Developments in Primatology: Progress and Prospects
Series Editor: Louise Barrett

Michel T. Waller *Editor*

Ethnoprimatology

Primate Conservation in the 21st Century

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Primate Conservation in the 21st Century

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Introduction

The fact that we *are* primates plays no small role when it comes to why we are drawn to them. We very clearly see ourselves in them and them in us. Nonhuman primates are empathetic and have morality. They fight and make war. They have sex for nonreproductive reasons. They have a complex communication system. They care for and create long-lasting bonds with their kin. They mourn their dead. They lie and cheat and steal and kiss and hug. Consequently, we worship nonhuman primates. We are eager to visit them in zoos. We want them as pets. We put them in movies. We experiment on them and study their behavior in forests and deserts and cities. We ingest their body parts in an attempt to gain their strength.

However, and in some case because of these connections, nearly half of all primate species are of serious conservation concern and face some type of threat (IUCN 2015). These threats include poverty and bushmeat hunting, habitat loss and infrastructure expansion, industrial agriculture, the effects of warfare and disease, and our seemingly insatiable demand to harness more power and develop greater resources. Indeed, it is difficult to consider the plight of nonhuman primates on our planet and not recognize a bleak future. Even with these challenges, however, I believe there is hope. That belief is founded on the research and hard work demonstrated by the authors of the chapters contained in this book (and others) and the shift in conservation strategies and tactics that they espouse. That shift is rooted in ethnoprimatology.

The field of ethnoprimatology examines the multifaceted interactions between human and nonhuman primates (Sponsel 1997) and has become an important tool for those interested in primate conservation. This holistic approach includes the study of hunting as well as the keeping of primates as pets, pathogen exchange, habitat alteration, mythology and folklore, tourism, and any other ways that human and nonhuman primates encounter each other (Wolfe and Fuentes 2007). By better understanding the broad array of interactions between human and nonhuman primates, conservationists are better equipped to encourage diverse groups of people to cooperate on issues of nonhuman primate survival (Fuentes and Wolfe 2002). Additionally, combining ethnoprimatology with conservation biology (i.e., Cowlishaw and Dunbar 2000) provides strategists with a more nuanced perspective of the many issues challenging human and nonhuman primates alike, placing them in a better position to make decisions. I think most conservationists would agree that policies aimed at setting aside areas of land for wildlife protection should continue. But given the increasing rates of infrastructure expansion, deforestation, and other habitat disturbances, designating refuges alone is unlikely to be sufficient for protecting all biological diversity, especially in the face of increasing human population density and consumption.

That is where this book comes in. The authors featured here include scholars who have studied primates for decades as well as graduate students who have been inspired by them. Their fields of study range from the densest tropical forests to the densest urban environments. You can find them at work in zoos or fetish markets and in Asia, Africa, and the Americas. Their subjects include the rarest lorises and the most prolific macaques—and, of course, humans.

One of the most important aspects of ethnoprimatology is a seemingly simple thing. We see ourselves and all humans as part of the natural world, not apart from it. While this is nothing new, the way ethnoprimatologists "perform" primatology is. We measure human behavior as an independent variable. We affect what we observe and quantify our own presence. We know that human ecologies and societies influence and are influenced by the behavioral ecology of nonhuman primate species in their areas. This bidirectional transfer of influence alters both human and nonhuman primate behavioral patterns and can affect access to resources (i.e., seed dispersal), agricultural practices (i.e., crop raiding), and cultural systems (i.e., mythology), to name a few. Comprehending the various sociocultural attitudes directed at primates is crucial to understanding the motivations behind human/nonhuman primate interactions. Ethnoprimatology, therefore, calls for the continuation and expansion of this new type of primatology in order to more fully elucidate the various perspectives born within a multitude of anthropogenic environments (Riley 2006).

And this is why I hope. Ethnoprimatology is progress. Ethnoprimatology is sensitive to the needs of people and wildlife. Ethnoprimatology acknowledges that there is value in cultural traditions while pragmatically assessing conservation threats. Conservation strategies and tactics based on an ethnoprimatologic approach seem possible. We have a long way to go to save primate populations on this planet, but the work presented here is a forward step and should set the tone for conservationists and primatologists working in the twenty-first century.

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Ethnoprimatology and Conservation: Applying Insights and Developing Practice

Agustín Fuentes, Amanda D. Cortez, and Jeffrey V. Peterson

Introduction

At its core the ethnoprimatological approach discards the perspective that the human–other primate interface is best seen, and is most often encountered, as a relationship of conflict and competition. While it is true that hunting/predation, deforestation/conflict, and primates as pets/pestilence are core foci for many investigations, such characterizations of the human–other primate interface are limiting in their scope and in what they can provide in regards to moving forward toward sustainability. Ethnoprimatology rejects the idea that humans are separate from natural ecosystems, accepts that humans have moral and ethical responsibilities to the landscapes we alter and modify, and mandates that multiple stakeholder approaches (including other primates) be included in behavioral, ecological, and conservation research with other primates (Fuentes and Hockings 2010; Lee 2010; Loudon et al. 2006; Riley 2010; Fuentes 2012; Malone et al. 2014). Because humans are primates ethnoprimatology discards the "us versus them" perspective inherent in much of the literature and in that vein we use the term "other" primates as opposed to "non-human primates" in this chapter.

To illustrate the current state of the relationships between ethnoprimatological approaches and conservation/management, we provide examples from recent and ongoing work in the following areas: long-term field sites, politics, education, kinship, and multi-stakeholder approach scenarios. Finally, we end with a specific focus on the interface of conservation management, ethnoprimatology, and the role of researchers as active agents in local ecologies. Via each of these topical lenses we demonstrate both how and why the ethnoprimatological approach matters for contemporary primate studies and conservation approaches.

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Kinship: Other Primates as Members of Human Societies

We begin with a few examples of the different ways that humans and other primates coexist. While many societies draw a sharp distinction between humans and other animals, others maintain more fluid relationships with other primates. In some human groups, these relationships represent deep connections, both biological and cultural. This fluidity includes primates as pets, food, sacred figures, and persons, often other primates occupy more than one of these roles in what at times seems to be a contradictory nature. Understanding the variety of human-other primate kinship bonds can have substantive implications for conservation.

For the Guajá people of Brazil, monkeys hold an important place as both kin and food. In her pioneering ethnoprimatological work Loretta Cormier (2002) wondered how this seemingly contradictory relationship could in fact be true. Here, monkeys take on social, cosmological, and nutritional roles. In large part, this diversity stems from a very different conception of what it means to be a person (everything in the forest has personhood, or better put shares in the elements that constitute personhood (see Kohn 2013)) and from a central role of endocannibalism, meaning "like eats like" (Cormier 2002: 78). Howler monkeys (*Alouatta belzebul*), in particular, are central to Guajá culture. While other monkey species are present as pets and food, howler monkeys are especially important because for the Guajá, howlers were created directly from humans (Cormier 2002). In Guajá culture, conceptualizations of the world emphasize the continuity between nature and culture, and kinship relations are extended to other life forms. These extended kinship relations allow for the practice of endocannibalism, a practice in which all life forms engage. This means that life forms eat other, related life forms, specializing in those most closely related. Just as Guajá prey on howler monkeys—which were created from Guajá people—Guajá are preyed upon by cannibal spirits, thus continuing the cycle of "like eats like" (Cormier 2002).

Along with their cosmological importance, monkeys also hold significance as pets and, more specifically, as adopted children for women. Orphaned monkeys enter the Guajá kinship system when hunters have killed their mothers. They are often given names, breast-fed, and otherwise treated as child-kin of the humans. Unlike hunted monkeys, these monkeys are not eaten. The primate-kin can also play a role in the ways in which humans represent themselves to one another: nursing an infant monkey can be desirable for women as it enhances both their appearance of fertility and attractiveness. In this way, monkeys play a role in the Guajá gender system and social development for females through both elevating social status and providing an opportunity to practice caring for a child (Cormier 2002).

Taking these perceptions into consideration when thinking about conservation strategies is beneficial for conservation scientists, local communities, and other primate species alike. Without such an understanding, non-Guajá humans may interpret Guajá cultural practices as destructive toward monkeys, giving them a fundamental misunderstanding of the relationships between Guajá and other primates. Such a misunderstanding could then risk damaging important cultural norms and practices. If primatological research takes local human perceptions of other primates seriously, we are better able to reconcile the differing desires that various human groups hold.

Ethnoprimatological research from both the Lindu highlands and Buton island of Sulawesi shows that despite a relationship fraught with competition for resources, humans can be generally tolerant of crop raiding macaques (*Macaca ochreata* and *M. tonkeana*). Riley and Priston (2010) note that this tolerance is due to the place that macaques hold in some human folklore. Sulawesi, like many contemporary landscapes, is transforming due to logging, transmigration, cash cropping, and increasing human population, which has increased the overlap and interactions of human and macaque populations. As Riley and Priston (2010) note, crop raiding in Sulawesi is not a new phenomenon: it has been present since before Dutch colonization. Recent human activities have, however, exacerbated the problem (Riley and Priston 2010). While relationships between humans and crop raiding macaques may seem purely negative, some farmers are tolerant of low levels of raiding because it can help in the harvesting of certain crops. This tolerance is exemplified with cashew nut crops on Buton. Farmers perceive raiding as beneficial because monkeys eat only the fruit and let the nut fall to the ground to be collected by farmers (Riley and Priston 2010).

Crop raiding is not the only way humans and macaques interact in Sulawesi, macaques also hold mythological importance. Amongst some peoples, like the Muslim Butonese, macaques are considered haram (forbidden), deterring humans from killing and/or eating them (Riley and Priston 2010). For other native Sulawesi groups, macaques are more strongly connected to humans through ancestry. The Kajang tribe believes that their ancestors became monkeys. Similarly, in the Lindu highlands, the Kaili Tado (To Lindu) people see Tonkean macaques (*Macaca tonkeana*) as kin and as guardians of traditional law (adat) (Riley and Priston 2010). Because of their biological similarities to humans, they are understood to be of human origin. The To Lindu people thus understand that they should not behave in negative ways toward, or speak negatively of, the macaques, lest they wish the monkeys to become their enemies (Riley and Priston 2010). While this case provides a different understanding of the human–other primate interface from the Guajá example, it demonstrates that examining certain interactions and relationships is beneficial for developing conservation programs, as local perceptions can provide insights as to why and how certain relationships exist.

A particularly interesting case of human–other primate kinships is that of the Japanese and macaques. Filled with contradictions, the relationships between the two have shifted greatly over time and reflect the complexities of coexisting with other primates. Mito and Sprague (2012) outline the history of human—macaque interactions in Japan, beginning with the role of monkeys in prehistoric and early historic era art and subsistence. A significant shift in perception of monkeys was brought about by the arrival of Buddhism, which brought with it a respect for all animals and a discouragement from hunting and eating them. In the Middle Ages, humans began to train monkeys for the saru-mawashi monkey performances. Around the same time, the Umaya-zaru custom, in which samurai kept their pet monkeys in stables to take on the diseases and misfortunes of horses, also appeared, as did crop raiding. By the nineteenth century, the hunting of wild animals increased. As a result, some went extinct and others, like monkeys, were hunted as both pests and commodities. In recent decades, increased crop damage has resulted in increased hunting of monkeys as pests (Mito and Sprague 2012). Although monkeys are still seen as pests by many, they have maintained their traditional role in Japanese cultural practices and thus their role as important cultural actors (e.g., as central figures in traditional children's stories) (Mito and Sprague 2012). Moreover, the Japanese people still believe that all things animate, and even objects such as stones and water, have a spirit and a personality. This aspect adds an interesting layer to the complexities and contradictions that characterize the relationships between the Japanese and macaques (Ohnuki-Tierney 1987).

Recently, monkey parks were introduced in an attempt to bring monkeys and people together. These parks encourage positive relationships by allowing humans to interact with the monkeys through food provisioning, while increasing tourism and the recovery of monkey populations (Mito and Sprague 2012). Monkey parks have been quite successful in Japan, but Mito and Sprague stress that despite their effectiveness in this context, such a solution will not work everywhere. Conservation strategies should not be developed in a "one size fits all" manner. Rather, "the actual solution to wildlife issues needs to be formulated with the cultural context of each place where humans and primates coexist" (Mito and Sprague 2012: 49).

As stated by Mito and Sprague (2012), there is no single answer for creating positive coexistence between humans and other primates. However, their case study, and those of Cormier (2002) and Riley and Priston (2010) show that understanding the context and details of particular human–other primate relationships can help significantly in trying to find solutions for conservation. From shared personhood to shared histories, considering these contexts can have great implications for conservation.

Long-Term Field Sites: Necessary for Developing Robust Knowledge Base

Long-term field sites are salient to the ethnoprimatological framework because they allow for a broader understanding of the local and global contexts that influence foci of ongoing research projects. Such studies are well suited to reveal diverse social, economic, and ecological relations between human and other animal species. Researchers involved in long-term research projects are in the best position to identify and understand the interdependencies tying together human and other animals. It is important to note, however, that long-term field sites themselves also have an impact on the local social, political, and ecological landscapes. We illustrate these themes and outcomes via four brief examples of multi-year ethnoprimatological projects.

Melissa Remis and colleagues have conducted research at the Dzanga Sangha Dense Forest Reserve in the Central African Republic (CAR) for nearly 15 years, enabling the substantive accumulation of diverse datasets (e.g., Remis and Jost-Robinson 2012, Chap. 3, this volume). For instance, Remis and Robinson conducted line transect surveys along the same paths across different years, allowing them to assess trends in ecological change between years for a specific transect. They found that there were less overall primate species along a single transect in 2009 than in 2002, and they also noted a decrease in the overall number of times the most common species were sighted between these years. Another form of data collection at their site includes multiple years' worth of interviews with local hunters. Working with hunters can be especially informative because they have a more intimate knowledge of the nearby primate populations, as well as the local flora and fauna in general, than those who are not engaged with forest-dwelling primates. Learning about specific hunting practices, such as the scale of killing and preferred targets (e.g., males), can further contextualize ecological data on shifts in the composition of local primate populations. Local community members, including those who engage in hunting practices, are more accessible and provide more reliable information at long-term field sites in which the researchers have established rapport with local residents. Ethnographic data collection in general is an integral facet of long-term ethnoprimatological studies because it acknowledges the importance of local human perception and behavior in relation to the broader socioecological niche to which other primates belong. Both of these methodological techniques are able to assess aspects of forest-use, impact, and change diachronically, with further reference to variables such as protected area demarcations and local primate home ranges. Combining ethnographic and survey/census methods in long-term contexts enabled this project to document ethnographic shifts in relation to ecological shifts, as well as contextualize primate behavioral data within the dynamic socioecological niche. One example of these shifting relations is the development of cryptic behaviors in some primate prey species to alleviate hunting pressure, which results in hunters modifying their own strategies to acquire prey by employing firearms (Remis and Jost-Robinson 2012). These authors conclude, however, that the primate anti-hunting strategies may not be able to keep up with such technological modifications to human hunting techniques.

The Padangtegal temple in Bali has been the focus of ethnoprimatological research for nearly the past 20 years (Wheatley 1999; Fuentes 2011; Brotcone 2014). The "field site" is open to all interested researchers, but much of the work has been conducted or overseen by Agustín Fuentes and an interdisciplinary team of colleagues. Padangtegal is an important site for understanding how long-term collaborations between researchers and locals can be employed effectively. Fuentes and colleagues (2007) provide a historical sketch of Padangtegal's development as a managed ecotourism destination, dating back to the 1980s. One conclusion emerging from comparisons of similar types of management systems is that such management programs must be flexibly conceived to account for the political-economic, ecological, and cultural dynamism of the human–other primate interface.

Research on other primates in folklore and mythology has been another important focus at Padangtegal. Researchers believed temple monkeys to be sacred early-on (cf. Wheatley 1999), but later work by Fuentes and colleagues (2005, 2007) demonstrated that perceptions of macaque monkeys at Padangtegal are rooted in more complex spatial, social, and economic interconnections (see also Schillaci et al. 2010). Interesting parallels exist between local Balinese people, such as tour guides, and long tailed macaques (*Macaca fascicularis*) in the socioecological niche of Hindu temples, including the mutual reliance on daily tourist income and food, respectively. As temple macaque populations increase, however, management strategies need to take into account the greater potential for conflict between people and macaques in these shared spaces and how that might affect local human perceptions of the macaques (Fuentes 2010).

Padangtegal has also been a valuable site for research focussed on understanding zoonotic pathogen transmission. For example, Engel and colleagues (2006) studied the transmission of Simian Foamy Virus between macaques and temple employees at this location (and subsequently across Asia: Jones-Engel et al. 2008). Fuentes (2006) situates such transmission in the context of human–macaque behavioral interactions that result in both species sharing this socioecological niche. Further, Lane and colleagues (2010) demonstrate that adverse health effects resulting from zoonotic transmission are bidirectional, meaning that members of both species can experience negative health impacts resulting from interactions in this shared space.

Macaque behavior at temple sites in Bali, such as Padangtegal, has also been monitored over time. In her recently published dissertation, Fany Brotcorne (2014) demonstrates more behavioral flexibility among macaques at Padangtegal than at other temple sites in Bali. She argues that this behavioral difference stems from the higher anthropogenically influenced diet for Padantegal monkeys relative to others. More direct human provisioning at Padangtegal allows for behavioral plasticity to emerge in the context of non-subsistence behaviors (Brotcorne 2014).

Multi-year research projects in other areas of Indonesia have made important contributions to the ethnoprimatology literature as well. In Central Sulawesi, Riley (2007) found that overlapping resource use between humans and macaques does not necessarily result in conflict between them. For example, strategic planting of unappealing buffer crops near the forest edge can reduce the possibility of such conflict. Furthermore, taboos on hunting or disturbing monkeys in some societies, such as the To Lindu in Central Sulawesi, can prevent threats to monkey populations via retributive hunting for crop raiding (Riley 2007). Such taboos, however, do not offer long-term stability due to the dynamic nature of cultural institutions, as well as the presence of people moving in from other areas who do not share the local taboos on hunting monkeys (Riley 2007).

Stemming from work conducted with silvery gibbons (*Hylobates moloch*) in Java, Malone and colleagues (2014) describe the importance of long-term fieldwork for conservation projects. These authors suggest that the scientific focus of conservation research must be considered in reference to its local political implications. Ethnoprimatological work in particular, with its emphasis on ethnographic data collection among local people in tandem with primate behavioral and ecological data collection, is in a good position to enlighten conservation projects regarding the local cultural and political issues that need to be addressed for the successful conservation of any given primate species (Malone et al. 2014). For example, rehabilitation and reintroduction programs, such as those proposed for silvery gibbons, stand to benefit from research in the ethnoprimatological framework as it is important to understand how local residents feel about the release of rehabilitated primates into nearby forests, and how these perceptions impact the long-term viability of such projects (Malone et al. 2014).

Politics: Unavoidable Realties of Fieldwork

An emerging focus of ethnoprimatological research brings political issues to the forefront. Just as the other primates can no longer be considered free from human influence, primatologists can no longer consider themselves separate from the sociopolitical circumstances of the regions in which they work. Such sociopolitical contexts can involve both local interpersonal conflict as well as tensions between the national and local levels. Furthermore, socioeconomic inequality and uncertainty are often pervasive in the regions that have been identified as conservation priorities.

Alejandro Estrada (2013) describes primate conservation projects as social issues that are necessarily connected to the local and global socioeconomic contexts of the area. Forested regions targeted for conservation, for instance, are often utilized by local people for subsistence and survival. In fact, "nearly 60 % of the world's poorest people inhabit fragile, vulnerable tropical landscapes" (Estrada 2013: 34). Therefore, primate conservation programs must recognize that they are often enmeshed in the socioeconomic realities of massive poverty, economic instability, and political oppression. In terms of policy, this means that the implementation of top-down projects alone, such as the establishment of new protected areas, will not be sufficient and may actually be unethical in the context of human rights. Researchers must address primate habitat conservation with complementary approaches, including shifting away from monocropping and increasing the use of agroecosystems, utilizing shade crops, establishing biodiversity conservation corridors, and initiating community-based conservation management programs (Estrada 2013).

In their chapter on the ethics of conservation, Matthew McLennan and Catherine Hill (2013) tease apart the relationship between chimpanzees, local people, conservation scientists, and national governments. Echoing Estrada (2013), they describe a paradox in which chimpanzees are granted legal protection by the Ugandan government, but that same government rarely supports the local people in conflict with chimpanzees (McLennan and Hill 2013). For example, government regulations on locals' land-use practices may be perceived as prioritizing chimpanzee livelihood by restricting human access to forest resources. The presence of Western scientists, who are often implicitly associated with the national government (and typically work under the auspices of governmental permits), may therefore cause concern among locals when their land-use practices are not in line with government regulations (McLennan and Hill 2013). Local people may also worry that conservation scientists conducting research in their region indicate impending changes to land-use regulations, such as the implementation of new protected areas or other loss of local autonomy in land use decisions. Researchers themselves may inadvertently be associated with existing political conflict at the local level regarding discourses on conservation initiatives. For instance, McLennan reports that Ugandans with whom he worked assumed that he was involved with an unpopular proposed ecotourism plan due to his association with a specific community member who was behind it (McLennan and Hill 2013).

McLennan and Hill (2013) also shed light on the embedded politics of acquiring research permits from the national to the local level. Often seen as a means of establishing informed consent for conducting a research project in a foreign country, the top-down nature of the permit process situates researchers as government-sanctioned workers by the time they arrive at their proposed field site with the signatures of high-ranking government officials in-hand. Therefore, local people are often powerless to speak up and deny foreign scientists permission to conduct research in and around their communities (McLennan and Hill 2013). They also note that this situation can create a perceived power imbalance between locals and researchers: foreign scientists (typically white, coming into an impoverished area) are often perceived to have money and status and relatively powerless locals may feel obligated to assist (McLennan and Hill 2013). While it is usually not the intention of the researcher to create power imbalances, they may become an inevitable result of field studies. Hiring locals to work as field assistants, a common way of building a more reciprocal relationship with local communities, also has inherent political issues. Employing only a select few individuals can cause issues of jealousy and resentment in the community and may interfere with previous or existing instances of interpersonal conflict amongst locals (Fuentes 2002; McLennan and Hill 2013). All of these scenarios demonstrate that one cannot simply be a "neutral outside researcher," but is rather always involved to some degree in local sociopolitical issues.

The commoditization of other primates is another political issue of importance for the ethnoprimatological framework. Agustín Fuentes (2013) discusses how macaques can be social as well as economic and subsistence commodities. In Japan, monkey performances are seen as related to important aspects of lived human experience and existence, which reflects the high degree of social inclusion for macaques in Japanese society (Fuentes 2013). As such, the role of these performing macaques can be characterized "as a social commodity, for the Japanese, while simultaneously acting as financial commodity for the monkey trainers" (Fuentes 2013: 112, see also Ohnuki-Tierney 1987, 1995). The other primates can also be commoditized as political symbols, as seen in the conflict between Spain and England over the isthmus of Gibraltar. The story of a nineteenth century Spanish attack thwarted by the alarm calls of startled macaques has become a common trope invoking a "naturalness" for

British control of the island (Fuentes 2013). The macaques of Gibraltar are also cultural commodities for local residents because they are the only free-ranging other primates in Europe (Fuentes 2013).

Through tourism, macaques are economic commodities in Gibraltar, as well as in parts of South Asia, Southeast Asia, and East Asia. In Bali, for example, monkey temples have greater numbers of tourists and generate more income than similar temples without resident monkey troops or than those with monkeys but a less developed tourist infrastructure (Fuentes et al. 2005). In other parts of Asia macaques are used as “laborers” similar to traction animals, such as oxen. Macaques in Thailand are a common example of this: they are trained from a young age to pick coconuts, which they do far more efficiently than humans (Sponsel et al. 2002). In Southeast Asia an array of primate species are also occasionally kept as “status” pets to demonstrate the owners’ high socioeconomic status. In these circumstances the primates are not necessarily economic commodities themselves, but are symbolic of their owners’ economic means (Fuentes 2013). Finally, many primates, and macaques in particular, are used as biomedical commodities in certain countries where such use is legal. Biomedical commodification of the other primates can occur from the local to transnational level, at which point the animals have become economic commodities as well. Understanding the role of primates as commodities in certain sociopolitical contexts sheds light on the social and economic value humans attribute to them, and the corresponding ways in which such interspecies relations are mediated by those perceptions of value (Fuentes 2013).

Multi-Stakeholder Approaches: The Reality of Complex Management Attempts

The most effective conservation strategies take into account the multiple actors that exist in and utilize an environment. Conservation programs that only focus on one actor, such as the target animal of the conservation program, are at risk of disempowering other groups, such as local people (Estrada 2013). Further, the most successful strategies weave together different disciplinary approaches to conservation such as understanding local wildlife, local perceptions of other life forms, and habitat protection in order to address the role that each group holds in the local ecology (Hockings and McLennan 2012). Many environments in need of conservation are characterized by the deeply intertwined relationships of different stakeholders, all of whom should be considered if a program is to be successful (Malone et al. 2014). Multi-stakeholder approaches to conservation are critical in areas where different groups use the same resources and ethnoprimatological work allows researchers to understand whether these various groups are aligned or at odds with one another over the uses of wildlife and the environment.

At their long-term field site in the CAR, Rebecca Hardin and Melissa Remis have identified changing patterns of human and other primate interactions and ways of existing (Hardin and Remis 2006). Due to an increase in overall human activity in the area and a proliferation of market-driven logging and hunting, interactions between humans and other primates are increasingly unsustainable as humans utilize more area and animal populations decline. In this context, economic developers, conservationists, and local humans focusing on bushmeat all interface with the wildlife, each with differing interests. This is, however, not always the case, different groups may align in their interest, as evidenced when researchers employ locals as field assistants or when locals participate in the global economy through employment in eco-tourism and conservation projects. In the CAR for instance, locals participate in these programs as guards or guides in gorilla eco-tourism and visits to sites where animals come together to bathe and socialize (Malone et al. 2014).

Remis and Hardin's (2009) concept of transvaluation is important for engaging with a multi-stakeholder approach because such a framework demonstrates the many roles that a single species can play in conservation and resource management. Further, transvaluation "helps to mobilize diverse stakeholders and provide new methods for monitoring forests—[they] emphasize the need for nuanced, site-specific approaches that recognize uniqueness of individual situations" (Malone et al. 2014: 18). This approach acknowledges that species such as gorillas have a local, regional, and global value. Further, it ensures that programs not only incorporate the different stakeholders, but can also help researchers, conservationists, and policy workers move beyond tired dichotomies of ethical versus material value of wildlife and landscapes (Malone et al. 2014) and instead understand the nuances of what it means to implement conservation programs in an area of deeply entangled relationships. Such entangled relationships provide the basis for what scholars call "situated collaborations," or processes of connecting "anthropological data and perspectives to conservation dilemmas" (Remis and Hardin 2009: 1589). Ethnoprimatology is in a privileged position for such collaborations because it allows researchers to understand both the perspectives—local, regional, and global—of other animals as well as wildlife behavioral data.

As mentioned previously, Kimberley Hockings and Matthew McLennan note that the most effective conservation strategies include multiple perspectives and various disciplinary approaches. Their research, which focuses on chimpanzees and crop-raiding activity across Africa, aimed to find effective conservation strategies from a multi-stakeholder approach (Hockings and McLennan 2012). They note that an increase in globalization has led to an increase of cash cropping. A combination of chimpanzee habitat loss and an increase of cash cropping has led to crop-raiding on the part of chimpanzees, a major source of conflict between humans and chimpanzees, and one that is not specific to just chimpanzees (see Riley 2007; McLennan and Priston 2013). Farmers often come to resent chimpanzees and fear for their safety (due to chimpanzee attacks, a result of increased contact), which sometimes leads to the killing of chimpanzees (McLennan and Hill 2013). Crop-raiding animals pose a threat to both people and their livelihoods, but as habitat destruction continues, chimpanzees and other primates need a source of subsistence. Effective solutions to this problem include collecting ethnographic data in order to understand the local context of why cash cropping is problematic for both local humans and wildlife, as well as behavioral data to understand patterns of crop raiding. Examined together, such information can be used to create positive, sustainable solutions for all parties involved.

In northern Peru, Sam and Noga Shanee run a conservation Non-Government Organization (NGO) that emphasizes local people as keystone stakeholders in the conservation process (Shanee et al. 2014). Believing that effective conservation programs happen from within local groups, they encourage a bottom-up model rather than a top-down one. The departments of San Martín and Amazonas in which Shanee et al. conduct research have some of the highest rates of deforestation in Peru. Migrants in Peru are frequently blamed for environmental destruction and are described in the literature as maladaptive, antipathetic toward the forest, and hungry for land and natural resources. Shanee et al. (2014) found these characterizations to be prevalent in the environmental discourse of northeast Peru. Such destruction is, however, largely due to economic and legal pressures on migrants and such characterizations are not accurate. Rather than apathy toward nature, migrants do not always have the resources for conservation due to state requirements and a lack of sustainable options. Understanding these pressures, and the ways that migrants actually perceive the environment, as well as encouraging locals to take on conservation initiatives on their own terms, is hugely beneficial for the sustained success of programs (Shanee et al. 2014, see also Chaps. 12 and 18 this volume).

Alongside government-protected areas, Peru allows private conservation areas and conservation concessions. However, these private areas are difficult to acquire due to a complicated, costly, and time-consuming process of registration (Shanee et al. 2014). As a result, many migrant communities opt to bypass such processes and instead initiate informal conservation plans. Shanee and colleagues conclude that conservation effectiveness depends on partnerships with local stakeholders; as conservationists, we should encourage local people to initiate their own programs and work to simplify the process for establishing private protected areas. Rather than primarily encouraging locals to enter into the global economy, we should focus on local initiatives. Increasingly, the (Peruvian) government is valuing conservation, not for the wellbeing of animals and the environment, but for economic development. It is thus crucial that locals become involved and create their own protected areas in order to promote conservation that will benefit multiple stakeholders, including the local people themselves (Shanee et al. 2014). Ethnoprimatology can aid in this process by acknowledging the various stakeholders and legitimizing the value that each group places on various primate species.

Education: The Emergence of the Central Feature in Effective Conservation and Management

A key assumption underlying many conservation projects is that educating locals of the merits of protecting a particular primate species and their habitat will increase the project's likelihood of success (cf., Remis and Hardin 2009). As such, conservation projects with a focus on education are often concerned with expanding local knowledge of a primate species' important role in the shared ecosystem. More consideration, however, should be given to educating local stakeholders as to how conservation programs benefit them as well. Relying on arguments for the "good of the ecosystem" may not translate easily to the social, political, and economic realities that are embedded in local stakeholders' daily lives. In light of this perspective, conservation efforts should move away from attempts at infusing ecological knowledge locally and focus instead on the sharing and mutual transmission of ideas.

Nancy Priston and Simon Underdown (2009) have undertaken a novel conservation-oriented project that emphasizes establishing a body of shared knowledge with locals. They focussed specifically on helping farmers who deal with crop-raiding, assess the amount of crop damage incurred by primates compared to the damage done by other animal species, as well as the potential for damage to particular crop species in the future (Priston and Underdown 2009). Measurements of actual crop damage and crop-specific risk are important because the perception that crop damage is caused by primates influences peoples' opinions of, and behavior toward, those species (Priston and Underdown 2009). Damage caused by the other primates can be overestimated due to their conspicuous appearance relative to other crop-raiding animals, such as forest rats (see Riley 2007). Therefore, educating farmers as to the actual level of crop damage caused by primates can help alleviate conflict where they are not as destructive as perceived. To do so, Priston and Underdown (2009) established a simple model that farmers can use to calculate the actual risk or susceptibility of specific crops to damage from other primates. The necessary calculations are based on the incidence rate (IR) of damage across farms for a specific crop species, divided by the sum of the available, but damaged, and available, undamaged crops (Priston and Underdown 2009). Such calculations can then be made for all crop species to determine those that have the highest risk of being damaged (Priston and Underdown 2009). Planting strategies can then be made to alleviate susceptibility of damage for those crops with the highest risk. For example, farmers can organize their crops in specific spatial patterns by placing those species with greater risk of being damaged farther from the forest edge (Priston and Underdown 2009). This strategy has the added effect of creating a buffer zone of low-risk crops near the forest that are less likely to draw crop-raiding primates into the gardens. Transparent use of this model allows farmers to continue making calculations and monitoring damage risk across seasons, thereby insuring that they are not reliant on outside researchers to understand the most important risk factors to their crops over time (Priston and Underdown 2009).

The work of Melissa Remis and Rebecca Hardin represents the shift from conservation education to a dialectical relationship between researchers and local communities that we described above—and couched in an ethnoprimatological approach. Remis, a biological anthropologist, and Hardin, a cultural anthropologist, have combined efforts since 1997 in order to gain a robust understanding of human–other primate interactions at Dzanga-Ndoki Park and Dzanga-Sangha Dense Forest Reserve (RDS) in the CAR. Central to disseminating conservation information within a dialectical framework is the concept of "transvaluation," which accounts for the comprehensive and multi-directional flow of resources (Remis and Hardin 2009). The complexity of transvaluation at sites of interest for conservation is necessarily reflective of the needs associated with the multiple stakeholders. Such "situated collaborations" are important because they contextualize the varied ways in which different actors (e.g., residents, tourists, researchers) value the habitat and wildlife (Remis and Hardin 2009). The information that emerges at each site on how multiple stakeholders interact with the local ecology can then be used to educate debates on conservation and land-use policy (Remis and Hardin 2009).

Another important dimension of conservation education from within a transvaluation framework comes from parents and other community members educating their children about the local ecology (Hardin and Remis 2006). When children accompany their parents into the forest for various activities, such as gathering food or medicinal plants and participating in hunting rituals, the local ecology becomes normalized and children learn about the flora and fauna in a hands-on, experiential fashion (Hardin and Remis 2006). Conservation programs should be cognizant of such situated education practices, especially when those programs limit who has access to the forest they are attempting to protect. For example, in some places a conservation strategy in which multi-generational camps of locals are no longer allowed within protected areas is being employed (cf., Hardin and Remis 2006). These policies disrupt the transmission of culturally situated ecological information between parents and children as described above, but also prevent nighttime song and dance performances that are powerful forms of storytelling directed at younger members of the community (Hardin and Remis 2006). Although such exclusive policies may be well-meaning, they also run the risk of disrupting the ways in which local people engage with, and transmit knowledge of, their surrounding ecology (Hardin and Remis 2006).

Finally, Shanee and colleagues (2014) describe salient forms of conservation education that operate at different levels among a location's multiple stakeholders. For example, NGOs can be important for educating local communities about national policies and the bureaucratic processes regarding the development and implementation of conservation programs (Shanee et al. 2014). They can also be key sources of funding for such programs, but those resources may be limited by the organization's ability to follow up long-term (Shanee et al. 2014). Another important level of conservation education occurs between local communities. Referred to as the "contagion effect," inter-community education results from knowledge of successful, locally administered conservation programs spreading throughout the region (Shanee et al. 2014). The contagion effect is a powerful force for conservation because it does not rely on the presence of NGOs or researchers to succeed, but is instead grounded in local practice. Furthermore, communities that begin administering conservation projects in this way will benefit by virtue of the transmitted practices having already been proven successful.

Conservation Management: Ethnoprimatology and the Role of Researchers as Active Agents in Local Ecologies

Gone are the days that primatologists can consider themselves merely observers: onlookers who have no influence on their surroundings, be they related to the environment, local human and other primate populations, or conservation and management efforts. The interconnectedness of humans and other primates extends beyond those relationships we study as scholars and includes the unintended consequences we create as researchers (McLennan and Hill 2013; Tsing 2004). Although sociocultural anthropologists realized this in the 1980s, primatologists have only recently come to terms with the fact that there is no “noninvasive” research, all research has repercussions and primatologists are becoming increasingly aware of their ethical, moral, and social entanglements (Malone et al. 2014; Strier 2010). Much, although not all, of the primatological research done today is conducted in areas that are of increasing interest for conservationists. What eventually becomes apparent to researchers, but is not always obvious to others, is the intense interconnectedness of multiple stakeholders that surround conservation work, making it difficult to determine a single trajectory for successful conservation. In this section, we explore the unintended consequences and researcher influence related to conducting field research and their connection to conservation and management efforts.

Karen Strier’s (2010) work with the critically endangered northern muriqui (*Brachyteles hypoxanthus*) in Brazil—which began in 1983—provides a critical reflexive moment in primatology. After 30 years of a strict “hands-off policy,” Strier was able to examine the extent to which her work was truly noninvasive. From the beginning of the study, she has been committed to the notion of noninvasive observational research, meaning no direct handling, capturing, or sedating the monkeys. Although this presents a trade-off (types and contexts of data collection are significantly limited by such an approach), Strier felt it was the best for the fragile population of muriquis. But was it truly noninvasive? What she found was that despite her and her collaborators’ efforts, the research process did alter the future of the group and the unintended consequences of her research have effects regarding conservation.

Her study population and the environment they inhabit underwent noticeable changes over the 30-year period as a result of her research team’s presence: most notably an increase in population size and an altered niche (Strier 2010). The muriqui population has grown to four times its initial size, potentially a positive element for the muriqui, but likely to have contributed to the decline in sympatric brown howler monkeys (*Alouatta guariba*). Moreover, the muriquis became less wary of observers and came into increasingly closer proximity to the human researchers. Finally, as a result of declining available space in relation to an increasing population, of habituation to humans, or a bit of both, there has been a 20-fold increase in the frequency of terrestrial use over a 22-year period. The monkeys have changed their behavioral niche from a mostly arboreal lifestyle to a mixed terrestrial/arboreal one and they now face new ecological parameters including pathogen exposure due to contact with feces and terrestrial predators (Strier 2010).

As active participants at field sites, researchers not only influence the other primate populations under study, we also impact both the humans who coexist with other primates and the environments in which our research takes place. Like Strier, McLennan and Hill (2013) make note of the unintended consequence of conducting field research and stress researcher influence, which should become a normal consideration in (ethno)primatological research.

McLennan's research with chimpanzees in western Uganda is a part of a larger project focusing on human–other animal relationships within commercialized rural production systems, land use change, and habitat destruction, all underpinned by conservation efforts for chimpanzees (McLennan and Hill 2013). The goal was to understand how chimpanzees, a protected animal under Ugandan law, respond and adapt to changes and fragmentation of unprotected habitat and increased contact with humans. This contact is often detrimental for humans either through crop-raiding or direct attack on humans. An important outcome of the study however is an examination of the ethical implications regarding humans and the effects outside researchers have on local human populations. These include: influences of the arrival of primatologists on social processes and political dynamics and the changing social relations resulting from locally employed field assistance, the top-down process by which researchers gain clearance in Uganda, resulting in power relationships between researchers and local people, the distinction between research and conservation and the complicated decision of when to act, and the issue of whether impoverished rural communities should be expected to live with and conserve bothersome and sometimes dangerous wildlife (McLennan and Hill 2013).

Primatologists may also find themselves stuck between fealties to the research objectives versus intervening in issues of conservation. Should we remain passive observers in the face of environmental destruction and species loss or are we ethically obligated to take action? One might also consider this: is it our place, despite our ethics and good intentions, to interject in matters we may not fully understand? How might stepping in have positive effects for animals and their environments but negative ones for humans? The most pressing issue facing a field researcher is this: is it worth it (Malone et al. 2010; McLennan and Hill 2013)? Further, who are we to say, as foreigners who do not live alongside potentially dangerous animals who threaten our livelihoods, that these creatures (chimpanzees in this case) carry the worth that we give them (McLennan and Hill 2013). Why is it that our classification as an important conservation target is more important than protecting the impoverished people inextricably intertwined with other primates? McLennan asks if it is indeed appropriate to conserve chimpanzees in such circumstances. While the circumstances he mentions are particular to his site, the question can and should be applied to all ethnoprimatological research sites.

The long-term research by Remis and Hardin (2007) in the CAR embodies the goals of ethnoprimatology while grappling with issues of conservation. Over many years, they have documented changing forest uses and how this interfaces with changing human perceptions of and relations with other primates. Specifically, they have looked at the ways that traditional forest uses such as hunting and gathering have been replaced by new ways of interacting with the landscape, which include logging and conservation (Remis and Hardin 2006). Their collaborative research provides insights into changing human uses and perceptions of the forest, variations in human and other animal adaptations to habitat alterations, and decreases in animal densities at research sites. Comparing findings from this study to that of their respective long-term research in the area reveals that humans are "both materially and ideationally impoverished by animal declines" (Remis and Hardin 2006, 273).

Combined methods from biological and cultural anthropology such as transect work and ethnography provide a lens for understanding an increase in gorilla predation and the connation to increased economic activity, human immigration in the RDS region, and social changes that may cause local declines of prey populations that are alternative options to gorillas (Remis and Hardin 2006). This work also complicates simplistic understandings of conservation and management work in areas with multiple stakeholders. As the authors note, the increasingly politically charged nature of conservation work has taken on an "us" versus "them" rhetoric, conservation is often understood as either counter to indigenous people's interests or connected to colonial discourses of understanding and controlling the natural world (Remis and Hardin 2006). Moreover, conservation can be interpreted as favoring one group's interests over others, such as protecting animals from human encroachment or protecting forest-dwelling humans against conservationists and other actors (Remis and Hardin 2006). Entangled interest in forest resources is far more complex than the simple "save the rainforest" ideology prevalent in many conservation ideologies. Ethnoprimatology and the work by Remis and Hardin help to elucidate these complexities because we can gain insight from multiple parties that will help us to understand the many different perceptions of other primates.

Looking Forward: Interlacing Ethnoprimatological Practice and Conservation Management

Humans are central figures in every context and ecology in which other primates are studied. Therefore, we recommend that the following foci be addressed in future primatological research.

- Primatological projects should collaborate with ethnographic projects in the same area to better understand both the important perspectives of local people and the roles of other primates in local people's lives.
- Researchers should take seriously the political ecology of the multi-stakeholder approach and further, primatologists should make themselves aware of the political, economic, and social contexts of the area *before* beginning research.
- Following Strier, primatologists need to consider the continuing impact of short and long-term field sites, as well as conservation programs, on local communities and ecologies.
- Along with considering different stakeholders, we must also look at the multiple problems that can interfere with the sustainability of ecological systems. Rather than having primatologists focus solely on conservation, we can work to create sustainable systems that address a range of different stakeholders' needs.
- Finally, long-term and broad-scale primatological research projects should be multidisciplinary in order to address the issues and examples outlined throughout this chapter.

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The Threat of Industrial Oil Palm Expansion to Primates and Their Habitats

Joshua M. Linder and Rachel E. Palkovitz

Introduction

Over the last few decades, agro-industrial enterprises have replaced small-scale farming and shifting cultivation as a leading driver of deforestation in many parts of the humid tropics (Butler and Laurance 2008; Gibbs et al. 2010). Of all the industrially produced crops, it is the relatively recent and rapid expansion of large-scale oil palm plantations that is among the greatest concern to tropical forest conservation. We review the history of large-scale, industrial oil palm expansion in the humid tropics and examine its ecological and social impacts to inform biodiversity conservation and human development strategies. We also assess global efforts to sustainably produce palm oil and offer recommendations on how to reduce the environmental footprint and improve the social benefits of producing palm oil.

The Rise of Industrially Produced Palm Oil

The African oil palm (*Elaeis guineensis* Jacq.) originated in Africa, where archaeological evidence suggests people have been cooking with palm oil for up to 6000 years in the tropical forest zones of West and Central Africa (Hartley 1988; Lynn 2002). A pioneer species, this member of the palm family (Palmae) thrives in tropical lowland areas with high rainfall and extensive sunlight. It begins to produce clusters of fruits 3–4 years after planting and can bear fruit for up to 60 years (Lynn 2002). Palm oil is extracted from the fruit pulp, while palm kernel oil (similar to coconut oil) is obtained from the hard seed embedded within the pulp. Per unit

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area, the African oil palm produces the highest oil yields and maintains the lowest production costs of any industrially derived vegetable oil (Rival and Levang 2014). Together, palm oil and palm kernel oil are used worldwide for cooking oil and as ingredients in soaps, cosmetics, detergents, lubricants, fertilizers, feedstuff, and biodiesel (Sheil et al. 2009).

The inter-continental trade in palm oil began as far back as the fifteenth century when European traders bought it from West Africans who extracted it from natural and sub-spontaneous groves (Lynn 2002). Palm oil became an important component of the transatlantic slave trade when it was used as a provision on slave ships and as a rub to enhance the marketability of slaves entering the New World (Watkins 2015). However, it was toward the end of the slave trade in the eighteenth and nineteenth centuries that brought about the more systematic and formalized export of palm oil from West African oil palm groves. By the late 1700s, the British began a sustained and extensive trade in palm oil and palm kernel oil from smallholder farmers in Africa's Upper Guinea and Gulf of Guinea regions as raw materials to help fuel an increasingly industrialized economy (Lynn 2002; Law et al. 2013). The development by the early twentieth century of large-scale industrial oil palm plantations started in Africa and Southeast Asia and stemmed from the inability of traditional palm oil extraction methods to meet a growing demand for the commodity. Large-scale, private enterprise-led oil palm plantations, compared with smallholder plots, would lead to greater yields, higher quality of palm oil, and lower production costs (Corley and Tinker 2003).

In Africa, the origins of large-scale, oil palm plantations can be traced to colonial Cameroon and the Congo (now the Democratic Republic of the Congo). By the late nineteenth century, the Germans were among the first colonial rulers in Africa to convert rain forest areas into plantation agriculture (Lanz 2000). In German-controlled Cameroon, cocoa plantations dominated at first, but were soon replaced in the early twentieth century by oil palm and rubber plantation crops (Gockowski and Dury 1999). Foreshadowing later agro-industrial developments in the tropics, early German plantation agriculture necessitated the expulsion and relocation of the indigenous people living in the concession area and led to a large influx of migrant workers living in company towns with poor living conditions (Konings 1993; Njoh 2002).

Around the same time, in the Belgian Congo, Sir William Lever (of the British soap manufacturing company, Lever Brothers) entered into a treaty with the Belgian colonial government in 1911 that eventually secured 750,000 ha of land, appropriated from the local population, on which his private company Huileries du Congo Belge would build modern processing facilities and monoculture plantations of oil palms to produce and export vast quantities of palm oil (Duignan and Gann 1975). Controlling the manufacturing, marketing, and distribution of palm oil along with the growing of oil palms revolutionized palm oil production (and industrial agricultural development, in general) and would temporarily vault the Congo into one of the top global producers of palm oil by 1935 (Dinham and Hines 1984). In 1930, Lever Brothers merged with the Dutch company Margarine Unie to form Unilever, now the world's largest buyer of palm oil (Oosterveer 2015), thus forming one of the first large-scale, industrial, multinational oil palm enterprises. Despite the African origin of palm oil and some of the earliest experiments with large-scale cultivation of oil palms, palm oil production in Africa remained primarily controlled by smallholder farmers for much of the nineteenth and early twentieth centuries and even today much of the palm oil production is in the hands of small- to medium-scale farmers (Poku 2002; Corley and Tinker 2003; Rudel 2013; Wich et al. 2014). As such, Africa was the largest producer of palm oil until 1972, when Asia emerged as the leading global palm oil producer (FAO 2015).

The first African oil palms made their way to Asia when the Dutch planted four seedlings of African oil palm in Java's Buitenzorg (now, Bogor) Botanical Gardens in 1848. In 1875, the progeny of these plants would be planted in Sumatra and by 1914 these palms would be developed into a 2600 ha commercial oil palm plantation. Similarly, in 1911 and 1912 these palms were also planted in Malaysia, which by 1917 developed its own commercial oil palm plantations (Hartley 1988). The African oil palm and its varieties were found to thrive in Southeast Asia due to favorable soil and rainfall conditions and the absence of pests and diseases that afflicted it in Africa, resulting in higher yields. The oil palm industry would, thus, expand quickly in Indonesia and Malaysia.

In contrast to the smallholder dominance of palm oil production in Africa, large-scale, industrial cultivation of oil palms in Malaysia rapidly increased starting in the 1960s when the government introduced schemes to reduce the country's dependence on rubber and diversify its agricultural production (Teoh 2002). As a result, by 1975 Malaysia was producing more palm oil than all of Africa, with 60 % of its oil palm hectarage in the hands of private enterprises and 10 % managed by smallholder farmers as of 2000 (Teoh 2002). Similarly in Indonesia, government initiatives from the 1960s through the 1980s increased palm oil production from plantations, 50 % of which is controlled by private enterprises (Colchester et al. 2006; Sheil et al. 2009). By 2013, Malaysia and Indonesia were responsible for over 85 % of the world's palm oil production, whereas the proportion of the world's palm oil produced in all of Africa and the Americas was 4.1 % and 5.5 %, respectively (FAO 2015). Despite the early introduction and extensive use of the African oil palm in South America and the establishment of semi-wild populations in Brazil during the slave trade, large-scale cultivation did not really take hold until the 1960s (Hartley 1988). Since then, Columbia has seen the greatest growth of oil palm plantations in Latin America and is now the region's largest producer of palm oil and the fourth largest producer worldwide (FAO 2015; USDA 2015).

Impacts of Industrial Oil Palm Plantations on Biodiversity and Human Livelihoods

Global production of palm oil has increased exponentially over the past 50 years, driven by increasing consumption from a rapidly growing human population and use as a raw material (Fitzherbert et al. 2008). Today, the top importers of palm oil are India, the European Union, and China, respectively (FAO 2015). Between 1961 and 2013, the average annual growth rate of the world's palm oil production was 7.4 %, with production more than doubling every 10 years, making oil palm one of the most rapidly expanding crops in the tropics (Koh and Wilcove 2008; FAO 2015). At the same time, the total land devoted to oil palms more than quadrupled from 3.6 million ha in 1961 to over 17 million ha, distributed across 43 countries, in 2013 (Koh and Wilcove 2008; FAO 2015). Palm oil consumption and use as a raw material, especially for the production of biofuel, are expected to increase considerably by 2025 (Kongsager and Reenberg 2012). While Indonesia and Malaysia are predicted to maintain their dominance in palm oil production, land-use policy changes in these countries (Varkkey 2012; Feintrenie 2013) have contributed to an increase in land acquisitions and prospecting by agribusinesses for the development of oil palm plantations in other suitable regions, especially the tropical forest zones of Africa and Latin America (Schoneveld 2011; Greenpeace 2012; Sayer et al. 2012).

The lucrative palm oil industry and the need for economic development have motivated countries in these emerging palm oil producing regions to offer attractive land acquisition terms, including low rental fees, taxation, and duties and rights to water, minerals, and/or timber in the oil palm concession area (Hawkins and Chen 2011; Nguiffo and Schwartz 2012). In the African tropical forest zone, these factors are contributing to a "new wave" of palm oil production (Linder 2013). An estimated 2.6 million ha of land, the majority of which is forested, has already been allocated or is expected to be allocated to industrial oil palm developments in west and central Africa (Greenpeace 2012). These and other non-protected forests suitable for oil palm expansion overlap extensively with the geographic ranges of apes and other primate species (Wich et al. 2014). Similarly, the tropical forest zones of Central and South America are considered to be prime areas for large-scale oil palm cultivation (Corley and Tinker 2003). Almost half of Brazilian Amazonia, for example, holds some of the greatest biophysical potential for growing oil palms (Butler and Laurance 2009) and Brazil has recently increased its investment in the palm oil industry (Villela et al. 2014, Monteiro de Carvalho et al. 2015). Meanwhile, in Asia, large-scale oil palm developments are expected to expand quickly in Thailand (Saswattecha et al. 2015), Papua New Guinea (Nelson et al. 2014), and Myanmar (Donald et al. 2015).

Forest Loss and Fragmentation

Although oil palms require less land to produce the same amount of oil as other vegetable crops, and despite claims by some authors that the environmental damage from oil palm development has been exaggerated (Lam et al. 2009; Tan et al. 2009; Boyfield and Ali 2011; Roberts 2011), evidence indicates that industrial oil palm expansion can lead to extensive deforestation. Wicke and colleagues (2011) examined land use changes in Indonesia and Malaysia from 1975 through 2005, relying on data gathered from various kinds of publicly available national and international statistics. They found that in Indonesia forested land experienced the largest changes, declining in extent by 30 % over the 30-year period as agricultural land expanded by over 25 % during the same period. Palm oil production accounted for approximately half of this expansion, but was largely concentrated in Sumatra and Kalimantan. Malaysian forests were reduced by 20 % as land use for oil palm cultivation increased nearly sixfold. Although the impact of oil palm expansion varied across different scales and regions, the authors concluded that it played a significant role in reducing forest cover.

Based on nationally reported statistics of cropland and forest area, Koh and Wilcove (2008) also assessed the extent to which oil palm plantations are destroying forests (including primary, secondary, and plantation forests, but excluding rubber plantations) in Malaysia and Indonesia. They found that between 1990 and 2005, between 55 and 59 % of oil palm expansion in Malaysia resulted in secondary forest (selectively logged) and plantation forest clearance. At least 56 % of oil palm expansion in Indonesia during this same time period resulted in forest loss. Although the data did not permit the authors to discern between primary, secondary, and plantation forest loss due to oil palm developments, subsequent analysis showed that almost 60 % of new plantations (oil palm and rubber) created in Southeast Asia between 1980 and 2000 occurred at the expense of intact forests (Gibbs et al. 2010).

Based on remotely sensed time series data and socioeconomic surveys in West Kalimantan in the Indonesian part of Borneo, Carlson and colleagues (2012) found that from 1989 to 2008, nearly half of all oil palm plantations were developed on intact, secondary, and logged forests, leading to a decline in forest cover outside of protected areas from 59 to 22 %. The great majority of the forest loss during this 19 year period was attributed to fires that were exacerbated by deforestation (Curran et al. 2004). However, by 2008, 27 % of deforestation (and 40 % of all peatland loss) was directly attributed to oil palm plantation expansion. This is likely an underestimate of forest loss because in many instances logging conducted or contracted by oil palm companies was responsible for the deforestation and this was not attributed to oil palm expansion in the analysis. While many oil palm plantations in Southeast Asia have been established on selectively logged timber concessions (Curran et al. 2004; Hansen 2005), there is also a more direct link between palm oil production and logging. Timber production commonly precedes forest conversion to oil palm monoculture as timber revenues can help offset the costs of establishing a large-scale oil palm plantation (Hansen 2005; Sandker et al. 2007; Obidzinski et al. 2012; Hewitt 2013; Greenpeace 2014; Lee et al. 2014). However, these logging operations are often illegal or are conducted without intention of converting the area into an oil palm plantation (Sandker et al. 2007; Greenpeace 2014).

Considering forest loss across the entire island of Borneo, Gaveau and colleagues (2014) found that between 1973 and 2010, Borneo lost over 30 % of its forests, with 33 % converted to oil palm and rubber plantations. By 2010, industrial oil palm plantations covered almost 9 % of Borneo. Along with rubber plantations, the authors concluded that oil palm expansion represents the primary driver of forest loss in Borneo.

Margono and colleagues (2012) quantified using remotely sensed time series data the loss of primary, intact, lowland forest in Sumatra between 1990 and 2010. Results show that primary forest extent was nearly halved over the 20-year study period with most of this loss occurring in the first decade as there was simply less intact forest remaining in the 2000s. Over two-thirds of Sumatra's primary intact forest loss was located in the province of Riau and mostly attributed to the establishment of oil palm plantations along with timber and pulp concessions.

Similarly, Lee and colleagues (2014) examined forest loss (mangrove, peatland, lowland, lower montane) in Sumatra from 2000 through 2010 from smallholdings, private enterprises, and state-owned oil palm plantations. They found that large-scale oil palm developments were responsible for almost 20 % of Sumatra's total forest losses over the 10-year study period—eight times the impact of smallholders. Private enterprise-managed plantations were responsible for over 88 % of the deforestation.

Large-scale oil palm plantations in Southeast Asia have, in general, expanded at the expense of peatland forests, unique ecosystems that harbor high concentrations of endemic plant and animal species and serve as important refuges for orangutans and other primate species (Yule 2010). From analysis of remote sensing data, Koh and colleagues (2011) found that by the early 2000s a large proportion of peatland forests were converted to oil palm plantations in Peninsular Malaysia and certain regions of Sumatra. Miettinen and colleagues (2012) also came to a similar conclusion examining peatland deforestation in Southeast Asia from 1990 to 2010. They determined that due to logging and plantation development (including the burning and draining of forests), Sumatra experienced the greatest loss of peatland compared with Peninsular Malaysia and Borneo. The total study area lost over half of its peatland over a 20 year period. Focussing just on Indonesia, Lee and colleagues (2014) found that peatlands lost the greatest absolute and relative amount of forest due to oil palm development (especially private enterprise-managed) from 2000 through 2010. In the state of Selangor, Malaysia, Abdullah and Nakagoshi (2007) using time series data from land use/cover maps found that between 1966 and 1995, peatland and mangroves became increasingly more fragmented than other forest landscapes due primarily to the expansion of oil palm plantations.

Although deforestation from oil palm development is not as well studied in Latin America as it is in Southeast Asia, the available evidence indicates a similar trend. From remotely sensed and field data, Gutierrez-Velez and colleagues (2011) assessed forest loss due to large-scale, industrial and small-scale, low-yield oil palm plantations in the Peruvian Amazon from 2000 to 2010. They found that 72 % of large-scale oil palm expansion occurred at the expense of forests, representing 1.3 % of total deforestation in Peru during that time period. In contrast to small-scale plantations, the large-scale, industrial developments tended to expand mostly into old-growth forests. In Costa Rica, Broadbent and colleagues (2012), using remote sensing and socioeconomic surveys, examined changes to forest cover around Manuel Antonio National Park from 1985 to 2008. They found that large-scale oil palm plantations expanded from 19 to 31 % of the surrounding study area on an increasing proportion of natural forests, including in the buffer zone of the park. In Columbia oil palm expansion has become one of the principle drivers of deforestation and forest fragmentation, especially of gallery forests (Carretero-Pinzón et al. 2009), with the land devoted to oil palm increasing from 157,000 ha in 2000 to 404,000 ha in 2010 (Marin-Burgos et al. 2015). In the Brazilian State of Pará, the country's largest palm oil producer, 20 % of all oil palm expansion led to deforestation including of primary forest between 1985 and 2008 (Villela et al. 2014). Total area of oil palm plantations in Ecuador increased from 72,210 to 207,285 ha from 1998 to 2008, replacing over 22,000 ha of Ecuador's coastal Chocó rainforest (Hazlewood 2012).

The literature indicates that industrial oil palm plantations have expanded at the expense of tropical forests including primary, secondary, peatland, and mangrove forests. Especially salient is the link between industrial oil palm development and selective logging, a subject we explore in more detail below (see "Sustainability" and Industrially Produced Palm Oil).

Effects on Animal Communities

Turner et al. (2011) summarized much of the literature on the impact of oil palm development on species richness and abundance. Not surprisingly, conversion of forest to oil palm plantation results in simplification of the vegetation and extreme losses of biodiversity across taxonomic groups. Compared with intact primary, secondary, and/or selectively logged forest, industrial oil palm plantations are species-poor and/or exhibit substantially lower diversity. Specifically, research from Asia, Latin America, and Africa document the negative effects of large-scale oil palm plantations on mammals (Danielsen and Heegaard 1995; Maddox et al. 2007; Bernard et al. 2009; Swarna Nantha and Tisdell 2009; Struebig et al. 2011; Wich et al. 2012), birds (Danielsen and Heegaard 1995; Waltert et al. 2005; Aratrakorn et al. 2006; Koh and Wilcove 2008; Edwards et al. 2010; Azhar et al. 2011; Lees et al. 2015), reptiles (Glor et al. 2001; Gallmetzer and Schulze 2015), amphibians (Iskandar and Erdelen 2006; Gallmetzer and Schulze 2015), ants (Room 1975; Brühl and Eltz 2010; Lucey and Hill 2012), beetles (Chung et al. 2000; Davis and Philips 2005), orchid bees (Livingston et al. 2013), aquatic "true bugs" (Cunha et al. 2015), butterflies (Koh and Wilcove 2008; Lucey and Hill 2012), and fish (Giam et al. 2015).

Generalist, invasive, non-forest species tend to dominate oil palm plantations while species lost due to forest conversion are typically specialists and/or of highest conservation concern (Fitzherbert et al. 2008; Foster et al. 2011; Gallmetzer and Schulze 2015). Forest-dwelling primates are particularly affected by forest conversion to oil palm plantations. While some primate species can exploit the oil palm for food or shelter, few species can permanently live in such a monoculture (Humle and Matsuzawa 2004; Marchal and Hill 2009; Estrada et al. 2012; Azhar et al. 2013; Ancrenaz et al. 2014).

Related Ecological Effects

The ecological effects of large-scale oil palm development extend far beyond the direct loss of forest, subsequent dramatic declines in local biodiversity, and significant changes to animal assemblages. Large-scale oil palm developments result in local increases in human population density, primarily due to the mass migration of laborers into the project area, and investments in infrastructure, including roads and facilities to house and care for plantation workers (Susanti and Burgers 2013; Schoneveld 2014). In many tropical areas this results in increased hunting intensity for wild meat in adjacent forests and forest patches located within the plantation as migrant workers bring with them a preference for wild meat over other protein sources (Butynski and McCullough 2007; Maddox et al. 2007; Rist et al. 2010; Cramb and Curry 2012; Norwana et al. 2012; Azhar et al. 2013; Dewi et al. 2013; Luskin et al. 2014). The roads allow easier access to adjacent forests and markets, while reducing transport costs of wild meat (Laurance et al. 2014). Finally, the influx of laborers leads to further deforestation as these migrants clear forest for farmland (Laurance et al. 2009; Susanti and Burgers 2013; Schoneveld 2014).

Oil palm plantations are often established beside (and sometimes within) protected areas (PAs) including national parks (Curran et al. 2004; Broadbent et al. 2012; Azhar et al. 2013; Linder 2013; Susanti and Burgers 2013; Schoneveld 2014, Friends of the Earth 2015). As oil palm plantations have expanded (combined with their demographic, agricultural, and infrastructure correlates), PAs have become increasingly isolated (Broadbent et al. 2012; Carlson et al. 2012; Rival and Levang 2014). Forest loss and degradation surrounding PAs not only limit dispersal of non-flying mammals between remaining forest blocks (Bernard et al. 2009), but also threaten the ecological integrity of the PA itself through increased edge effects, hunting, encroachment, and pollution (Harvey et al. 2008; Laurance et al. 2012). Consequently, expansion of large-scale oil palm plantations near to PAs will likely result in increased rates of population extinction within the PA for many animal species. Primates are especially vulnerable to the synergistic interaction of inhospitable matrices and increased hunting intensity (Brashares et al. 2001; Gonedele Bi et al. 2012; Benchimol and Peres 2013).

Livelihood Impacts of Industrial Oil Palm Developments

Industrial oil palm development has been heralded as an effective strategy to improve rural development and alleviate poverty in developing countries (Härdter et al. 1997; Susila 2004; Basiron 2007; Lam et al. 2009; Tan et al. 2009; Deininger and Byerlee 2011; Roberts 2011; World Growth 2011). Some have suggested that NGOs have exaggerated the negative socioeconomic impacts of large-scale, industrial oil palm development (Tan et al. 2009; World Growth 2011) and overstated the conflicts that arise between agribusiness, government, and local communities (Rival and Levang 2014). A deeper consideration of the literature, however, indicates that oil palm development may have serious negative social, economic, and health consequences for local, especially indigenous, populations.

Rural and indigenous communities across Asian, Latin American, and African tropical forest zones exercise customary land tenure, but such rights are often unrecognized or ineffectively secured and protected (McCarthy and Cramb 2009; Colchester et al. 2011; Gerber 2011; Schoneveld 2014; Brad et al. 2015; Friends of the Earth 2015). Agribusinesses and national governments exploit this uncertain legal framework to gain control over forested lands, laying the foundation for the expansion of agro-industrial development throughout the tropics (Friends of the Earth 2008; McCarthy and Cramb 2009; Côté and Cliche 2011; Hazlewood 2012; Obidzinski et al. 2014; Brad et al. 2015; Rein 2015). This leads to the failure of many agribusiness to effectively follow national and international laws that give rights to affected communities to obtain free, prior, and informed consent (FPIC) in all phases of plantation development (Vermeulen and Cotula 2010; Hazlewood 2012; Colchester and Chao 2013; Nelson and Lomax 2013; Larsen et al. 2014; Friends of the Earth 2015; Global Witness 2015). Such large-scale land deals often suffer from lack of transparency regarding land allocation, resource rights, and contract details (Rosenkrantz et al. 2003; Friends of the Earth 2008; McCarthy and Cramb 2009; Rist et al. 2010; Vermeulen and Cotula 2010; Colchester et al. 2011; Hoyle and Levang 2012; Assembe-Mvondo et al. 2013; Schoneveld 2014). Consequently, without independent counsel and other experts advocating on their behalf, local community members (usually with only modest education levels) report confusion over rights, responsibilities, and obligations of stakeholders (Rosenkrantz et al. 2003; Rist et al. 2010; Vermeulen and Cotula 2010; Greenpeace 2013a; Nguiffo 2013; Brad et al. 2015; Friends of the Earth 2015). Local resistance, opposition, and other forms of conflict over land use, resource claims, and contractual obligations often follow (Ashley 1987; Mingorance 2006; Acciaioli 2008; Friends of the Earth 2008; McCarthy and Cramb 2009; Sirait 2009; Rist et al. 2010; Côté and Cliche 2011; Gerber 2011; Li 2011; Obidzinski et al. 2012; Väth 2012; Greenpeace 2013a; Schoneveld 2014; Castiblanco et al. 2015; Global Witness 2015; Marin-Burgos et al. 2015). Conflict occurs between local communities and the agribusiness and/or the government, among local communities that vary in acceptance of the plantation, among members within local communities, and between migrant workers and people native to the area (Colchester et al. 2011).

In addition to the links between industrial oil palm and human rights issues, claims that industrial oil palm development is a boon to local and national economies and livelihoods may have been exaggerated in some cases. Economic analysis suggests that the heyday of industrially produced palm oil profitability witnessed in the last decade may be coming to an end. Increasing production costs (especially labor costs), a declining global market price of crude palm oil, and overall declining cost competitiveness compared with other vegetable oils indicate that investments in large-scale oil palm ventures may not be as profitable in the near future as they were in the past (Rein 2015). While the industrial oil palm sector is an important source of employment, its proponents may be overestimating the number and quality of local jobs it generates

(Li 2011). Oil palm plantations profit by employing cheap, abundant labor. In Malaysia and Indonesia, this was largely accomplished through massive transmigration programs, moving mostly poor Javanese smallholders to oil palm plantation sites, marginalizing customary landholders (McCarthy and Cramb 2009). A similar strategy has been implemented in the Nigerian palm oil industry (Schoneveld 2014). Furthermore, oil palm development creates mostly seasonal and casual employment (Li 2011; Schoneveld 2014; Rein 2015). Converting forests and farmland to large-scale oil palm monocultures can also reduce income diversity, increase income inequality, and expose rural farmers to global commodity market volatility (Belcher et al. 2004; Dewi et al. 2005; McCarthy and Cramb 2009; Dauvergne and Neville 2010; Balachandaran et al. 2013; Elmhirst et al. 2015; Rein 2015). While the overall health impacts of industrial oil palm development on affected local communities are understudied, research shows that loss of forest and farmland to an export commodity threatens local food security and dietary quality, especially among women (Elmhirst et al. 2015), through declining access to non-timber forest products, reduced production of subsistence crops, and increased daily expenses on food (Norwana et al. 2012; Väth 2012; Balachandaran et al. 2013; Ickowitz et al. 2014; Schoneveld 2014; Sneyd 2014). In fact, Indonesia's rise to the world's top producer of palm oil came at the expense of its domestic food production; since 2011 the country has spent more money on importing food than it earned from exporting palm oil and rubber (Rein 2015). Finally, local populations can be affected by water contamination from plantation agrochemicals (Rosenkrantz et al. 2003; Hazlewood 2012; Marin-Burgos et al. 2015) and are at a high risk of malaria infection in plantation landscapes (Pluess et al. 2009).

This is not to say that industrial oil palm development always leads to adverse social and economic outcomes, nor is it the case that every agribusiness violates procedures of FPIC or causes social conflict (Susila 2004; McCarthy and Cramb 2009; Feintrenie et al. 2010; McCarthy 2010; Rist et al. 2010; Feintrenie 2012; Norwana et al. 2012; Obidzinski et al. 2012; Väth 2012; Beggs and Moore 2013). Indeed, economic benefits can be significant, particularly at the national level. Socioeconomic impacts of large-scale, industrial oil palm expansion are, however, highly variable (Zen et al. 2005; Sandker et al. 2007; McCarthy 2010; Rival and Levang 2014) and the socioeconomic risks involved with large-scale oil palm ventures are rarely, if ever, communicated to local people. The research cited above points to many detrimental social and economic consequences of industrial oil palm plantations that cut across time periods and all tropical regions where industrial oil palm is expanding. So, while there may be "winners" in the palm oil "sweepstakes," notably governments, agribusinesses, and elites, the "losers" stand to lose a lot (Belcher et al. 2004).

"Sustainability" and Industrially Produced Palm Oil

We have relied on peer-reviewed sources and the gray literature to illustrate that across regions where palm oil is produced, industrial oil palm development has been and continues to be a leading driver of tropical deforestation and biodiversity loss, threatens the integrity of protected areas, and can lead to significant social, economic, and health costs for local populations. Combined with overhunting and the activities of other agricultural and extractive industries, the rapid expansion of industrial oil palm plantations in the Neotropics and African tropical forest zones, assuming a "Business As Usual" (BAU) approach, is a harbinger of significant declines in tropical forest biodiversity.

In response to the problems associated with the palm oil industry, the World Wide Fund for Nature (WWF) conceived of and initiated the Roundtable on Sustainable Palm Oil (RSPO), a voluntary, multi-stakeholder effort formally established in 2004 to improve through independent certification the environmental and social impacts of the palm oil industry (Schouten and Glasbergen 2011). As national governments were largely unwilling or unable to forestall deforestation from industrial oil palm development, an alternative strategy of "partnered governance" was established whereby the palm oil industry from across the "supply chain" (e.g., palm oil producers, buyers, retailer, traders) collaborates with civil society organizations, which represent ecological and social interests, to implement minimum standards for "sustainable" palm oil (Nikoloyuk et al. 2010). Through the application of a set of principles and criteria (P&C), the RSPO certifies that palm oil is produced by "legal, economically viable, environmentally appropriate, and socially beneficial management and operations" (Roundtable on Sustainable Palm Oil 2013). From the ecological perspective, the RSPO has focussed on compelling palm oil producing members to establish plantations on "degraded land" and to protect areas of "High Conservation Value" (HCV), defined on the basis of species diversity, ecosystem services, the presence of rare, endemic, flagship, or threatened ecosystems or species, community needs, and cultural values (Roundtable on Sustainable Palm Oil 2013). As of April 2016, 3.66 million ha across eleven countries have been certified by the RSPO resulting in the production of over 13.7 million tones of certified sustainable palm oil, representing 21 % of global production (www.rspo.org).

The apparent success of the RSPO to shift the palm oil industry from a BAU approach to one of "sustainability," however, has been tempered by its critics. It has been argued that values held by palm oil producers, buyers, and traders dominate the RSPO system at the expense of environmental protection and local community rights (Laurance et al. 2010; Nikoloyuk et al. 2010; Paoli et al. 2010; von Geibler 2013) and that membership in the RSPO is too easy to acquire (Laurance et al. 2010). Critics have also cited the lack of effective oversight and enforcement of P&C as a major weakness of the RSPO (Siagian 2008; Laurance et al. 2010; Yaap et al. 2010; Schouten and Glasbergen 2011). There are many instances of members violating RSPO P&C including Herakles Farms/SG Sustainable Oils (Linder 2013), First Resources (Environmental Investigation Agency 2012; Parker 2013), Sinar Mas (Greenpeace 2009), United Plantations (Greenpeace 2008), Kuala Lumpur Kepong (Rainforest Action Network 2014), and the Wilmar Group (Friends of the Earth 2007; Greenpeace 2013c), challenging the credibility of the RSPO. Although the RSPO has established a formal grievance process to address complaints against RSPO members, this system has its limitations. To be successful, grievances require extensive evidence of violation, which require substantial resources and may involve entering the concession illegally (Pesqueira and Glasbergen 2013; Ruysschaert and Salles 2014; Marin-Burgos et al. 2015). In practice, grievances are typically filed by large NGOs often acting on behalf of local affected populations who may lack the capacity to do it themselves, and resolution can take up to 36 months (Ruysschaert and Salles 2014). Local community members and independent researchers who attempt to “blow the whistle” on powerful agribusinesses, which are often backed by national governments, risk intimidation, harassment, imprisonment, and death (Bird 2013; GRAIN 2014; Rainforest Action Network 2014). Without such NGO oversight, violation of P&C by RSPO members would likely go undetected by the RSPO.

Many have argued that weak and imprecise P&C allow national governments and palm oil producers to interpret the guidelines in ways that allow deforestation; including and especially of peatland and high carbon stock forests (Laurance et al. 2010; Nikoloyuk et al. 2010; Edwards et al. 2012; Greenpeace 2013a; Ruysschaert and Salles 2014). Among the most confusing yet critical concepts central to the RSPO sustainability approach is that of “degraded” land, on which members are encouraged to establish plantations so long as HCV is not present or is identified and protected. To date, the RSPO has not defined “degraded,” despite calls to do so in 2010 (Roundtable on Sustainable Palm Oil 2010), in part because degradation is a value judgement and, as such, there is no widely accepted definition of or method for delineating degraded land (McCormick et al. 2014). The P&C, however, imply that an area of land is either degraded or not degraded. In other words, the RSPO presents the process as a binary decision and that growers should select one over the other. In reality, degradation is a far more complex concept that is site specific and that falls along a continuum in terms of degree (e.g., lightly vs. severely) and scale (e.g., land/soil, habitat, ecosystem) (McCormick et al. 2014). Furthermore, protecting fragments of HCV forest within presumed “degraded” landscapes, as required by the RSPO, contributes little to broader biodiversity conservation efforts (Wilcove and Koh 2010). This RSPO conservation strategy also fails to account for delayed extinctions following forest loss and fragmentation (Kuussaari et al. 2009). As a result, biodiversity loss from conversion of land to industrial agriculture is likely being underestimated. A focus on identifying HCV and degraded land also ignores the importance of overall landscape heterogeneity in promoting biodiversity (Azhar et al. 2015).

Actors in the Malaysian and Indonesia palm oil industry have argued that industrial oil palm expansion has occurred primarily in previously logged, degraded land and, therefore, has not lead to the extensive deforestation and biodiversity losses suggested by environmental NGOs (Koh and Wilcove 2008). Selectively logged forests, however, have been found to retain relatively high levels of biodiversity, especially for primates (Meijaard et al. 2005; Berry et al. 2010; Putz and Redford 2010; Didham 2011; Gibson et al. 2011; Edwards and Laurance 2013; Ramage et al. 2013) and can become floristically similar to surrounding intact forest blocks within a few decades (Van Gemerden et al. 2003). Thus, logged forests are degraded relative to unlogged forests but still retain important conservation value and should be protected from conversion to industrial agriculture (Gaveau et al. 2014). With over 30 % of Central Africa's dense, humid forests under logging concessions (Laporte et al. 2007), Africa would stand to lose a significant proportion of forest biodiversity if it were to follow the Malaysian and Indonesia model of converting logged forests to oil palm plantations.

To further illustrate how the interpretation of the RSPO's "degraded" land and HCV approach can lead to forest loss and social conflict, we turn to the case of American agribusiness Herakles Farms (HF) and its subsidiary SG Sustainable Oils, which in 2009 signed an agreement with the government of Cameroon to establish an industrial oil palm plantation on over 73,000 ha adjacent to four protected areas including two national parks. HF, a member of the RSPO at the time of starting its development, claimed that the concession area was degraded because it had been heavily fragmented from years of commercial logging and slash and burn agriculture and was, therefore dominated by secondary forest of low biodiversity value (Asamoah 2011; Herakles Farms 2012). The HF formal assessment of HCV, submitted to the RSPO and Cameroon government, indicated that within this degraded landscape only small (mostly <25 ha), isolated patches of HCV forest primarily restricted to hilltops and steep-sided ridges would be spared from conversion (Asamoah 2011). The relevant Cameroon ministries generally concurred with this evaluation and management plan. HF further argued that they secured the support of local communities in the form of signed Memorandums of Understanding. The HF development may have been given permission to clear forest by the RSPO had it not been for the efforts of local community members and Cameroonian and foreign NGOs and scientists who brought the HF issue to international attention and filed an official grievance with the RSPO. Years of data gathering by this group (including interviews, ecological surveys, remote sensing, and investigations into HF) indicated that the concession area primarily consisted of dense, intact, high canopy forest with carbon stocks higher than the regional average and contained many kinds of threatened and/or narrowly endemic plant and animal species distributed throughout the planned plantation area (Maschler 2012; Greenpeace 2013b; Kupsch et al. 2014). Furthermore, HF allegedly failed to obtain the FPIC of local communities, resulting in extensive conflicts with (and among) local stakeholders (Nelson and Lomax 2013). Thus, contrary to claims made by HF and the Cameroon government, critics argued that the proposed plantation area was composed almost entirely of HCV forest and not suitable for conversion, local communities were not given the opportunity to give their informed consent, and the process by which HF obtained the land lease would not meet RSPO standards. In response to the grievance file, the RSPO asked HF to engage in bilateral discussions with only one of the dozens of complainants (WWF-Cameroon) to resolve issues related to HCV areas, FPIC, and legal compliance (Roundtable on Sustainable Palm Oil 2012). In other words, despite the depth and breadth of violations allegedly committed by one of its members, the RSPO was evidently still willing to certify as sustainable the palm oil produced by HF so long as the company could resolve its issues with only one of the complainants. In spite of these outstanding issues, the sustained campaign against HF would lead the company to withdraw from the RSPO and abandon some of its oil palm nurseries, while the Cameroon government reduced the concession area to 20,000 ha. This example lends strong support to many of the accusations leveled by critics of the RSPO and illustrates how RSPO weaknesses can be easily exploited by agribusiness members, who use their membership to greenwash their activities (McCarthy and Zen 2010).

In view of the problems with the RSPO, it could be argued that ecologically sustainable palm oil has yet to be produced on an industrial scale. Rather, in its present form, the RSPO provides minimum standards for palm oil production that improve upon BAU approaches but fall short of eliminating (or, significantly reducing) deforestation, biodiversity loss, and social and economic risks associated with the industrial palm oil industry. As such, if the RSPO "sustainability" approach were to rapidly expand in emerging palm oil producing regions (e.g., African tropical forest zones and Latin America) we can continue to expect large-scale losses in forest cover, biodiversity, and ecosystem services as well as increased social conflict.

Palm Oil Is Not Bad, It Is Just Produced That Way

While the industrial production of palm oil on large plantations has greatly contributed to the biodiversity crisis (Laurance 2007), the African oil palm and its varieties are not inherently damaging to biodiversity (Colchester et al. 2006). Given the global demand for palm oil, the immense productivity of the oil palm, and its near ubiquity in tropical forest regions, the oil palm holds a unique opportunity to help bridge the divide between local and national aspirations for economic development and global concerns for biodiversity. Many of the authors cited in this chapter have offered solutions to the environmental and social challenges of producing palm oil on an industrial scale and we encourage readers to refer to their suggestions. Here, we aim to supplement those recommendations with a few of our own.

The evidence presented in this chapter indicates that those concerned with biodiversity conservation, human rights, and socioeconomic development should be wary of industrial oil palm developments (even RSPO certified ones) as a means of rural development, poverty alleviation, and as a "win–win" for people and the environment. Most worrisome is that industrial oil palm plantations are rapidly expanding in areas of high conservation concern including biodiversity hotspots (Myers et al. 2000; Mittermeier et al. 2004), threatened ecoregions (Olson and Dinerstein 1998), and regions characterized by exceptionally high plant and animal endemic species richness (Fa and Funk 2007; Kier et al. 2009). Conservation, development, and human rights NGOs should collaborate with local actors to invest resources in oversight of industrial oil palm developments and in providing legal counsel to locally affected communities. Such expansive coalitions are especially necessary to investigate RSPO members and file grievances when appropriate. Results from well-researched, scientifically grounded studies can also be used successfully to influence agribusiness activity and government support of agribusinesses that violate national and international agreements and laws (Ongolo 2015). As in the case with Herakles Farms, such research can be elevated to the international stage to overcome agribusiness greenwashing and public relations campaigns. To maintain credibility, NGOs must present to the public factual information about the environmental, socioeconomic, and legal issues surrounding industrial oil palm developments without inflating claims or resorting to scare tactics (Koh et al. 2010).

While the negative effects on the environment are clear, there remain many unanswered questions regarding the socioeconomic and local human health impacts of large-scale, industrial oil palm plantations. A deeper understanding of the factors that influence social and economic effects is desperately needed. For example, will the variables that make industrial oil palm "good for some" (Rival and Levang 2014) in Malaysia and Indonesia also apply to other regions of the world? How will the concerns over the social and economic risks of industrial oil palm development, presented by many of the authors cited above, be incorporated in national land use and agricultural policies and legal responsibilities of agribusinesses? How will the diets and health of local community members living in and around oil palm plantations change through time as landscape heterogeneity declines?

As governments in the tropics look to bolster their economy and invest in the agricultural sector, alternative strategies for producing palm oil besides on large-scale plantations need to be investigated. This is especially salient for the African tropical forest zones where smallholders control up to 80 % of planted oil palm areas (Wich et al. 2014). What role can smallholders and their agroecological systems play in expanding production of palm oil? With proper technical and financial capacity building, can investments in smallholder agriculture improve palm oil productivity to the extent that large-scale monocultures are unnecessary while maintaining some degree of habitat heterogeneity through agroforestry techniques?

Tropical forest conservation, including and especially primate conservation, in the 21st century will require innovative strategies for conserving biodiversity not only in protected areas but also in human modified landscapes where palm oil and other agricultural commodities are produced (Chazdon et al. 2009). In his critique of large-scale land acquisitions for farming, De Schutter (2011) argues that we need to examine whether land leased to agribusinesses for large, monoculture plantations could, instead, be used more productively, in ways that reduce environmental impacts and socioeconomic risks. Toward this end, the conservation, development, and human rights communities should work in concert to influence land use policies in regions where industrially produced palm oil is expanding.

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Monkeys on the Menu? Reconciling Patterns of Primate Hunting and Consumption in a Central African Village

Carolyn Jost Robinson, Lesley L. Daspit, and Melissa J. Remis

Introduction

Most human populations in the Congo Basin rely on wildlife for protein (Bennett et al. 2007; Bowen-Jones and Pendry 1999; Eves and Bakaar 2001; Fa et al. 2002a, 2002b). Such use and extraction of wildlife has become popularly referred to as the bushmeat trade, which is defined as the commercial hunting and sale of wildlife (BCTF 2000). It is a trade that is often characterized as a "crisis" because of its illegal and unsustainable characteristics. Throughout the Congo Basin, burgeoning economies of wildlife, increased human migration, changing technology, and the presence of conservation and development projects threaten the viability of wildlife populations and the human communities dependent upon them (Barnes 2002; Fa and Brown 2009; Linder and Oates 2011; Jost Robinson et al. 2011; Milner-Gulland and Bennett 2003). Milner-Gulland and Bennett (2003) note that bushmeat is consumed on a "massive scale" and that this high level of consumption is directly linked to both global and local economies. At the local level, consumption is based

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on the intersections of local ecology, subsistence practices, economics, and preferences. Preferences for bushmeat are culturally based and shaped by various factors including tradition, taste preferences, education level, and migration status (Daspit 2011; East et al. 2005; Fa et al. 2003; Schenck et al. 2006).

The continued and increased consumption of bushmeat has been found to be related to both wildlife abundance and preferences for wild meat alongside the high costs of protein alternatives and the low availability and productivity of domestic livestock in tropical forests (Fa and Brown 2009; Wilkie and Godoy 2001; Wilkie et al. 2005). More recently, research has demonstrated the fundamental importance of wild game to human nutrition and health in poor communities throughout the tropics (Blaney et al. 2009; Golden et al. 2011; Fa et al. 2015b). Studies have also explored ways to substitute local diets with other forms of protein; however, this may harm rather than help local inhabitants who depend on the bushmeat trade as a source of income where few alternatives exist (Milner-Gulland and Bennett 2003). The cultural significance of food, specifically bushmeat, is particularly important for human communities in the Congo Basin (de Garine 1997; de Garine and Pagezy 1990; de Merode et al. 2004; Motte-Florac et al. 1993). The importance of wild meat in the diets of local human populations results in greater challenges for conservation and development programs that overlook the cultural significance of bushmeat (Fa et al. 2015b).

In these cases, it may be neither feasible nor appropriate to provide communities with protein alternatives (Robinson and Bennett 2000). In a large-scale analysis, Fa et al. (2015a) recently determined that in some cases, it might be sustainable for smaller, low-density human communities to subsist on faster-reproducing species of game meat. Yet, before we can adequately address the issues of sustainability (Weinbaum et al. 2013), we must develop a better understanding of the complex nature of the relationships that exist between humans and wildlife, including nonhuman primates.

Regional market surveys have been used as a rapid assessment tool to measure faunal extraction and changes in relative proportion of wildlife to inform regional management plans (Fa et al. 2000, 2015a). Increases in the relative frequency of primates for sale at markets may signal an increase in human disturbance and reduction in preferred ungulate species rather than a preference for primates. Areas that have large human populations and road networks have fewer elephants, large duikers, buffalos, and red river hogs (Blake et al. 2008; Laurance et al. 2006; Wilkie et al. 2000). Additionally, an influx of guns and hunters' adoption of them as faster, more accurate hunting technology, increases the threats to primates, especially arboreal species (Kümpel et al. 2008; Noss 1998). Moreover, increases in the representation of fast-reproducing species in wildlife markets have been seen as indicators of overexploitation of primary prey species (Cowlishaw et al. 2005; Dupain et al. 2012). However, market surveys only capture a fraction of what is hunted, consumed, or traded outside of the formal market context. It is thus essential that we more holistically address "what is on the menu," or in the cooking pots, of local communities from multiple methodological perspectives. This will help to deepen our understanding of the dynamic relationships between humans and prey species and the relative vulnerability of primate populations. These relationships will have ecological and economic consequences beyond declining primate diversity and food insecurity for populations in primate habitat countries. Research demonstrates that the loss of primates and other frugivorous prey species (e.g., *Artiodactyls* and rodents) from ecosystems has knock-on effects across trophic levels (Abernathy et al. 2013; Henschel et al. 2011; Klailova et al. 2013).

Initially, the bushmeat crisis was portrayed as a primate problem—especially that of slow-reproducing great ape species. Primatologists and biologists owe a great debt of gratitude to the remarkable photographic work of Karl Amman and other conservation researchers who were able to draw initial international attention to multifarious issues surrounding the hunting, trade, and consumption of nonhuman primates and other wild game (BCTF 2000; Bowen-Jones and Pendry 1999; Peterson 2003). In fact, regional research has suggested that in many Congo Basin forests, primates are not the most preferred source of meat (Crookes et al. 2005; Fa et al. 2000, 2002a, b, 2015a; Njiforti 1996). Regardless of preference, nonhuman primates are nonetheless hunted (Abernathy et al. 2013; Fa and Brown 2009; Jost Robinson 2012), especially wherever gun hunters are common. Game depletion and the relative percentages of ungulates and primates sold in markets are highly correlated with human population density and anthropogenic activity (Fa et al. 2015a). Given their larger body size and slow rates of reproduction, we know that many primate populations cannot tolerate even modest levels of hunting.

Studies emphasizing the unsustainable hunting of nonhuman primates and other wildlife for trade and consumption in local and international markets are not novel. However, the ways in which we study, engage with, and understand the interconnected issues of conservation, poverty, and food security require us to incorporate additional methods into our approach. Here, we provide a case study that demonstrates the utility of assessing natural resource use (e.g., hunting) and primate conservation within theoretical and methodological frameworks of ethnoprimatology and multispecies ethnography (Fuentes 2012; Malone et al. 2014; Jost Robinson and Remis 2014). To better determine the degree to which monkeys are on the menu, we address the consumptive use of primates within a larger socio-ecological setting within the Dzanga-Sangha Protected Areas (APDS), Central African Republic (CAR). We do this by investigating the ecological patterns of forest presence, and off-take as they intersect with economic and cultural patterns of commerce and consumption of monkeys and other nonhuman primate species across three contexts: the forest, the market, and the cooking pot.

Methods

The data presented in this study were collected in the APDS, CAR located in the southwestern part of the country (2°13′26N, 16°11′26E, Fig. 1), from January 2008 to August 2009. Conservation and development activities in the southwestern CAR

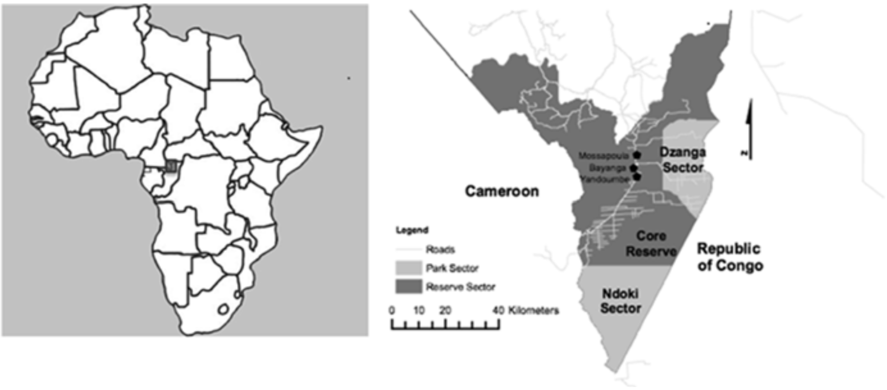

Fig. 1 Dzanga Sangha Protected Areas (APDS), Central African Republic (CAR)

began in the mid-1980s (Carroll 1986) with the APDS officially designated as a park (1200 km^2) and multiple-use reserve (3360 km^2) in 1990. Within the APDS park sectors, only research and tourism are permitted. Cable snares are prohibited, but were commonly used through the 1980s and 1990s (see Noss 1998). In the reserve, gathering of plant and animal products, traditional spear, cross-bow and net hunts as well as regulated shotgun hunting during daylight hours are permitted.

The APDS was selectively logged at low intensity in the 1970s and again between 2002 and 2005. Human in-migration to APDS (Blom et al. 2004), greater access to arms, and a reduction in preferred ungulate prey are related to the increased hunting and trade of primates (Daspit 2011; Fa et al. 2005; Jost Robinson et al. 2011). Rainfall in the APDS averages 1400 mm per year. The forests can be broadly classified as mixed secondary forest (low canopy forest with dense understory) although mixed primary forest (high canopy forest with a relatively open understory) is also common (Remis 2000).

Line Transect Surveys

The ecological data reported here are a subset of a larger, longitudinal ecological monitoring dataset collected by Remis (1997–2005) and Jost Robinson (2008–2009). Remis and Jost Robinson have worked to maintain overlapping members of the field teams to increase accuracy and comparability of datasets. Here, we report on the 2002 ($n = 100$ km) and 2009 ($n = 135.4$ km) datasets. We focus solely on direct observations of monkey species on census walks on straight-line transects. Following patterns documented at other sites (i.e., Croes et al. 2006), our data indicate that changing antipredator tactics among cercopithecoid primates in APDS affect the accuracy of auditory detection on transects (Jost Robinson 2012; Remis and Jost Robinson 2012).

Using line transect surveys (Plumptre 2000; Plumptre and Cox 2006), we monitored large mammal species including diurnal primates (*Cercopithecus pogonias*, *C. nictitans*, *C. cephus*, *C. neglectus*, *Lophocebus albigena*, *Cercocebus agilis*, *Colobus guereza*, *Procolobus badius*, *Pan troglodytes*, and *Gorilla gorilla gorilla*), Elephants (*Loxodonta africana*), Suids (*Potamochoerus porcus*), and duikers (*Philantomba monticola*, *Cephalophus callipygus*, *C. dorsalis*, *C. leucogaster*, *C. nigrifrons*, *C. sylvicultor*) at intervals from July to August 1997 and August 2008 to June 2009.

At each of our research sites, we established four to six 5-km line transects, perpendicular to drainage patterns, using an abandoned primary logging road as a baseline. At each site, we located at least two transects within 500 m, of and parallel to, a secondary logging road, and two transects more than a kilometer from the nearest secondary road. Following methods described in White and Edwards (2000) teams of at least two trained observers walked transects between 0700 and 1300 h at a pace of 1 km/h. On the transects, we documented direct observations and calls of large mammals, noting species, age/sex (if possible), location on transect, and perpendicular distance from transect and animal-observer distance (Fashing and Cords 2000; Marshall et al. 2008). During data collection, we also recorded all indications of human activity on transects, including logging and hunting signs (indication of logging trails, stump cuts, snares, or gun shots) and other human traces.

Hunter Off-Take and Interview Data

Ethnographic semi-structured interviews ($n=210$) with hunters from APDS included information on hunting methods, preference and returns, as well as their knowledge of hunted wildlife species. Given the potentially sensitive nature of hunting-related topics, we used snowball sampling to opportunistically select individuals who were willing to participate in this study (Bernard 2002; Trotter and Schensul 1998) in order to minimize the risk to human participants. Additionally, 34 weeks of surveys with 15 local hunters (cable = 5, registered firearm = 5, artisanal firearm = 5) yielded data for 793 hunting trips. Surveys included data on munitions taken, and animals captured by age (adult/juvenile) and sex class.

Market Data and Interview Methods

The primary market and ethnographic data were collected from the central town of Bayanga, in addition to four other satellite villages and forest camps. We emphasize and present the data for Bayanga only, as during our study period (2008–2009) this was the location of the single central marketplace for bushmeat and other wild and domesticated foodstuffs, including beef (sold by the Kg) and whole chickens (see Table 1 for wildlife species). Data collected in 2008 are compared to a 2006

Table 1 Species available in the marketplace of Bayanga, 2008

Latin name	English name
Ungulates	
Philantomba monticola	Blue duiker
Tragelaphus eurycerosa[a]	Bongo
Loxodonta africana[a]	African forest elephant
Syncerus caffer	Buffalo
Hippopotamus amphibious[a]	Hippopotamus
Cephalophus spp.[b]	Red duikers
Potamochoerus porcus	Red river hog
Tragelaphus spekei	Sitatunga
Hyemoschus aquaticus[a]	Water chevrotain
Cephalophus sylvicultror	Yellow-backed duiker
Hylochoerus meinertzhageni	Giant forest hog
Primates	
Cercocebus galeritus	Crested mangabey
Colobus guerza[a]	Black and white colobus
Pan troglodytes[a]	Chimpanzee
Cecopithecus pogonias	Crowned guenon
Cercopithecus neglectus	DeBrazza's monkey
Gorilla gorilla gorilla[a]	Western lowland gorilla
Cercopithecus nictitans	Greater white-nosed monkey
Lophocebus albegina	Gray-cheeked mangabey
Cercopithecus cephus	Mustached monkey
Other	
Bat (unknown)	Bat
Corythaeola cristata	Great blue turaco
Civettictis civetta	African civet
Smutsia gigantea[a]	Giant pangolin
Cricetomys emini	African pouched rat
Atherurus africanus	Brush-tailed porcupine
Snake (general)	Snake
Nandinia binotata	Palm civet
Phataginus tricuspis	Tree pangolin
Genetta servalina[a]	Servaline genet
Kinixys spp.	Tortoise

[a] Indicates a completely protected species

[b] Includes the following species with number of individuals observed: *C. dorsalis*, *C. nigrifrons*[a], *C. callipygus*, *C. leucogaster*

market study using identical methodologies (Hodgkinson 2009). At other villages within APDS, the sale of wild meat occurred from homes, on roadsides, or across international borders. Additionally, ethnographic interviews (informal and semi-structured) were conducted with the ten primary bushmeat sellers in Bayanga's marketplace in order to understand their bushmeat commerce from multiple socio-economic perspectives.

Results

The Forest

Of the eight nonhuman primate species present in APDS, three species (*C. guereza*, *P. badius*, *C. galeritus*) were not detected on transects during either sampling year. Direct observations of monkeys species on transects have declined over time at APDS between 2002 (Avg=0.73, *n*=73) and 2009 (Avg=0.26, *n*=40). For those species detected (see Fig. 2), there were discernible declines in rates of observation on transects between years.

In addition to ecological transect data, we include results related to hunter off-take rates and hunting technology within the context of "forest" datasets, as these are a reflection of prey availability and the ways in which hunters interact with primates. Our datasets document a large increase in guns relative to other forms of hunting since 2006 (Daspit 2011; Jost Robinson 2012). Jost Robinson (2012) interviewed 91 self-identified gun hunters in/from Bayanga, confirming that a large percentage of guns in the region are undocumented or artisanal.

Prior to the 2000s, firearms were rare in APDS. During this earlier time, hunters relied on illegal cable snares and other traditional methods (i.e., nets and spears). Cable snares, unlike firearms, do not allow hunters to choose their prey, as catches are opportunistic. Thus, mostly ground-dwelling species, both protected and not, are trapped within snares. Moreover, the use of snares reduced the importance of arboreal primate species as a prey base for hunters. Some hunters may still rely on illegal cable snares and/or nets, given their low cost. However, firearms, both registered and artisanal (i.e., illegal) have become the prominent hunting tool in the

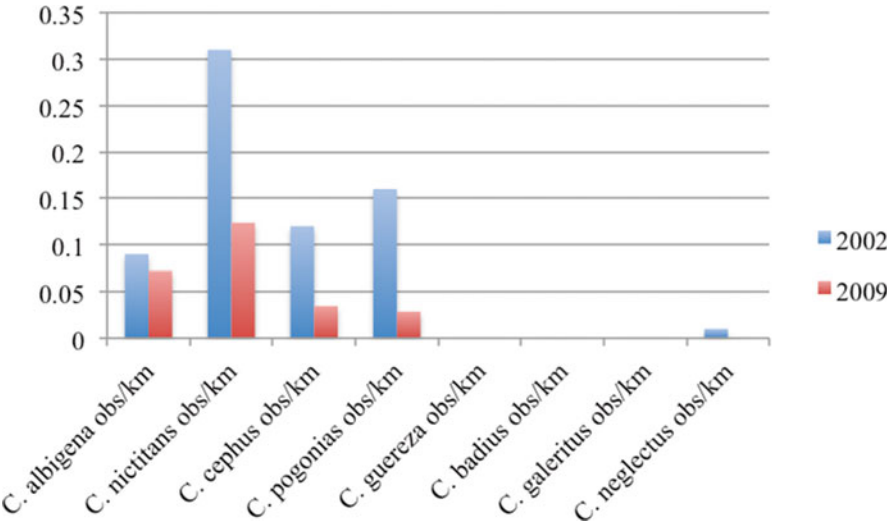

Fig. 2 Differences in monkey observation encounter rates over time in APDS, 2002 vs. 2009

APDS. The number of firearms has increased along with continued human in-migration to the area, as well as increased overall circulation with civil conflict in neighboring countries. During a short period of time, registered guns in the APDS increased from 8 in 2006 to 53 in 2009 (Hodgkinson 2009; Nabane pers. comm.); of course this number does not account for illegal, artisanal guns, which are also present and increasing in numbers. As such, hunters target-specific prey species, catch more individuals per hunting trip, and have increased their economic returns.

The increase in the numbers of guns in the region is likely responsible for the tenfold increase in quantities of primates hunted since 1994 (see Noss 1995). Using data on rates of prey off-take, we estimate that 90 gun hunters were able to hunt roughly 10,473 cercopithecoid primates during the 2008–2009 field season. The percentage representation of each species in hunter off-take is represented in Fig. 3. *C. nictitans* (blue) and *L. albigena* (red) were the two most common species in hunter off-take, followed by *C. cephus* (green) and *Cercocebus galeritus* (purple).

The Market

Between 2006 and 2008, market data from Bayanga showed a slight increase (6.62 %) in the annual estimated number of carcasses for all wildlife species (Daspit 2011). Broadly, researchers examined the proportions of species types in the marketplace, including ungulates, primates, and other species (including rodents and carnivores), in order to determine the approximate health of prey populations in the region (Cowlishaw et al. 2005; Fa et al. 2000; Noss 1998). In 2009, ungulates were the most prevalent species in the market (primarily species of blue and red duikers), representing 80 % of all carcasses available, followed by primates (19 %) and other species (1 %), including rodents, tortoises, birds, and small-bodied carnivores. There were some notable changes in the species composition across years, however,

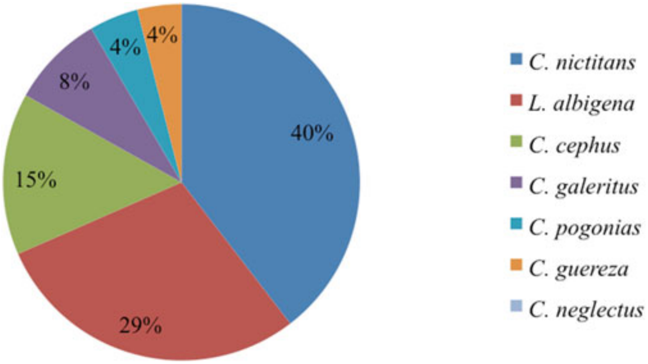

Fig. 3 Percentage representation of monkeys in hunter catchments, 2008–2009

which mirror trends observed in other West and Central African markets where declines in ungulate populations from overexploitation are buffered by an increase in the hunting of nonhuman primates and rodents (Cowlishaw et al. 2005; Fa et al. 2000, 2005). In this particular market in Bayanga, there was a 9 % decrease in ungulates species available in the market place coupled with a 9 % increase in primate off-take between 2006 and 2008 (see Daspit 2011; Hodgkinson 2009). Figure 4 compares the percentage of primate species present in hunter off-take with those documented in market profiles. When we compare the proportional representation of what comes out of the forest with what appears in the market we see some interesting differences.

C. nictitans and *L. albigena* were still the two most common species. However, the third most common species in the market in 2009 was *C. pogonias*. This species, which is taboo among many ethnic groups, was the fifth most common in hunter catchment but the third most common in the market. We saw a similar trend for the black and white colobus (orange), also a taboo species. *C. pogonias* and *C. guereza* are taboo species for some local ethnic groups as they are thought to cause bodily harm or be lethal to pregnant women, nursing mothers, and infants. Both *C. pogonias* and *C. guereza* were more common in the marketplace than expected given their representation hunter catchments.

For the case of *C. pogonias*, ethnographic interviews with hunters and market women suggest that this is possibly related to taboos regarding *C. pogonias* as well as gendered differences in commerce and economic practices. Because hunters were less often able to target their preferred prey species (i.e., duikers, *Philantomba monticola* and *Cephalophus* spp.) and many aspects of traditional food culture have eroded, all species are hunted regardless of taboos. Hunters noted that they often sold taboo species to market women and did not keep them for home consumption, thereby exercising choice in what was kept for domestic use and what was sold. We should note that *C. pogonias* sold for more money than that of the smaller *C. cephus* monkeys. However, hunters would occasionally sell *C. pogonias* to the local market

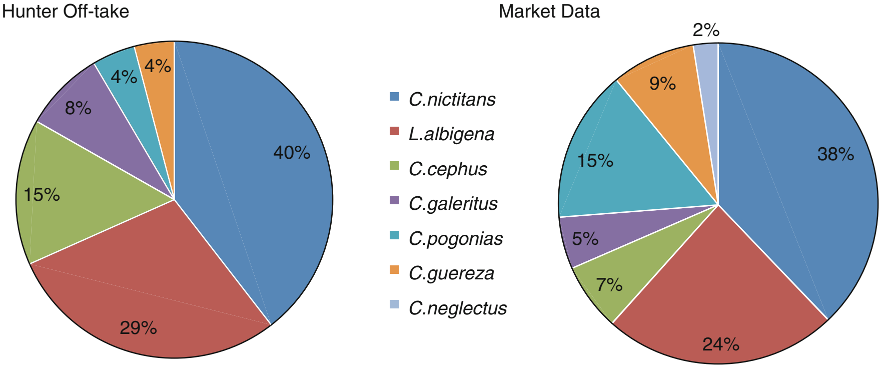

Fig. 4 Comparison of percentage representation of monkeys in hunter catchment vs. market availability

because they did not want to consume taboo species rather than for its potential higher profit. This was a rare instance we noted where profit was not the primary motivation for species sales.

However, many market women did not appear to have the luxury to exercise choice in the same way that hunters do, as they needed to have something to sell each day. The more senior market women in Bayanga, who occupied the tables within the interior of the marketplace, would not sell monkeys but preferred species of duikers (*Philantomba monticola* and *Cephalophus* spp.). In interviews with Daspit, these market women indicated their preference for purchasing red duikers (*Cephalophus* spp.) followed by blue duikers (*Philontomba monticola*) from hunters, explaining that these are what local women preferred to purchase for their daily meals. As such, offering cuts of blue and red duikers for sale would better contribute to women's market profits. Overall, information gathered from hunters, market women, and consumers further highlights the strategic aversion to the hunting and consumption of monkeys when other preferred species are available.

The Cooking Pot

The final context in which we must address the hunting and consumption of monkeys is in the home. In the APDS, hunters, market women, and consumers, whether they were born within the area or were a recent or longer term migrant to this region, all reported preferences for ungulates. Further, in everyday life, we observed that people preferred to purchase and fill their cooking pots with duiker species rather than primates. This observation was further supported by Hodgkinson's (2009) surveys, conducted in 2006, which showed that people not only preferred but also consumed ungulate species more than primate species (Kilograms consumed/yr: Primates = 3749 (6 %), Ungulates = 57,037 (90 %)) (Fig. 5).

Discussion

So how do we reconcile these patterns where primates are hunted although not desired? We found that monkeys have both declined and become increasingly cryptic on transects over time (Remis and Jost Robinson 2012), but we also know that overall off-take increased tenfold over a 15-year period. Guns have likely helped to facilitate greater overall off-take of wildlife in this protected area as evidenced by higher carcass numbers reported in both hunter off-take and formal market surveys. Taboo species of monkeys have also become more frequently hunted, signaling the erosion of particular cultural traditions. However, when hunted, these species are likely to be sold to women who sell their foodstuffs on the outskirts of the central marketplace rather than to the market women who sell daily on tables rented within the marketplace. The more common, yet illegal, practice of night hunting (i.e.,

Fig. 5 A young woman prepare a blue duiker (*P. monticola*) for a traditional meal

"jacklighting") may temporarily diminish the threat of hunting to monkey species in this region, but as preferred ungulate species decline primates will take their place at the dinner table. This pattern has already been observed at West African sites (Covey and McGraw 2014).

In Bayanga, the formal market data have already begun to signal this important change from the hunting of desired prey species to secondary prey. In just 2 years during our study, small, but meaningful differences were seen in the decline in ungulates coupled with an increase in monkeys available in the marketplace. In addition, our ethnographic data suggest that what local communities were consuming was beginning to change during this time period, apparently out of necessity rather than preference. This was especially evidenced on days observed in 2008 when few to no carcasses made it to the marketplace in Bayanga, leading to a perceived scarcity of wild meat. Both market women and the women who came to the market to purchase their daily stew's ingredients commented on the difficulty in finding meat in the market and even at individuals' homes, a pattern told to Daspit as being a more recent phenomenon.

We suggest that a combination of ethnographic and primatological approaches helped us to better understand patterns of primate hunting and consumption (Jost Robinson and Remis 2014). In the APDS, while monkeys have not been traditionally top menu choices for many local residents, they have come to fill people's cooking pots more frequently over time under specific and changing socio-ecological contexts. While guns were not yet exclusively associated with increased primate off-take during our study period, they allowed hunters unprecedented access to these species compared to previous time periods. We thus posit that future household and market surveys will likely point toward the increasing importance of primates to local diets, mirroring shifts in the 2008 market data as compared to 2006. The expected increase in primates will become a necessity as ungulates become less available due to the increased number of guns in the APDS, as well as, their efficiency in depleting populations of preferred prey species. It is at this point that the bushmeat trade within APDS will shift toward/become primarily a primate crisis. The hunting pressure for nonhuman primates was low during our data collection period, as local hunters preferred to target duiker species at night. Yet, as duiker populations decline, we predict that gun hunters in the APDS will revert to daytime hunting, relying more heavily on arboreal primates. Given that shifts toward primates may not result from traditions or food preferences suggests it might be possible to influence or reduce the consumption of primates if sufficiently low-priced alternatives were available (also Wilkie and Godoy 2001). Schenck and colleagues (2006) in Gabon found no strong preference for bushmeat in paired choice trials, suggesting the potential viability of domesticated alternatives.

Ethnographic understandings of wildlife off-take from multiple perspectives combined with quantitative research in forests and markets provide stronger platforms from which research can inform conservation policy, perhaps providing a silver lining for primate species. Hunters would prefer to hunt ungulates, and although we do not suggest that ungulates should be sacrificed, we do suggest they are a keystone species whose populations may be successfully maintained using active approaches to management in transitioning ecosystems and economies such as in the case of the APDS (Fa et al. 2015a).

To more effectively understand the state of nonhuman primate populations and their future in the Congo Basin, it is necessary to contextualize their numbers and threats in relation to other mammalian species that are important to local and regional diets and material economies. The successful conservation of nonhuman primates cannot be accomplished in isolation of complex, interrelated ecological, economic, and cultural practices. We must draw upon theory in anthropology, ethnoprimatology, and historical ecology to develop integrated conservation efforts that aim to provide best management practices for active management of preferred prey populations under conditions of relatively high human density. Maintenance of these populations will be key to the maintenance of nonhuman primate species in this forest. Decline of critical key prey species will have cascading effects for other wildlife species such as nonhuman primates that may be even less resilient to hunting pressures.

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Conservation Medicine: A Solution-Based Approach for Saving Nonhuman Primates

Sharon L. Deem

Introduction

The pressures limiting the long-term survival of many wildlife species, including nonhuman primates (NHP), are largely human-driven (anthropogenic). These pressures include climate change, habitat degradation and fragmentation, invasive species, trade in wildlife, and exposure to emerging pathogens, all of which are associated with the human population growth which surpassed seven billion individuals in 2012. In fact, these anthropogenic changes have led many to contend that the Earth is presently in a new “Anthropocene” epoch (Crutzen 2002). Simply stated, humans are the drivers of planetary health.

Humans have transformed between one-third and one-half of the land surface, and now appropriate over 40 % of the net primary terrestrial productivity, consume 35 % of the productivity of the oceanic shelf, and use 60 % of the freshwater run-off each year (Vitousek et al. 1986; Pauly and Christensen 1995; Postel et al. 1996; Rojstaczer et al. 2001). Additionally, with an estimated 50 % increase in animal-based protein for human consumption by the year 2020, it is inevitable that human use of resources will continue to rise (Delgado et al. 2001). Lastly, the estimated billions of live wildlife animals and animal products, including NHP, that are traded annually also place heavy burdens that threaten the long-term survival of species (Rosen and Smith 2010). In addition to the direct impacts of the wildlife trade on conservation are the potentially devastating impacts from cross-species microbial mixing and exposure to novel pathogens.

There are many examples of disease-related population declines and extirpations, as well as an increasing number of species’ extinctions related to pathogen exposure (Cunningham and Daszak 1998; Skerratt et al. 2007). (In this chapter, the

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word pathogen will be used for all infectious and parasitic agents including viruses, bacteria, fungi, and parasites.) Diseases have ecological impacts on multiple scales, affecting individuals (survival, reproduction), populations (population size, gene flow), communities (shifts in dominant or abundant species, changes in species composition), and ecosystems (changes in ecosystem structure, function, and resilience) (Deem et al. 2008). All these potential disease-related impacts should be considered in NHP conservation initiatives, since an increasing number of disease events have been demonstrated to influence NHP populations (Wallis 2000). During the recent decades of increasing anthropogenic conservation challenges, including the threat of diseases, the need for a holistic approach for conservation and health care—conservation medicine—was realized.

Conservation medicine is an ecologically driven and conservation-minded approach which first appeared in the literature in the 1990s (Koch 1996). Although there are a number of definitions for conservation medicine, at the core is the realization that the health of environments, and the animals and people within, are intimately related. Conservation medicine may best be defined as a transdisciplinary approach to study the relationship between human, animal, and ecosystem health to ensure the conservation of all biodiversity, including *Homo sapiens* (Koch 1996; Deem et al. 2000; Aguirre et al. 2002; Jakob-Hoff and Warren 2012; Deem 2015). In its simplest form, it is the application of medicine to augment the conservation of wildlife and ecosystems, while ensuring human public health. A conservation medicine approach may involve the documentation, evaluation, monitoring, modifying, and/or prevention of diseases in wildlife (Deem et al. 2001). Following on the heels of this holistic conservation medicine approach, for planetary health care was a "new" initiative termed One Health.

Starting in the 2000s, the One Health initiative has become widely accepted in both human and veterinary medicine, although initially the human medical profession may have more fully embraced the term, due in large part to the increasing recognition of globally significant zoonotic emerging infectious diseases (EIDs) that threat human public health (Taylor et al. 2001; Kahn et al. 2007). However, the veterinary community also now embraces One Health, and indeed historically, it was a veterinary epidemiologist who coined the term One Medicine in the mid-twentieth Century (Schwabe 1984; Gibbs 2014). Many view this term as the building block for both conservation medicine and One Health. And if one wishes to go further in history, it was as early as the 1800s that a physician, Rudolf Virchow stated "Between animal and human medicine, there is no dividing line—nor should there be" (Klauder 1958).

A One Health approach may be based less on an ecological understanding than conservation medicine. In fact, an early definition of the One Health concept stated that One Health is an initiative that aims to merge animal and human health science to benefit both (Enserink 2007). This definition, with the lack of ecosystem as one component of the triad, may miss the underlying, "Anthropocene" drivers of the health concerns that increasingly threaten human and animal health and biodiversity conservation. However, similar to conservation medicine, there have been a number of newer definitions of One Health that factor ecosystem health alongside humans and animals. One unifying theme has been that One Health is a strategy that strives to expand transdisciplinary collaborations and communications to improve health care for humans, animals, and the environment (Kahn et al. 2012). This defining theme is rather analogous to conservation medicine and thus semantics aside, we may see One Health and conservation medicine as two names for across discipline strategies to improve health care for the planet. In this chapter, we will call this holistic health care approach, focusing across ecosystems, animals and humans, conservation medicine since our primary objective is the long-term conservation of NHP species globally.

Conservation Challenges Threatening NHP Survival

The long-term survival of many NHP species demands a conservation medicine approach. In today's "Anthropocene epoch," threats to NHP conservation are similar to other taxa and as such are mostly anthropogenic. Habitat loss and degradation, encroachment of humans and their domestic animals into NHP habitat, hunting for the pet and bushmeat trades, and increasingly infectious disease events continue to intensify and threaten NHP survival (Walsh et al. 2003; Chapman et al. 2005; Wich et al. 2011; LeBreton et al. 2012; Schwitzer et al. 2014). Human population growth and the rapid destruction of forested habitat are bringing humans and NHP into ever-increasing contact (Fig. 1).

Although the exact number of NHP species is unknown, as new species are still being discovered and taxonomic reshuffling occurs, the IUCN Red List of threatened species has 92 % of all NHP species classified as critically endangered,

Fig. 1 A confiscated orphaned chimpanzee interacting with people at a café on the beach in Gabon. © Sharon L. Deem

endangered, vulnerable, near threatened or of least concern (http://www.iucnredlist.org, accessed January 24, 2015). For example, all of the great apes are listed as endangered or critically endangered, and 94 % of the world's lemur species are listed as critically endangered, endangered, or vulnerable (Walsh et al. 2008; Schwitzer et al. 2014).

One major component of NHP conservation, and human public health, is the current realization that infectious diseases increasingly threaten species across the globe. In fact, anthropogenic global modifications are the most important variables associated with disease events in wildlife, including NHP, today (Dobson and Foufopoulos 2001). As the threat of EID has become a tangible risk for NHP and human public health, this area of study has become increasingly important within NHP conservation (Wolfe et al. 1998; Wallis and Lee 1999; Wallis 2000; Daszak et al. 2000; Chapman et al. 2005). Zoonotic pathogens—those agents shared between animals and humans—comprise 60.3 % of EIDs in humans, and of these, 71.8 % have originated from wildlife hosts and include sudden acute respiratory syndrome (SARS), avian influenza, Ebola, monkeypox, and West Nile virus (Jones et al. 2008). Although all animals may serve as a reservoir of zoonotic pathogens, NHP are one of the most common taxa to share infectious agents with humans.

One reason that pathogen sharing between NHP and humans is so common is because as our closest relatives they are the weakest barrier to cross-species transmission. An expression of this lack of a barrier is that primates constitute only 0.5 % of all vertebrate species but have contributed about 20 % of our major human diseases (Wolfe et al. 2007). Conversely, it has been well documented that infection with human pathogens may have fatal consequences for immunologically naïve NHP in captivity (Ruch 1959; Brack 1987). Now there is evidence of similar events, with potentially catastrophic effects, in free-living NHP populations (Wolfe et al. 1998; Wallis and Lee 1999; Leroy et al. 2004). Chimpanzees, bonobos, and gorillas, as the NHP most phylogenetically similar to humans, are also the most highly susceptible to human pathogens, especially viruses (Benirschke and Adams 1980; Brack 1987; Ott-Joslin 1993; Wallis and Lee 1999; Wolfe et al. 1998; Murphy 2012; Gilardi et al. 2014).

Of most concern at the NHP-human interface is hunting. Primates can make up over 10 % of captured animals in some areas (Wilkie and Carpenter 1999; Fa et al. 2003; Willcox and Nambu 2007). The handling and consumption of NHP bushmeat provides an effective means for the spread of pathogens from NHP to humans. The best-known example for NHP-human transmission is the emergence of HIV, which originated from the simian variant of the virus SIV (Gao et al. 1999; Hahn et al. 2000; Wolfe and Switzer 2009). Other important examples involve HTLV-1, which originated from STLV-1, simian foamy viruses, and Ebola virus (Morell 1995; Makuwa et al. 2004; Engel et al. 2006; Wolfe and Switzer 2009). Ebola is a grave public health concern, but is also capable of extreme great ape population impacts including a documented 80 % decline of gorilla and chimpanzee populations in the Gabon/Republic of Congo border region in the early 2000s (Huijbregts et al. 2003; Walsh et al. 2003; Leroy et al. 2004).

The opposite transmission event—human-to-NHP (anthropozoonoses)—historically has been less frequently reported. Few cases of human to NHP pathogen transmission have been demonstrated conclusively, but examples include giardia, sarcoptes mange, metapneumonia and other respiratory viruses, and herpes virus into NHP through ecotourism and conservation activities (Nizeyi et al. 1999; Cranfield et al. 2002; Kalema-Zikusoka et al. 2002; Kaur et al. 2008; Köndgen et al. 2008; Gilardi et al. 2014). Other examples of infectious agents of NHP conservation concern that have a human link include Cryptosporidium, *Plasmodium knowlesi*, and measles (Hirsch et al. 1995; Wolfe et al. 1998; Rouquet et al. 2005). These human-to-NHP transmission events are significant for NHP conservation, but also substantiate the fact that pathogen sharing is bidirectional (Chen et al. 2011; Palacios et al. 2011).

Although possibly less direct than pathogen exposure, potentially devastating impacts for NHP survival from human presence are those stressors (e.g., habitat fragmentation and degradation) that may cause behavioral modifications, reproduction decline, and poor immunity, along with traumatic injuries (e.g., snares), all of which may contribute to poor population viability (Chapman and Peres 2001; Junge et al. 2011; Cranfield et al. 2002, Oates 2013). Additionally, a number of research projects and management efforts for NHP conservation involve handling of animals that may require anesthesia and other veterinary techniques (Deem et al. 2001). Conservation medicine offers a transdisciplinary approach and in this chapter, we will present some of the more common applications that are imperative for the long-term survival of NHP populations (Fig. 2).

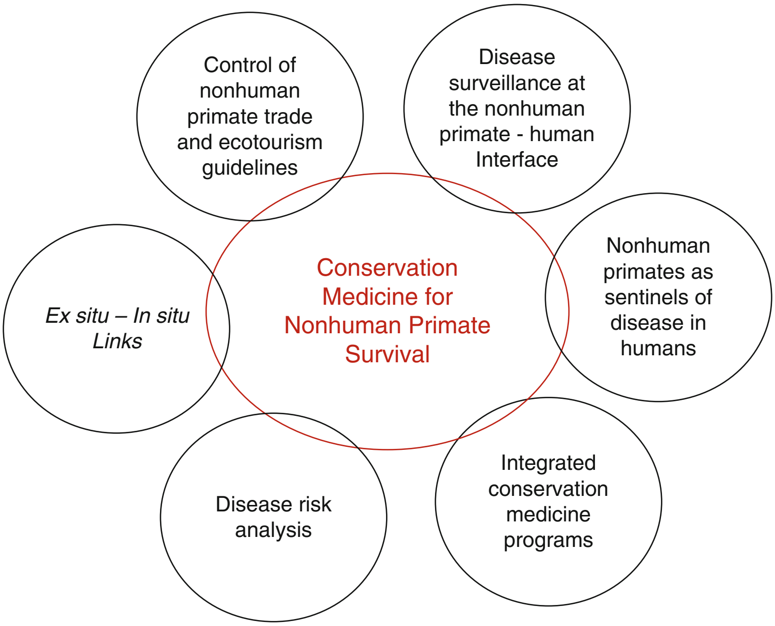

Fig. 2 Conservation medicine approaches for nonhuman primate survival

Conservation Medicine for NHP Conservation

Surveillance and Sentinels

Pathogens as part of any living community are known to drive evolution (Deem et al. 2010). In fact, the evolution of a wide variety of behaviors observed in primates, ranging from the consumption of medicinal plants to fly-swatting and other behaviors aimed at reducing contact with insect vectors of disease are driven by these agents (Huffman 1997; Dudley and Milton 1990). Therefore, a first step in understanding the role of pathogens in primate ecology is by surveillance to improve our knowledge of primate pathogens and their occurrence in natural populations (Nunn and Altizer 2005). Data gleaned from surveillance programs that may be crucial for conservation efforts include knowing which pathogens are present, what percentage of any given population is infected, and how these pathogens impact NHP population viability (e.g., morbidity and mortality). Yet these data are still sadly limited. For example, even in lemurs, a taxa with a number of critically endangered species, the first exogenous viruses of any lemur species were just described (Lim et al. 2015).

Surveillance programs of NHP populations may also indicate the risk of EID for humans, serving as important “sentinel species” for predicting human disease outbreaks (Wolfe et al. 1998; Rouquet et al. 2005; Leendertz et al. 2006). Programs such as the USAID PREDICT project will help to determine pathogen presence and provide missing data necessary for zoonoses preparedness, while gathering data important for conservation (Morse et al. 2012). Other programs such as the Great Ape Health Monitoring Unit (GAHMU) is a transdisciplinary approach for the diagnoses of pathogens in great apes, with an objective to create a long term, systematic sampling system (Leendertz et al. 2006). This program provides detailed health monitoring on wild great ape populations to establish baseline infectious agent exposure data of healthy animals, as well as to determine pathogens potentially causing morbidity and mortality. Similar surveillance programs exist for NHP populations in Asia and South America (Engel et al. 2006; Vitazkova 2009; Arajújo et al. 2013). In fact, it is in Asia, with temple monkeys, and South America, with urban green centers providing habitat that may harbor a growing number of NHP, that close proximity of NHP and humans is increasing and the surveillance of pathogens in these populations is imperative.

Disease Risk Analysis

Disease Risk Analysis is another conservation medicine approach that has gained momentum in recent years to help with our understanding of the health challenges that threaten wildlife conservation (Deem 2012). Disease risk analysis is a formal procedure for estimating the likelihood and consequences of adverse effects occurring in a specific population, taking into consideration exposure to potential hazards and the nature of their effects (Thrusfield 2007). Components of a disease risk analysis consist of four interconnected phases: (1) hazard identification, (2) risk assessment, (3) risk management, and (4) risk communication (Thrusfield 2007; Deem 2012). All the phases are interactive with the others, and therefore the process should be iterative and not simply flow from phase 1 to 4. Hazard identification may be viewed as the identification of what may go wrong. It is important to identify what diseases have potential effects harmful enough to warrant inclusion in the disease risk analysis. These hazards may be infectious (e.g., Ebola virus) or noninfectious (e.g., snare wounds), with the criteria for inclusion in the disease risk analysis dependent on the potential for negative impacts. Risk assessment is the range of calculations required to estimate release, exposure, and consequence parameters for infectious diseases, or for noninfectious diseases the likelihood and consequences of a disease occurring in a population. Risk management provides conservationists with a focus on those responses that may decrease the likelihood of an adverse outcome and/or reduce the consequences if such an outcome occurs. This element of risk analysis may best be viewed as the reason for performing the analysis so that science may move into action. The fourth component, risk communication is a continuous process, necessitating respectful communication among the multiple stakeholders throughout the risk analysis (Office of International Epizootics 2004). For a more in-depth discussion of this important tool for non-human primate conservation, please see Thrusfield (2007) and Deem (2012).

A number of disease risk analyses for free-living NHP populations have been conducted. One example is an analysis using retrospective health data from the long-running Gombe chimpanzee study (Lonsdorf et al. 2006). This study provides an excellent example of how retrospective data may be used within a disease risk analysis framework. The analysis enumerates various factors, including a better understanding of disease threats to an endangered species, a guide to improve health data collection, and proper risk communication to advance high-quality health care standards. A second study was derived from a workshop on Southeast Asian Macaque Risk Analysis. Field and laboratory data and expert opinion were combined to develop a model to predict transmission of simian foamy virus between temple macaques and humans accurately (Engel et al. 2006). This study provides an example of integrating real data with expert opinion for a better understanding of zoonotic pathogens at the interface of semiwild NHP and humans.

A disease risk analysis in African great apes was performed using GIS overlay of data (Sleeman 2005). Human demographic data and core human health indicators for African great ape range countries were evaluated. The combined indicators of environmental stress/vulnerability (as a proxy measure of human–great ape contact), and infant mortality rate and healthy life expectancy were used as separate indicators of disease burden among the human populations living in great ape ranges. These indicators were analyzed to create maps of critical areas with both environmental stress and high burden of human diseases, both significant for great ape conservation (Sleeman 2005).

In Situ–Ex Situ Links

An ex situ–in situ NHP conservation medicine approach exists at a growing number of zoos and primate centers. Many of the veterinary techniques (e.g., anesthesia) and preventive, diagnostic, and therapeutic care available for primate conservation projects are first perfected with collection animals (Ølberg 1997; Sleeman 1997; Williams and Junge 1997; Calle and Joslin 2012; Murphy 2012). Much of what we have learned about NHP infectious diseases, and their zoonotic potential, were first discovered with animals in captivity but have implications for free-living populations (Ruch 1959; Brack 1987). One project that offers a fence to field link is the great ape heart program which strives to better understand the cardiovascular health challenges in great ape species (http://greatapeheartproject.org/ accessed on January 24, 2015).

Another important fence to field connection is the outreach and education these facilities provide to inspire people to care about NHP. Many zoos and primate centers participate in recovery plans that focus on the health and reproduction of collection animals as insurance populations and species' ambassadors, while also providing money, time, and resources to free-living NHP conservation efforts.

Increasingly this ex situ–in situ link is also conducted at NHP sanctuaries and rehabilitation centers globally. These centers often provide humane care for injured and confiscated NHP. Unfortunately, the close human to NHP contact at these sanctuaries and centers may lead to zoonotic disease issues, and conservation challenges if repatriated NHP carry human pathogens back into the wild. For example, a confiscated juvenile eastern lowland gorilla that had significant human contact during care was diagnosed with a clinical case of human herpes simplex virus type 1 (Gilardi et al. 2014). As a potentially chronic infection, the release of this gorilla back to the wild could serve as a vehicle of introduction of a human pathogen into the free-living population. The need for these centers to provide health care using a conservation medicine approach that ensures healthy animals and healthy people is being increasingly supported (http://www.pasaprimates.org/ accessed January 24, 2015).

Control of the Trade in NHP and Ecotourism Guidelines

As discussed above, the NHP bushmeat trade is one of the biggest conservation challenges faced by many NHP species, but also has dire public health implications as best exemplified by Ebola and HIV. The use of NHP for food and within the pet trade places serious pressures on free-living populations while also providing a perfect vehicle for pathogen transmission between NHP and humans. The benefit of understanding this risk of pathogen transmission may allow for these data to help establish regulations to limit the trade in NHP. Poverty and hunger complicate the strength of this information. However, using a conservation medicine approach by working for alternative food sources while emphasizing human health, NHP populations may be better protected due in part to knowledge of zoonotic disease concerns (Golden et al. 2014).

A second growing use of NHP has been in ecotourism. A sustainable version of tourism, ecotourism is a significant proportion of all tourism which is estimated to generate more than 9 % of the global domestic product and may account for almost half of the gross domestic product in developing countries with biodiversity-rich areas (Muehlenbein and Ancrenaz 2009). The need to perform ecotourism in a manner that does not harm the very NHP that tourists are keen to visit, leads to the need for preventive measures to ensure that the health of both human and NHP participants is not jeopardized. In the case of great ape ecotourism, which necessitates habituation, the stress of human proximity as well as the potential for zoonoses and anthropozoonoses makes the need for a conservation medicine approach imperative (Nutter and Whittier 2001; Woodford et al. 2002; Macfie and Williamson 2010).

Integrated Conservation Medicine Programs

Combining all these approaches into an integrated conservation medicine program for NHP conservation is best exemplified by the mountain gorilla program in Central Africa. This program is structured with a clear understanding that the conservation of mountain gorillas is inextricably linked to the health of their ecosystem, the health of humans who frequently contact gorillas, and the health of the animals themselves (Cranfield et al. 2002). Documenting that infectious diseases are only second to trauma as a cause of death in this species, a conservation medicine approach that includes habitat health, preventive and therapeutic medicine for human and NHP alike is crucial (Mudakikwa et al. 2001). And with 70 % of all traumatic lesions from 1971 to 1995 snare related, veterinary intervention for these injured gorillas may be a necessity for the long-term survival of the species (Cranfield et al. 2002).

The Kibale EcoHealth Project is another example of a conservation medicine approach in that the aim is to better understand the health links at the interface of humans-animals and the ecosystem in a region with high NHP biomass (Goldberg et al. 2012). This project has demonstrated the transmission of infectious agents from humans and their domestic livestock to primates in the region (Goldberg et al. 2007; Rwego et al. 2008). Therefore, one of the big goals of the project, to promote human livelihoods and health, helps to ensure NHP conservation.

Conclusions

The many conservation challenges that threaten the long-term survival of NHP species are complex. These mostly anthropogenic threats, from habitat degradation to hunting to zoonoses/anthropozoonoses may differ depending on the species of NHP and/or geographical region, but most present serious health concerns for free-living NHP populations. The continuum from infectious disease epidemics, that may extirpate entire populations, to the more chronic stressors of habitat degradation and human encroachment, decreasing immunity and reproductive success, demand a conservation medicine approach. Additionally, with the zoonotic link between NHP and humans, which is predicted to become more serious as stable ecosystems and large genetically diverse populations of NHP are increasingly stressed by humans, the need for a conservation medicine approach has never been more urgent. Transdisciplinary conservation medicine teams may include ecologists, primatologists, veterinary and medical professionals, sociologists, anthropologists, and politicians, along with local stakeholders and laypersons. These teams are necessary to achieve the primary goal of minimizing the human created stressors and diseases that threaten the survival of NHP. As they say, “it takes a village.”

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How Do Primates Survive Among Humans? Mechanisms Employed by Vervet Monkeys at Lake Nabugabo, Uganda

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Introduction

Between 2000 and 2012, it is estimated that 2.3 million km^2 of forest was lost globally and in the tropics forest loss increased by 2101 km^2 per year (Hansen et al. 2013). As a result, in most countries degraded forests now exceed areas covered by primary forests (FAO 2005). It is estimated that in the 1990s secondary forests replaced at least one of each six hectares of primary forest deforested in the 1990s (Wright and Muller-Landau 2006) and that secondary forests now represent 35 % of all remaining tropical forests (Emrich et al. 2000). Cropland in tropical countries

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expanded by 48,000 km^2 per year between 1999 and 2008, largely at the expense of forest (Phalan et al. 2013), suggesting that many tropical areas that once were forested habitats are currently or will become a mixture of agricultural land and regenerating forest. One estimate suggests that approximately one billion hectares of additional agricultural land, primarily in developing countries, will need to be converted to agriculture by 2050 to meet the demands of the growing human populations—an area larger than Canada (Laurance et al. 2014).

Given these trends in land use, the conservation opportunities potentially available in degraded or severely humanized landscapes are dramatically increasing. However, the field of primatology has only recently turned to evaluating the conservation value of habitats other than old-growth forest and has rarely evaluated the most dramatically modified habitats. This bias likely stems from the historical objectives of the field. In early studies of primate behavioural ecology, there was an emphasis placed on studying primates in their natural environment, often with the goal of understanding the selective pressures that shaped their social organization (Struhsaker 1975; Terborgh 1983). Possibly, the need for information on the conservation of primates and because of recent interest in the transmission of diseases among humans and non-human primates, there has recently been a shift towards researching very disturbed habitats (Jones-Engel and Engel 2006; Chapman et al. 2007; Pozo-Montuy et al. 2013). In fact, a recently published book on primates in fragments (Marsh and Chapman 2013) had chapters dealing with primates in villages (Carretero-Pinzón 2013), large cities (Gordo 2013), around Buddhist temples (Aggimarangsee 2013), and in sacred forests (Cameron and Gould 2013). There are now a number of studies in Central America that focus on highly modified landscapes, such as those that demonstrate that howler monkeys walk along barbed wire among forest fragments, forage in isolated trees, or use introduced *Eucalyptus* plantations (Serio-Silva et al. 2006; Bonilla-Sanchez et al. 2012; Hagell et al. 2013; Pozo-Montuy et al. 2013). It is these sorts of highly disturbed habitats that we consider here.

In the past, conservation biologists have typically responded to change and attempted to take corrective action after negative situations have occurred (Caughley 1994; Chapman and Peres 2001); however, it would be much more effective if researchers were able to predict negative change prior to it occurring and proactively prevent population declines. This makes sense, as it is typically easier to prevent declines rather than rebuild populations, which typically involves restoring parts of the population's ecosystem. Furthermore, population decline itself results in negative situations where factors such as the risk of disease spread through small populations or loss of genetic potential must be considered in conservation/management plans. To predict declines, and not simply respond to change, conservation biologists must find general patterns across taxa and locations. However, finding such generalities has proven difficult. For example, Chapman et al. (2000, 2010) censused primates in logged and unlogged areas of Kibale National Park, Uganda, and found that red colobus (*Procolobus rufomitratus*), blue monkeys (*Cercopithecus mitis*), redtail monkeys (*C. ascanius*), and grey-cheeked mangabeys (*Lophocebus albigena*) were all negatively affected by logging, but black-and-white colobus

(*Colobus guereza*) appeared to do well in some disturbed habitats. In contrast, just a few hundred kilometres away in Budongo Forest Reserve, Plumptre and Reynolds (1994) found that black-and-white colobus, blue monkeys, and redtail monkeys were more abundant in logged than in unlogged areas. Given such variable responses, it may be valuable to look for new means of identifying the mechanisms primates use to respond to habitat degradation. Therefore, it seems reasonable to suggest that understanding the mechanisms species use to survive in highly humanized landscapes can aid in the construction of general management plans.

The objective of this research was to investigate the mechanisms that allow vervet monkeys (*Chlorocebus pygerythrus*) to survive and prosper in the highly modified humanized landscape surrounding Lake Nabugabo Field Station, Uganda. Our study group lived in a highly modified landscape where private land owners have extensive agricultural plots, grazing areas, and trees are left in marginal agricultural land. There was one main dirt road that was not heavily used by cars, but was frequently used by small motorbikes. The monkeys cross this road at least twice a day; often by using over-hanging trees, but occasionally by running across it. The human population density in the area is 229 individuals/km^2, and the area has a population growth rate of 2.2 %. The majority of these people in the district practise small-scale agriculture, but around Lake Nabugabo fishing is also an important economic activity, but fish stocks are declining (Vaccaro et al. 2013). With the decline in fish stocks former fisherman return to agriculture, causing its intensification, and making charcoal from local trees, thus is increasing deforestation (Vaccaro et al. 2013).

Methods

Study Site and Subjects

This study was conducted at Lake Nabugabo, Masaka District, central Uganda (0°22′-12°S and 31°54′E). Lake Nabugabo (8.2×5 km) is a satellite lake to Lake Victoria lying at an elevation of 1136 m (Fig. 1). The lake was formerly a bay of Lake Victoria, which became isolated from the main lake by an extensive swamp and sandbar approximately 5000 years ago (Stager et al. 2005). Now, much of the lake's perimeter consists of a dense wetland (Chapman et al. 2003), but the landscape on the west side of the lake is modified by humans and is a matrix that includes grasslands, patches of forest, areas with natural regenerating vegetation, farmer's fields, and a few buildings.

One habituated group of vervet monkeys called M group was the subject for this study. At the beginning of the study in June 2011, the group contained 22 individuals (2 adult males, 7 adult females, 1 subadult male, 6 subadult females, 2 juveniles, and 4 infants). By July 2012, the group contained 24 individuals (2 adult males, 5 adult females, 3 subadult males, 3 subadult females, 11 juveniles and infants). Finally, when what we report on here ended in May 2014 the group contained 30 individuals (5 adult males, 8 adult females, no subadult males, 3 subadult females, 14 juveniles and infants).

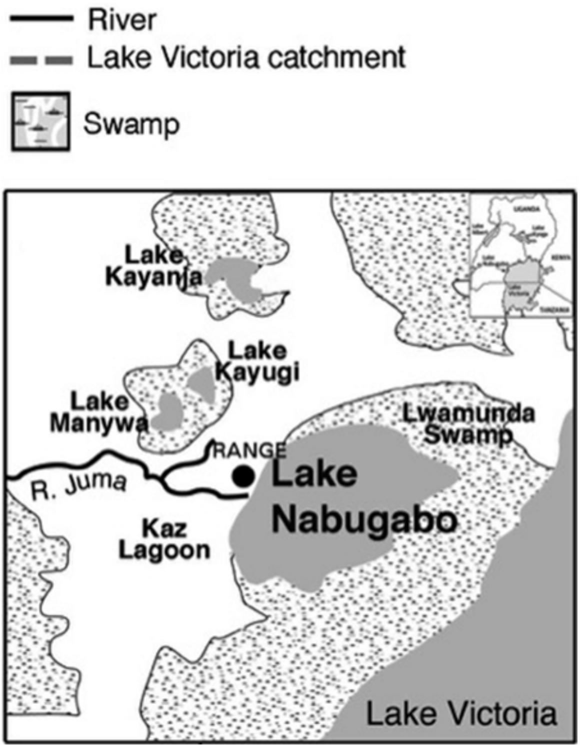

Fig. 1 A map of the location of Lake Nabugabo in Uganda, and the home range of the group next to the Lake, with the colour of the grid cell indicating how frequently the group used that cell

Behavioural Observations

The M group was followed by either the investigators or field assistants from June 2011 to April 2014 (46 months), for approximately 9 h per day (7:30 to 16:00), 10 days a month. During group contact, scan samples were taken every 30-min on general activity data with detailed data on foraging (e.g. food species, part, height from ground while foraging, and when possible, feeding rate). In addition, 2 months of intensive dawn to dusk follows were completed by JAT from June to July 2012 for 5 days per week (41 days) to calculate detailed rates of interactions and behaviours involving interactions with people and their crops. In addition to focusing on a study of the vervet monkeys' cognitive abilities (Teichroeb and Chapman 2014; Teichroeb et al. in press), during these intensive observations we were able to obtain very accurate data on the crop-raiding rate per hour, food raiding from kitchens, feeding by tourists, and events that cause alarm in the animals, such as approaches by people or being chased by dogs. The vervet group was scored as scared by people or their actions when they fled, reversed their travel direction, or alarm called in response to the event involving people (Table 1). During regular observations, data were also collected

Table 1 Rates of interactions among the vervet monkeys of Lake Nabugabo, with people and dogs during 41 days of intensive dawn-to-dusk observations that focused on these interactions

Interaction	Freq.	Rate (h)	Mean duration
Crop raiding	17	0.0407	38.8 min
Food raiding from a restaurant	1	0.0024	15 min
Fed by tourists	1	0.0024	45 min
Scared by adults	5	0.0120	
Scared by children	9	0.0216	
Scared by dogs	45	0.1078	
Dogs/children sent to chase monkeys out of crops[a]	4	0.0096	

[a] Events also included in the "scared by children" and "scared by dogs" rows

continuously on an ad libitum basis on the groups' interactions with people, their crops, dogs, or any other human disturbance. Finally, diaries were kept to record all important events, such as births, deaths, immigration, emigration, major fights or dominance disputes, wounding, dog attacks, and negative human actions taken against the group.

Phenology of Non-crop and Crop Foods

To evaluate the temporal variation in food availability, we constructed a phenology trail system in June 2011. This system (see Chapman et al. 2005 for a detailed description of this system) involved monthly monitoring of the phenological state of an average of 74 individuals from 27 tree or shrub species that previous ad libitum observations made over 20 years indicated were eaten by the monkeys in this area. If a tree on the phenology trail was cut down by the local community members, a new individual of that species of roughly the same size was added in the subsequent month or second month as it took time to find suitable replacements. We attempted to monitor five individuals of each species, but for nine species of fruiting trees, only one tree of that species occurred in the group's home range. Thus, we monitored an average of 2.7 individuals per species (range 1–5 individuals). At the end of the monthly collection of behavioural data, we recorded the amount of ripe fruit, unripe fruit, flowers, mature leaves, and young leaves for each of the individually marked trees. DBH of each tree was recorded and used as an index of fruit production (Chapman et al. 1992).

People planted crops along one stretch of forest edge within the group's home range and the vervets frequently raided these crops (see below). This was the only area where crops were close to the safety of trees and thus the only area crop raiding was possible without the vervet monkeys placing themselves in great danger from free ranging dogs. To quantify crop availability and stage of ripeness, one observer measured all vegetation types along this stretch of forest. This included fallow land (grass and bushland), the crop species, and its stage of ripeness. Behavioural observations of crop raiding was used to inform us of the particular stages where each crop was a suitable food (e.g. vervets eat beans as soon as the stems are emerging and once the bean fruit is ripe but rarely this plant in other states).

Ranging

Every 15 min the location of the group was determined using a grid cell system overlaid on a Google Earth Image of the area. The image was of a high enough resolution that many individual trees known to the observers could be identified on the image, enabling us to accurately determine the location of the group at all times. The cells were approximately 36 × 36 m. The frequency of use of each cell was determined over the course of the study. To quantify ranging, first the google image was georeferenced to the local grid system using ArcGIS (ESRI Version 10). Here, the origin of the coordinates was selected to be identical to the hand-drawn Cartesian coordinate system superimposed on the original image. Therefore, the bottom left corner of the image served as the 0,0 point, whereas the *X* and *Y* coordinates matched the values of the 1 cm long co-ordinates along the map (i.e. one unit of the georeferenced image (36 m) was equal to 1 cm).

Subsequently, the *X* and *Y* locations for each observation, as recorded in the field, were extracted from an excel file and converted to a GIS layer containing points representing each observation in ArcGIS. Further, a GIS layer was created where each cell of the hand-drawn grid system was converted into a polygon. We then counted the total number of observations (as points in the GIS layer) per cell of the hand-drawn grid. This total count is shown using equal-interval choropleth mapping, where darker hues highlight cells with higher number of observations.

Results

Behaviour

For animals (excluding infants), approximately one third of their activity budget involved feeding (34.3 %). They also travelled a great deal (21.2 %) and spent approximately 18.3 % of their time resting (Fig. 2). The average amount of time spent playing was 5.5 %, but this high value was driven by play of subadults who spent 4.5 % of their time playing, while adult males only spent 0.4 % of their time playing. Clear differences among age and sexes were

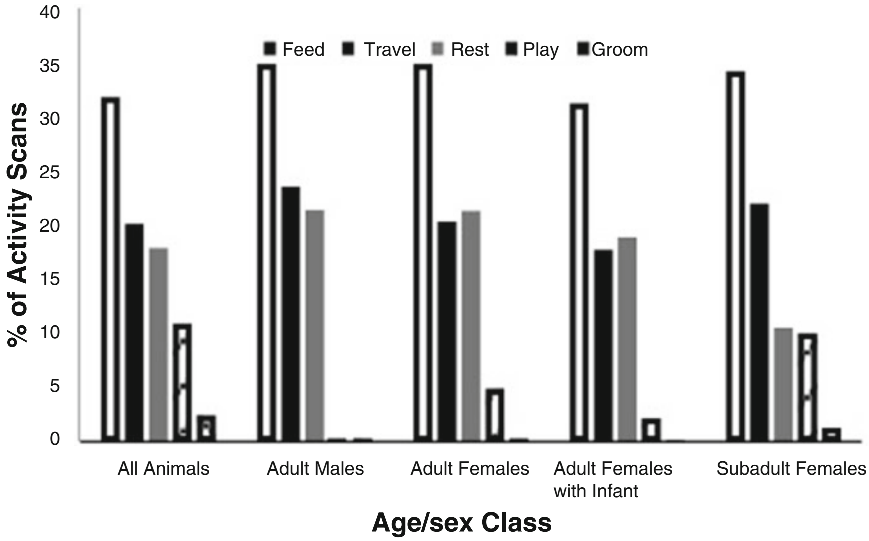

Fig. 2 The average activity pattern of a group of vervet monkeys living in the very humanized landscape near Lake Nabugabo Research Station, Uganda

evident as was variation associated with whether or not a female had an infant. There was little seasonal variation in the group's activity pattern (data not shown), which may have been driven by the fact that, with the exception of a peak of rain in April, rainfall was not highly variable resulting in relatively constant fruit production as proxied by the proportion of trees on the phenology trail bearing fruit (Fig. 3).

Diet

The group was observed feeding on 4690 food items. The animals frequently fed on an item rapidly and only ate one or a very few of these items, except when they fed in large fruiting trees. The 3757 instances where we positively identified the food item indicated that they are very reliant on fruit, which made up 77 % of the plant parts consumed (59 % ripe, 17.9 % unripe) and 69 % of all feeding events, including those feeding events on insects (Fig. 4). Flowers (7.6 %) and young leaves (4.0 %) made up only a small portion of the plant diet. Insects, were relatively important in their diet making up 10.6 % of feeding events and the vervets ate a great variety including dragon flies, termites, cicada, beetles, and many insects that could not be identified as the vervets typically grabbed the insect and rapidly ingested it. In 20 % of these events, the item could not be positively identified as a particular plant species and the item (e.g. fruit, young leaves, and flowers) could not be recognized in 83 % of the unidentified events because

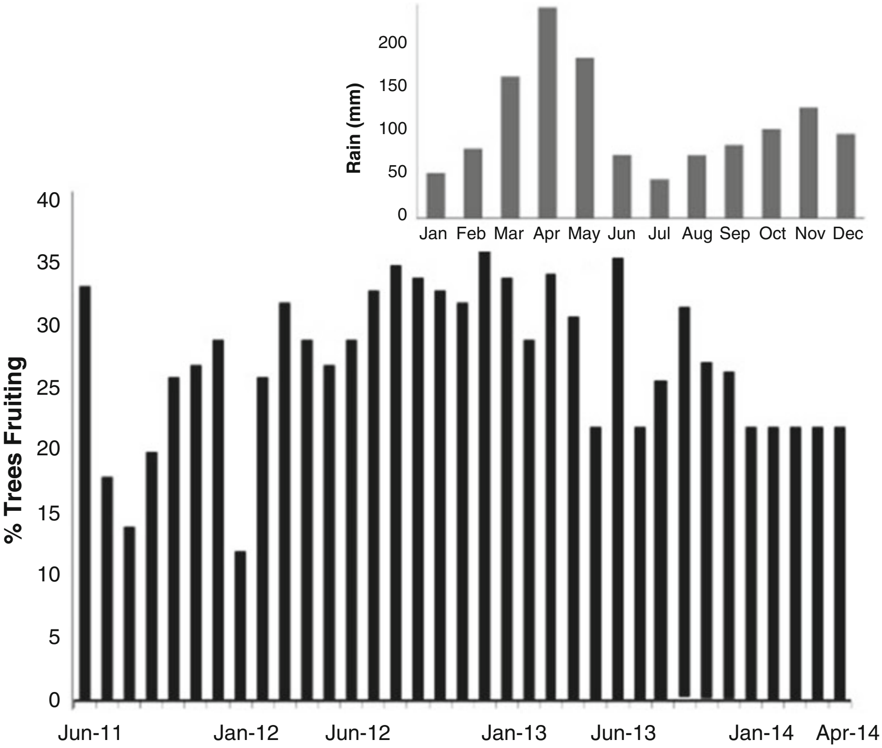

Fig. 3 The percentage of vervet monkey plants (trees and shrubs) that were fruiting between June 2011 and April 2014 (46 months; on average 74 plants were monitored each month) in the Lake Nabugabo area of Uganda. Inlaid into this figure is the average monthly rainfall of 2010 and 2011

the animal was obscured from clear view, but could be seen to be eating (11 %), or the event was of very short duration (6 %).

Given the degraded nature of their home range, it was surprising that their plant diet was fairly rich and 49 species of food items (e.g. soil) made up 90 % of the diet (Table 2). The five most important plant species were *Pseudospondias microcarpa* (8.9 %), *Lantana camara* (7.7 %), *Maeosopsis eminii* (6.3 %), *Ficus natalensis* (5.2 %), and *Pycanthus angolensis* (4.5 %). The vervets primarily ate the fruits of these species when seasonally available, with the exception of *Lantana camara*, which is an exotic shrub that fruits year round. Just these five species made up a third of the group's plant diet.

Of the plants eaten, 17 were native, 16 were exotic to the region, 9 were edible crops planted for human consumption, and 7 were species of trees planted for fuelwood. It is likely that a number of the native tree species were also planted because many of them are good timber trees useful for the construction of boats. As might be expected for a degraded habitat where large trees are extracted for timber for building or for the construction of boats, the average size of the trees (shrubs, like *Lantana camera*, excluded) was small (mean = 38.2 dbh, median = 32, range −2 to 144, $n = 2191$ (Fig. 5); compare to Bonnell et al. (2012).

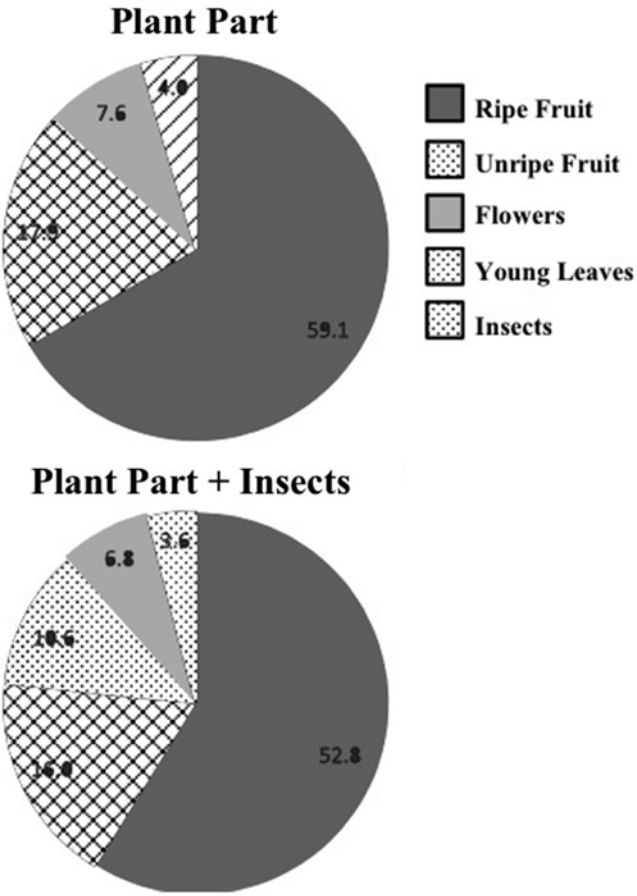

Fig. 4 The percentage of scans where a vervet monkey of the Lake Nabugabo, Uganda study group were observed feeding on different plant parts between June 2011 and April 2014 (46 months), excluding (**a**) and including (**b**) foraging on insects

Ranging

Summing the number of cells used indicates that the group used an area of 11.6 ha. The intensity of grid cell use (Fig. 6) was highly variable from 1 (areas of open pasture that the group ran through) to 312 (a forested area with many fruiting trees). In general, the areas of most intense use were forested areas far from crops. The group frequently travelled along the very edge of the lake on a cliff side, which likely made a very safe travel route where dogs, their only terrestrial predator, could not access them on the ground.

Table 2 The food species and frequency of consumption of items eaten by the vervet monkeys of Lake Nabugabo, Uganda

Species	Common name	Total	Frequency	Cumulative percent
Pseudospondias microcarpa		333	8.9	8.86
Lantana camara		290	7.7	16.58
Maesopsis eminii		236	6.3	22.86
Ficus natalensis	Fig	195	5.2	28.05
Pycnanthus angolensis	African nutmeg	168	4.5	32.53
Rauvolfia vomitaria		143	3.8	36.33
Elaeis guineensis	Oil palm	119	3.2	39.50
Syzygium		118	3.1	42.64
Garcinia huillensis		107	2.8	45.49
Pachystela brevipes		84	2.2	47.72
Manihot esculenta	Cassava	81	2.2	49.88
Harungana madagascariensis	Haronga	73	1.9	51.82
Ficus congensis	Fig	70	1.9	53.69
Alchornea cordifolia		67	1.8	55.47
Baikiaea isignis		62	1.7	57.12
Securinega virosa		61	1.6	58.74
Beilschmiedia ugandensis		60	1.6	60.34
Soil		60	1.6	61.94
Mangifera indica		*58*	*1.5*	*63.48*
Blighia unijugata		*57*	*1.5*	*65.00*
Dead wood		*57*	*1.5*	*66.52*
Senna siamea		*55*	*1.5*	*67.98*
Ficus exasperata	*Fig*	*49*	*1.3*	*69.28*
Senna sp.		*47*	*1.3*	*70.54*
Lantana camara		*47*	*1.3*	*71.79*
Teclea nobilis		*44*	*1.2*	*72.96*
Hibiscus sabdariffa	*Hibiscus*	*43*	*1.1*	*74.10*
Kisuula	*Local name*	*42*	*1.1*	*75.22*
Kakupa	*Local name*	*41*	*1.1*	*76.31*
Prunus africana		*38*	*1.0*	*77.32*
Red Berry	*Local name*	*35*	*0.9*	*78.25*
Calistamom citrus	*Bottle brush*	*34*	*0.9*	*79.16*
Psidium guava	*Guava*	*33*	*0.9*	*80.04*
Jacaranda	*Jacaranda*	*32*	*0.9*	*80.89*
Trichilia emetica		*30*	*0.8*	*81.69*
Mussapiem	*local name*	*29*	*0.8*	*82.46*
Dovyalis macrocalyx		*28*	*0.7*	*83.20*
Carissa edulis		*27*	*0.7*	*83.92*
Ekebergia senegalensis		*25*	*0.7*	*84.59*
Ipomea batatas	*Sweet potato*	*25*	*0.7*	*85.25*

(continued)

Table 2 (continued)

Species	Common name	Total	Frequency	Cumulative percent
Monodora myristica		*24*	*0.6*	*85.89*
Morus alba	*Mulberry*	*24*	*0.6*	*86.53*
Zea mays	*Corn*	*23*	*0.6*	*87.14*
Grevilia robusta		*23*	*0.6*	*87.76*
Spathodea campanulata		*22*	*0.6*	*88.34*
Musa	*Banana*	*22*	*0.6*	*88.93*
Balanites wilsoniana		*18*	*0.5*	*89.41*
Citrus sinensis	*Orange*	*18*	*0.5*	*89.89*
Antiaris toxicaria		*17*	*0.5*	*90.34*

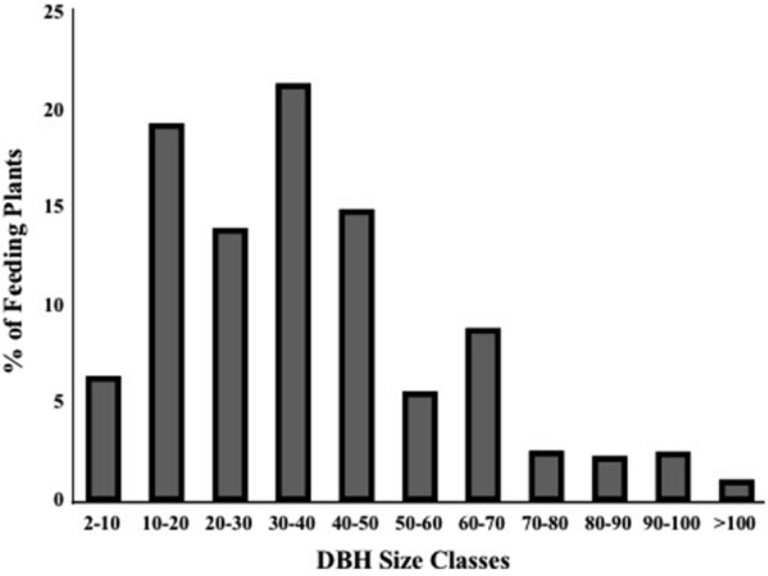

Fig. 5 The average size (DBH) of food trees used by the vervet monkeys of Lake Nabugabo, Uganda. The categories go from 2 to 10, 10.1 to 20, 20.1 to 30, etc., but the 0.1 was omitted for simpler presentation

Interactions with Humans

The vervet monkeys of Lake Nabugabo live in a humanized landscape and interactions with people and associated animals and products are frequent. We focused on these interactions during 41 days of observations. The monkeys raided crops approximately once every second day for a mean duration of 38.8 min per day (Table 1). The group was scared by people or dogs 59 times (on average 1.2 times a day).

Over the entire 46 months, more dramatic events occurred on rare occasions. These included seven animals who were poisoned by bananas baited with herbicide with the

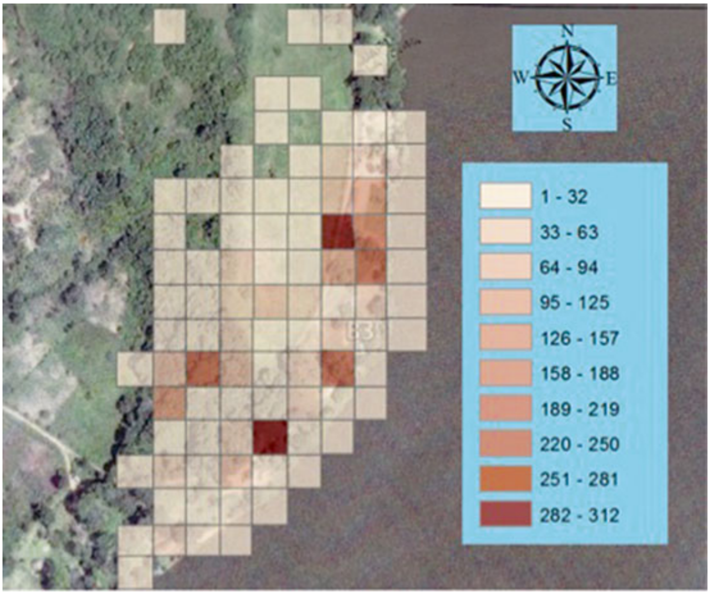

Fig. 6 The range of the vervet monkeys study group at Lake Nabugabo, Uganda. The cells were approximately 36 m by 36 m and the intensity of the colour indicate the intensity of grid cell use

intention of decreasing crop raiding, one animal who was speared because the hunter liked the skin, two animals that were captured and kept as pets (both eventually escaped and joined groups), one animal was electrocuted on power lines and died (two animals were electrocuted and survived), and two animals that were killed by dogs.

The vervet's landscape was also dynamic. In 2011, two areas were cleared for the production of charcoal (~3600 and ~6600 m^2), while numerous small areas were left to regenerate or were regenerating for a year or more only to be cleared again for agriculture. A much larger area was cut in a neighbouring forest reserve for timber and charcoal, and it is possible that this could occur in our study site. It is the cutting of large trees that likely has the most serious impact on the vervets because many of their most frequently eaten foods came from species that only bear fruit once they reach a large size (Table 2).

Discussion

As different regions experience forest loss due to anthropogenic land conversions and climate change, understanding the adaptive behaviours that facilitate the use of fragments and landscapes like Nabugabo becomes critical to predicting which species will be most threatened in the future. The vervets of Lake Nabugabo were very capable of surviving in this type of environment and the increase in group size and the numbers of infants and juveniles at the end of the study suggests that they can at times even prosper in highly humanized environments. This is despite some very negative interactions with the local human community that included such events as the intentional poisoning of seven animals, the spearing of another, and the constant danger of dogs. Given their ability to persist in this humanized landscape, the question is what are the mechanisms they use to respond to habitat degradation and the dangers that this environment presents? We suggest that mechanisms to deal with disturbance might be most evident in severely degraded habitats such as the one we studied.

Activity budgets can be variable depending on group size and composition (Isbell and Young 1993; Henzi et al. 1997, 2013); nonetheless behavioural patterns at the human-modified Lake Nabugabo were not very different from those reported for vervets at other less disturbed sites (Table 3). This might be because crop raiding and food obtained from other human sources was still a relatively small part of the diet at Nabugabo compared to foods eaten from the forested areas. When human food has been found to make up >50 % of the diet, vervets have been reported to feed for a smaller proportion of the day and rest and socialize more (Saj et al. 1999). This is a pattern also observed in other primate species living in environments, where human food sources are readily available (e.g. *Papio anubis*, (Forthman-Quick 1986); *P. cynocephalus*, (Altmann and Muruthi 1988); *Macaca sylvanus*, (Fa and Southwick 1988); *M. mulatta*, (Marriott 1988; Jaman and Huffman 2013)). Presumably these animals benefit from having easily accessible, high-calorie food sources and can spend less time searching for resources compared to populations living in areas undisturbed by humans.

Two mechanisms that vervets use to adapt to humanized landscapes become apparent from our data. The first is that they appeared to be able to prosper using the food they had available to them. This was generally much reduced compared to that found in old-growth tropical forest (Chapman et al. 2002), but not reduced relative to woodland (Struhsaker 1967, 1976) where they also thrive. As a result, we suggest that their evolution in areas such as riverine forests and woodlands may have pre-adapted them to survive in degraded humanized landscapes. They have a generalized digestive system and show great variability in their diets depending on where they are located (Lee 1984; Clemens and Malaoiy 2009). Additionally, they raid crops (Naughton et al. 2011) and take advantage of occasional opportunities, such as food handouts from locals or tourists. We would like to point out that Lake Nabugabo is somewhat of an idiosyncratic or unique setting; likely all areas are atypical in some way. For example, a number of the large food trees are on land owned by relatively wealthy land owners who have positive attitudes towards nature and can afford to have these attitudes (e.g. this land owner is not struggling to get school fees for their children for the next year). One of the best examples of this is that one of the largest and most frequently used *Pseudospondias microcarpa* trees (the most frequently eaten plant) is on the land of the Lake Nabugabo Field Station, and we have no intention or need to cut the tree down.

The second mechanism that likely facilitated the survival of the vervets in this humanized landscape is the sentinel behaviour of the males; a relatively unique behaviour for a primate. During sentinel behaviour typically males will take a prominent position, often relatively high in a tree on the forest edge and scan for approach-

Table 3 Mean activity budgets for vervets (*Chlorocebus pygerythrus*) in anthropogenically disturbed versus undisturbed environments

							Social			
Site	Disturbed?	Human food	*N*	Feed	Rest	Travel	Total	groom	play	Reference
Samara, South Africa	N	Low	2	31.7	33	24.6	10	NR	NR	Pasternak et al. (2013)
Blydeberg, South Africa	N	Low	1	42	17	15	26	NR	NR	Henzi et al. (2013)
Windy Ridge, South Africa	N	Low	1	32.8	30.6	18.4	NR	6	NR	Baldellou and Adan (1998)
Amboseli, Kenya	N	Low	3	40	32	25	5	NR	NR	Lee (1984)
Amboseli, Kenya	Y	High	1	18.9	43	16.5	20	NR	NR	Brennan et al. (1985)
Entebbe Zoo, Uganda	Y	High	1	26.3	44.3	14.2	11	NR	NR	Saj et al. (1999)
Nabugabo, Uganda	Y	Medium	1	34.3	18.3	21.2	x	X	5	This study

ing predators, giving alarm calls if a predator is seen (Cheney and Seyfarth 1981; Horrocks and Hunte 1986). We know the free ranging dogs are dangerous for our population as two animals were killed by dogs. Mortalities caused by domestic dogs have also been described for *Alouatta pigra* (Ramírez-Julián et al. in prep) and *Cebus nigritus* (Oliveira et al. 2008) populations. Thus, the vervet's antipredator behaviour may reduce human-related mortality.

The question that logically stems from this research is: "what can be done to promote conservation in these very humanized landscapes?" Redtail monkeys (*Cercopithecus ascanius*) and mangabeys (*Lophocebus albigena*) were once common in this area, but are now only found in distant forest reserves, but maybe this situation can be changed. Angolan colobus monkeys (*Colobus angolensis*) are still found in the larger forest patches. In such situations, for any conservation initiative to be successful, community involvement becomes critical. The conservation model of Juan Carlos Serio-Silva and colleagues (including CAC) for the howler monkeys of the fragmented habitats of the Municipality of Balancán of Mexico provides a possible roadmap for a conservation approach (Ramírez-Julián et al. in prep), but it will have to be adjusted to the local situation. First, it would be critical to work at all political levels to obtain agreements concerning forest conversion and prohibitions against negative human activities, such as poisoning. Second, in Mexico they established a protected area for the howler monkeys. This is possible in the Nabugabo region as some government controlled forest reserves still exist. However, these areas would have to receive adequate protection against further extraction of any sorts (Mugume et al. 2015). Third, it would be necessary to promote environmental education and to inform the community of the perspective that wildlife, including vervets, and the forest are important and of value. This will be difficult given the crop-raiding behaviour of the monkeys. One element the community may relate to is the fact that the vervets disperse the seeds of many of the important timber and fruiting trees in the region. The fourth element of the Mexican plan was to make the official declaration of the importance of primate widely known to the local community. This involved a celebration that involved popular lectures, workshops offered simultaneously, for children and adults, cultural activities such as dancing, singing, poetry, theatre, painting of a mural, and movies (all primate related). Fifth, in Mexico school children planted trees to help connect fragments and limit terrestrial locomotion in an effort to limit predation by dogs. Limiting terrestrial locomotion may not be critical for the more terrestrial vervets, but planting food trees away from crops may help both sustain the population and draw the vervets away from crops. Finally, since there is tourism in the area around the lake, training field guides to take tourists for local guided walks would increase the exposure of the importance of the vervets and other primates and their habitat, providing much needed jobs and revenue for the community.

It is our hope that these activities will be initiated in the near future and will connect the results of the research to real conservation that will operate on a landscape level on privately owned land. This outreach and the fate of the monkeys are being monitored so we can determine the value of this conservation model.

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Indigenous Peoples, Primates, and Conservation Evidence: A Case Study Focussing on the Waorani of the Maxus Road

Sarah Papworth

Introduction

The Historical Context of Conservation and Indigenous Peoples

Historically, the prevalent ideology in conservation was one of humans as a source of unnatural disturbance (e.g., Young et al. 2005), rather than an integral part of the natural environment. This conservation paradigm prompted an expansion of protected areas in wilderness or pristine landscape, which now cover 15.4 % of global terrestrial area (Juffe-Bignoli et al. 2014). Within newly created protect areas, human activities such as hunting, shifting cultivation, and natural resource use have been viewed as undesirable and even criminalized. Local communities were excluded and evicted from national parks without their consultation, and local histories rewritten to deny the long-term tenancy of communities in these areas (Dowie 2009). One example of this in primate conservation is the eviction of the Twa from national parks in the tri-border area of Rwanda, Uganda, and the Democratic Republic of Congo, which were established to protect mountain gorillas (*Gorilla beringei beringei*, Kidd and Zaninka 2008). Before their eviction, the Twa were dependent upon the surrounding forest, however they did not hunt the gorillas for food and have even expressed horror to the thought of eating them (Kidd and Zaninka 2008). Although Twa snares did occasionally harm gorillas, the relatively pristine state of the forest in this area is testament to the low-impact lifestyle and culture of the Twa (Dowie 2009). Nevertheless, the presence of the Twa was assumed to be a problem for gorilla conservation and they were excluded from national parks in the tri-border area without any compensation (Colchester et al. 2008). For the Twa, entry to the forest and the collection of natural resources or

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visits to sacred sites are restricted. Due to the lack of farming skills or land, the Twa were unable to participate in the largely agrarian local economy and they were reduced to a poverty-stricken life living on the margins of the forest (Kidd and Zaninka 2008). The forest is now only accessible to park officials, researchers, and tourists. Although ostensibly part of the high tourist fee goes to help local people, little of this money reaches the local communities (Adams and Infield 2003). The mountain gorilla conservation project is viewed as a success in ecological terms due to the increasing size of the gorilla population (Gray et al. 2013), but this success has come at the cost of Twa livelihoods and culture. The Twa were potentially excellent guardians of the forest who could have acted in conjunction with park authorities to detect poachers and transient occupation within the forest (Dowie 2009).

Primates, Indigenous Peoples, and Conservation

The view of humans as unnatural fails to recognize the long histories of human occupation, co-adaptation, and natural resource management by communities, which shaped these "pristine" landscapes in remoter areas. Very few primates live in entirely human-free habitats (Fuentes 2010), and many primates are negatively affected by human activities (Chapman and Peres 2001). Even in species which are typically associated with remote locations, such as the orangutan (*Pongo* spp.), healthy populations can be found in human-modified landscapes (Russon et al. 2001; Wadley and Colfer 2004). Human-modified landscapes are the dominant landscape globally (Ellis and Ramankutty 2008), and insights from ethnoprimatology may be critical for primate conservation in these landscapes. Ethnoprimatology contrasts with traditional research on wild primates, by viewing humans as an integral part of the primate ecosystem, rather than a source of disturbance or unnatural behavior (Fuentes 2006, 2012; Malone et al. 2014; Riley 2006). Ethnoprimatology has paid particular attention to human–primate interactions and areas where primates form some part of local culture, whether through consumption, mythology, or other relationships (Sponsel 1997). Those peoples with substantial cultural interactions with primates are frequently part of indigenous cultures. Indigenous cultures often have a long history of occupation in a specific locality and shared cultural values and heritage, particularly associated with resource use. How to define indigenous peoples is highly contentious, and any definition is likely to exclude certain groups or individuals which consider themselves indigenous (Corntassel 2003). From a practical perspective however, those interested in working with local communities for primate conservation should allow communities to define for themselves whether or not they are indigenous.

Although it is easy to argue that geographic and social exclusion of indigenous peoples has reduced, with changing attitudes and conservation approaches, the reality is these communities continue to be excluded (e.g., Costanza Torri 2011). In a review of all references to community eviction for national park creation, Brockington and Igoe (2006) found that almost half were of indigenous peoples.

Conservation has been responsible for human rights violations in the past (Dowie 2009) and within this context, it is particularly important to ensure that conservation issues are accurately and fairly identified, and indigenous people's rights to self-determination on their own land are supported. Part of this process is consulting local communities about potential conservation issues and developing culturally relevant solutions (Gadgil et al. 1993). I argue here that evidence-based conservation which recognizes local community rights is particularly important when measures to address potential issues could have a negative impact on local or indigenous communities (Hill 2002). To explore this approach, I use here the example of the Waorani living along the Maxus Road in Amazonian Ecuador.

Hunting Sustainability of the Waorani in Amazonian Ecuador

In spite of there being only a few hundred Waorani living along the Maxus Road, their hunting and conservation behavior has received substantial attention in the academic literature. There are numerous peer-reviewed articles which argue that the Maxus Road has a negative conservation impact as it increases access to markets and thus the profitability of hunting (Suárez et al. 2009; Suárez et al. 2013), by allowing hunters access to areas which would otherwise be inaccessible (Espinosa et al. 2014). Current evidence does suggest that Waorani communities are hunting increasing volumes of meat (Espinosa et al. 2014), and that they are substantial contributors to a local wildmeat market (Suárez et al. 2009). Yet this increase in hunting by the Waorani is only a problem if hunting is currently unsustainable or if hunting is projected to increase to unsustainable levels. If hunting is sustainable, commercial selling of wildmeat (usually called bushmeat in Africa, though wildmeat is used here to reflect the global nature of trade in wild animal meat) can provide a sustainable income for families where the only other source of cash is casual work for a large oil extraction company.

Various methods to measure the sustainability of hunting exist (Robinson and Redford 1994), and many of these have been applied to Waorani hunting along the Maxus Road. Suárez et al. (2013) compared densities of various species along the Maxus Road with densities at a nearby site without hunting. Although comparing densities at hunted and unhunted sites can be problematic as the two sites may have other differences apart from hunting pressure (Robinson and Redford 1994), Suárez et al. (2013) conclude that "wildlife has been severely impacted in this area [the Maxus Road], underscoring the importance of the indirect effects associated with the presence of roads and the oil industry" (Suárez et al. 2013, p. 269). Yet individual species with density estimates at both sites all have overlapping 95 % confidence intervals, and some density estimates (for example the howler monkey, *Alouatta seniculus*) are based on observations of a single individual. The species with the greatest number of observations is the squirrel monkey (*Saimiri sciuereus*), with 32 observations, this is still below the minimum of 60 recommended by Buckland et al. (2001) for reliable density estimates using line distance sampling.

These density estimations can be considered unreliable and these comparisons therefore provide insufficient evidence to conclude that Waorani hunting is unsustainable.

Franzen (2006) compared 2002 hunting offtake profiles in three communities of differing ages, Timpoca (founded 2001), and Dicaro and Guiyero (founded 1993–1994). Hunters in Timpoca used a much smaller hunting area and harvested more spider monkeys (*Ateles belzebuth*) per day of hunting, "the clearest evidence for the local depletion of spider monkeys near the communities of Guiyero and Dicaro" (Franzen 2006, p. 42). Although comparing hunting profiles in Dicaro and Guiyero with that of Timpoca does suggest spider monkey populations are depleted, this does not conclusively prove Waorani hunting of spider monkeys in those two communities is unsustainable. In a separate study assessing hunting profiles in another Amazonian community over 10 years, Vickers (1988) found that after an initial change in hunting profiles, offtakes stabilized as animal densities became stable at new levels. Guiyero and Dicaro may have experienced this same change in animal densities, and the lower offtakes may reflect sustainable extraction at these new, lower densities of spider monkeys. A second study of hunting offtake in the same communities along the Maxus Road by Espinosa et al. (2014) showed that compared to 2002 levels, offtake and hunted area had increased. Increasing hunting area could mean local expiation of species so hunters have to travel further to maintain offtake, but as Espinosa et al. (2014) also observed greater harvests, these observations do not conclusively indicate hunting is unsustainable. To conclude hunting is unsustainable in these communities, decreases in animal populations over time need to be demonstrated (Weinbaum et al. 2013). Unfortunately, there are no density estimates currently available which will allow changes in populations to be examined directly, but there is sufficient information available to model the sustainability of Waorani hunting of ateline species (*Alouatta seniculus*, *Ateles belzebuth*, and *Lagothrix lagotricha*), collared peccary (*Pecari tajacu*), and red brocket deer (*Mazama americana*) along the Maxus Road.

It has not been demonstrated that Waorani hunting along the Maxus road is unsustainable, yet management measures which would restrict either hunting area or volume have been suggested (Espinosa et al. 2014). Such statements, based as they are on inconclusive evidence, label the Waorani on the Maxus Road as a conservation problem waiting to be solved. Yet their way of life, local resource extraction by a few thousand people living in several thousand square kilometers of forest, is more likely to be sustainable than that of many other communities. This chapter models the sustainability of Waorani hunting of the three sympatric ateline species, the collared peccary, and red brocket deer along the Maxus road using two models. The first is a stable model based on hunting information from Franzen (2006), and assumes that Waorani hunting behavior is constant over time. The second model allows Waorani hunting behavior to change and to adapt to changing prey densities during the first 7 years of the model, changing from the hunting area and offtake observed in 2002 to that observed in 2008, effectively adapting to changing prey availability.

Methods

The Waorani on the Maxus Road

Before first Western contact was made in the 1950s, the Waorani lived in small, highly mobile family groups which moved between hilltop longhouses built on terra firme (Rival 2002). At this time, the population was estimated at approximately 600 individuals which lived throughout the area now known as Yasuní National Park and the Waorani Ethnic Reserve. The Waorani had a reputation with surrounding communities for fiercely defending their territory from non-Waorani intruders. This fierce reputation is still preserved by some Waorani subgroups which still live in voluntary isolation in the south and east of Yasuní National Park. These groups—the Tagaeri and Taromenane—still follow a traditional lifestyle and have been responsible for the lethal spearing of illegal loggers within their territory (Proaño García and Colleoni 2008). Attacks against all outsiders isolated the Waorani from surrounding ethic groups, and is likely to be responsible for the uniqueness of their genetics and language—Wao terero—which is not related to any known language.

Deaths from illness or accident were believed to be caused by other Waorani individuals, so spearing raids between households were common, resulting in up to 42 % of deaths from intra-tribal spearing (Beckerman et al. 2009). Longhouses were frequently relocated, partly to avoid revenge killings, but also when monkeys in the area were perceived to have run away (Rival 2002). The Waorani used few cultivars, mostly collecting wild foods from the forest. Avoiding the riverine areas around their territory where non-Waorani groups were settled, fish played a less important part in traditional Waorani diet than terrestrial animals and wild plants. Hardwood spears were used to hunt white-lipped peccaries (*Tayassu pecari*), and blowpipes with arrows tipped in curare poison were used to hunt monkeys and birds. Other species, such as the tapir (*Tapirus terrestris*) and capybara (*Hydrochaeris hydrochaeris*), were considered taboo and were not eaten (Rival 2002).

This chapter focuses on the Waorani living on the Maxus Road, which runs into Yasuní National Park from Pompeya on the Napo River (Fig. 1). Numerous Waorani settlements were founded on the 150 km of the Maxus Road after its construction in the 1990s (Franzen 2006). Repsol, the company which currently owns the contract for oil facilities on the road (Pearson 2010), provides bus transport along the road for all three communities. This bus is used for visiting friends and relatives, as well as to gain faster access to hunting areas further from communities, and to transport surplus meat to market (Franzen and Eaves 2007). Access to the road is controlled by Repsol where it meets the Napo River, and only residents and authorized individuals (e.g., those working for the oil company or biological research stations) are allowed to pass, effectively preventing new migration into the area (Pearson 2010; Suárez et al. 2013). Life in these communities does differ from the traditional way of life described above, though

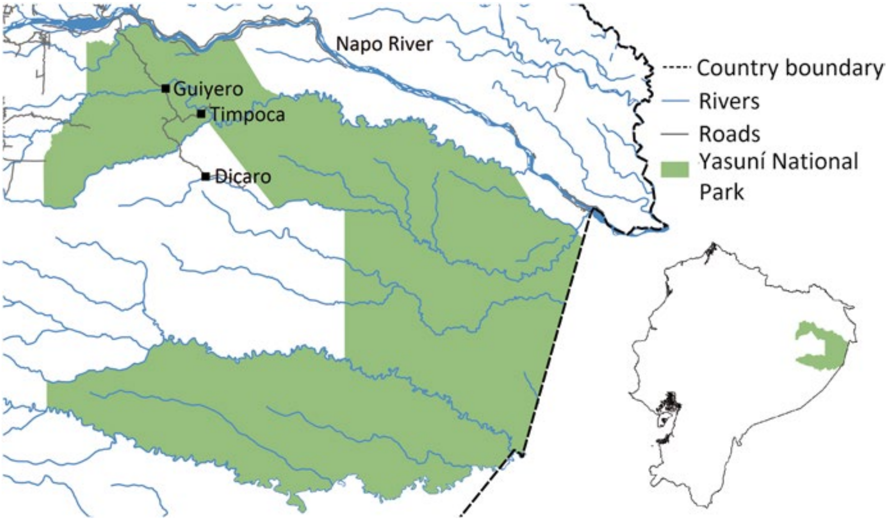

Fig. 1 Locations of the Waorani communities of Guiyero, Timpoca, and Dicaro in the Ecuadorian Amazon. Communities included in this study are shown with a *black square*

many similarities remain. Communities are still based on extended families, and matrilocal residency after marriage remains common. Although the oil company has built concrete houses in the communities, traditional structures made from palms are still used, and are preferred by many individuals as they have better ventilation. Most individuals under 50 have some primary education, though few have secondary education. In order to receive secondary education, individuals must leave the communities and live in distant towns. Although Ecuador is largely Catholic, many Waorani reject Christianity as an outside religion and traditional beliefs and stories are still widespread.

Participation in the cash economy is either by selling wildmeat or handicrafts in the local market or through occasional work for the oil company, as grass cutters or construction workers (Franzen and Eaves 2007). Most waged income is from the oil company (Doughty et al. 2010) and household average monthly income over a 5-month study in 2002 was USD246 (Franzen and Eaves 2007). Wildmeat can be sold in the market for USD3-6/kg Espinosa et al. (2014) and is the only source of income for some households. This money is used to buy food items such as rice, coffee, or sugar, and pay for secondary school fees. Most activities are part of a subsistence economy based on small-scale farming, hunting, and gathering. Women tend crops, mostly yuca and plantain, in small clearings created by cutting trees and controlled burning of the area. Women also collect wild fruits, plants, and honey from the forest, and palms and seeds to make hammocks, baskets, and other handicrafts. Most protein comes from fish and wildmeat although some households keep chickens. Children start learning to hunt small birds with half or three-quarter size blowpipes and Waorani hunting is still predominately for subsistence (Franzen 2006). More recently many individuals have changed their hunting methods from traditional spears and blowpipes to guns and dogs (Franzen 2006; Mena et al. 2000). Hunters are also now hunting and eating species that were previously considered taboo, such as the tapir (*Tapirus terrestris*) (Rival 1993). Although men are the main hunters, some women also hunt, though this is usually opportunistically, such as killing animals with a machete when encountered near the community (Papworth 2012).

Primates near the Maxus Road

Twelve primate species are present in Yasuní National Park, although not all are found in the area around the Maxus road (Table 1). Although biological research is conducted throughout Yasuní National Park, the majority of research conducted has focussed on the areas near two research stations in the north of the park; Tiputini Biodiversity Station and Yasuní Research Station. All primate species in the park have experienced some degree of study (e.g., Carrillo-Bilbao et al. 2005, Di Fiore et al. 2009). It has previously been shown that the Waorani also consider the olingo (*Bassaricyon alleni*) and kinkajou (*Potus flavus*) as a sort of monkey (Papworth et al. 2013). In addition to consumption, primates are often kept as pets, and the tails of saki monkeys (*Pithecia aequatorialis*), squirrel monkeys, and the kinkajou are reportedly used to decorate traditional crowns. Although Waorani favor the taste of peccary (*Tayassu pecari*, *P. tajacu*) and paca (*Cuniculus paca*), their preferred primate meat is that of the woolly monkey (*Lagothrix lagotricha*), which is said to be rich in fats (Papworth et al. 2013).

Table 1 Species observed near the Maxus Road, Yasuní National Park, and considered "monkeys" by the Waorani

Common name	Scientific name	Wao terero name
White-bellied spider monkey	*Ateles belzebuth belzebuth*	*Deye*
Poeppigi's woolly monkey	*Lagothrix poeppigii*	*Gata*
Red howler monkey	*Alouatta seniculus seniculus*	*Iwa*
White fronted capuchin monkey	*Cebus albifrons aequatorialis*	*Bogi*
Common squirrel monkey	*Saimiri sciureus macrodon*	Gekirè
Noisy night monkey	*Aotus vociferans*	*Amönka*
Red titi monkey	*Callicebus discolour*	Gänaroca
Equatorial saki monkey	*Pithecia aequatorialis*	Cuwïncu
Pygmy marmoset	*Cebuella pygmaea*	Gatomo
Golden-mantled tamarin	*Saguinus tripartitus*	*Mimö*
Olingo	*Bassaricyon alleni*	*Ganata*
Kinkajou	*Potus flavus*	*Gamönga*

Sustainability of Harvests Along the Maxus Road

Sustainability of harvests was calculated in R version 3.2.0 (R Core Development Team 2015) using a simple harvest model (Milner-Gulland and Rowcliffe 2007) where:

$$N_{t+1} = N_t + P_t - H_t \tag{1}$$

Thus the population in the next year is equal to the population in the previous year (N_t), plus the productivity of the population (P_t), minus population harvesting (H_t). Productivity is calculated using:

$$P_t = r_{\max} N_t \left(1 - \frac{N_t}{K}\right) \tag{2}$$

where $r_{\max}$ is the maximum intrinsic rate of natural increase and K is the carrying capacity. Values for $r_{\max}$ were taken from Robinson and Redford (1986). The highest density estimate for each species ($D_{\max}$) was used to calculate carrying capacity, where:

$$K = D_{\max} A_t \tag{3}$$

Hunting area (A_t) estimates and annual primate harvests for three communities (Guiyero, Timpoca and Dicaro) were calculated from Franzen (2006), based on data collected in 2002, and from Espinosa et al. (2014) based on data collected in 2008. Population densities of ateline species were taken from surveys conducted in the Proyecto Primate plot along the Maxus Road in 2005 (Derby 2008) and 2005–2006 (Suárez et al. 2013). Population densities of red brocket deer and collared peccary were taken from Suárez et al. (2013). Although white-lipped peccary (*T. pecari*) was the most hunted species in the studies of Franzen (2006) and Espinosa et al. (2014), there is no density estimate available to model population change. Initial population sizes were calculated using:

$$N_{t0} = D_0 A_{t0} \tag{4}$$

where D_0 is population density in the area before hunting occurs, and A_{t0} is area of extraction in km^2 in the first time step. D_0 was calculated from the mean value of available density estimates.

Two models were considered, one where hunting area and annual primate harvest changed linearly from the values observed in 2002 to those observed in 2008 (adaptive model), thus:

$$N_{t+1} = N_t + r_{\max} N_t \left(1 - \frac{N_t}{D_{\max} A_t}\right) - H_t + D_0 \left(A_{t+1} - A_t\right) \tag{5}$$

and then maintained a stable offtake and area at 2008 levels until 2021, thus:

$$N_{t+1} = N_t + r_{\max} N_t \left(1 - \frac{N_t}{D_{\max} A_{2008}}\right) - H_{2008} \tag{6}$$

The second model maintained hunting offtake and area stable at 2002 levels until 2021 (stable mode):

$$N_{t+1} = N_t + r_{\max} N_t \left(1 - \frac{N_t}{D_{\max} A_{2002}}\right) - H_{2002} \tag{7}$$

Population changes were calculated separately inside the hunting area of each community. Hunting sustainability of spider monkeys and red brocket deer were not modeled for the community of Guiyero as none of these animals were harvested during Franzen's study of hunting in 2002 (Franzen 2006). Harvests of both species were observed in Guiyero in 2008 (Espinosa et al. 2014).

Percentage of populations harvested from inside hunting areas in 2002 and 2008 were calculated using:

$$\text{Percentage harvested} = 100\left(\frac{H_t}{D_0 A_t}\right) \tag{8}$$

For 2008, hunting area and offtake from two additional communities were included: Ganeka and Oña. Minimum densities to maintain observed harvest levels in each period were also calculated using:

$$D_{\min} = \frac{H_t}{r_{\max} A_t} \tag{9}$$

Sensitivity Analysis

As many of the parameter estimates are based on single data points, there is some uncertainty about whether these estimates are typical of the populations studied. Sensitivity analyses can be used to identify which parameters have the most impact on model results (Cariboni et al. 2007). If parameters which have higher impacts on the model results are based on a single data point, there is greater uncertainty in the model results. Sensitivity analyses were conducted to understand the impact of changes in the parameter estimates on the model predictions. Latin hypercube sampling from the R package pse was used (Chalom et al. 2014), with 250 parameter sets generated from a uniform distribution between the minimum and maximum observed value across the five focal species. Sensitivity analyses were conducted separately for the adaptive and stable model.

Results

Hunting Offtakes along the Maxus Road

Based on the calculated size of the hunted area, offtake and densities, annual harvests of ateline primates vary between 0.7 % and 4.6 % of total population sizes in the hunted areas around the Maxus Road (Table 2). Hunting of collared peccary and red brocket deer were calculated to exploit a far greater percentage of the population, varying between 12.5 % and 34.6 %. Minimum densities to sustain extraction levels in 2002 and 2008 (based on $r_{\max}$ values from Robinson and Redford 1986) were lower than mean density estimates for all species (*L. lagotricha*, 18.95 individuals/km^2; *A. belzebuth*, 6.64 individuals/km^2; *A. seniculus*, 2.91 individuals/km^2; *P. tajacu*, 0.75 individuals/km^2; *M. americana*, 0.46 individuals/km^2).

Hunting Sustainability over 20 Years

After 20 years of Waorani hunting in three communities, an increased density for most populations was predicted under both the adaptive and stable models (Fig. 2). Around the communities of Guiyero and Dicaro, woolly and howler monkey populations increased over 20 years in both scenarios, with an average increase of 239 ± 128 (SD) % for ateline populations across the three communities in the adaptive model. However, when harvest and hunting area were held constant at 2002 levels in the stable model, all three ateline species showed decreased populations around the

Table 2 Percentage of population harvested and minimum densities to maintain observed extraction levels of ateline primates, collared peccary, and red brocket deer along the Maxus Road

Species	Year	Individuals hunted per year	Hunting area (km^2)	Percentage of population harvested	Density where extraction is equal to $r_{\max}$
Alouatta seniculus	2002	96[a]	719.2[a]	4.6	0.79
	2008	78[b]	1616[b]	1.7	0.28
Ateles belzebuth	2002	139[a]	719.2[a]	2.9	2.76
	2008	71[b]	1616[b]	0.7	2.76
Lagothrix lagotricha	2002	199[a]	719.2[a]	1.5	1.98
	2008	270[b]	1616[b]	0.9	1.19
Pecari tajacu	2002	67[a]	719.2[a]	12.5	0.07
	2008	416[b]	1616[b]	34.6	0.21
Mazama americana	2002	45[a]	719.2[a]	13.5	0.16
	2008	150[b]	1616[b]	20.1	0.23

[a] Data from Franzen (2006)

[b] Data from Espinosa et al. (2014)

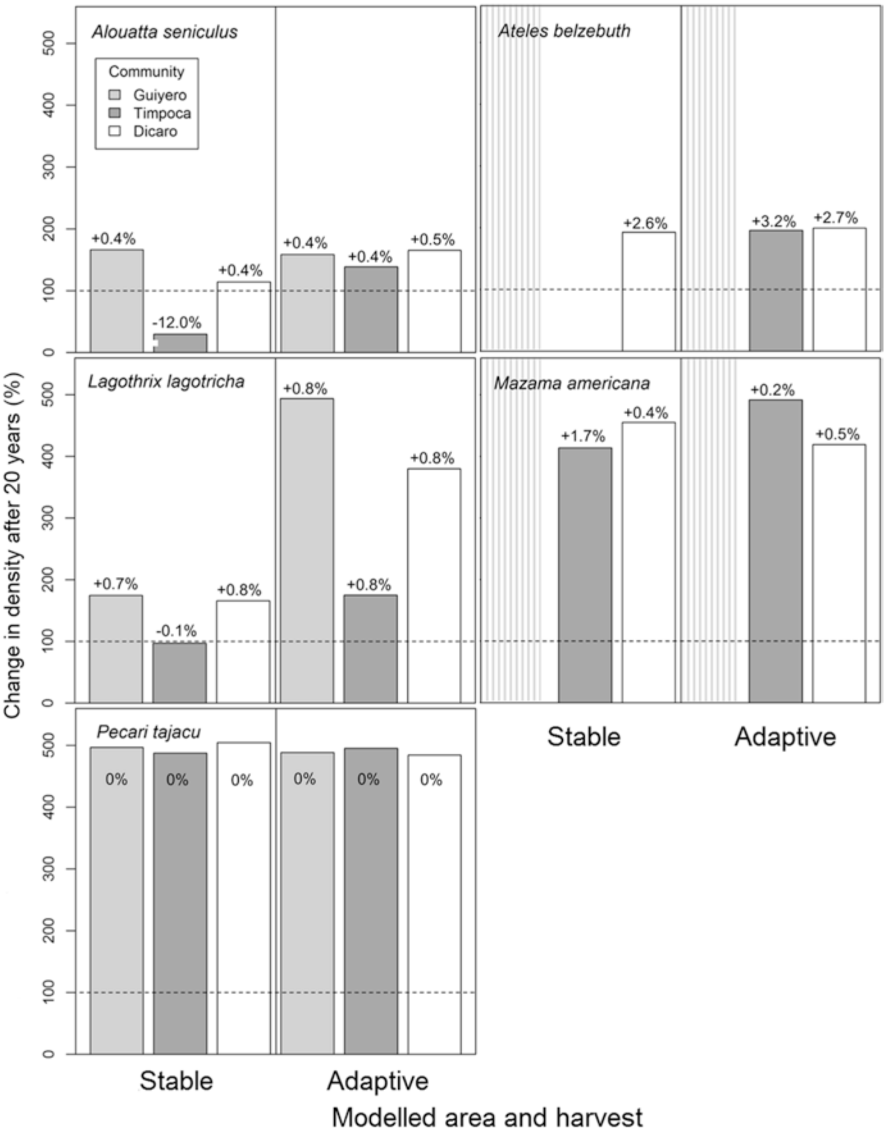

Fig. 2 Predicted density change for ateline primates, collared peccary, and red brocket deer after 20 years of hunting by three communities along the Maxus road, Amazonian Ecuador. Stable and adaptive models of hunting area and offtake are shown, and percentage population change between year 19 and 20 are shown for each population. Spider monkey and collared peccary populations at the community of Guiyero are shown as a *striped bar* as they were not modeled

community of Timpoca, with the spider monkey population going locally extinct. Populations of red brocket deer and collared peccary increased under all scenarios and around all communities, although this increase was greater for the adaptive model where hunting area and harvest changed between 2002 and 2008. The greatest population density change in the final year of the model was observed for the stable model of howler monkeys around the community of Timpoca, with a decrease of 12 % (Fig. 2). In the adaptive model, the greatest population increase was also observed around the community of Timpoca, but for spider monkeys (3.2 % increase in 1 year). No density change was observed in the final year for any of the models of peccary populations, most likely as the populations had increased to carrying capacity.

Sensitivity Analyses

Sensitivity analyses showed that the direction of effect was consistent between the stable and adaptive model for all parameters except initial hunting area in 2002. In the stable model, initial hunting area (A_{2002}) was positively correlated with population density, whereas in the adaptive model there was a negative correlation. The output density after 20 years for both the stable (Fig. 3) and adaptive models (Fig. 4) was most strongly correlated with the maximum density (D_{max}). Models with higher maximum densities had higher final densities, as did models with higher maximum

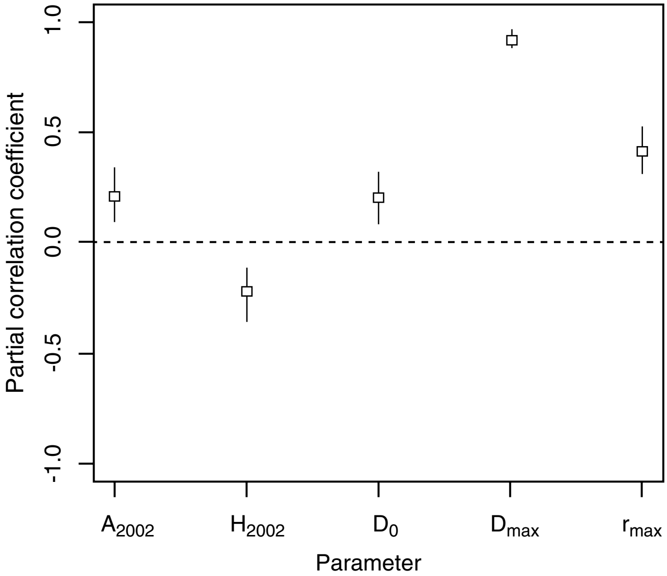

Fig. 3 Impact of parameter estimates on observed population density after 20 years in the stable model, measured using Latin hypercube sampling. Positive values indicate positive linear associations between the parameter and the estimated population density, negative values indicate negative linear associations

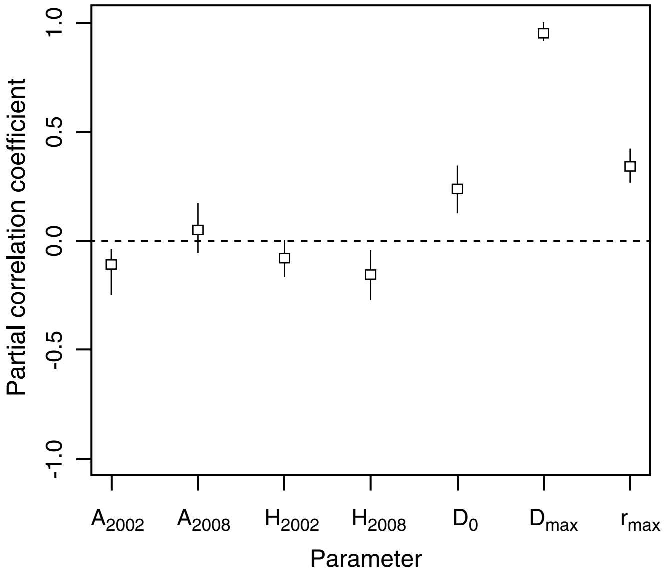

Fig. 4 Impact of parameter estimates on estimated population density after 20 years in the adaptive model, measured using Latin hypercube sampling. Positive values indicate positive linear associations between the parameter and the estimated population density, negative values indicate negative linear associations

intrinsic rates of natural increase (r_{max}). There were negative correlations between population harvesting (H_{2002} and H_{2008}) and density: as harvesting increased, densities decreased.

Discussion

Evidence for Hunting Sustainability Near the Maxus Road

Although previous research on hunting along the Maxus road has suggested Waorani hunting is a potential conservation problem, these results suggest that hunting volumes of woolly and howler monkeys in Guiyero and Dicaro, spider monkeys in Dicaro, and collared peccary and red brocket deer around all communities may be sustainable over 20 years, even when hunting area and offtake are maintained at the levels observed by Franzen (2006). In Timpoca however, woolly and howler monkey populations would decrease, and spider monkey populations would become locally extinct under this scenario. However, the maintenance of hunting offtakes and areas were not observed, and when the hunter behavioral changes observed by Espinosa et al. (2014) are incorporated into the model, hunting of all species around all communities may be sustainable. Collared peccary and red brocket deer have been observed at lower densities than ateline primates along the Maxus Road

(Suárez et al. 2013) and if these density estimates are accurate, a greater proportion of collared peccary and red brocket deer populations are harvested. Yet greater increases in population were predicted for these species than for the ateline primates, suggesting these species are more resilient to harvesting.

Nevertheless, it is difficult to state that current hunting is sustainable for several reasons. Firstly, the model uses maximum intrinsic rate of natural increase thus estimates maximum possible population increases and excludes mortality from sources other than hunting (Weinbaum et al. 2013). Wild animal populations experience mortality apart from human hunting pressure, such as from disease, injury, or non-human predators and additional sources of mortality may be substantial. For example, a 30-year study of an unhunted howler monkey (*Alouatta seniculus*) population yielded yearly survival of 0.81–0.92 depending on age–sex class (Wiederholt et al. 2010). Secondly, there is uncertainty about the parameter estimates used in the model process. The models are sensitive to the parameter estimates used, particularly maximum density ($D_{\max}$), which is difficult to estimate accurately even in unhunted areas due to habitat heterogeneity (McLeod 1997). Maximum intrinsic rate of natural increase estimates were taken from Robinson & Redford (1986), some of which are calculated from very small sample sizes in captive populations (Bowler et al. 2014). The models also used density estimates by Suárez et al. (2013), which as noted above, are based on low sample sizes. Some of this uncertainty in density estimates was mitigated for the ateline primates by averaging these estimates with the density estimates from Derby (2008), but the sensitivity analyses highlight the importance of accurate density estimates. Thirdly, the adaptive model assumed that Waorani hunting behavior changed at a constant rate between 2002 and 2008, then remained constant after 2008, but hunting behavior between these points is unknown, as are potential future changes in behavior. Finally, in addition to uncertainty in the parameters used, there are certain assumptions about the model which could affect the results. For example, the model assumes that hunters do not target specific age or sex classes, yet Waorani hunters often target females with young to keep as pets (Papworth 2012), potentially exacerbating the impact of hunting.

To conclusively demonstrate whether Waorani hunting along the Maxus road is sustainable, changes in density estimates and extraction levels would need to be observed over time (Weinbaum et al. 2013). Even if density decreases were found, these would have to be observed over time, as hunting of some species (such as some guenons in Equatorial Guinea, Kümpel et al. 2008) can initially reduce densities but remain sustainable over time. Although Waorani hunting along the Maxus road may be unsustainable, as yet there is insufficient evidence to support this theory. Collecting this information would be time consuming, but the data produced would establish whether hunting was sustainable. Otherwise, conservation projects to address Waorani hunting on the Maxus road would risk investing money and effort to manage a system which is already sustainable. If hunting was unsustainable, this monitoring could be used to assess evidence-based approaches to conservation interventions (Sutherland et al. 2004). In the absence of evidence for unsustainability, Waorani autonomy to manage their own resources should be respected and supported. Historically, biodiversity conservation has been dominated by opportunistic gazetting of protected areas which require funding, training, and locally placed park rangers to maintain (Blaustein 2007). These initiatives cost substantial amounts of money and are intrinsically unsustainable, as national parks often prohibit commercial and subsistence exploitation, which could fund the cost of running the park. These conflicts between protected areas and exploitation have led to downgrading, downsizing, and degazettement of protected areas (Mascia and Pailler 2011). In contrast, protected areas with indigenous people or indigenous-led community conservation areas have a sustainable work force, plus ownership and land tenure allows collective management of resources so people can support themselves and others while participating in conservation activities such as patrolling to prevent incursions from non-community members (Alcorn 1993). One example of this approach in Latin America is the Alto Fragua—Indi Wasi National Park in Amazonian Colombia, where the Ingano people manage 68,000 ha of forest (Oviedo 2006), offering sustainable management of hunting for at least nine species of primate (Correal et al. 2009), and maintaining a deforestation rate ten times lower than in the surrounding area (Rodríguez et al. 2012).

Implications for Conservation Management Along the Maxus Road

Although there is inconclusive evidence that Waorani along the Maxus road are hunting unsustainably, numerous papers have made management suggestions which could have negative impacts on local communities and affect Waorani self-determination. Suárez et al. (2009) suggested that the provision of free bus transport along the Maxus Road encourages greater hunting by the Waorani as it lowers the entry cost for trading and allows hunters to transport more individuals from the forest to the community. This analysis ignores the other benefits gained by the bus service, such as access to markets, health services, transporting children to school, and allowing easy social visits between communities. Selling wildmeat at the market is also one of the few sources of cash for communities along the Maxus road. The average price paid for a woolly monkey by trader at the market is USD12.90, based on average woolly monkeys weight in Franzen (2006) and average price for mammals per kilogram in Pompeya market from Suárez et al. (2009). This price makes hunting profitable, particularly when compared with the USD15 per half day paid by the oil company Repsol for grass cutting and other manual tasks (Pearson 2010).

The bus service has also been criticized for allowing access to larger areas of forest, leading Espinosa et al. (2014) to state that: "[f]or wildlife to persist, harvest must be managed (e.g., by establishing and enforcing hunting quotas) or large areas must remain inaccessible to hunters in order to serve as refugia" (p. 13). Yet, our understanding of sink-source dynamics is currently insufficient to conclude whether prey sustainability is better maintained by intensive hunting in smaller areas (as would occur in the absence of roads), or more disperse hunting over a larger area (accessed by road). If the second is true, the road and bus service may actually increase the sustainability of hunting effort. Although Waorani also recognize the potential negative impacts of roads (Lu Holt 2005), they have other concerns, and identifying Waorani priorities and solutions is more appropriate for effective long-term conservation (McSweeney and Pearson 2009). For example, Waorani may not see hunting as an issue, but they may be interested in long-term solutions that prevent migrants from settling inside their territory. Immigration to the Maxus road is currently prevented by a Repsol run checkpoint where the road meets the Napo river (Suárez et al. 2013), but this may not be sustained if oil extraction discontinues.

If hunting is identified as a problem, rotating hunting areas may be more effective than harvest quotas. Although the reasons for relocation by the Waorani are complex and varied, including feuds with neighboring groups, Rival (2002) reports that groups relocated when the monkeys were perceived to have run away. When a longhouse was no longer able to easily find large bodied primates such as woolly and spider monkeys at close distances, they concluded that their hunting had scared the monkeys away and moved to a new location were the monkeys were not afraid. These new locations could be an entirely new area or a return to a previously occupied. Although a scientist hearing this narrative may conclude that the monkeys were locally expiated through hunting, they can recognize changing monkey populations and the behavioral solution applied by the Waorani, or adaptive natural resource management. Relocation, regardless of the narrative behind it, is an effective way to allow local animal populations to recover, or as the Waorani view it, to return to the area. This is one example of how an ethnoprimatological approach could identify new, culturally appropriate solutions for primate conservation. Ethnoprimatology draws from a number of disciplines to understand human primate interactions from multiple viewpoints (Malone et al. 2014), and using this approach will likely generate conservation strategies that are locally distinct rather than globally applicable.

Primate Conservation and Indigenous Communities

There are numerous benefits for biodiversity conservation when working with, rather than against, local communities (Gadgil et al. 1993; Stevens 1997). Projects that have local community support are likely to experience increased compliance if rules are introduced. Local community members can act as forest guardians, such as the local community members who work to protect the cross-river gorilla (*Gorilla gorilla diehli*, Nicholas et al. 2010). Local management of the ecosystem is also often beneficial and can maintain existing systems. Although this is widely recognized in European conservation where grazing by domestic livestock is essential to maintain certain ecosystems (WallisDe Vries et al. 1998), the benefit of local management is less recognized in tropical conservation. There are examples, however, such as ungurahua (*Oenocarpus bataua*) stands in the Amazon, which may be anthropogenic (Miller 2002) and form an important part of the diet for peccary and large-bodied primates. Identifying and understanding potentially positive local management practices, and working with local communities to preserve and support their culture can therefore have positive outcomes for conservation. Finally, the big threats to biodiversity are often driven by global markets for agricultural or mineral products, rather than small-scale use of the local environment (DeFries et al. 2010). For example, although hunting is a threat for orangutans (*Pongo* spp.), by far the biggest threat is forest clearance for commercial oil palm and other agricultural products (Swarna Nantha and Tisdell 2008). Working with local communities to ensure land tenure may prevent these more destructive industries from being granted land-use rights.

The ethnoprimatological approach has potential overlap with rights-based approaches to conservation with and by indigenous peoples. Supporting and working with indigenous-led conservation can support indigenous lifestyles, practices, and rights (Alcorn 1993; Gadgil et al. 1993; Stevens 1997; Adams et al. 2014), and have positive outcomes for primate conservation. It is important to be aware that working with indigenous communities in this way means that indigenous peoples define the conservation problem and solution, possibly in conjunction with outside individuals (Adams et al. 2014). These problems and solutions may not directly relate to primates, although they could indirectly benefit primate populations. For example, rotating hunting areas as hunters are worried about declining peccary populations would also allow primate populations in the unhunted areas to increase. To be successful when working with indigenous communities, the ethnoprimatological approach should take an inclusive view of primate conservation which recognizes the complex interactions between humans, primates, and other species. Ethnoprimatology is a western discipline which takes a particular interest in primates, yet this interest may not be shared by the communities in which ethnoprimatologists work (Papworth et al. 2013). In some cases, local communities may be decidedly against the conservation of certain local primates. One example of this is the aye-aye (*Daubentonia madegascariensis*) in Madagascar, which is believed to be a portent of death, although the death can be prevented by killing the aye-aye (Simons and Meyers 2001). Aye-aye's are feared and killed on sight, so support for their conservation may be difficult to gain in Madagascar. Indeed, even after education programs on the aye-aye, little change in attitudes to the species were found (Rakotomamonjy et al. 2014).

In this study, assessing the sustainability of select primate and non-primate populations showed that the non-primate populations were more likely to withstand predicted harvesting levels, but it is unlikely these results are generalizable to all other hunted primates and non-primates. If a conservation project discouraged primate hunting, hunters may compensate by increasing pressure on other species that are sensitive to overhunting. In this case, demonstrating increasing primate populations would not necessarily be a positive outcome for conservation if other species were going locally extinct. One example that can illustrate the disadvantages of a narrow focus on primates is the sacred monkey forests of West Africa. At the Boabeng-Fiema Monkey Sanctuary in Ghana, black and white colobus (*Colobus vellerosus*) and Campbell's monkey (*Cercopithecus campbelli lowei*) are protected from hunting by two local communities (Fargey 1992). In the sanctuary, populations of these two species have increased and substantial numbers of national and international tourists come to visit the monkeys. Unfortunately however, this focus on protecting monkeys from hunting has not extended to other animals or the forest which the monkeys live in, thus the forest has been substantially reduced, potentially threatening the long-term viability of the monkey populations (Saj et al. 2006). The ethnoprimatological approach which focuses exclusively on primates is therefore not a silver bullet for primate conservation, but must form part of a larger suite of conservation strategies aimed at preserving species and ecosystems for future generations. When working with indigenous communities, the ethnoprimatological approach may open dialogue between local communities and researchers, revealing novel solutions for conservation. This dialogue may help researchers recognize the potential benefits of supporting communities to manage their own resources and ensure that conservation interventions do not negatively impact communities.

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The Role of Nonhuman Primates in Religious and Folk Medicine Beliefs

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Introduction

People interact with different animals in different ways (Alves 2012). Because of phylogenetic, biological, and behavioral connections between humans and nonhuman primates, the relationships between the two groups have multiple levels of significance (Fuentes and Wolfe 2002). Over the ages, nonhuman primates have played a wide range of roles in people's lives. These roles vary depending on human cultural practices and local environments. People worldwide use primates as food, watch them on television or in zoos and safaris, keep them in their houses as pets, use primates products in folk medicine, and conduct scientific experiment on them. In addition to their utilitarian importance, primates play an important role in cultural expressions such as art, music, literature, and other different cultural manifestations. Animals (including nonhuman primates) are valuable to people not only because they provide economic benefits, but because they have also been incorporated into our sense of place and are enshrined in long-standing cultural practices (Shephard 1996). Many human cultures have mythologies and many show close integration and connections with totemic, ancestral, or mythological (imaginary) animals or animal-gods, which are said to have been present throughout human history (Allaby 2010; Alves 2012; Kemmerer 2011).

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These human/nonhuman primate relationships form core components in conservation and represent an emerging area of discourse across anthropology (Fuentes 2006). These connections can be investigated by ethnoprimatology, a subdivision of ethnozoology. Such studies are imperative to understanding the social, economic, and cultural factors that influence these interactions and can aid in the development of sustainable management plans, thus, they are essential to conservation efforts. This chapter provides a brief review on the main forms of interactions between people and primates in religious and folk medicine contexts and the resulting conservation implications.

Primates, Religion, and Mythology

Religious beliefs and practices have long influenced human perception and the use of natural resources (Berkes 2001; Tomalin 2004). In relation to fauna, this is even more evident, since virtually all manner of beliefs have involved animals (Bowman 1977), which have played and continue to play an important role in religious practices worldwide (Alves et al. 2012; McNeely 2001). Among the main animals that play an important role in magic-religious context are the nonhuman primates. This is not surprising considering the phylogenetic similarity of these animals with humans. Since ancient times, nonhuman primates were and remain associated with religious and magic practices and they have been identified with human qualities or gods in paintings or other artistic products (Alves et al. 2013; Mittermeier et al. 2007). For instance, from the beginning of Egyptian history through at least the beginning of the Christian period, baboons held a very consistent and important role in ancient Egyptian religious beliefs and were represented as both demon and protector. They became associated with a number of the most important Egyptian gods, as well as the king, even though they would have had to be imported from abroad (Dunn 2014).

In some human societies, nonhuman primates are considered divine or able to interact with gods. A good example of the important role of primates in religious practices is *Hanuman the Monkey*, which in some tales is said to be an incarnation of Shiva, considered the Supreme God within Shaivism, one of the three most influential denominations in contemporary Hinduism (Lutgendorf 2006). *Hanuman* is revered for his bravery, strength, loyalty, devotion, and dedication to justice. Every year, his birthday is celebrated "on the full-moon day of Chaitra (April) at sunrise." Monkeys in general are revered in several parts of India for bearing the likeness of Hanuman (Jokinen 2014).

Another example is recorded in Mesoamerica, where *Hun Batz*, the howler monkey god in the Mayan book Popul Vuh (Urbani and Cormier 2015) is frequently represented in sacred pottery (Bruner and Cucina 2005; Coe 1977, 1978). As described by Braakhuis (1987), *Hun Batz* has multiple roles. This deity is represented in Mayan vases as a diviner with a pivotal role in the Mayan calendar. In addition, *Hun Batz* has other sacred functions. In conjunction with the god *Hun*

Chuen (the spider monkey deity), they forged humankind and served as artisan creators (Braakhuis 1987).

There are also cases in which the zoomorphic gods have morphology associated with nonhuman primates. In ancient Egypt, for example, the gods and goddesses often had a human torso and the head of an animal (Sax 2002). These include, among others, Thoth, who was originally a moon god. Thoth gradually became seen as a god of wisdom, magic, and the measurement and regulation of events and of time (Assmann 2001). Sometimes, Thoth was depicted as a baboon holding up a crescent moon, as the baboon was seen as a nocturnal and intelligent creature. The association with baboons led to him occasionally being said to have as a consort Astennu, one of the (male) baboons at the place of judgment in the underworld. On other occasions, Astennu was said to be Thoth himself (Rogers 2014). Because of these beliefs, in ancient Egypt, the baboon was considered a sacred being and was treated with great respect (Morris 2013). Another interesting example is Hanuman, the monkey-god, who is generally depicted with a human body, a red monkey's face and a tail.

Furthermore, primate sculptures are used to decorate altars and religious temples in different countries of the world. In a number of regions from Africa to Tibet, primates are revered as guardians of human settlements, as animals that bring good luck, as reincarnations of the spirits of ancestors, and as embodiments of gods (Petter 1977). Representation of sacred baboons, for instance, is found in artistic production from the Protodynastic chronologies (end of the fourth millennium-2695/2640) up to the Christian era, in which period the worship of the baboon persisted (Osborn and Osbornová 1998). Particularly famous are the hamadryas evoked in the wall-paintings of Tutankhamun's burial chamber, where they are supposed to guard the young pharaoh as he passes through the 12 sections of the underworld on the first night after his death (Masseti and Bruner 2009).

In Africa, the sacred role of primates has been recorded in several places. In Ghana, for example, the people of Fiema and Boabeng villages have considered the monkeys sacred (Appiah-Opoku 2007). In these areas, two species of primates (the ursine black and white colobus, *Colobus vellerosus*, and the Campbell's monkey, *Cercopithecus campbelli lowei*) are taboo when it comes to hunting because community members consider them to be the children of the gods who protect the villages. The taboo carries with it the requirement of "caring for the monkeys," which translates into a hunting ban (Saj et al. 2006). Even non-believers have to refrain from killing the monkeys around the villages (Saj et al. 2006). Fargey (1991) reports that a former Nkoranzahene who did not believe in the taboo regularly killed monkeys around Boabeng (even mistaking people picking fruit in trees for monkeys and killing them). The angry villagers cut off the Nkoranzahene's head (Saj et al. 2006). Another example is the case about the mythical monkeys of Soko (Department of Bondoukou), in the east of Côte d'Ivoire, where, according to the legend, ancient humans were transformed into monkeys to escape the attack of enemies, but the process was irreversible. Therefore, the monkey has become the totem animal, a sacred animal that should not be killed or eaten. The mythical nature of those primates causes them to become the sacred animals most protected in the region

(Jean-Pierre 2013). Likewise, taboos involving primates and the beliefs regarding not disturbing, collecting, or killing them are well known from Madagascar, where there are specific taboos concerning different species of lemur (Jones et al. 2008; Vargas et al. 2002; Wilson et al. 1989).

Similarly, throughout various parts of Asia, there have been a number of monkey deities in the past and, although in modern times they have largely lost their power to inspire worship, they still play an important role in oriental folklore (Morris 2013). In different places, primates have been traditionally considered sacred and, because of this, are treated with great respect. For example, the Hanuman langurs *Semnopithecus* spp. or macaques *Macaca* spp. are revered as ancestors or as deities (Zinner et al. 2013), with populations persisting locally where they otherwise almost certainly would have perished (Nijman and Nekaris 2014). In Tibet, monkeys are said to be the primordial ancestor of the Tibetan people alongside the Bodhisattva Avalokitesvara, killing them is seen as a transgression of religious principles (Hongyan et al. 2000). In early India the langur monkey acquired a godlike status and is still worshipped to this day, despite increasing complaints from many members of modern Indian society (Morris 2013). Interaction between humans and others primates is particularly intensive at religious sites that are commonly referred to as “monkey temples” or “monkey forests” (Schilaci et al. 2010). On the island of Bali, for example, today there is a sacred Monkey Forest where long-tailed macaques are treated as sacred animals and allowed to roam around the temples there (Morris 2013). In Siberut, off the west coast of the Indonesian island of Sumatra, hunting was forbidden for Kloss’ gibbons *Hylobates klossi* and the pale (but not the black) morph of *Simias concolor*, despite primates being amongst the largest mammals on the island (Mitchell and Tilson 1986). In north Sulawesi, Indonesia, a clear taboo, based in local folklore, prohibits harming Tonkean macaques (*Macaca tonkeana*), despite their frequent crop-raiding behavior (Riley 2010).

Mythology, which is closely connected to religion, is another cultural expression in which nonhuman primates can be extremely important. As pointed out by Sakalauskaite (2010), gods, animals, and certain creatures that have elements of both humans and animals, are main characters in mythological and folktales and play a major role in the development of the behavior of the human being. In this scope, examples of the importance of primates appear in various contexts. In China and India, the Monkey mythology is an important part of both Hindu/Buddhist lore (India) and Zodiac/Buddhist lore (China) (Schumacher 2013). In Costa Rica, *Alouatta palliata* is considered an evil omen that brings bad luck, and, so, when found near a village it is shot (Gonzalez-Kirchner and Sainz de la Maza 1998). Similarly, in Madagascar the aye-aye (*Daubentonia madagascariensis*) may be killed on sight as crop pests or harbingers of evil (Manh Ha et al. 2008). Due to its evil reputation, the aye-aye is never eaten, but is used in ritualized ceremonies (Nekaris et al. 2008; Nekaris and Jayewardene 2004). In Sri Lanka, valuable material from the eyes is extracted by holding a loris above a fire until the eyes burst (Nekaris and Jayewardene 2004). Some people fear their cry as an ill omen (Lewis 1917). The mournful tone of the cry is thought to bring misfortune, usually resulting in their being stoned to death (Nisbett et al. 2003).

A broad category of beliefs encountered in Amazonian cultures attribute either positive or negative traits to monkeys that can be transferred to humans (Hamada et al. 2007), this influences on hunting, use, and consumption of these animals. This is well exemplified in several South American groups. For example, Crocker (1971) reported a kind of magical prohibition among the Bororo people that keeps them from eating monkeys, which are considered to epitomize speed and grace. In multiple Amerindian societies, howler meat is avoided for reasons including magical contagion, ritual couvade, or simply due to taste preferences (Urbani and Cormier 2015). According to Lizarralde (2002), the Barí of Venezuela view red howler monkeys (*Allouata* sp.) as similar to three-toed sloths (*Bradypus variegatus*) in terms of lethargy and lack of cleverness, and so avoid these primates to prevent acquiring their negative qualities. Howler monkeys are considered to be of low intelligence and speed, and they are not kept as pets nor are their teeth valued as charms. On the other hand, they keep spider monkeys as pets and believe that wearing spider monkey teeth necklaces will confer manual dexterity to the owner. A similar perception was recorded in the Matsigenka mythology, in which howler monkeys are considered to be lazy and capuchins are considered thieves, and they believe that these traits can be transferred to humans who eat them (Shepard 2002). This is reflected in another example that bridges couvade and contagion, in which Vilaça (2002) reported a Warí shaman telling two parents that their child was turning into a monkey because they had not followed the correct protocol for preparing and eating capuchins. Among the Kagwahív (Parintintin), monkeys are kept as pets, but are avoided as food, due to their similarity to human beings (Kracke 1978). On the other hand, the Kalapalo, who consider most land animals disgusting, do eat monkeys, because they are classified as "like-human-beings" (Basso 1973).

Alves et al. (2010, 2013) published recent revisions on the primates' species associated with folk beliefs or used for magical/religious purposes, which is summarized in Table 1. These authors found that at least 60 species are associated with folk beliefs and magical/religious practices. They also found that the interactions between people and primates are influenced by the way animals are associated with local cultural practices and which can result in positive or negative aspects for conservation of nonhuman primates (Alves et al. 2010). Such cultural aspects, mainly based on folk beliefs and religion, are among the main reasons for hunting or not hunting primates. Islam, Hinduism, and Buddhism, for instance, have various restrictions or beliefs that prevent followers from eating or killing primates (Mittermeier 1987). A well-known example is the Hindu-based protection of monkeys in parts of Asia, such as long-tailed macaques (*Macaca fascicularis*) in Bali, Indonesia (Srivastata 1999), and rhesus macaques (*M. mulatta*) and gray langurs (*Semnopithecus* spp.) in India and the neighboring region (Bennett et al. 1987; Fitch-Snyder 2001; Gray 2001). Nahallage and colleagues (2008) in their study in Sri Lanka reported that people are generally tolerant toward animals due to religious beliefs, and the major threat to their survival is more likely to be the loss of their forest habitats. The authors also highlighted that hunting primates for food was not a common practice in most of surveyed areas since most of the people are Buddhists and against the killing of any animal. Another interesting belief of people in the

Table 1 Primates used in magic-religious rituals or practices. Adapted from Alves et al. (2013)

Family/species	Region or country(ies)	Use(s)
Callitrichidae		
Cebuella pygmaea (Spix, 1823)	Peru	Considered magical and potentially dangerous creatures
Saguinus midas (Linnaeus, 1758)	Suriname, Brazil	It is considered sacred
Cebidae		
Alouatta seniculus (Linnaeus, 1766)	Peru	Considered to be lazy; this undesirable character trait could be passed on to children who consume their meat. Also known to be infested with botfly larvae, rendering their meat less attractive
Aotus azarae (Humboldt, 1811)	Bolivia	Implies a potential threat on the spiritual level, used to prevent dribbling in babies
Aotus infulatus (Kuhl, 1820)	Brazil	Folk uses
Alouatta palliata (Gray, 1849)	Costa Rica	Evil omen that brings bad luck
Ateles paniscus (Linnaeus, 1758)	Peru, Suriname	Animal spirits considered capable of stealing the souls of children and making them ill. It is considered sacred in Suriname
Alouatta belzebul (Linnaeus, 1766)	Venezuela	“Folk uses”
Cebus kaapori (Queiroz, 1992)	Brazil,	Folk uses
Saimiri sciureus (Linnaeus, 1758)	Brazil	Folk uses
Cercopithecidae		
Cercopithecus mona (Schreber, 1774)	Nigeria, Congo DR, Ghana	Charms or amulets, aid in quickening child walking, used by palm wine tappers to climb successfully, victory in competition, used in funeral rituals, protected by local beliefs and traditions
Cercopithecus neglectus (Schlegel, 1876)	Congo DR	Used in funeral rituals
Cercopithecus petaurista (Schreber, 1774)	Ghana, Ivory Coast	Considered sacred
Cercopithecus diana (Linnaeus, 1758)	Ghana	Considered sacred
Chlorocebus tantalus (Ogilby, 1841)	Nigeria	Considered sacred
Chlorocebus sabaeus (Linnaeus, 1766)	Ivory Coast	Considered sacred

Family/species	Region or country(ies)	Use(s)
Colobus angolensis (P. Sclater, 1860)	Congo DR	To cure supernatural diseases
Colobus polykomos (Zimmermann, 1780)	Ghana	Purification and strengthening of widow/widower, protected by local beliefs and traditions, spiritual strengthening after birth of tenth child, Considered sacred. Miscarriage
Colobus vellerosus (I. Geoffroy, 1834)	Ghana	It is locally considered sacred
Erythrocebus patas (Schreber, 1775)	Nigeria, Sudan	Charm preparations
Macaca fascicularis (Raffles, 1821)	Indonesia	Considered sacred
Macaca fuscata (Blyth, 1875)	Japan	Has positive religious associations as one of the animal reincarnations of the Buddah; however, in sharp contrast, monkeys also appear as morally dubious or unfavorable animals in Japanese folklore
Macaca mulatta (Zimmermann, 1780)	India	The palm or finger or skull of *M. mulatta* is hung above the main door to propitiate evil spirit
Macaca nigra (Desmarest, 1822)	Indonesia	Some incorporation into traditional belief systems
Macaca pagensis (Miller, 1903)	Indonesia	Part of belief system
Macaca tonkeana (Meyer, 1899)	Indonesia	It is considered sacred
Papio hamadryas (Linnaeus, 1758)	Saudi Arabia, Ethiopia, Eritrea, Indonesia	Considered sacred
Papio anubis (Lesson, 1827)	Nigeria, Kenya, Uganda	Used in cultural ceremonies, viewed as malicious, cunning, and dangerous
Papio cynocephalus (Linnaeus, 1766)	Kenya, Uganda	Viewed as malicious, cunning, and dangerous
Papio ursinus (Kerr, 1792)	South Africa	Protective charm, court case charm
Procolobus badius (Kerr, 1792)	Africa	Spiritual use
Procolobus verus (Van Beneden, 1838)	Ivory Coast	Considered sacred
Semnopithecus entellus (Dufresne, 1797)	India	Amulets, sacred primate to Hindus, charms prepared from dismembered digits of a monkey's paw strung together on a thread are believed to treat paralysis, bones subjected to black magic rituals are considered auspicious and bring recognition

(continued)

Table 1 (continued)

Family/species	Region or country(ies)	Use(s)
Trachypithecus pileatus (Blyth, 1843)	India	Magical/religious practices
Theropithecus gelada (Rüppell, 1835)	Not mentioned	To procure their manes for ceremonial headdresses
Pitheciidae		
Chiropotes satanas (Hoffmannsegg, 1807)	Brazil	Folk uses
Callicebus torquatus (Hoffmannsegg, 1807)	Venezuela, Brazil	Folk uses
Chiropotes chiropotes (Humboldt, 1811)	Venezuela, Brazil	Folk uses
Hominidae		
Gorilla gorilla (Savage and Wyman, 1847)	Nigeria, Cameroon	Charms or amulets, to obtain victory in competition. In Cameroon, this species is considered sacred
Pan troglodytes (Blumenbach, 1775)	Nigeria, Guinea, Sierra Leone, Liberia, Mali, Guinea, Senegal, Uganda, Tanzania, Cameroon	Amulets, regard the chimpanzee as a sacred totem and a reincarnation of their ancestors, considered sacred, piece of the dried bone of chimpanzees is tied around the waist or wrist of infants in the belief that it makes them stronger as they grow into adulthood, chimpanzee's central incisors were procured to be worn as amulet around the waist of infants to protect them and give them power over others in their cohort, magic rituals
Pan paniscus (Schwarz, 1929)	Congo DR	It's locally considered sacred
Pongo pygmaeus (Linnaeus, 1760)	Indonesia, Malaysia	Spiritual use. It's considered sacred in Malaysia
Pongo abelii (Lesson, 1827)	Indonesia, Malaysia	Spiritual use
Loridae		
Loris lydekkerianus (Cabrera, 1908)	Sri Lanka and India	Religious practices

Family/species	Region or country(ies)	Use(s)
Loris tardigradus (Hill, 1942)	Sri Lanka, India, Indonesia, Myanmar	Used in religious practices, using its eyes in native medicines and love potions, charms
Nycticebus bengalensis (Lacépède, 1800)	Lao PDR	They are believed to be a spiritual animal
Nycticebus pygmaeus (Bonhote, 1907)	Lao PDR	They are believed to be a spiritual animal
Daubentoniidae		
Daubentonia madagascariensis (Gmelin, 1788)	Madagascar	*D. madagascariensis* may be killed on sight as crop pests or harbingers of evil. Due to its evil reputation the aye-aye is never eaten, but is used in ritualized ceremonies
Indriidae		
Propithecus verreauxi (A. Grandidier, 1867)	Madagascar	Protected or sacred in some areas
Propithecus tattersalli (Simons, 1988)	Madagascar	Used in ritual practices
Propithecus edwardsi (A. Grandidier, 1871)	Madagascar	Species that are considered to embody dead ancestors
Propithecus perrieri (Lavauden, 1931)	Madagascar	It is locally considered sacred
Avahi laniger (Gmelin, 1788)	Madagascar	Species that are considered to embody dead ancestors
Indri indri (Gmelin, 1788)	Madagascar	Protected or sacred in some areas
Lemuridae		
Lemur catta (Linnaeus, 1758)	Madagascar	Protected or sacred in some areas
Eulemur rufus (Audebert, 1799)	Madagascar	These are ancestors in animal form
Eulemur rubriventer (I. Geoffroy, 1850)	Madagascar	These are ancestors in animal form
Hylobatidae		
Hylobates moloch (Audebert, 1797)	Indonesia	It is considered sacred
Hylobates klossii (Miller, 1903)	Indonesia	It is considered sacred
Nomascus concolor (Ma & Wang, 1986)	Lao PDR	It is considered sacred

south is that monkey organs (heart and lungs) are being used in the cities for organ transplants in humans due to their close similarity to humans. Some believe that the monkey's right leg contains human flesh, and even if they eat the meat they usually avoid eating this part (Nahallage et al. 2008).

Primates may also be protected by social taboos (Shepherd et al. 2004). For example, the exploitation of some primate species in Africa is largely prohibited because local communities adorned them with ritual meanings, regard them as animal totems or value them as fetishes or aids to traditional medicine practice (Adams and McShane 1996; Osemeobo 1991). In addition, traditional knowledge in the form of local taboos that restrict or regulate the exploitation of wildlife is thought to have contributed significantly to preventing the extinction of some wild primates (Rose et al. 2003). In a study about traditional beliefs associated with the Cross River gorilla (*Gorilla gorilla diehli*) in Lebialem Division, Cameroon, Etiendem et al. (2011) reported that most research respondents believed that if the totem gorilla is killed, the human counterpart also dies unless he/she seeks immediate disconnection from the soul of the deceased totem by treatment from a traditional healer. The authors also found that the fear of human death resulting from the death of gorillas seems to be the strongest reason why people do not want to hunt the species. Likewise, some chimpanzee (*Pan troglodytes*) populations are not hunted because of their physical similarity to humans or folklore regarding an ancestral relationship with humans (Kortlandt 1986; Putra et al. 2008; Silva et al. 2005; Takeda 1998). In the village of Bossou (Republic of Guinea), Manon people consider chimpanzees sacred, as the reincarnation of their ancestors, and believe that their ancestors' souls rest on the sacred hill of Gban (Kortlandt 1986). As the chimpanzee is a totem of the most influential family of Bossou, it is strictly forbidden to hunt or eat the chimpanzee (Yamakoshi 2005). This author proposes that Gban was important for village protection during years of tribal conflict, the current peaceful coexistence between man and chimpanzee may have historical war roots. Chimpanzees regularly crop-raid and are known to attack villagers occasionally. However, due to the local people's strong cultural beliefs, humans and chimpanzees have been able to coexist in such close proximity over many generations (Akowuah et al. 1975; Yamakoshi 2005). A recent review of the literature on primate taboos, among indigenous Amazonian peoples identified *Alouatta* as the most frequently prohibited taxon (Cormier 2006). The situations mentioned above show that taboos are not uniform, meaning that in some societies the beliefs associated with nonhuman primates vary according to the human communities that interact with these animals. As pointed by Urbani and Cormier (2015), most avoidances or taboos of primates are associated with the social or ritual status of the group members, including their age/sex and reproductive status.

Among diverse Amazonian peoples, many primate species have mythological or symbolic importance and are subject to taboos, restrictions, or dietary avoidance (Ganzhorn and Abraham 1991; Shepard 2002). Shepard (2002) noted that Matsigenka hunters generally avoided taking woolly and spider monkeys from the peak of the dry season (July–August) through the early rainy season (November–December). This is because fruits are scarce at that time and monkey meat is lean and tough, and likely to elicit disparaging comments from their wives. Monkey hunting is instead concentrated in the late rainy season and beginning of the dry season (March–June) when these animals are fat. The Matsigenka also believe that certain monkeys (especially large adult males) and other game animals have vengeful spirits that can "take revenge" on the hunter's family, causing illness in young children. Matsigenka women use special fragrant herbs to protect newborn babies from the musk-smell and vengeful spirits of monkeys and other game animals. The examples cited above reinforce the view that traditional socio-environmental concepts could provide ideological frameworks for future conservation measures (Shepard 2002).

However, traditional beliefs and practices related to primates have not always carried a positive potential for the conservation of involved species (Alves et al. 2010, 2013; Etiendem et al. 2011). For example, Critchley (1968) reported the use of apes (gorillas and chimpanzees) in traditional medicine and as fetishes. Even today, those who own bones or skulls of these animals are respected traditionally, and in some cases, are given chieftaincy positions within community social structures (Etiendem et al. 2011). In India, skulls of various species of primates are hung outside tribal dwellings in Arunachal Pradesh and other northeastern states to ward off evil spirits or simply as objects of ornamentation (Alves et al. 2010). These authors pointed out that products derived of 67 primate species are used in traditional folk medicine. In some areas of Sri Lanka, for example, Nahallage et al. (2008) reported that people believe that monkey meat can cure certain illnesses and some eat the purple-faced langur (*Trachypithecus vetulus*) for medicinal purposes. In the Southern Province, it is a common belief that the meat of the purple-faced langur is good for asthma or that it can cure sight defects. Of course, none of this has been medically proven (Nahallage et al. 2008).

Primates and Folk Medicine

Recent publications have shown that the number of medicinal primates' species used in traditional folk medicine is expressive, encompassing at least 110 species (Alves et al. 2010, 2013) in different socio-cultural contexts throughout the world, comprising 52 countries, mainly in Latin America, Africa, and Asia (Alves et al. 2013). The whole bodies of primates may be used in the preparation of many traditional medicines, but various parts of these animals, such as fur, legs, fat, oil, eyes, bile, blood, gall bladder, viscera, bone, meat, brain, and skull are used most commonly in preparation of traditional remedies (Alves et al. 2013). A similar trend has been observed for other animals used in traditional medicine in which extracted zootherapeutical remedies are derived from body parts that are often not used for any purpose (Alves and Alves 2011; Alves et al. 2013; Ashwell and Walston 2008; El-Kamali 2000; Sodeinde and Soewu 1999; Van and Tap 2008; Vázquez et al. 2006). Moura and Marques (2008) pointed that one characteristic in common among all zootherapeutic products, whether whole animals or their parts, is their lack of use for other purposes. The same trend has been observed for primates used in popular medicine, it is remarkable that in most cases, the medicinal products of primates are byproducts from animals hunted for other purposes (Alves et al. 2013). These multiple uses (including medicinal) of fauna and their impact on animal populations must be properly assessed and taken into consideration when implementing recovery plans for these species, especially those that are highly sought after.

Zootherapeutic products are consumed in several ways. Hard parts (e.g., bone and fur) are generally sun-dried, grated, and crushed to powder to be administered as tea or taken during meals. Meat, brain, oil, fat, and blood can be ingested, or used as an ointment (Alves et al. 2013). Products derived from primates diseases have been used for treating various diseases. In India, for example, Adi people occasionally use rhesus monkey (*Macaca mulatta*) meat to treat epidemic diseases like malaria, typhoid, cholera, and pox, etc. (Geissmann 2007). The Marring Nagas people grind the loris skull, mix it with water, and take it orally to cure epidemics like cholera (Duckworth et al. 1999). In Indochina, gibbons are sometimes hunted for medicinal purposes (Rijksen and Meijaard 1999) and there have been claims that some people there will eat the meat of orangutans as an aphrodisiac (Campbell et al. 2008). In Vietnam, primates are hunted for food or medicinal purposes and it is a common occurrence to find them in bottles in alcohol, not as zoological specimens, but as tonics for medicinal use or for sipping as monkey wine (Fruth et al. 2008). In addition, in the same country, primates in alcohol are used as “energy drinks” (Geissmann et al. 2000; Tang and Li 1957). Another belief of people in the south of Sri Lanka is that monkey organs (heart and lungs) are being used in the cities for organ transplants in humans due to their close similarity to humans (Horowitz 1998) although it is unclear how this affects people perception of monkeys.

The use of primates in traditional folk medicine is influenced by religious, mythological, and magical beliefs (Alves et al. 2010). This is not surprising given that cultural issues are recognized as important components of health care (Zweber 2002). As noted by Straker (1994), the supernatural world is as relevant in the diagnosis of illness as the natural world, with the main causes of illness being magical, mystical, and animistic forces. Alves and Rosa (2006) highlighted that animals provide the raw materials for prescribed remedies using the clinical method and are also used in the form of amulets and charms in magical/religious diagnosis, seeking, especially, the prevention of spiritual diseases. As suggested by Alves and colleagues (2007), in traditional medicine, animals are employed with a magical-prophylactic perspective with the purpose of warding off diseases of “unnatural” origin—a practice that encompasses perceptions related to the belief that supernatural forces are involved in causing diseases as well as in their treatment.

Unsurprisingly, in different traditional medical systems, primate parts are used to prepare clinical remedies as well as to make amulets or charms used in magical/religious diagnoses. One form of spiritual treatment involves the use of amulets containing primate parts to protect the user against diseases. An example is recorded by Hanson-Alp and colleagues (2003) in Sierra Leone, where sometimes a piece of dried chimpanzee bone is tied around the waist or wrist of infants in the belief that it makes them stronger as they grow into adulthood. Also in Sierra

Leone, chimpanzee central incisors were procured to be worn as amulets around the waist of infants to protect them and give them power over others in their cohort (Chan et al. 2005). In India, the eye of the Hanuman langur (*Semnopithecus entellus*), worn in amulets, is believed to increase courage and strength and charms prepared from dismembered digits from a monkey's paw strung together on a thread are believed to treat paralysis (Ham 1998). The hyoid bone of *Alouatta seniculus* is used by *campesinos* in the upper Magdalena and Cauca valleys of Colombia as a grinding device and some believe that it possesses therapeutic properties for curing goiters (Garbutt 1999). Similarly, in some parts of the Brazilian Amazon, drinking from an *Alouatta* hyoid has been thought to ease labor pains and to treat asthma while in Surinam it has been thought to cure stuttering (Albignac 1987; Alves and Rosa 2007, 2010).

Some treatment methods recorded are eccentric. In India, it is thought by many that eating monkey brains (i.e., *Macaca assamensis* and *M. mulatta*) will treat rheumatism and that drinking monkey blood will cure asthma. For treating rheumatism, a special table with a device is used. The monkey's head (live animal) is introduced through a hole on the top of the table and a chain tied to the bottom part of the table holds its legs. Boiling water is then poured over the head and face of the primate causing extensive scalding and peeling away of the fur and skin. A sharp rap with a small hammer cracks the skull and the "doctor" pours several tubes of ointment into the skull. The patient, who is seated at the same table, inserts a spoon into the cranium of the monkey and eats the brain, alternately mashing and mixing in medicinal drugs. For asthma, the patient drinks the monkey's blood (Ham 1998).

Conservation Implications

Many human cultures across the world interact with nonhuman primates, hunting and eating them, but also adopting nonhuman primates as pets. Furthermore, hunting practices remain the greatest threat to primate survival in the wild in many areas. However, beyond the utilitarian value of these animals, many primate species play an important role in many types of stories, fables, folktales, myths and proverbs, legends, and in magic-religious rituals. As a result, the inclusion of nonhuman primates in various cultural practices influences the interactions with these animals and affects human attitudes toward those nonhuman primate species, with obvious implications for the conservation of these animals.

Primate species that are associated with folk beliefs and religious practices highlight the importance of understanding such uses in the context of primate conservation. The literature reveals that human perceptions of nonhuman primates are often one of the contradictions, typified by extremes. In some cultures and contexts primates are viewed as sacred, in others, they are mythical creatures of cunning and deviousness, while for most of the world's subsistence farmers living in close proximity to monkeys and apes, they represent a significant crop pest. In many cultures, these two views overlap, resulting in both a love and loathing of the creatures, such that they may be worshipped at a temple and killed on the farm next door (Alves et al. 2010; Srivastava and Mohnot 2001).

It is noted that in some circumstances, folk beliefs, religious doctrines, and species-specific taboos can be important in the conservation of declining or threatened species, therefore such practices must be stimulated and valorized (Alves et al. 2010). This becomes increasingly urgent as present indicators show that traditional practices are generally on the decline. This has been occurring in many parts of Africa (Hens 2006) due to changes in the belief systems of people due to the spread of new influences (e.g., Christian sects) (Etiendem et al. 2011). Obviously, there are situations where cultural traditions alone are not sufficient to promote the conservation of species. Etiendem et al. (2011) point out that the conservation of gorillas without the conservation of the forests in which they exist will mean their eventual demise.

It is recognized that habitat losses and hunting have been considered the principal threats to nonhuman primate populations (Ganzhorn and Abraham 1991; Lamabaddusuriya et al. 1992; Mittermeier 1988; Tashiro et al. 2007). In this context, primate conservation cannot be dissociated from natural habitat protection (Mittermeier 1988). Thus, conservation strategies intended to protect primates should consider the direct interactions between people and nonhuman primates, but also be extended to environmental protection where these (and other animals) live. It is important to stress that in some places, cultural aspects that provide protection for primates also extend that protection to their habitats. These situations show that in some places, the importance of primates can be even more relevant, since these animals can be used as a "flagship" or "umbrella" species to help conserve other wildlife (Mittermeier 1988). In Brazil, for example, two of the Atlantic forest primate species stand out among the rest: the muriqui (*Brachyteles arachnoides*), which is the largest and most apelike of the South American monkeys, and the golden lion tamarin (*Leontopithecus rosalia*), which is surely one of the most beautiful of all mammals (Mittermeier 1988). These animals are representatives of the two highly endangered genera that are endemic to the Atlantic forest and they have been subjects of two major public awareness campaigns (Dietz 1985; Mittermeier et al. 1985). They have really become the flagship species for the entire region and the campaigns using them as symbols are excellent examples of the way in which key groups of animals can be used to sell the whole issue of conservation, both in the tropical countries and in the developed world (Mittermeier 1988).

With human populations increasingly encroaching on primate habitats and vice-versa (Schilaci et al. 2010), interactions between them tend to intensify, showing that, more and more, strategies of primate conservation must consider environmental and cultural aspects that rule these interactions. Human attitudes toward primates and their habitats differ by species and by region and are essential to consider the different realities in the design and implementation of primate conservation strategies. Whatever the situation, interactions and traditional uses of primates must be considered together with other anthropogenic pressures affecting the populations of primates in the world, especially the loss of habitat, hunting, and the illegal wildlife trade.

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Problematic Primate Behaviour in Agricultural Landscapes: Chimpanzees as 'Pests' and 'Predators'

Kimberley J. Hockings and Matthew R. McLennan

Human–Primate Interactions in Agricultural Landscapes

Extensive transformation of natural habitats to other land uses such as agriculture is ongoing throughout the World's most biodiverse regions (Koh and Wilcove 2008; Gibbs et al. 2010). In response to these human-driven environmental changes, wild animals must adjust their behaviour, migrate, or else perish (Sih et al. 2011). While human encroachment into natural habitats is associated with declines in many populations of nonhuman primates (hereafter primates) (Cowlishaw and Dunbar 2000), a diversity of primate taxa are now known to utilise modified habitats including agroecosystems in proximity to people (Estrada et al. 2012). Primate responses to increasingly cultivated landscapes occur along a gradient ranging from local extinction, where primates are unable to cope with the changing conditions (especially if hunted or persecuted), to apparent benefit where primates show flexible behaviours that enable them to exploit cultivated environments successfully (Else 1991; Gautier and Biquand 1994). Habitat conversion increases proximity between people and primates, which can lead to direct competition over space and resources (Paterson and Wallis 2005). On the one hand, human activities such as agricultural and settlement expansion erode

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wild food supplies for primates. On the other, they provide opportunities for primates to feed on novel foods such as cultivars, garbage, and in some cases domestic animals. Crop feeding by primates (commonly referred to as 'crop raiding') is a particularly widespread driver of conflict between humans and primates in rural environments (Hill 2005; Lee and Priston 2005; Campbell-Smith et al. 2010; Priston and McLennan 2013). Other less common causes of conflict include predation on domestic animals, human-directed aggression, and damage to property by primates (discussed below). Understanding how primates respond to human-induced habitat changes such as agriculture is not only of theoretical importance for examining primate flexibility (Nowak and Lee 2013), it is fundamental for informing effective conservation management (Hockings and McLennan 2012).

In this chapter, we first summarise some characteristic behaviours and traits of primates that are commonly labelled agricultural 'pests'. We then determine to what extent chimpanzees (*Pan troglodytes*)—an endangered species of great ape—exhibit traits associated with primate pests. We further consider the conservation implications of pest-like and other problematic behaviours in this species, including aggressive and predatory behaviour towards humans and domestic animals. We discuss why chimpanzees might be tolerated by local human communities in some anthropogenic habitats but not in others, and how tolerance of chimpanzees is liable to change with increasing human pressures on land and resources.

Primates as Agricultural 'Pests'

Although many primates fare badly in habitats highly disturbed by humans, there are notable exceptions. In particular, certain members of the genera *Macaca* (macaques), *Papio* (baboons), and *Chlorocebus* (vervet and tantalus monkeys) can prosper in the mosaic of habitats created by human settlement, cultivation, and pastoralism, incorporating human foods as a supplementary or predominant portion of their diet (Maples et al. 1976; Richard et al. 1989; Saj et al. 1999). Aside from rural environments, populations of these genera are sometimes also found in or on the outskirts of towns and other urban or semi-urban areas, such as tourist lodges and religious sites, where they become dependent on direct (handouts) or indirect (garbage, raided food, religious offerings) provisioning (Brennan et al. 1985; Biquand et al. 1994; Southwick et al. 2005; Gumert et al. 2011). Most especially, macaques have a long history of commensalism with humans in some Asian nations, where human cultural attitudes imbue these monkeys with religious or symbolic significance, resulting in complex social-ecological and economic interconnections (e.g. Lane et al. 2010; Radhakrishna et al. 2013; Riley and Fuentes 2011).

Crop feeding is inherently risky for primates because of the potential for hostile encounters with humans seeking to protect their livelihoods (Hill 2005).

However, cultivated foods offer foraging advantages over many natural foods, tending to be energy-rich, highly palatable, easily digestible, and spatially concentrated in fields or plantations (Forthman-Quick and Demment 1988; Lodge et al. 2013; Riley et al. 2013). Certain members of *Macaca*, *Papio,* and *Chlorocebus* cause substantial damage to agricultural crops throughout their distributions and are most frequently labelled as primate 'pests'. Such species are not usually classified as Endangered by the International Union for the Conservation of Nature (IUCN), and some have been classified as vermin in some countries (e.g. *Papio anubis*, *P. cynocephalus,* and *Chlorocebus pygerythrus* in Tanzania) (Mascarenhas 1971). Not surprisingly, macaques, baboons, and vervet monkeys feature prominently in publications dealing with agricultural conflicts between people and primates (e.g. Else 1991; Boulton et al. 1996; Naughton-Treves 1997; Hill 2000; Saj et al. 2001; Chalise and Johnson 2005; Sprague and Iwasaki 2006; Engeman et al. 2010; Warren et al. 2011; Priston and McLennan 2013, Chapman et al. Chap. 5). These 'classic' primate pests share a variety of traits that facilitate their exploitation of cultivated landscapes, including high intelligence and curiosity, large complex social groupings, flexible and omnivorous diets, high manual dexterity, extreme agility, a high degree of terrestriality but with the ability to utilise arboreal habitats, and rather aggressive or audacious temperaments (Else 1991; Hill 2005). Traditional non-lethal measures to protect crops from wildlife including guarding, basic fences or barriers, throwing objects, and chasing can be labour intensive and are often ineffective against these intelligent and agile primates (Strum 1994; Osborn and Hill 2005; Hill and Wallace 2012). Thus, lethal control methods may be favoured by farmers, sometimes leading to local extirpation if primates are heavily persecuted through hunting, trapping, or poisoning (Paterson 2005). Even so, removal of pest primates from one agricultural area can simply create a 'sink' into which new populations flow from surrounding areas (Else 1991; Paterson 2005).

While these most-typical pest primates have traditionally dominated the human–primate conflict literature, recent studies demonstrate that a diversity of primate taxa are found in mosaic landscapes and consume agricultural crops (e.g. bearded capuchin (*Cebus libidinosus*), de Freitas et al. 2008, ring-tailed lemur (*Lemur catta*), LaFleur and Gould 2009, Uganda mangabey (*Lophocebus ugandae*), Fungo et al. 2013, Thomas's langur (*Presbytis thomasi*), Marchal and Hill 2009), including species of high conservation concern (e.g. Mountain gorillas (*Gorilla beringei beringei*), Madden 2006, orangutans (*Pongo* spp.), Meijaard et al. 2011; Campbell-Smith et al. 2011, Zanzibar red colobus (*Procolobus kirkii*), Siex and Struhsaker 1999, highland mangabey (*Rungwecebus kipunji*), Bracebridge et al. 2013, purple-faced langur (*Trachypithecus vetulus*), Moore et al. 2010). However, no evidence suggests these species *prosper* in cultivated habitats around people. Nevertheless, their use of human-altered landscapes and human foods is of considerable theoretical and applied interest since it implies these primates—many of which are not generalist omnivores—are using behavioural strategies to cope with changing environments (see Nowak and Lee 2013 for a review of 'specialist' primate flexibility in response to anthropogenic habitat alteration).

Primate Predation on Livestock

Compared to crop feeding, predation by primates on livestock and domestic animals is rare. Among the commonly cited primate pests only baboons, which include small mammals in their natural diet (Harding 1973), seem to pose a risk to livestock. For example, chacma baboons (*P. ursinus*) on Gokwe Communal Land, Zimbabwe, were regarded as serious predators of young goats and sheep. Over a 3-year period, 52 % of 241 livestock killings were attributed to chacma baboons—more than any other predator including lions and leopards (Butler 2000). Similarly, around Pendjari Reserve, Benin, olive baboons *P. anubis* were reported to cause 25 % of 752 livestock mortalities, mostly of sheep and goats (Sogbohossou et al. 2011). However, Holmern et al. (2007) reported a much lower frequency of livestock depredation (0.4 %) attributed to yellow baboons (*P. cynocephalus*) in villages outside Serengeti National Park in Tanzania ($n = 33$ cases, all goats). Baboons can also kill domestic dogs. Adult male chacma baboons on Gokwe Communal Land killed 11 dogs, though this was apparently in defence and not predation since the dogs were being used to chase baboons from crops or livestock when they were killed (Butler et al. 2004).

Human-Directed Aggression by Primates

While baboon attacks on livestock may be the result of predation, attacks on people by free-ranging ‘pest’ primates occur predominantly in the context of tourism and food provisioning, and mostly in urban or semi-urban locales, where primates have lost their fear of humans (e.g. *Chlorocebus pygerythrus*, Brennan et al. 1985, *Macaca thibetana*, Zhao and Deng 1992, *M. mulatta*, Southwick et al. 2005, see also Ritz et al. 2009). By comparison, in rural environments, where active provisioning is uncommon, attacks by wild primates on local persons are seldom reported in the literature. This contrasts with attacks by other wild animal groups such as carnivores which occur more frequently (e.g. Löe and Röskaft 2004). For example, Treves and Naughton-Treves (1999) report that 5.4 % of wildlife attacks on people between 1923 and 1994 in Uganda ($n = 5636$ casualties and fatalities in official records) were by primates (olive baboons and chimpanzees). This compares to 61.1 % for large carnivores.

Although most primates are fearful of humans and exhibit avoidance behaviours, ‘pest’ primates seem to have a higher propensity to display bold behaviour towards humans, including threats and aggression. For example, in rural locales macaques may show aggressive behaviour towards humans (e.g. *M. fuscata*, Knight 1999) but—unlike at provisioning sites—physical attacks by wild macaques appear to be infrequent. Hamada et al. (2007) reported an attack by a pig-tailed macaque (*M. nemestrina*) on a woman on a village path in northern Lao PDR, but considered such incidents rare. The causes of physical aggression towards people by wild primates are often obscure because details of the circumstances, including human behaviour, at the time of an attack are seldom available. For example, Mitchell et al. (2011) reported that a 6-year-old boy was severely bitten on the face by a vervet monkey (*Chlorocebus* sp.) in a rural village in Tanzania, but no further contextual details were provided. Owing to their size, strength and formidable canines, baboon attacks can be severe. Of recorded baboon attacks in Uganda, a high proportion were fatal (70.9 %, $n=31$). However, this apparent deadliness might reflect biased reporting towards the most serious incidents, which typically involved children guarding crop fields (Treves and Naughton-Treves 1999). In these cases, it is unclear whether primate attacks on humans were motivated by predatory instincts or not.

Property Damage

A further potential cause of conflict is damage to property by primates. In some towns and cities in Asia, macaques (e.g. *M. mulatta* and *M. fascicularis*) invade homes and offices to steal food, clothes, and other loose items. They cause damage to roofs, television antennas, and other electrical wires and may 'vandalise' gardens (Gumert et al. 2011; Priston and McLennan 2013). However, property damage by non-provisioned monkeys beyond that caused to gardens during crop 'raids' appears to occur only very rarely in rural environments (but see Enari and Suzuki 2010 for damage to household property by Japanese macaques (*M. fuscata*) in rural Japan).

Are Chimpanzees Another 'Pest' Primate?

Like many primates, great ape populations are declining due to ongoing habitat loss and hunting, as well as epidemic disease (Caldecott and Miles 2005; IUCN 2014). An estimated 300,000–400,000 great apes remain in the wild, and all species and subspecies are listed as Endangered or Critically Endangered (IUCN 2014). Great apes require large spaces yet are increasingly forced into highly restricted ranges, often outside of protected areas, and exposed to agriculture (e.g. the West African chimpanzee (*P. t. verus*), Kormos et al. 2003, the Bornean orangutan (*Pongo pygmaeus*), Wich et al. 2012). In fact, most long-term great ape research sites are impacted by humans and their activities in one way or another, including commercial and/or subsistence agriculture, hunting, extractive industries, roads, and settlements (Hockings et al. 2015). However, unless heavily hunted, great apes can exploit modified habitats including degraded forests, secondary vegetation, plantations, and forest–farm ecotones near human settlements (chimpanzees (*Pan troglodytes*): Hockings et al. 2009; McLennan 2013, gorillas (*Gorilla* spp.): Goldsmith et al. 2006; Madden 2006: orangutans (*Pongo* spp.): Meijaard et al. 2010; Campbell-Smith et al. 2011, bonobos (*Pan paniscus*): Idani et al. 2008).

Chimpanzees have the broadest current geographical distribution of the great apes. They are found in a variety of habitat types across equatorial Africa from dense lowland rainforest to dry savanna woodland and montane forest (Caldecott and Miles 2005). Today, chimpanzees are sympatric with humans across large parts of their distribution. In some regions, chimpanzees and people have a long history of coexistence, for example, at Lopé, Gabon; humans have shared an environment with both chimpanzees and gorillas for at least 60,000 years (Tutin and Oslisly 1995). Where human population density is low and encroachment on natural habitat is not extensive, human–chimpanzee interactions are mostly neutral, with both species exhibiting mutual avoidance (Leciak et al. 2005; Duvall 2008; Hockings and Sousa 2013). However, where human population densities are higher, and where chimpanzees are not traditionally hunted for food, chimpanzees can persist in highly fragmented and degraded habitat in remarkably close proximity to people (e.g. Uganda: Reynolds et al. 2003; McLennan 2008, Guinea: Hockings 2009). For example, wild chimpanzees at Bulindi, Uganda, and Bossou, Guinea, inhabit forest–agricultural mosaics and both communities exploit a variety of human foods (McLennan and Hockings 2014). Chimpanzees at Bulindi have experienced recent rapid habitat alteration, with extensive logging and clearance of forest for agriculture since c.2000 to the present. Persistent crop-raiding and use of farmland by chimpanzees is considered ‘recent’ by villagers (McLennan and Hill 2012). Chimpanzees at Bossou have a longer history of coexistence with farmers for whom the apes are a totem and have exploited agricultural crops for generations. While considerable deforestation has occurred at Bossou, remaining forest is sacred in local mythology and has not recently experienced very high rates of clearance and logging as witnessed at Bulindi (Matsuzawa et al. 2011). Persistence of chimpanzees in heavily modified human-dominated environments is largely a contemporary phenomenon, resulting from swelling human populations, and rapid land use changes (e.g. McLennan 2008). In such circumstances, people and chimpanzees may utilise the same space and resources and encounter one another frequently, leading to competition and conflict (Hockings and Humle 2009).

Chimpanzees as Crop ‘Pests’

Primate diets occur along a continuum from highly specialised to broadly generalist, and many primate species—including the chimpanzee—fall somewhere between these categories. Unlike most wild mammals commonly associated with cultivated landscapes, chimpanzees are not dietary generalists. Although chimpanzee natural diets are broadly omnivorous, comprising diverse plant and animal foods, their diets in all habitat types are dominated by ripe fruits (e.g. Goodall 1986; McGrew et al. 1988; Tutin and Fernandez 1993; Newton-Fisher 1999; Basabose 2002; Pruetz 2006). During periods of fruit scarcity, they consume other, less nutritionally dense plant foods such as leaves, fibrous pith, and bark in greater amounts while continuing to pursue a predominantly fruit-based diet (e.g. Wrangham et al. 1998; Tutin and Fernandez 1993; Yamagiwa and Basabose 2009; McLennan 2013). Furthermore, chimpanzees exhibit socioecological adaptations to enable them to pursue a fruit-dominated diet year-round, including fission–fusion dynamics, which is not observed in true generalists. Thus, chimpanzees are usually considered ripe fruit specialists (Wrangham et al. 1998; Watts et al. 2012). Some authors have proposed that chimpanzees show dietary conservatism (Kortlandt 1967; Takasaki 1983), which contrasts with the opportunism characteristic of 'classic' pest primates. However, among primates not traditionally labelled 'pests', chimpanzees emerge as a particularly frequent and widespread consumer of agricultural crops (see Hockings and McLennan 2012 for a review; Hockings and Humle 2009).

Recent research at sites in East and West Africa has revealed how chimpanzees in forest–agricultural mosaics integrate human foods into their seasonal foraging strategies. Contrary to more generalist primate crop-feeders, chimpanzees show a strong species-typical preference for agricultural fruits over other crop types such as vegetables and tubers (Hockings and McLennan 2012; McLennan and Hockings 2014) (Fig. 1). Despite differences in the degree of human impact at Bossou and Bulindi (as outlined above), crop feeding by chimpanzees was recorded at a similar overall frequency at both these sites (McLennan and Hockings 2014). Chimpanzees consumed agricultural fruits most often during periods of wild fruit scarcity, showing increased willingness to take risks when the need is greatest (Hockings et al. 2009; McLennan 2013). At Bulindi, it was suggested that feeding on agricultural fruits when forest fruit was scarce helped chimpanzees maintain a high-quality diet and a high degree of frugivory year-round (McLennan 2013). Even so, certain temporal crops (e.g. mango fruit at Bossou and Bulindi, maize cob and rice pith at Bossou) were targeted when available seasonally, irrespective of wild fruit availability (Hockings et al. 2009; McLennan 2013).

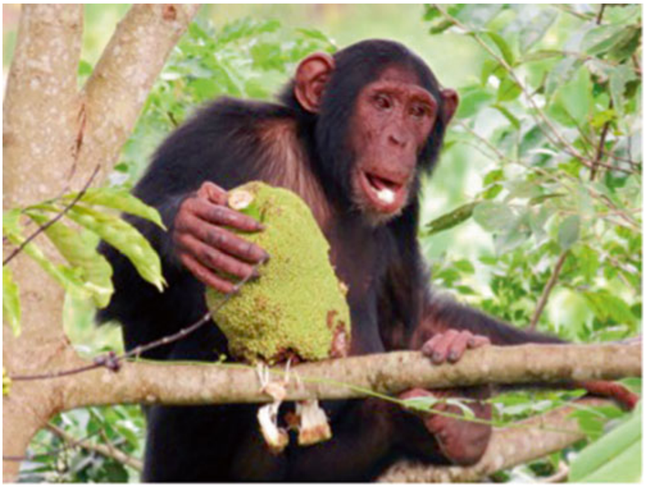

Fig. 1 Subadult female chimpanzee at Bulindi, Uganda, feeding on cultivated jackfruit 'raided' from a homestead alongside the forest (Photo: Matthew McLennan)

Although chimpanzees target sugary fruit crops predictably, evidence from Bossou and Bulindi indicates their selection of agricultural crops becomes more omnivorous over time (i.e. with increased exposure) to include more non-fruit items such as underground storage organs and staple food crops. In other words, chimpanzees show foraging adaptations to cultivated landscapes by exploiting a greater diversity of crops over time (McLennan and Hockings 2014). Where exposure to agricultural foods is high, crops can form an important part of the chimpanzee diet. For example, on average 8.8 % of chimpanzee feeding time at Bossou was devoted to crops, and there was an inverse relationship between time spent feeding on wild foods and time spent on crops (Hockings et al. 2009). Nevertheless, chimpanzees are not known to depend on human foods to the extent of some populations of more-typical 'pest' primates (e.g. Maples et al. 1976; Richard et al. 1989; Saj et al. 1999). Although detailed studies of chimpanzee foraging strategies from additional forest–farm ecotones are needed, available data from other sites lend support to the idea that exploitation of human foods by these great apes is selective and/or strategic (Dunnett et al. 1970; Sabater-Pí 1979; Naughton-Treves et al. 1998; Reynolds et al. 2003; Krief et al. 2014; Bessa et al. 2015).

The more selective use of human foods by chimpanzees compared to other crop-feeding wildlife influences how local farmers view them. Specifically, the chimpanzees' broad preference for domestic fruits such as mango, papaya, and banana, as opposed to staple human food crops like potato, cassava, and beans, may promote greater tolerance of these apes. This contrasts with other crop feeding primates that cause considerable damage to food crops and are commonly perceived as vermin by farmers (e.g. olive baboons and tantalus monkeys *Chlorocebus tantalus* in Uganda: Hill and Webber 2010; McLennan and Hill 2012). However, where chimpanzees learn to exploit non-fruit crops such as human staple foods (McLennan and Hockings 2014), or where they consume cash crops (e.g. sugarcane and cocoa in Uganda: Reynolds et al. 2003; McLennan 2008), local attitudes towards chimpanzees are liable to harden and farmers may regard them as troublesome crop pests (McLennan and Hill 2012). Nevertheless, in some circumstances humans and chimpanzees can exploit the same cultivated resource with minimal competition and conflict. For example, chimpanzees in Cantanhez National Park, Guinea-Bissau feed on cashew, a major cash crop. But whereas humans mostly use the marketable nut, chimpanzees consume only the surrounding pseudo-fruit, and most farmers described the chimpanzees' habit of placing cashew nuts in manageable piles as a benefit because it makes it easier for people to harvest them (Hockings and Sousa 2013).

Chimpanzee Predation of Livestock

Wild chimpanzees are frequent predators of sympatric wildlife, particularly small to medium-bodied mammals like monkeys, bush pigs, and small antelopes (e.g. Goodall 1986; Boesch and Boesch 1989; Watts and Mitani 2002). Chimpanzee populations living near human settlements may also come into contact with common domesticated species such as cows, goats, sheep, chickens, pigs, and dogs. Their reactions towards such animals vary from indifference to aggression, play, or predation (Hockings et al. 2012). In Uganda, chimpanzees reportedly depredate domesticated species, in particular chickens (Reynolds 2005; McLennan 2008). As domestic animals are mostly found in predictable locations and tend to show reduced fear and avoidance of other animals, they are likely easier to capture than many wild species. Even so, available data indicate that chimpanzee predation on domestic animals and livestock is overall rare. At Bulindi, evidence of predation on chickens was found only twice during a 13-month study of the chimpanzees' diet (McLennan 2010a): once, a chicken kill was encountered near chimpanzee nests shortly after the apes had vacated the site, villagers at a nearby home complained that a chimpanzee had taken one of their chickens the previous evening. In the second case, three chimpanzee faecal specimens contained skin and tissue that appeared to be chicken. Again, a local man claimed that a chimpanzee took a chicken from a nearby home the day before. In 2011, an adult male at Bossou was observed capturing a chicken, but the bird was not eaten which is consistent with this population's non-consumptive behaviour towards wild birds (Hockings et al. 2012). At Bulindi, a chimpanzee killed a piglet following an altercation with the sow, apparently by beating or slapping it, but did not eat from it (McLennan, unpublished data).

Domestic dogs pose a threat to chimpanzees in agricultural areas because local people sometimes use them to hunt chimpanzees or chase them from crops (McLennan 2008, 2010a). Like baboons, chimpanzees may respond to a threatening dog with aggression, sometimes injuring or killing it (McLennan and Hill 2010). At Bossou, between 1997 and 2009, direct physical contact was never observed between chimpanzees and any domesticated species, but chimpanzees sometimes engaged in noncontact interactions with dogs and goats. On two occasions, immature chimpanzees exhibited playful behaviour (e.g. play face) towards a dog and goats, although no contact was made. In contrast, when adults encountered dogs on three occasions, they mostly exhibited fear responses (e.g. fear grin), but an adult male once chased and displayed towards a dog (Hockings et al. 2012).

Chimpanzee Aggression Towards Humans

Wild chimpanzees generally react fearfully to humans, perceiving them as a threat (Tutin and Fernandez 1991; Hicks et al. 2013). However, where direct hunting pressure is low, and where chimpanzees encounter humans frequently, they may exhibit bold, confrontational, or aggressive behaviour towards humans (McLennan and Hill 2010; McLennan 2010b), in rare instances leading to physical attacks (Wrangham 2001; Reynolds 2005; McLennan 2008; Hockings et al. 2010). At Bossou and Bulindi, where chimpanzee–human interactions have been studied in most detail, physical attacks occurred at a rate of less than once per year, even though chimpanzees at both sites encounter local people daily (Hockings et al. 2010; McLennan and Hill 2010). Local accounts of circumstances surrounding aggressive incidents are often vague. However, chimpanzee attacks at these sites seem to occur most commonly in response to harassment by people, such as when children throw stones, or over competition for 'right of way' when chimpanzees encounter humans on a footpath or road (Fig. 2, see McLennan and Hockings 2016 for detailed characterisation of attacks). In some instances, directing aggression towards local people might be a means for adult males to display boldness and assert their dominance in front of group members (Hockings et al. 2010).

The primary perpetrators of attacks on humans by wild chimpanzees seem to be adult males, and their targets are overwhelmingly children (Wrangham 2001; Reynolds 2005; Hockings et al. 2010). Although fatalities are uncommon, chimpanzees can inflict severe injuries on humans (see Khalil et al. 2011 for an assessment of injuries sustained by an adult woman following an attack by a captive male chimpanzee). Most seriously, chimpanzees in agricultural areas have been found to prey on human children as food. Unambiguous cases of chimpanzees targeting young children as prey come from two East African sites (Kibale National Park, Uganda: Wrangham 2001, Gombe, Tanzania: Goodall 1986; Kamenya 2002). At Kibale, eight attacks against children on agricultural land bordering the park were thought to have been carried out by a single 'rogue' adult male (Wrangham 2001), whereas two predatory attacks at Gombe were isolated incidents. However, increased interactions between humans and wild chimpanzees may not necessarily lead to predatory attacks against children. No evidence indicates that attacks at Bossou and

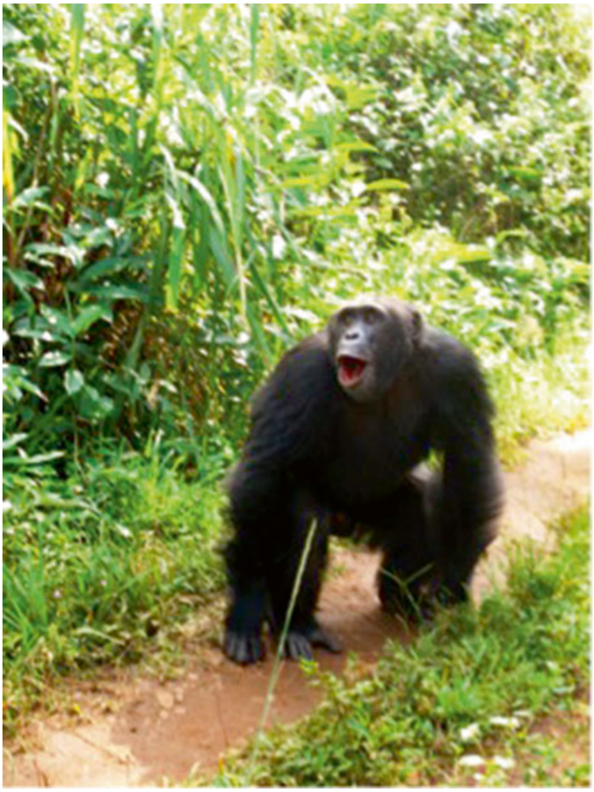

Fig. 2 Adult male chimpanzee at Bossou, Guinea, displaying towards local people on a path utilised by humans and chimpanzees that borders agricultural fields and forest (Photo: Kimberley Hockings)

Bulindi to date were motivated by predation (McLennan and Hockings 2016). While hunting and meat eating is prevalent in many chimpanzee populations, hunting frequencies vary among sites as does the prey species available (Newton-Fisher 2007). Chimpanzee populations also show some variation in the species they target (i.e. they have a 'specialised prey image', Boesch and Boesch 1989; Hockings et al. 2012). Neither chimpanzee community at Bulindi nor Bossou regularly eat meat. At Bossou diurnal primates are absent due to past human hunting activities (Hockings et al. 2012), whereas at Bulindi suitable prey are present (e.g. black and white colobus monkeys, *Colobus guereza*) but no evidence to date suggests the chimpanzees eat them (McLennan 2010a and unpublished data). Therefore, the risk of predatory attacks against children might be greatest at human-impacted sites where chimpanzees regularly hunt and consume sympatric monkeys.

Notably, the perpetrators of some recorded chimpanzee attacks were well habituated for research or tourism (e.g. Bossou chimpanzees). This might imply that a loss of fear of humans increases the risk of physical aggression by chimpanzees. It is important to note, however, that most records of chimpanzee attacks on local persons involve semi-habituated (Bulindi chimpanzees) or entirely unhabituated individuals (e.g. predatory chimpanzee(s) at Kibale) (McLennan and Hockings 2016).

Chimpanzee Damage to Property

Aside from brief forays to obtain agricultural foods, chimpanzees tend to avoid human settlements. Only one published study reports damage to human property by wild chimpanzees (McLennan 2010b). In this unusual case, adult male chimpanzees at Bulindi made repeated visits to a homestead bordering the forest, initially attracted by fruiting mango trees. However, the house had a glass-panelled door in which the chimpanzees could see their reflections. Excited by this 'mirror', the males would display in front of the door. On one occasion, a male broke a glass pane by flailing a branch against it, after which the house owner covered the glass with cloth (McLennan 2010b). Chimpanzees may also cause minor damage to traditional fences on agricultural land, for example, by separating fence poles or wires during travel or to access crops. Non-consumptive crop damage can be an additional source of provocation, for example, when chimpanzees knock or pull down standing crops during displays (e.g. banana plants or maize stems). At Bulindi, chimpanzees damaged tobacco—an important cash crop for local households—by treading on seedlings (McLennan and Hill 2012).

Conclusions: Pests, Perceptions, and Human Tolerance

Chimpanzees undoubtedly share some of the characteristics associated with more-typical 'pest' primates including high intelligence, high mobility and terrestriality, bold temperaments, ecological flexibility, and a tendency to consume agricultural crops. Like baboons, wild chimpanzees ranging within cultivated landscapes can be aggressive towards people and occasionally prey on domestic species (and, rarely, human children). But there are also important differences. Chimpanzees use human crops to supplement a wild diet, and they show more selectivity in crop feeding than most 'pest' primates, which tend to be generalist feeders. While crops can be important items in the diet of some populations, it is not yet established if any community of 'village chimpanzees' depend on human foods for their survival. Moreover, chimpanzees feed on crops when agriculture impinges on their natural habitats, and there is no evidence that chimpanzees migrate into agricultural areas from adjacent uncultivated habitat. Furthermore, chimpanzees appear unable to exploit more extreme anthropogenic habitats, such as urban or semi-urban areas or near tourist resorts, as some populations of 'pest' primate do. And chimpanzees never form commensal relationships with humans, as some macaque populations in Asia do (Radhakrishna et al. 2013). Perhaps most critically, no evidence indicates that chimpanzees 'prosper' (i.e. reach their highest numbers) in cultivated landscapes or in association with people. On the contrary, available data suggest very close human–chimpanzee coexistence is most likely a temporary phase prior to eventual local extinction of the apes (see below). Therefore, in most respects chimpanzees are not 'another pest primate'.

Whether a primate species is considered a pest or not depends mostly on how it is viewed in the local human culture. While the degree to which a species exhibits problematic behaviours such as crop damage and aggression towards people is important, perceptions of primates are also driven by social, cultural, and economic factors (Hill and Webber 2010). For example, traditional folklore around Lore Lindu National Park, Sulawesi, envisions tonkean macaques (*Macaca tonkeana*) as biologically and culturally related to humans, and harming macaques is traditionally taboo despite the damage they cause to cacao—an important cash crop regionally (Riley 2010; Riley et al. 2013). Chimpanzees are afforded special significance in some African cultures in recognition of their shared physical and behavioural affinity with people, which promote tolerant attitudes towards them. For example, in parts of West Africa local taboos and/or totemic beliefs that consider apes ancestors serve to protect them from hunting (Yamakoshi 2005; Hockings 2009). The chimpanzee's protected legal status, along with its perceived potential to generate income through tourism (McLennan and Hill 2012; Sousa et al. 2014), may also promote greater tolerance of these great apes compared to other primates more often labelled 'pests'.

Despite the tolerance sometimes afforded chimpanzees by human cultural beliefs, and their capacity to persist in modified cultivated habitats, we suggest a 'tolerance threshold' exists beyond which local people are no longer willing or able to coexist closely with these great apes. As discussed above, when chimpanzees damage staple food crops, and particularly cash crops—which today are more widely farmed in chimpanzee habitats than previously—traditionally benign local attitudes may give way to intolerance. An additional constraint to coexistence is that local communities sharing landscapes closely with these great apes often fear them (McLennan and Hill 2012). Chimpanzees are large-bodied and, as discussed above, are potentially dangerous, which probably limits people's tolerance towards having daily encounters with them. Where human–chimpanzee encounters become frequent as a result of human population increase and/or habitat encroachment, aggressive or threatening behaviour by apes, including attacks on children, can supersede concerns about crop damage (Hockings et al. 2014). People might move beyond viewing the animals as mere crop pests, towards an understanding of them as real problems. When this happens, some local people may feel prompted to act to resolve the problem, regardless of local taboos or fear of prosecution.

Evidence suggests that chimpanzee populations decline at sites with high human population densities and high levels of habitat disturbance. Since systematic research began at Bossou in 1976, the number of chimpanzees remained stable at around 20 individuals, but in the last decade community size has decreased during periods of deforestation (Sugiyama 2004), following a flu-like epidemic (Matsuzawa et al. 2011), and after three adults disappeared for unknown reasons. There has been no female immigration since research, most likely owing to challenges to migrating females in semi-isolated landscapes dominated by human activities and settlements. Only nine individuals currently remain. At Bulindi, community size has declined from an estimated 30 or more individuals in 2007 (McLennan and Hill 2010) to 19 chimpanzees in 2015 (McLennan, unpublished data). Although the cause of this decline is unconfirmed, several chimpanzees have had to be rescued from large steel traps set to protect crops at this site (McLennan et al. 2012). Further, bananas with a colourless substance detectable in small piercings made in the fruits have twice been found placed on chimpanzee trails at Bulindi (McLennan 2010a). According to local field assistants, the substance was probably carbofuran, an insect pesticide that has been used to poison 'problem' wildlife in various parts of the world, including in Uganda (Ogada 2014). However, there was no indication that chimpanzees ate the fruits on either of these occasions.

When chimpanzees come to be viewed as too problematic by local people, we expect that individuals are 'picked off' through retaliatory killings or trappings (whether intentional or not), leading to population declines (Reynolds 2005; McLennan et al. 2012; Halloran et al. 2014). Chimpanzees have slow reproductive rates and slow life histories, and consequently populations living alongside people may be unable to recover from killings, even if these occur at a low frequency. Finally, close human–chimpanzee interaction increases risk of pathogen exchange between them (Goldberg et al. 2007; Krief et al. 2010). Thus, diseases of human origin are likely a further source of chimpanzee population declines in cultivated landscapes.

In conclusion, although chimpanzees exhibit behavioural flexibility, which enables them to exploit the forest–farm interface (i.e. persistent raiding of nutritious but sometimes valued and guarded crops, and occasional aggressive behaviour towards people), these behavioural responses might be viewed as 'maladaptive' since they promote human intolerance that might lead to their extirpation (McLennan and Hockings 2014; Hockings et al. 2015). Chimpanzees are less likely to 'bounce back' from reprisal killings and eradication attempts compared to primates more typically labelled 'pests' (although such species also suffer extirpation if heavily persecuted). Very close coexistence between high-density human populations and chimpanzees may be considered inherently unstable, and in most cases probably represents a temporary phase prior to local ape population decline and extinction. However, at sites where chimpanzee communities are not yet isolated (i.e. where migration still occurs) and human population density is relatively low, long-term coexistence is more likely. Chimpanzee conservation in landscapes dominated by people raises ethical issues because of the potential threat the apes pose to human livelihoods and safety, and ultimately benefits of coexistence to humans must outweigh the costs (McLennan and Hill 2013).

Effective 'human–primate conflict' resolution requires multifaceted technical, social, and economic approaches that need to be combined flexibly at different spatial and temporal scales. These can involve both short-term (e.g. guarding, fencing, and visual/acoustic repellents) and long-term (e.g. land-use planning, research, and community conservation initiatives) approaches. However, we must acknowledge that conflict is not simply a result of economic loss or threats to human physical safety, it also stems from deep-rooted cultural values and clashes among human groups (including local persons, wildlife managers, conservation practitioners, academics, and policy makers) with different interests and values (Hill 2015). Culturally sensitive conservation actions to promote coexistence should aim to promote tolerance and reduce fear of chimpanzees, through promoting or developing existing positive attitudes towards them, while working with people to develop practical measures to reduce pest-like and other problematic behaviours (Hockings and Humle 2009; Hill and Wallace 2012). The ability for humans and primates to coexist therefore depends partly on the willingness of stakeholders to identify problems as being shared and to discuss them openly and collaboratively.

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Competition Between Chimpanzees and Humans: The Effects of Harvesting Non-timber Forest Products

Michel T. Waller and Jill Pruetz

Introduction

The combination of an increasing human population and worsening financial situation is causing more people living in tropical areas to meet their day-to-day needs through the extraction of "free" wild resources (Hutton and Leader-Williams 2003) for family consumption and commercial trade (Kim et al. 2008). While hunting and the bushmeat trade is clearly an important part of this (see Chaps. 3 and 6), less well understood is the collection, consumption, and trade of non-timber forest products (NTFPs). NTFPs for this study are defined as plants and plant parts (flowers, seeds, fruits, roots, leaves, bark) that act as food, medicine, or have some other utilitarian purpose (i.e., rope, cosmetics, clothing, construction materials) and have economic value or are important in terms of sustenance, protection from the elements, cultural practices, or other day-to-day functions. Thought by some to be a conservation strategy that could incentivize local people to protect their forests in order to preserve the economic and cultural benefits of NTFPs (i.e., Myers 1988; Nepstad and Schwartzman 1992; Viana et al. 1996; Freed 2001; Pacheco et al. 2012) while discouraging larger, more destructive forest practices such as logging and agricultural conversion, the use and overuse of these resources has drawn increasing scrutiny (Ambrose-Oji 2003; Ticktin 2004; Quang and Anh 2006; Ndangalasi et al. 2007; Belcher and Schreckenberg 2007).

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The purpose of this chapter is to highlight the socioeconomic and ecologic complexities interlaced within the harvest of NTFPs by humans.

The Benefits of Collecting NTFPs

Over 800 million people live in the forests and woodlands of the tropics and many of them live on less than $2 a day (Buys 2007). As such, the NTFPs found within these ecosystems play an important role in the economic and cultural lives of millions of people. From an economic standpoint, estimates suggest that the collection of NTFPs may value over $11 billion (Shanley et al. 2002), providing Earth's poorest people with much needed income. The emergence of "green markets" and an increase in the commercialization of "natural" products may further fuel the benefits of collecting NTFPs for some in the tropics (Belcher and Schreckenberg 2007). Of primary interest to conservationists, the use of NTFPs in some areas may act as an "economic buffer" that can stem the more destructive forces facing forests (i.e., mechanized logging, large-scale agriculture) by providing rural people with an economic incentive to protect local resources. For example, in central Borneo, the collection of *Gaharu*, a fungal infected wood used for incense, clothing, drawers, traditional medicines, and perfumes and soap, is very profitable leading to wages for collectors that can amount to triple the average villager's wage (Paoli et al. 2001) while creating local interest in protecting the forest from corporate timber extraction or agricultural conversion (Wollenberg 2001).

There are other examples that show similar benefits. In South Africa, Shackleton and Shakleton (2004) examined the role of NTFPs in the daily lives of rural people. They found that products such as wild spinach, firewood, wooden utensils, and other forest products were found in 85 % of households. Indeed, they discovered that rural communities regularly use between 200 and 300 different plant species. Furthermore, the NTFPs there served as an important economic safety net when other resources or job opportunities were unavailable. Similarly, a study of 2000 households in the Eastern Arc Mountains of Tanzania found that the trade of charcoal, firewood, poles, thatch, and other NTFPs was estimated at $42 million per year and highlights a trade-off between conservation policies aimed at land use restrictions and the consequent increase in poverty (Schaafsma et al. 2011).

NTFPs are also an important economic resource for women in Africa. With increased attention focused on poor women's socioeconomic empowerment as a way to combat global poverty, the harvest of NTFPs by women in the rural tropics has been and will continue to be an important means of subsistence (Shackleton et al. 2011). In a study that looked at the role of women in the economics of NTFPs, Shackleton and colleagues (2011) found that when it came to internationally important NTFPs such as gum olibanum (frankincense), gum arabic, and honey, women perform a variety of functions along the value chain yet are constrained economically due to social-cultural barriers. They suggest that greater recognition of informal markets, greater roles for women in export markets, and improved support for collective action would give women a greater voice, more negotiating power, and help with economies of scale (training, technology, and child care) creating more gender awareness overall. These and other studies like them show that the use of NTFPs may be more benign than deforestation or agricultural conversion while providing sustenance and other important economic and cultural capital for many of the poorest people on the planet, potentially empowering marginalized individuals and groups by creating a modicum of economic strength.

The Costs of Collecting NTFPs

There are a number of potential drawbacks to the collection of NTFPs. Belcher and Schrenkenberg (2007) illuminate the various economic elements (i.e., value chains, poorly developed markets, small volumes, use of technology, resistance to certification) that can combine to make the collection, trade, and consumption of NTFPs inefficient or may favor actors in developed countries who are better suited to maximize profits (as opposed to the poor who do most of the labor.) This inequality may lead to overexploitation, which in turn drives a number of ecological ramifications.

The clearest ecological effect of the harvest of NTFPs is a change in the rate of survival, growth, and reproduction of the plant being collected (Ticktin 2004). In some cases, this effect is minimal (i.e., some barks, flowers, fruits). In other cases, the harvest of some parts results in the death of the entire organism (i.e., roots, leaves). In the Sudano-Guinean region of Benin, Gaoue and Ticktin (2007) studied the use of foliage and bark of the *Khaya senegalensis* tree. They found that high harvest areas had significantly lower seedlings and saplings when compared with low harvest locations. Similarly, Singh (1999) studied the collection of NTFPs in India and found that rising market demand, increasing population density, and changes to sociocultural and socioeconomic values led to an increase in the collection of medicinal plants resulting in the local extinction of some of the more common ones.

At the community level, the harvest of fruits and seeds can affect the diversity and density of frugivorous and granivorous mammal and avian species (Ticktin 2004). This type of competition arises whenever two or more parties endeavor for the same goal (i.e., acquisition of a resource), which cannot be shared (Townsend et al. 1996) and is most often over foods, but can also occur over plants considered by humans as medicines or as utility resources. It is a reminder that humans are a part of the ecosystem and overtly compete with other community members for resources. For example, Galetti and Aleixo (1998) found that the harvest of *Euterpe edulis* palm hearts by humans resulted in a decrease in the abundance of two bird species known to eat the hearts.

It is well documented that, for most animals, an increase in human presence has negative consequences (Happold 1995). With more people venturing into the forests in search of NTFPs, there will be more human/nonhuman animal interactions including bushmeat hunting. Etiendem and colleagues (2013) studied the extraction of NTFPs in the Mawambi Hills of Cameroon and found that areas of heavy human activity coincided with the nest sites of the critically endangered cross river gorillas (*Gorilla gorilla diehli*) and the endangered Nigeria-Cameroon chimpanzees (*Pan troglodytes ellioti*), suggesting that these great apes face an uncertain future due to the exploitation of NTFPs and corresponding increase in bushmeat hunting.

Chimpanzees living in Senegal face many of these same issues. The few remaining populations there must compete with people for access to valuable resources including water, honey, and wild fruit species (Carter et al. 2003). The inability of chimpanzees to access these important resources could have several consequences. For example, chimpanzee groups moving out from their traditional range in an effort to find sufficient foods may come into territorial conflict with neighboring communities. Additionally, the lack of adequate resources may increase the amount of crop raiding, reducing the tolerance of humans for the presence of chimpanzees within their region (Carter et al. 2003). As such, the chimpanzees of Fongoli and the people living near to them make an excellent case study to highlight the complex issues surrounding the use of NTFPs, specifically the fruit of *Saba senegalensis*.

The Fruit of Saba senegalensis

Saba senegalensis is characterized as an upland evergreen species that continuously replaces its leaves (de Bie et al. 1998). The fruit of the *Saba* vine varies in size, but averages 7.6 cm in length and 6.3 cm in width and has an average weight of 197 g. Initially green, the fruit changes to an orange color as it ripens. The exterior of the fruit is hard and can be difficult to open. Each fruit contains an average of 21 large seeds with relatively little fleshy pulp (Knutsen 2003). The vines grow over 20 m in length and the fruit can be found from ground levels to the highest point of the vine. It is at its ripest in July. Humans use *Saba* fruit in a variety of ways. As the fruit ripens at the beginning of the wet season, people living in the area gather it for sale or personal consumption. It is commonly harvested and eaten straight from the vine or later mixed with sugar and water to make juice. For many people, it is an ingredient in daily meals and, along with other wild resources, constitutes an important nutritional addition to the diet (Knutsen 2003). Political instability in the Casamance region of southern Senegal, where it was traditionally harvested, created a niche for extraction of the fruit in the Fongoli region. The value of a 50-kg sack of *Saba* (approximately 500 fruits) varies depending on supply and demand and can range from CFA 2500 (US$5.00) to CFA 15,000 (US$30.00). Because it is shipped to far-off markets such as Dakar and Bamako, Mali, it is often picked before it is ripe. For women living there, the collection of *Saba* can account for up to 50 % of their annual income (Knutsen 2003).

The Chimpanzees of Fongoli

Since 2001, study of the Fongoli community of chimpanzees has been continuous. Field observations have led to the identification of a minimum of 27 chimpanzees (Pruetz 2006) in this community. Nest surveys conducted throughout southeastern Senegal, however, have concluded that chimpanzees in the region occur at a density of 0.09 individuals per km^2 (Pruetz et al. 2002), suggesting that the Fongoli site may be an area of relatively high chimpanzee density compared to other areas in Senegal.

Unlike most chimpanzee study sites, the ratio of males to females is high. Reasons for this are unknown but may be related to the killing of mothers and the extraction of infants for sale as pets or a bias in habituation regarding males. These chimpanzees are unique in that they use caves during the hottest times of the year (Pruetz 2003) and hunt bushbabies (*Galago senegalensis*) using tools (Pruetz and Bertolani 2007). Other primates living within the area include Guinea baboons (*Papio hamadryas papio*), vervet monkeys (*Chlorocebus aethiops*), patas monkeys (*Erythrocebus patas*), and the aforementioned northern lesser bushbaby.

The *Saba* fruit is vital for chimpanzees. During the months of May, June, and July, *Saba* seeds were found in 87 %, 89 %, and 95 % of all chimpanzee fecal samples collected, respectively, between 2001 and 2004 at the Fongoli study site. No other food source was found in more than 50 % of fecal samples in a single month over that same time period, highlighting the importance of the fruit to chimpanzees (Pruetz 2006). The seeds are swallowed whole and defecated intact. It is not uncommon to find chimpanzee feces with small *Saba* seedlings sprouting. Consequently, as large frugivores, chimpanzees are primarily responsible for the dispersal of *Saba* seeds (Pruetz 2006).

The People of Fongoli

Several small villages are found within and around the chimpanzees' core range area (50 km^2). The people living in these villages are Malinké, Bassari, or Peul and engage in subsistence farming, pastoralism, hunting, and gathering to provide food or money. Due to political, economic, and demographic factors, the number of people collecting *Saba* is increasing at a rate that may not be sustainable (Knutsen 2003; Pruetz and Knutsen 2003). For humans living in the area, the fruit represents a needed source of income at a time when crop stores are depleted and new crops have yet to produce. Traditionally collected by women, the income derived from the *Saba* harvest is used to buy clothing, food, and medicines (Knutsen 2003).

The villages of Ngari, Djendji, and Fongoli (Fig. 1) are the focus of this study. Ngari consists of approximately 130 people and is situated on the main road connecting Kedougou and Tambacounda, the two largest towns in southeastern Senegal. Because of its location and the ease with which large trucks can access the village, it is a main deposition spot for *Saba* fruit harvested throughout the area.

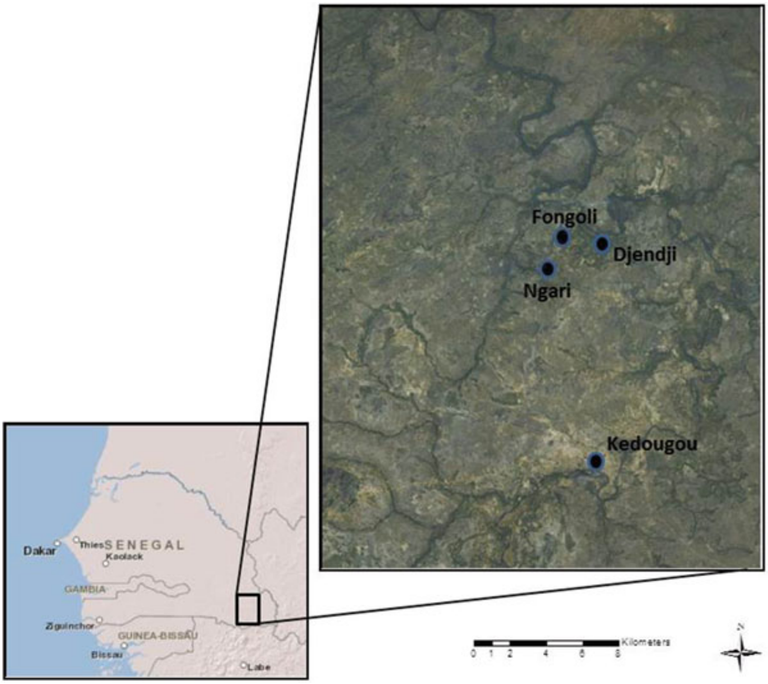


Fig. 1 This map shows the location of the three focal villages for this study (Ngari, Fongoli, and Djendji) as well as Kedougou, the economic hub of this part of southeastern Senegal

Djendji is a village of approximately 140 people. The area has many hills and valleys and is relatively more remote than the other two villages, with roads navigable only during the dry season. Trucks entering the village to collect *Saba* are rare. Djendji is approximately 1.5 km from a permanent water source used by chimpanzees and other animals.

The village of Fongoli is a cluster of homes with a population that fluctuates depending upon the time of year. During the dry season, the population decreases, while in the wet season, when crops are being planted, more people enter the area. Approximately 30 people live there permanently. The village is accessible by road year-round, but due to the small human population, trucks transporting *Saba* fruit are not as common as they are at Ngari. Fongoli is the main departure area for researchers studying chimpanzees in their core area.

Methods

The goal of this project was to examine chimpanzee and human extraction of *Saba* and more fully comprehend human use of the wild resources within the home range of the Fongoli chimpanzee community. Specific research objectives were to determine: (1) amounts of *Saba* extracted by chimpanzees and humans; (2) habitat use by chimpanzees and humans during *Saba* season; and (3) the importance of *Saba* and other wild plants to humans and chimpanzees inhabiting the area. By integrating ecological and cultural anthropological field techniques, the intention of this study was to analyze the *Saba* system in an effort to assess the risks to chimpanzee caused by human behavior and apply results to any future conservation plans.

Study Site

The Fongoli study site (12° 39′N 12° 13′W) is best described as a mosaic of grassland plateau, grassland, woodland, ecotone, and gallery forest habitats (Pruetz et al. 2002) punctuated by areas of disturbed lands where crops such as corn, millet, and cotton are grown. Plateaus are broad, level sheets of bauxite or laterite on top of which few woody plant species prosper (Hunt and McGrew 2002). Grassland consists of seasonal tall grasses with scattered trees (Baldwin et al. 1982). Humans frequently burn these areas during the dry season. Woodlands are composed of gentle slopes with the majority of trees less than 10 m in height and a partially open canopy that allows a sparse understory (Hunt and McGrew 2002). Ecotone forest occurs where water runoff creates patches of transitional, woody, evergreen forests (Pruetz et al. 2002). Gallery forest is described as growing from steep-sided watercourses in thin alluvial valleys dissected by erosion through laterite pans (Hunt and McGrew 2002). These forests are home to the tallest trees and densest canopies of the various habitat types (Pruetz et al. 2002).

The year consists of two seasons: wet (June–September) and dry (October–May) (Ba et al. 1997). In Kedougou, 10 km to the south of the Fongoli study site, the average annual rainfall ranges between 900 and 1100 mm and the average annual temperature is 28.2 °C, with an average monthly minimum of 25 °C in December and an average monthly maximum of 33 °C in May (Ba et al. 1997). These conditions are similar to those found at Mt Assirik 45 km northwest of Fongoli. Chimpanzees in Senegal endure the hottest and driest conditions recorded to date (McGrew et al. 1981; Hunt and McGrew 2002).

Line-Transects

In an effort to compare chimpanzee and human extraction of *Saba* among the three villages of Djendji, Fongoli, and Ngari, 15 stratified, line-transects were monitored from May through July 2004. Five parallel transects were made at 500 m intervals, ranging from 500 to 2500 m from each village. The transects were 1000 m in length and 40 m wide based on detection distances determined by Pruetz et al. (2002). Each line-transect was walked in 90 min increments a total of seven times throughout the study period. The initial survey counted the fruit on each *Saba* plant, marked the plants on a handheld Global Positioning System (GPS), and noted the habitat types in which they grew. The second survey measured the amount of each habitat within each transect using a GPS unit. One survey was dedicated to measuring the distances between nests and *Saba* vines. Three surveys focused on direct (sightings) and indirect (nests, feces, feeding remains) chimpanzee "signs" and recorded the habitat in which they were found. All surveys counted the number of *Saba* fruit remaining on each plant and recorded evidence left under each liana in an effort to determine which species extracted the fruit.

The difference in *Saba* counts from the first survey and the last survey was scored as due to human, chimpanzee, or monkey (vervet) extraction. Fruit that could not be scored was marked as "unknown." Fruit still on the vine was scored as "remaining." Human scores were based on signs left under the vines that included: bamboo poles (Fig. 2) used to reach fruit in the upper levels of the vines, bark rope used to fasten blades to the bamboo poles, and twigs of the vines,

Fig. 2 Man with bamboo pole for collecting *Saba* fruit

which are often cut during the process of extraction and which show distinct patterns of breakage from the bladed bamboo poles. Chimpanzee scores were based on the presence of feces and the manner in which the exterior of the fruit was halved, with little tooth or scratch marks on husks. Monkey scores were attributed to vervet monkeys and based on the presence of uneaten seeds and particular scratch and tooth marks found on the exterior of the fruit. Additionally, monkeys tend to break the husks into smaller pieces as opposed to the larger "halves" that is characteristic of chimpanzee feeding. In the event of multiple signs, the scores were split. Because monkeys do not disperse seeds and less is known about their diet in this area, the focus of this study will be on chimpanzees and humans.

Nest Distance to **Saba senegalensis**

In order to better understand the importance of *Saba* to chimpanzees, the distance of nests to *Saba* plants was measured to see if the proximity of fruit played a role in nesting location. Nests were recorded as fresh, recent, old, or rotted based on criteria established by Tutin and Fernandez (1984) but revised to fit the Fongoli site. Nests with all green leaves and traces of urine were considered fresh. Nests with mostly green leaves were considered recent. Nests with all brown leaves were considered old. Nests lacking leaves were considered rotted. Fresh and recent nests were assumed to have been created when the *Saba* was ripe (May–June), while those determined old or rotted were considered to have been constructed before May, when *Saba* is not considered a main portion of the chimpanzees' diet based on fecal samples collected. The nest distances were measured from the base of the *Saba* plants to the trunk of the tree using a standard field tape measure. In circumstances where *Saba* vines were intertwined with nesting trees, a distance of 1 m was recorded.

Interviews

To more fully comprehend the importance of *Saba* in relation to the people inhabiting the area, human harvesting of the fruit was assessed, interviews were conducted with the villagers, and observations of fruit collection and use were made. The interviews and observations were conducted opportunistically at the end of the study period when humans no longer harvested *Saba* fruit. Interviewees were asked to rank the most important wild-growing plants found in the area and list their uses. Comparisons were then made with plants used by chimpanzees within the area based on a list created by Pruetz (2006). Data were also collected on the number of 50-kg rice sacks of *Saba* fruit each person collected.

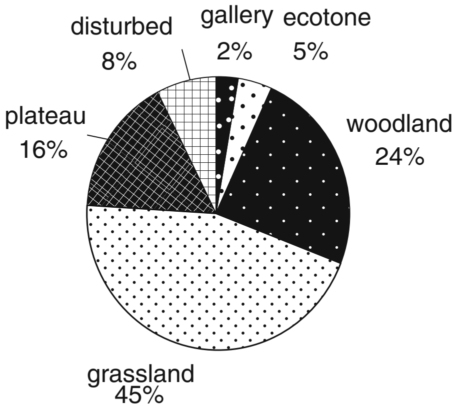
Results

Habitat

Results of the habitat measurements (Fig. 3) show that grassland predominates, accounting for 45 % of the area within the line-transects. Woodland, plateau, and disturbed areas accounted for 24 %, 16 %, and 8 % of the total areas surveyed respectively. Ecotone forest accounted for 5 % of the area, while gallery forest comprised 2 %.

All three villages had high proportions of wooded grassland and low proportions of gallery forests (Fig. 4). Djendji had the highest proportion of disturbed and grassland habitats. Fongoli had the highest proportion of woodland and the

Fig. 3 The percentage of habitat types at the Fongoli study site



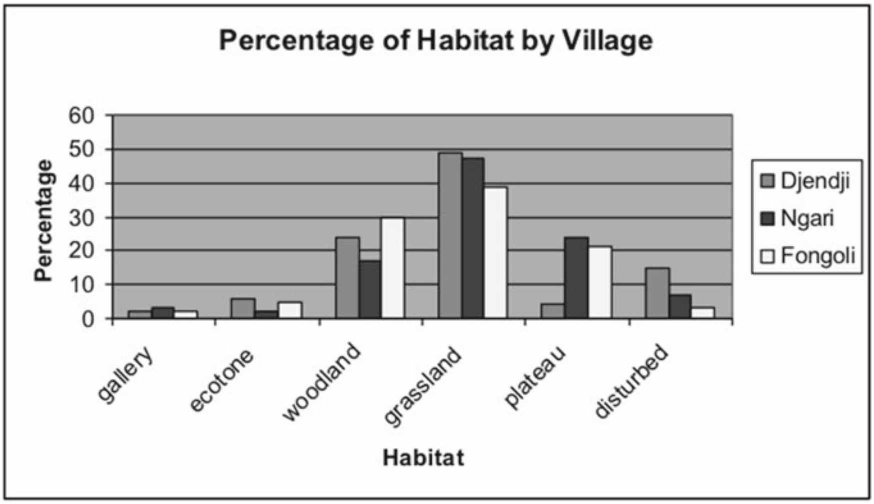


Fig. 4 Percentage of habitat types measured near Djendji, Ngari, and Fongoli

lowest proportions of disturbed habitats. Ngari had the highest proportion of gallery forest and plateau and the lowest proportion of woodland habitats. Grassland makes up the majority of habitat near all villages while gallery forest accounts for the least amount.

Saba senegalensis *Counts*

The initial survey of *Saba* found a total of 2868 fruit (4780 fruit/km^2) growing on 119 plants along the line-transects. The average number of fruit was just over 24 per plant and ranged from 1 to 74 fruits per plant. The amount of fruit recorded differed significantly between habitats ($\chi^2 = 706.18$, d.f. = 8, $p < 0.0001$, Fig. 5). The majority of fruit was found in woodland areas (1795, 63 %) followed by gallery forest (492, 17 %), grassland (464, 16 %), and ecotone (117, 4 %). *Saba* was not found growing in disturbed or plateau habitats. The density of fruit within each habitat also differed substantially (Fig. 4). In gallery forest, *Saba* density was 41,000 fruit/km^2. In woodland habitat, *Saba* density was 12,465 fruit/km^2. In ecotone forests, *Saba* density equaled 3900 fruit/km^2. In grassland habitat, *Saba* density equaled 1719 fruit/km^2.

The initial *Saba* counts also revealed significant differences between Djendji, Ngari, and Fongoli and the habitats in which the fruit was found ($\chi^2 = 508.6609$, d.f. = 6, $p < .0001$, Fig. 6). Line-transects near Djendji included 568 fruit with a density estimated at 2840 fruit/km^2. At Ngari, 886 fruit were recorded with an estimated density of 4430 fruit/km^2. Fongoli had the highest number of fruit with a total of 1414 and a density estimated at 7070 fruit/km^2. Overall, fruit density was highest in gallery forest habitat near Fongoli and lowest in grassland habitat near Djendji.

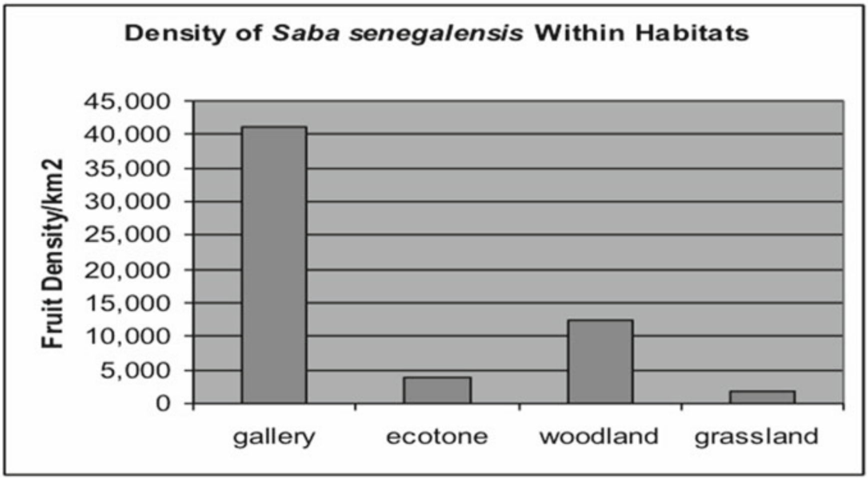


Fig. 5 Density of *Saba senegalensis* fruit within each habitat. The fruit density is over three times as high in gallery forest as it is in woodland

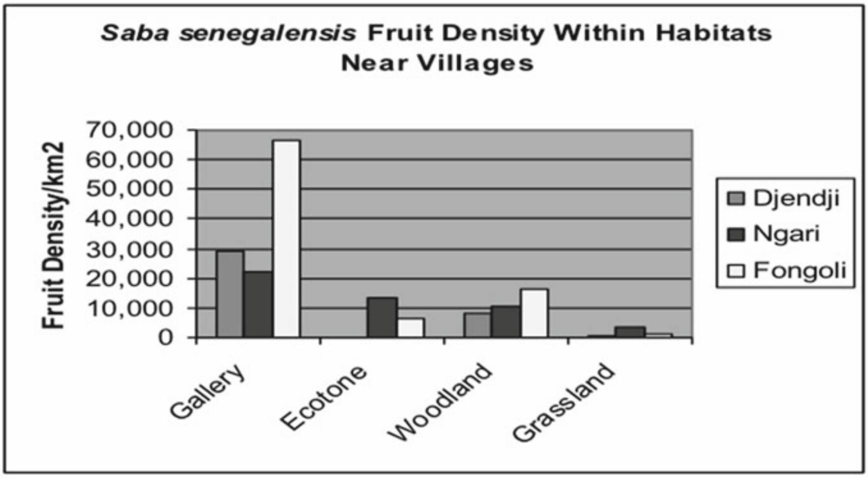


Fig. 6 The density of *Saba senegalensis* fruit recorded in each habitat near each village

Saba senegalensis *Extraction*

The difference in the number of fruit counted during the first and last survey was used to score the extraction of *Saba* fruit (Fig. 7). Based on evidence at each vine, results suggest that chimpanzees, humans, and monkeys removed 12.5 % ($n = 359$), 24.2 % ($n = 694.5$), and 13.7 % ($n = 392.5$) of fruit, respectively. A total of 32.6 % ($n = 935$) of the fruit remained on the vines while another 17 % ($n = 487$) of the fruit could not be reliably scored and was marked as “unknown.”

Results also showed that harvesting *Saba* by humans differed significantly at each village. Humans extracted more fruit ($n = 388.5$) from the area near Ngari than from any other region. Chimpanzees used more fruit near Fongoli ($n = 349$) while using very little fruit near the other villages ($n = 10$ at Djendji, $n = 0$ at Ngari). In general, chimpanzees were found to use *Saba* most often in areas near Fongoli while humans primarily harvested the fruit near Ngari.

The use of *Saba* by chimpanzees and humans differed significantly ($\chi^2 = 487.50$, d.f. = 3, $p < .0001$) according to habitat types. Over 62 % ($n = 224$) of fruit used by chimpanzees was taken from gallery forests while nearly 20 % ($n = 71$) was taken from ecotone forests and another 18 % ($n = 64$) was taken from woodland. Of the fruit extracted by humans, over 60 % ($n = 419$) was from woodland habitats, while more than 25 % ($n = 177$) was taken from grassland. Humans used gallery and ecotone forests to a much lesser extent, as each habitat accounted for 8 % ($n = 57$) and 6 % ($n = 41.5$) of the total number of fruit harvested respectively. Chimpanzees were found to utilize fruit in gallery forest habitats while humans harvested fruit primarily from woodland habitats.

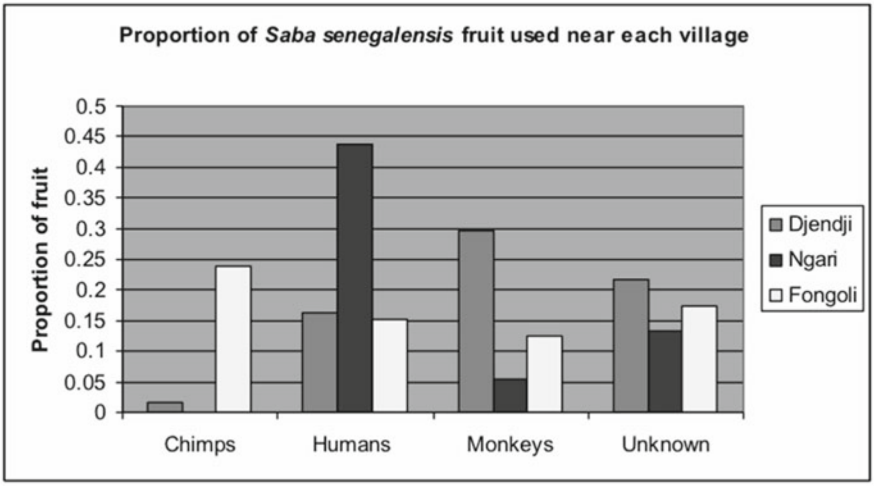


Fig. 7 The proportion of *Saba senegalensis* fruit scored at each village

Nest Distance to Saba senegalensis

A total of 25 nests were marked as fresh or recent. The remaining 42 nests were marked as old or rotted. Distances from fresh and recent nests to *Saba* vines were significantly different compared with nests marked old or rotted (ANOVA $F=7.63$, d.f. = 66, $p<0.0001$). Fresh and recent nests averaged 11.8 m from *Saba* vines and ranged between 1 and 58.1 m from the vines. Old and rotted nests averaged 28.3 m from *Saba* vines and ranged from between 1 and 216.4 m from the vines. Nests were observed in disturbed forest (1.5 %, $n=1$), gallery forest (16 %, $n=11$), woodland (27 %, $n=18$), and ecotone (55 %, $n=37$) habitats. Nest ages along transects near villages also differed. Of the 25 nests marked fresh or recent, 23 were along transects near Fongoli, 2 near Djendji, and none near Ngari. Of the 42 nests marked old or rotted, 14 were near Fongoli, 22 near Djendji, and 6 near Ngari.

Interviews

Interviews with 47 people (25 males, 22 females) were conducted opportunistically throughout the area. Subjects were asked to rank the five most important wild plants used in this region. Interviewees named 47 plants that grew in the area. Scores were given to each plant (five being the most important, one being less important, see Table 1). The shea butter tree (*Vitellaria paradoxa*) was the highest ranked plant species. Its seeds are used to make cooking oil and the fruit is eaten. *Saba* was the second highest ranked plant. The majority of plants were used for food ($n=25$) although several were used for medical purposes ($n=15$). Other uses included ropes, soap, boats, wood, and patches for bicycle tires. Of the 47 plants ranked, only

Table 1 The 16 most important wild plants in the Tomboronkoto region of southeastern Senegal as ranked by humans who use them. *Based on indirect (fecal samples) and direct observations (Pruetz unpublished data)

	Scientific name	Malinké name	Human use	Chimpanzee use*
1.	*Vitellaria paradoxa*	Se	Food/oil	Yes
2.	***Saba senegalensis***	**Kaba**	**Food/rope/meds**	**Yes**
3.	*Adansonia digitata*	Sita	Food/rope/meds	Yes
4.	*Tamarindus indica*	Timbingo	Food	Yes
5.	*Cola cordifolia*	Taba	Food/meds	Yes
6.	*Pterocarpus erinaceus*	Keno	Meds/animals	Yes
7.	*Combretum* species	Djambakata	Meds	No
8.	*Cordyla pinnata*	Dougata	Food/meds	Yes
9.	*Zizyphus mauritania*	Djib-djib	Food	Yes
10.	*Parkia biglobosa*	Nette	Food/meds	Yes
11.	*Mitragyna inermis*	Djungo	Meds	Unknown
12.	*Ceiba pentandra*	Bantan	Food/meds	Yes
13.	*Khaya senegalensis*	Djallo	Food/soap/pirogue	Unknown
14.	*Ficus ingens*	Sayho	Food	Yes
15.	*Spondias mombin*	Minkon	Food	Yes
16.	*Landolphia heudelotii*	Fole	Food/bicycles	Yes

29 were identified (Table 2). Of those, 25 are known to be used by chimpanzees (Pruetz 2006). The competition between chimpanzees and humans for plant resources is high at least, with respect to identifiable species.

The interviewees were also asked to list the amount of *Saba* fruit collected in terms of the 50 kg rice sacks typically used for transport. Of the 25 men interviewed, 16 of them collected a seasonal total of 154 sacks (average 9.63, range 1–39). Using Knutsen's (2003) estimates of 500 fruit per sack and 21 seeds per fruit, this study suggests that the men interviewed extracted a total of 77,000 fruit, or 1,617,000 seeds in 2004. Of the 22 women interviewed, 15 collected at least one sack of fruit. The total number of sacks collected by these women was 63 (average 4.2, range 1–10). Again using Knutsen's (2003) estimates, the women interviewed extracted approximately 31,500 fruits, or 661,500 seeds in 2004. Using these numbers, it is possible to extrapolate that the 300 people who inhabit these villages have extracted a total of 692,553 fruit, or 14,543,617 seeds in 2004.

Discussion

Saba senegalensis *and Chimpanzees*

With the highest density of *Saba*, it is not surprising to find that chimpanzees primarily forage for this fruit in the gallery forest habitat near the Fongoli village. Despite evidence of chimpanzee use (direct observations and nests) and the initial

Table 2 The 29 identified wild plants used by humans in southeastern Senegal, their uses, and whether they are used by chimpanzees

Scientific name	Malinke name	Chimpanzee use	Human uses
Acacia ehrenbergiana	Ganinkoyo	Yes	Food
Adansonia digitata	Sita	Yes	Food/rope/medicine
Afzelia africana	Lenke	Yes	Medicine
Allophylus africanus	Irindingo	Yes	Wood
Cola cordifolia	Taba	Yes	Food/medicine
Combretum spp.	Djambakata	No	Medicine
Cordyla pinnata	Dougata	Yes	Food
Daniella olivieri	Santango	Yes	Food
Diospyros mespiliformes	Kukuo	Yes	Food
Ficus ingens	Sayho	Yes	Food
Khaya senegalensis	Djallo	Unknown	Food/soap/pirogue
Landolphia heudelotii	Fole	Yes	Food/bike tires
Lannea acida	Bintinklingo	Yes	Food
Lannea microcarpa	Fekho	Yes	Food
Mitragyna inermis	Djungo	Unknown	Medicine
Nauclea latifolia	Battio	Yes	Food
Oxytenanthera abyssinica	Bo	Yes	Wood
Parkia biglobosa	Nete	Yes	Food/medicine
Piliostigma thonningii	Fara	Yes	Rope/food
Pterocarpus erinaceus	Keno	Yes	Medicine
Saba senegalensis	**Kaba**	**Yes**	**Food/rope/medicine**
Spondias mombin	Minkon	Yes	Food
Sterculia setigera	Kunkusita	Yes	Food
Strychnos spinosa	Kara	Yes	Food
Tamarindus indica	Timbingo	Yes	Food
Vitellaria paradoxa	Se	Yes	Food/oil
Vitex madiensis	Kutifingo	Yes	Food
Zizyphus Mauritania	Tomborongo	Yes	Food
Ximenia Americana	Sene	Yes	Food

presence of large amounts of *Saba* fruit in woodland habitats, chimpanzees did not forage for *Saba* within these habitats as often. There are two possible reasons for this. The high density of fruit within gallery forests may provide chimpanzees with an ample amount of fruit. As has been seen at other sites, the chimpanzees at Fongoli may limit their daily ranging behavior to areas of high fruit density, while at the same time increasing foraging efficiency (Baldwin et al. 1982; Doran 1997). Alternatively, humans may be removing *Saba* fruit from woodland habitats before chimpanzees can exploit it. The combination of the relative ease in which humans can move in woodland compared with gallery forest (personal observation) and the fact that humans extract *Saba* early in the season when the fruit is not fully ripe to ensure freshness when it arrives at distant markets (Knutsen 2003), suggests that the fruit may be largely depleted in woodland habitat.

Even given a relatively high percentage of gallery forest habitat, chimpanzees were not found foraging for *Saba* fruit in the area near Ngari. Of the relatively few traces found, all were old or rotted nests. Chimpanzee avoidance of the area near Ngari may be the result of a higher percentage of disturbed land, higher human population density, or the consequences of long-term *Saba* extraction by humans.

The low density of *Saba* fruit and the subsequent absence of chimpanzees in the area around Djendji may be explained by the varying topography and the large amount of disturbed land. The chimpanzee traces that were discovered there might also be attributable to the presence of a permanent water source in the area. This suggests that, as the wet season developed, the importance of this water source decreased and chimpanzees were then capable of selecting areas based on food rather than water availability. Consequently, of the 24 nests along the line-transects near Djendji, only 2 were considered fresh or recent, while 22 were marked as old or rotted.

According to Pruetz (2006), *Saba* fruit is likely to be the most essential food resource for the Fongoli community of chimpanzees during the months of May–June. This study supports that claim. Chimpanzees were found to extract 12.5 % of the fruit counted along the line-transects. The percentage of fruit extraction near the Fongoli village was even higher, where chimpanzees used nearly 25 % of the total fruit initially counted in the area. The importance of *Saba* fruit to chimpanzees is also evident in nesting behavior. Results show that chimpanzees nested significantly closer to *Saba* vines during periods when the fruit was ripe compared to periods when it was not. Additionally, data on chimpanzee feeding behavior at Fongoli during the study period revealed that *Saba* was the food most often eaten. These results suggest that chimpanzees adjust their behavior in relation to the location and abundance of *Saba* at this study site.

Importance of **Saba senegalensis** *to Humans*

Results from both field observations and interviews reveal that *Saba* fruit is an important plant for many people living in the Tomboronkoto region of southeastern Senegal. Human extraction accounted for over 24 % of the *Saba* removed from the area. In Ngari, where humans extract the most fruit, people were responsible for the removal of nearly 44 % of the *Saba* initially counted. These numbers are most likely underestimations, as humans are capable of extracting *Saba* fruit without leaving evidence. It was not surprising to find that, among the villages, humans extracted more *Saba* fruit at Ngari than either Fongoli or Djendji. Located on the main road that connects Kedougou to the rest of Senegal, Ngari is an obvious and easy stop for trucks transporting the fruit to distant markets. In an examination of habitat use, human extraction of *Saba* fruit was greatest in woodland habitats. This may be attributed to the abundance of the fruit there and/or the ease in which humans can move within this habitat. Because of the influx of humans, chimpanzees may be avoiding woodland habitats, although factors such as heat stress should be considered (Pruetz, personal communication).

Interviews conducted determined that wild plant resources are important to the people living in this area. A total of 47 plant species were listed and ranked. *Saba* was the second highest ranked plant, demonstrating its usefulness as a means of subsistence and income. Knutsen (2003) reported that *Saba* fruit was an important source of money for women who used the income earned to buy the necessary food, clothing, and medicine for their entire family. Once considered a task for women and children (Knutsen 2003), men are increasingly harvesting the fruit as the *Saba* market becomes more commercial and profitable. Since men are not responsible for the cooking and daily household chores and are thus capable of collecting more fruit, this shift from primarily female to male harvesting may impact economic values as well as the relationship between chimpanzees and humans in the area.

Demographic changes may also be a factor. Due to the increasing population within the region, there are more people using more resources at a more intense level (Knutsen 2003). Wild and Mutebi (1996) note that, as resources become more commercialized, the chances for sustainable use decrease. As the fruit of the *Saba* vine becomes successfully marketable, one can predict that the extraction of this fruit within the Fongoli study area will increase. Evidence for this already exists in the increasing number of men who are participating in the *Saba* harvest. With the number of people collecting *Saba* increasing and the density of the fruit near Ngari decreasing, people living in this area may range farther into the surrounding areas and habitats, further depleting the region of *S*aba seeds and restricting the availability of fruit for chimpanzees.

Conservation Strategy

The socioeconomic–ecologic ramifications of gathering NTFPs highlight the need for a case-by-case approach for managers of natural resources. Conservationists and policy makers must acquaint themselves with the ecologic, economic, and cultural complexities entwined within the harvest of NTFPs. Cowlishaw and Dunbar (2000) list four principal components necessary to formulate a successful conservation plan: (1) define the strategic goals; (2) identify the relative units of conservation (species, communities, ecosystems); (3) evaluate the units and rank them in order of urgency, taking into account the strategic goals, time limits, and resources available; and (4) present realistic tactics that have the potential for rapid implementation. Several other components such as budgets, research proposals diagnosing specific threats, and criteria for evaluating success may also be included (Cowlishaw and Dunbar 2000).

Studies such as this one provide data that help achieve a successful conservation plan. Carter and colleagues (2003) suggest that, in order to conserve chimpanzees in Senegal, complete surveys must be conducted, educational activities that raise awareness must be initiated, legislation must be revised, and solutions to competition between chimpanzees and humans over access to resources must be sought. Pertaining to competition between chimpanzees and humans over S*aba*, Carter et al. (2003) recommend that a survey of fruit density and distribution be conducted in areas of high chimpanzee density and that a moratorium on *Saba* harvesting should be imposed until the level of sustainability has been assessed. Other possible tactics should include more stringent control of the harvest in the form of paid permits, identifying specific areas for chimpanzee harvests and those for humans, and rotating areas of harvest from year to year to allow fruit to regenerate (Carter et al. 2003). Without knowing the regeneration rate of *Saba*, however, it is difficult to estimate the sustainability of human extraction. Given the large number of seeds removed by humans estimated by Knutsen (2003) and this study, current levels of extraction may not be sustainable over the long term. While Carter and colleagues (2003) recommend a moratorium on *Saba* harvests, caution is advised. As Wild and Mutebi (1996) have shown, the prohibition of wild resource use by humans ultimately leads to a higher demand, increased value, and more people illegally extracting the product. Furthermore, the elimination of an important resource for people may alter attitudes and increase animosity toward local chimpanzees. Likewise, the use of paid permits, designated extraction sites, and rotational periods may be problematic. Without the resources to guarantee proper enforcement, these tactics will likely fail.

The creation of small-scale *Saba* plantations does hold some promise. According to Pacheco and colleagues (2012), people in the Kolda and Casamance regions of Senegal have had success through management committees that includes local people. The plantations require the construction of supporting structures for the vines to climb and means of irrigation, but early indicators suggest that these plantations may provide an alternative to collecting the fruit in the wild. Conservationists working in southeastern Senegal should certainly look into the feasibility, limitations, and potential liabilities of plantations near the Fongoli area.

Many issues must be addressed to ensure the long-term survival of the Fongoli community of chimpanzees. The single most beneficial plan of action would be the establishment of a chimpanzee refuge where the agricultural alteration of land is prohibited and the extraction of wild resources such as *Saba* is monitored. To do this successfully, community support for the initiative must be sought. The key to mobilizing this support lies in demonstrating the benefits of such a refuge to local inhabitants. Tourism and employment are potential sources of income created by refuge areas, while the promise of long-term availability of resources such as *Saba* should also be emphasized. Once community awareness and support have been raised and a refuge established, policies including the use of paid permits, rotational areas, and designated chimpanzee sites could be enacted.

While the establishment of a protected refuge would clearly benefit chimpanzees, such an endeavor may be financially out of reach. The staggering amount of foreign debt owed by Senegal ($4.7 billion, 30 % of GDP[1]) may preclude the country from investing in infrastructure, education, health facilities, and conservation. As long as people are unable to receive clean water, essential medicines,

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[1] http://web.worldbank.org/WBSITE/EXTERNAL/COUNTRIES/AFRICAEXT/-accessed 8/27/15

and a basic education, the chances are high that they will commodify *Saba* and other NTFPs in search of the cash needed to buy food, clothing, and medicine. Until the poverty that drives human behavior in regions like Senegal is addressed, conservation programs that look to limit human use of valuable lands and resources face formidable obstacles.

Conclusion

Socioeconomics play a major role in determining how humans impact their local ecology. Indeed, people are part of the ecology and this study illustrates that by comparing human and chimpanzee use of *Saba*. Studies such as this one emphasize the need for a bio-cultural approach to best understand the multifaceted challenges facing primate conservationists. That is where ethnoprimatology comes in. Primatologists would be wise to consult with their cultural anthropology and economics colleagues when attempting to fully comprehend the many issues involved in the collection of NTFPs. Here, we show that it is highly likely that the human extraction of *Saba* affects chimpanzee ranging behavior and habitat use as well as human economics and well-being. As more *Saba* is removed from the area, decreasing the number of seeds available for germination, both humans and chimpanzees may be forced to face a future without this important food.

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The Effects of War on Bonobos and Other Nonhuman Primates in the Democratic Republic of the Congo

Michel T. Waller and Frances J. White

Introduction

More than 90 % of the major armed conflicts held between 1950 and 2000 occurred within countries that contain biodiversity "hotspots" (Hanson et al. 2009). And while there may be a few areas in the world such as the Demilitarized Zone between North and South Korea where standoffs result in a "war-zone refuge" that benefits wildlife (Martin and Szuter 1999), the majority of studies that have investigated the effects of war on biodiversity reveal a much bleaker picture. For example, chemical and biological warfare can alter landscapes and contaminate ecosystems. Herbicide combinations such as "Agent Orange" were sprayed on the forests of Vietnam in order to reduce cover for North Vietnamese soldiers (Westing 1971). Decades later, chlorinated dioxin contamination was measured in wildlife (Olie et al. 1989) and people (Schecter et al. 2001) and Agent Orange has been linked to cancer (Frumkin 2003), spina bifida (Ngo et al. 2010), and the decimation of mangrove forests in Vietnam (Arnaud-Haond et al. 2009).

Warfare is also coupled with extreme poverty due to a breakdown in economic systems, the disruption of governmental services, the collapse of infrastructure, and the reallocation of capital towards militarization (Collier 1999; Dudley et al. 2002). As a result, people living in war zones are often starving and malnourished and may be forced to turn to wild resources, exacerbating the stress that wildlife within these nations, most of which are developing, already face. Primates may be particularly

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susceptible to the effects of war. Many species are social and loud and therefore easy to hunt when other game is scarce. Moreover, while they are not always thought of as preferred prey (Chapter 3 this volume), an influx of weapons combined with starving populations can lead to an increase in primate hunting. With the number of armed conflicts increasing since the 1950s (Dudley et al. 2002), it is important to understand how humans and wildlife respond in order to protect endangered populations. The goal of this chapter is to better understand the armed conflicts of the 1990s and 2000s in the Democratic Republic of the Congo (DRC) and their effects on nonhuman primates living within and near the war zones with a specific focus on the primates living in the Lomako Forest.

The Great African War

In the mid-1990s, war erupted in the DRC. The "Great African War" (1996–2006), as it became known (Reyntjens 2009), was the result of complex interactions between nine African governments, warlords, several insurgent and rebel groups, and local people attempting to protect themselves (Williams 2013). The devastating war and resulting civil unrest that destabilized the social, political, and economic conditions within the DRC resulted in a massive human and environmental crisis. An estimated 3.9 million people died in the country due to the conflict and subsequent starvation (Coghlan 2004) making it the deadliest war in terms of human casualties in modern African history.

Wildlife suffered as well. The warfare spilled into protected areas, hundreds of park rangers were killed, and the extant threats to animals and the areas they inhabited grew. The influx of weapons and ammunition circulating in the country increased (Draulans and Van Krunkelsven 2002) while a variety of military factions and other people increasingly entered the forests in search of protection from other militarized groups and food (Nackoney et al. 2014). Hunting, the trade in ivory, and illegal timber harvesting increased as officials from Uganda and Rwanda used the political instability in the DRC as an opportunity to exploit those resources. Soldiers were also seen with live monkeys and parrots captured for use as pets (Draulans and Van Krunkelsven 2002).

One study in particular showed the effect of war on nearby wildlife. More specifically, de Merode and Cowlishaw (2006) investigated the amount and diversity of animals sold in a bushmeat market in the DRC. Their research focused on the bushmeat trade in Garamba National Park using market surveys, interviews, and direct observations. They found a significant increase in the number of protected species sold in an urban market during the war when compared with peacetime results. Most notable was the increase in elephants, buffalo, hippos, and antelope. They also noted a slight increase in the number of monkeys (multiple species) sold in a village market, although the change was not statistically significant. In general, they found that protected species accounted for over half of the bushmeat sold during peacetime and increased fivefold during the war due to a change in the commodity chain brought about by the war's overall instability and an increase in access to protected areas for other actors.

Perhaps no species suffered as much during the war as the gorillas living in the North Kivu region of the DRC. Categorized as Critically Endangered by the IUCN (Robbins and Williamson 2008), the 700–800 remaining mountain gorillas (*Gorillas beringei beringei*) live near areas with some of the highest human population density levels in Africa (400–600 people per km^2) and have been threatened by habitat loss and poaching for decades (Harcourt and Fossey 1981; Weber 1995; Weber and Vedder 2001). Ecotourism, education, and antipoaching patrols have helped stabilize the number of mountain gorillas to some degree, but few could have predicted the challenges gorilla populations would encounter as a result of the war. In Virunga National Park, between 12 and 17 gorillas (4–5 % of the entire population) died as a direct result of military activity with detrimental effects likely for surviving groups (Kalpers et al. 2003), as the loss of a silverback male often leads to the migration of females with infants, increasing the risk of infanticide to infants under 3 years old (Robbins 1995). Even after the war officially ended, mountain gorillas continued to face threats. In July of 2007, seven mountain gorillas living in Virunga were killed, not for food, but for political and economic purposes as their removal allowed increased exploitation of resources within the park (Jenkins 2008). Like the mountain gorillas, Grauer's gorillas (*Gorilla beringei graueri*) were also slaughtered in greater numbers during the war (Kasereka et al. 2006).

Gorillas were not the only ape species affected by the war. Bonobos populations living in the DRC have also decreased (Vogel 2000). Bonobos are endangered (Fruth et al. 2008) and face many of the same challenges of other nonhuman primates such as habitat loss and bushmeat hunting (Mohneke and Fruth 2008). As with gorillas, however, the war seems to have exacerbated these problems for bonobos. In the Wamba Forest, Idani and colleagues (2008) returned after the war and found a decrease in the population of three groups while three other groups were missing from their former ranges altogether. Additionally, one of the groups that did survive was forced to expand their range. These researchers speculate that the depreciation of the DRC currency and the decrease of employment opportunities forced many of the people to leave the area or turn to the forest to feed their families. Furthermore, they suggest that local taboos against eating bonobos (due to beliefs that these apes are ancient relatives) may have been lifted in the face of starvation.

Human activities also threaten bonobos at Lac Tumba (Inogwabini et al. 2008) and Salonga National Park (Hart et al. 2008). Meanwhile, the number of orphaned bonobos confiscated from the pet trade and brought to the Lola ya Bonobo sanctuary in Kinshasa increased dramatically during the war (André et al. 2008). It is clear, given the humanitarian and ecological pressures that were present in the DRC, that bonobos were killed or captured in large numbers during the war. This study looked at bonobo populations living in the Lomako Forest by analyzing changes in party size and ranging behavior from studies conducted before and after the war. Additionally, we looked at the changes in population density and group size estimates of monkeys living in the same area. Lastly, we comment on the people living there and how research projects affect bonobo conservation.

Methods

The Site

The N'deli site in the Lomako Forest (0.7994° N, 21.143° E) is located in the Congo River Basin within the Equateur Province of the DRC (Fig. 1). The 40-km^2 study area consists of climax evergreen and primary rain forest (75.2 % of study site) with smaller areas of swamp forest (12.6 %), bolafa (*Gilbertiodendron*) forest (9.9 %) and secondary forest (2.3 %) tracts (White 1992). The study area is also home to several primate species including bonobos, black and white colobus monkeys (*Colobus angolensis*), red-tailed monkeys (*Cercopithecus ascanius*), Wolf's mona monkey (*Cercopithecus wolfii*), DeBrazza's monkey (*Cercopithecus neglectus*), Black-crested mangabeys (*Lophocebus aterrimus*), Allen's swamp monkey (*Allenopithecus nigroviridis*), Demidoff's dwarf galagos (*Galagoides demidovii*), and the Eastern potto (*Perodicticus potto*).

The history of nonhuman primate studies at Lomako dates back to the early 1970s when preliminary studies on bonobos were conducted (Badrian and Badrian 1984; Susman et al. 1980). Long-term research, however, did not commence until 1980 when US-based researchers originally from the State University of New York at Stony Brook (Susman 1984; White 1992) and Yale (Thompson-Handler 1990) maintained a semi-permanent presence throughout the decade. During the 1990s, field seasons were carried out by Thompson-Handler (1990) and White (1996) and

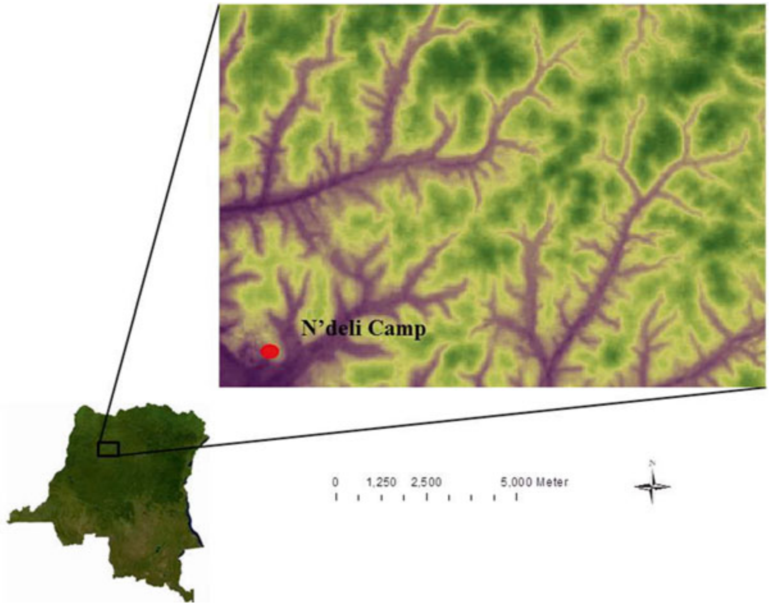


Fig. 1 This map shows the location of the N'deli field site in the Lomako Forest, DRC

her graduate students as well as researchers from the Max Planck Institute in Leipzig, Germany (Hohmann and Fruth 2002). Increasing difficulties from political unrest and the developing war resulted in evacuations and eventual complete exclusion in 1998.

For the US-based researchers, the local people were an important part of their studies and community conservation efforts. Belonging to the Lingala speaking Mongo ethnic group, the people who live along the Lomako River subsist primarily on small horticultural gardens, fishing, hunting, and gathering wild resources. Their knowledge of the forest and willingness to partner with researchers with formal agreements at high local levels made them indispensable as guides and local partners while providing them income and creating incentive to refrain from hunting in and around the study area.

Prewar Primate Populations

Data presented here comes from two separate eras of research that represent "prewar" and "postwar" periods. The "prewar" bonobo data was collected by FW during field seasons conducted from October 1984 to July 1985, June–August 1991, and June–August 1995. Her studies at Lomako focused on two communities of bonobos: the Bakumba community in the western portion of the study area and the Eyengo community in the east (Badrian and Malenky 1984; White 1998; Hohmann and Fruth 2002). Using age, sex, and facial characteristics, researchers were able to identify 28 individuals in the Bakumba community including four adult males, 11 adult females, and 13 sub-adults, adolescents, and infants. The Eyengo community consisted of 30 identifiable individuals including 10 adult males, 11 adult females, and nine sub-adults, adolescents, and infants. Party size estimates were based on focal animal sampling (see Chapman et al. 1994). Data presented here comes from 200 sightings and 448 h of focal animal observations.

To understand habitat use and ranging behavior, the trail system at Lomako was mapped using GPS in 2007 and imported into a GIS program (ArcGIS 9.3). The locations of sightings during the prewar period were hand-plotted into the program based on notes and hand drawn maps used by FW. All maps were made using a Transverse Mercator projection and the WGS 1984 UTM Zone 34 N coordinate system. Once plotted, the location data were analyzed using the RANGES8 (Anatrak Ltd. 2010) software program in order to determine the range area of the two communities for each field season and for all field seasons combined. This program uses fixed-kernel analysis to calculate a home range area in hectares (see Waller 2011).

There have been fewer studies on monkey populations at Lomako. McGraw (1994) conducted a preliminary census on the monkey species that lived in the N'deli study area before the wars began. The results included densities (individuals/km^2) and average group size for *Lophocebus aterrimus* (73.1, 10.2), *Colobus* *angolensis* (5.8, 5), *Cercopithecus ascanius* (42.8, 12.7), and *Cercopithecus wolfi* (44.2, 12). Altogether, McGraw found 165 monkeys/km^2. We use these data as the "prewar" numbers for the monkey density in the Lomako Forest.

Postwar Primate Populations

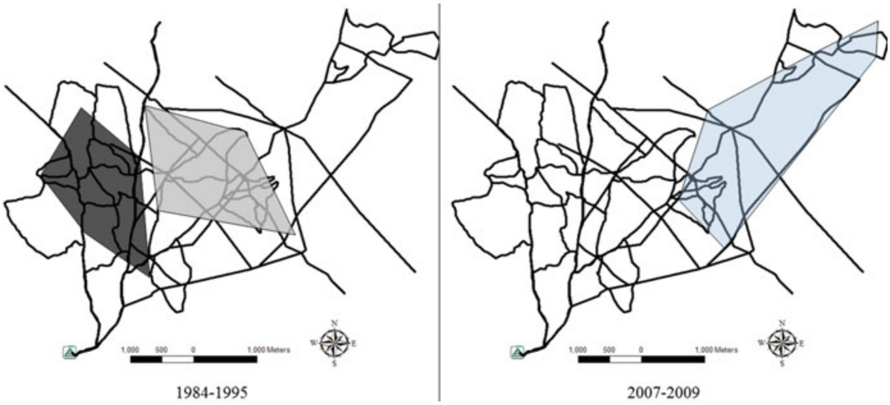
Field research resumed in 2007, after an initial visit in 2005, following the cessation of the war and the return of a modicum of political stability within the DRC. Informal interviews with local people about the war were conducted and researchers and guides searched the trails for signs of bonobos. When bonobos were located, focal animal sampling occurred and GPS points were taken. Because of the long time span between field seasons as well as research that suggests bonobo community composition may be more fluid over longer time spans than previously believed (Hashimoto et al. 2008), the relationship of the bonobos living near the study area to past groups is unclear. One female with a particularly striking facial complexion was recognized by FW as a former Eyengo community member. As such, the ranging behavior of the newly designated "New Eyengo" community (NE) located in the northeastern portion of the study area was used to look at changes in ranging areas of the Eyengo community since 1995. Although there were traces of bonobos in the Bakumba's original range in the form of recent *Haumania* feeding remains in 2005 and 2007, these traces were sparse, northeast of their former range, and no members of the Bakumba community were located or observed. Data was collected on the NE group (18 sightings, 39 follow hours) during field seasons in June–August 2007 and June–August 2009. We were able to identify 16 individuals in the NE group including 2 adult males, 9 adult females and 5 sub-adults, adolescents, and infants. The composition of all the groups fluctuated to some degree during the field seasons and the data analyzed for this study are limited to individuals clearly identifiable within a community. As with the prewar population, the locations of the bonobos were analyzed using the ArcGIS and RANGES8 (Anatrak Ltd. 2010) software programs in order to determine the community's ranging area.

Transects were monitored for monkey populations using methods similar to McGraw (1994) with the exception of detection distances used. We used detection distances of 20 m, whereas the detection distances used by McGraw varied depending on the species being counted. Surveys were conducted along established trails on 18 days in 2007 and on 26 days in 2009. The transects consisted of 5 km-long segments of the trails and counted monkeys that were 20 m on either side of the trail. A total of 90 km and 130 km from 10 different trails were included during the 2007 and 2009 field seasons, respectively. The surveys were conducted between 6:00 AM and 12:00 noon. Observations were made from the trail only and recorded the number of groups for each species, number of individuals per group, and whether the monkeys were in polyspecific groups.

Results

Bonobos

The extent to which local people, soldiers, and commercial bushmeat hunters entered the study area is not well understood. Evidence from bonobo ranging and local people gives us some hints, however. The changes in the observed locations of bonobos were used to assess the ape's response to the use of the forest by local people and soldiers during the war (Fig. 2). According to our guides and other local people, soldiers raided the local village and the research camp forcing families to flee into the forest. Food was scarce. As a result, hunting in the Lomako Forest increased during the period of instability (Dupain et al. 2000). At N'deli, the local guides moved into temporary camps in the study area, one within the Bakumba range, and one in the Eyengo range. According to the local guides, soldiers entered the research camp and shot monkeys around the camp area but did not enter the forest or shoot any bonobos. As the research camp is maintained approximately an hour's walk from the southernmost point where bonobos have been observed, it is possible that soldiers at this site would not have seen any of the bonobo study groups. On first contact with the Eyengo group after the war, there was no sign of alarm at observers. In subsequent field seasons, only younger individuals who were not previously habituated to observers showed any marked reaction to researchers. Nonetheless, there was evidence of monkey hunting around the research camps (see below) and habitat disturbance around the temporary hiding camps that the guides had used during the war. As mentioned above, surveys of the area formerly used by the Bakumba community found only some fresh feeding remains in 2005 but no nests or sightings, suggesting that those bonobos may have moved outside of the



1984-1995

2007-2009

Fig. 2 These maps show the change in bonobo ranging and habitat use from field seasons conducted before the war (1984–1995) and after the war (2007–2009). In the first map, the Bakumba group's range is illustrated by the *black* polygon while the Eyengo group's range is shown by the *grey* polygon. The second map shows the ranging area of the New Eyengo group in *blue* study area, either permanently or temporarily. Moreover, while it is difficult to say with certainty that the Eyengo and NE community are the same, we find that it is likely based on the presence of one recognizable female and the proximity to the old ranging area. Initial data shows that community size and average party size has decreased, while the ranging area has increased (Table 1).

Monkeys

The transects used to investigate monkey populations living in the Lomako Forest found the same four monkey species living there as McGraw's census conducted in 1994. *Lophocebus aterrimus*, *Colobus angolensis, Cercopithecus ascanius*, and *Cercopithecus wolfi* all still live in the forest, but the population density (Table 2) and average group size (Table 3), however, had changed. For each species with the exception of *angolensis*, the population density decreased. In fact, the overall population density of monkeys decreased notably from 165 to 83.6 individuals/km^2 in 2007. Of equal interest is the increase in population density from 2007 to 2009 to 109.6 individuals/km^2 suggesting that these populations may be rebounding. Similarly, the average group size for all four species decreased from 1994 to 2007

Table 1 This table shows the differences in community size, average party size, and ranging area of the communities at Lomako

Community	Community size	Average party size	Range area (ha)
Bakumba (1984–1995)	28	8.26	247.4
Eyengo (1984–1995)	30	7.86	225.95
NE (2007–2009)	16	5.5	480.67

Table 2 Population density (individuals/km^2) of the four species of monkeys found during transects conducted at Lomako

	Lophocebus aterrimus	*Cercopithecus ascanius*	*Cercopithecus wolfi*	*Colobus angolensis*	All species combined
1994	73.1	42.8	44	5.8	165
2007	32	23.8	20.6	6.4	83.6
2009	37.3	34.2	26.2	11.9	109.6

Table 3 Average group size of the four species of monkeys found during transects conducted at Lomako

	Lophocebus aterrimus	*Cercopithecus ascanius*	*Cercopithecus wolfi*	*Colobus angolensis*
1994	10.2	12.7	12	5
2007	2.6	3.1	2.8	2.9
2009	2.5	5.6	5.6	2.7

with a slight increase in *ascanius* and *wolfi* group sizes from 2007 to 2009. The monkeys at Lomako were also found in polyspecific associations often. Of the 211 separate observations recorded, 77 included polyspecific associations. The most common associations were between *aterrimus*, *ascanius*, and *wolfi* (Waller, unpublished data).

Discussion

The Great African War was a catastrophic event for humans and wildlife living in the DRC. The data presented here quantifies the effect of the war on wildlife at Lomako to some extent. For the two bonobo communities, the increased human traffic in the forest altered their population size and ranging behavior. The Bakumba group appears to have moved out of the study area following the war and only future surveys and monitoring will tell if they will return. An interview with a local woman suggests that they may have moved to the east of the site, but attempts to locate signs of bonobos (i.e., sightings, nests, feces) were mostly unsuccessful. The Eyengo group seems to have moved north of the study area to an area outside of the trail system. Their numbers appear to have decreased and they have been forced to range over a larger area in order to find resources.

The monkey population at Lomako also appears to have decreased during the war. All four species regularly recorded during McGraw's census in 1994 showed marked decreases in population density and average group size with *Lophocebus* decreasing the most. And while slight differences in methodology may account for some of this decrease, particularly in regard to average group size, the reduced overall monkey density and density of each species suggests that the monkeys living in the field site were subjected to an increase in hunting pressure. Worthy of mentioning, however, is the fact that monkey populations seemed to have recovered slightly from 2007 to 2009.

It should also be pointed out that N'deli is very close to another field site in the Lomako Forest known as Iyema (Dupain et al. 2002). Yet because N'deli is more accessible from the river (a 2 km hike as opposed to a 9 km hike to Iyema) and had a more developed trail network, soldiers who entered the area during the war likely hunted more often at N'deli than at Iyema. While the results of this study show that bonobos and monkeys at N'deli were affected by the war, a recent survey at Iyema suggests that populations there were relatively unaffected (Waller, unpublished data).

The results of studies such as this have added to the discussion of ethical considerations field primatologists must weigh. Recently, it has been proposed that the habituation of primates should be carefully thought out (Fedigan 2010; Malone et al. 2010; Gruen et al. 2013). More specifically, it has been suggested that the habituation process and the presence of primatologists has the potential

Fig. 3 This photo shows confiscated bushmeat including an individual *Lophocebus* from the Lomako Forest

to make nonhuman primates more susceptible to hunting and capture for the pet trade by diminishing their fear of humans (Fedigan 2010). Other costs may include an increased chance of disease transmission, increased stress, and increased vulnerability to predators. Humans living near habituated primates may also incur costs. Nonhuman primates that are unafraid of humans may aggress against local people or researchers, conduct crop raids or engage in other pest-like behavior, and can increase the risk for zoonotic disease transmission.

Yet there are benefits too. Research projects bring in money, educate people about the importance of biodiversity, and instigate local conservation projects. For example, it is unlikely that the Reserve de Faune de Lomako-Yokokala (RFLY), officially protected as of 2006 under DRC law, would have been created without the efforts of bonobo researchers such as Jef Dupain and the African Wildlife Foundation (AWF). Furthermore, AWF along with the Institut Congolais pour la Conservation de la Nature (ICCN) have trained local people to protect the reserve from poachers and confiscate bushmeat found in the area (Figs. 3 and 4). It may also be possible that the return of researchers to the area played a role in the slight recovery seen between 2007 and 2009 in monkey density.

Fig. 4 This photo shows a confiscated leopard pelt taken from the Lomako Forest

Decisions regarding primate research that involves habituation should incorporate as much information on the economic, ecological, and ethical ramifications as possible. The fieldwork at Lomako demonstrates the challenges such decisions include. In essence, one has to ask whether the animals at Lomako would have been better off unhabituated and unstudied. The financial benefits brought to the area likely led to fewer local people using the forest and its inhabitants for food while promoting the area as suitable for protected status. But these benefits may only apply during periods of peace as the instability of wartime, transect system, and proximity to the river may have increased access of several primate populations to increased human contact. With new techniques such as genotyping and noninvasive hormonal assessments becoming more readily available, the need to habituate nonhuman primates may be decreasing. These new techniques should be considered in places where political stability is absent.

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Primate Taxonomy and Conservation

Dietmar Zinner and Christian Roos

Introduction

“Only what we know, we can appreciate and protect.” This short version of a famous quote by *Baba Dioum*, a Senegalese environmentalist, nicely depicts the relationship between conservation and taxonomy. We have to name and classify things and organisms in order to know them and hence appreciate and preserve them. Taxonomy, as the science of classification, usually refers to the theory and practice of describing, naming, and classifying organisms, whereby classifying refers to “the ordering of [organisms] into groups (or sets) on the basis of their relationships” (Simpson 1961, p. 9). A taxonomic classification is the basis for most other biological disciplines, such as ecology, phylogeny, and evolution, and it is essential for an understanding of biodiversity and its conservation. The basic unit of taxonomy is the taxon (plural taxa) which is according to Simpson (1961, p. 19) “a group of real organisms recognized as a formal unit at any level of a hierarchic classification.” For instance, the species *Papio hamadryas* (hamadryas baboon) is a taxon, but also the genus *Papio* (baboons) and the family Cercopithecidae (Old World monkeys) are taxa.

The taxon “species” is of particular importance in taxonomy and species are also the fundamental units of evolutionary biology, macroecology, biogeography, and conservation. Many conservation issues are concerned with the protection and preservation of species (e.g., Endangered Species Act in the United States 1973) and the diversity, abundance, and distribution of species is used to prioritize conservation

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areas. Species are crucial to conservationists and also to policy-makers, who use them as units for formulating national and international conservation laws. It is understandable that these people rather prefer stable taxonomies. On the other hand, taxonomy is a biological hypothesis and is open to changes if new data become available. Progress in biological research and conservation is often hampered by widespread taxonomic uncertainty and, in particular, the delimitation of species is thus crucial for conservation biology. In our contribution we will briefly sum up the history of taxonomic research with a focus on primates, touch on the problems of species concepts, and delve into the impacts on primate taxonomy and conservation. Comprehensive introductions into primate taxonomy can be found in, e.g., Groves (2001, 2004, 2011, 2012, 2014).

Extinction of Species and the Biodiversity Crisis

Biodiversity is a term used to describe the variety of life on Earth and an essential proportion of this variety is the diversity among species (Wilson 1988). Within the last decades we witnessed an escalating loss of species due to human activities and thus a decline in species diversity, so that some authors already speak about a sixth mass extinction, after five earlier events in geological times, as suggested by fossil evidence (Casetta and Marques da Silva 2015). The human-caused increase of extinction risk also affects nonhuman primates. Currently (August 2015) the IUCN lists 430 extant primate species of which 259 (60.2 %) are Vulnerable, Endangered, or Critically Endangered (IUCN 2015). Several of these threatened species are already down to less than a few hundred individuals (Schwitzer et al. 2014). Due to various reasons, species differ in respect to their extinction risk and, because of the scarcity of time and financial resources, not all threatened species can be protected and managed at the same time. Conservationists have to set priorities and for decision-making they use, among others, data on population sizes, distribution, and threats, which all rely on information on the taxonomic status of respective populations under consideration. If conservation legislation and conservation work is focused on the preservation of species, a classification of a threatened population as a subspecies or species can make a critical difference.

Consider the case of the Hainan gibbon (*Nomascus hainanus*). With less than 30 individuals it is close to extinction and is regarded as Critically Endangered by IUCN. This species has been recently elevated from subspecies *N. nasutus hainanus* to species (Roos et al. 2007) and a species-specific conservation action plan was implemented. This measure most likely would not have been employed if the status would have remained at the subspecies rank. Another example is orangutans (*Pongo* spp.). Previously Sumatran (*P. abelii*) and Bornean orangutans (*P. pygmaeus*) have been considered as one species and animals from both provenances have been kept and bred together in captivity. Genetic studies however showed that Sumatran and Bornean orangutans are genetically so distinct that they qualify as separate species (Xu and Arnason 1996; Steiper 2006). A moratorium was placed on producing hybrid orangutans and each species has now its own species survival plan (SSP) to prevent genetic admixture.

Genetic admixture of populations or closely related species that are adapted to different local conditions can result in outbreeding depression, which leads to a reduction in fitness caused by the breakdown of coadapted gene complexes (Templeton 1986). Outbreeding depression is now recognized to be a problem in wildlife conservation and captive breeding programs similar to inbreeding depression (Storfer 1999; Waller 2015). On the other hand, if closely related but genetically impoverished populations were not elevated to species rank, genetic exchange between these populations as a management tool to improve genetic diversity (genetic rescue, Frankham 2015) would be an option to prevent possible negative effects of inbreeding.

Anyhow, for conservation decisions, reliable information on the taxonomic status of populations are therefore relevant and the demarcation of species becomes an important prerequisite for species conservation. It is thus comprehensible that the application of specific species concepts is one of the most hotly debated issues not only in taxonomic research but also in conservation biology (Rojas 1992; Cracraft 1997; Dubois 2003; Isaac et al. 2004; Mace 2004; Zink 2004; Gippoliti 2007; Morrison et al. 2009; Blair et al. 2011; Frankham et al. 2012, Gutiérrez and Helgen 2013, Zachos et al. 2013a, b; Melville et al. 2014; Shirley et al. 2014; Rylands and Mittermeier 2014).

Taxonomy

People at all times and in all places most likely ordered living things in a hierarchical system based on how organisms appear, that is, on similarities and dissimilarities in how they look, smell, taste, sound, or behave (Yoon 2011). Such classifications are often organized by particular interests for particular uses, e.g., beneficial versus noxious, edible versus inedible, harmless or dangerous (Atran 1998). In some cases taxonomic sophistry was employed to make animals useful. In medieval times the Catholic Church declared, among others, the beaver (*Castor fiber*) as “fish” so that its meat could be eaten even during Lenten seasons. In most cases, however, classifications are much more detailed, constituting a vernacular naming system also referred to as “folk-taxonomy”. Comparisons of folk-taxonomies of indigenous people from various parts of the globe with respective scientific taxonomies of the same regions revealed that both classifications come up with strikingly similar numbers of species and even higher taxonomic groupings (e.g., birds on New Guinea: Diamond 1966; Diamond and Bishop 1999, in the Philippines: van der Ploeg and van Weerd 2010, fish in the Amazon: Begossi et al. 2008). Furthermore, the indigenous knowledge of vertebrates and plants is most often not limited to economically important species, but represent in depth knowledge of the alpha diversity of the respective groups. But there are exceptions. For example, the Kalam of New Guinea deny that cassowaries fall under the bird category, not only because flightless cassowaries are physically unlike other birds, but also because they are ritually prized objects of the hunt (Bulmer 1967).

Humans everywhere classify animals and plants into species-like groups as obvious to a modern scientist as to a Maya Indian (Atran 1999). This apparently ubiquitous tendency of people to classify the organic world into "species" is often considered as an indication for the reality of species, independent of elaborate species definitions by western taxonomists (e.g., Mayr 1969).

Similarly, nonhuman primates were also named and classified in a system and one can imagine that their obvious similarity with humans qualified them into special classes. Primates have been often seen as distant relatives, ancestors or fallen ancestors and they became part of the local mythology and were often protected by taboos (e.g., Fuentes 2012; Zinner et al. 2013a). Two prominent examples of primates becoming important figures in mythology or religion are the hamadryas baboons of ancient Egypt and the Hanuman langurs (*Semnopithecus* spp.) of India. In ancient Egyptian the baboon held several positions in mythology. The name of the baboon god Babi or Baba, who was worshipped in Pre-Dynastic times for its intelligence and sexual lustfulness, may be the origin of the animal's common name (English baboon, French babouin). Later the baboon was closely associated with Thoth the god of wisdom, science, and measurement and it was often depicted on temples and monoliths. The Hanuman langur's common name originated from the Hindu deity Hanuman, who is sometimes considered a reincarnation of Lord Shiva. Traditional Hindus belief that each individual langur represents the living embodiment of this god and therefore is warranted protection. How local folklore affects the protection of monkeys in Africa is illustrated by the treatment of the white-thighed colobus (*Colobus vellerosus*) and Mona monkeys (*Cercopithecus mona*) by villagers in the Boabeng-Fiema Monkey Sanctuary in central Ghana. Local hunting taboos, based on an association of these monkeys with their gods, resulted in their protection since the nineteenth century.

The history of scientific taxonomy began in the eighteenth century with *Carl Linnæus* (Carl von Linné). He developed a hierarchical and nested system, in which animals, plants, and even minerals have been ordered according to their similarities (Table 1). With his "Systema Naturæ" he laid the foundations for the biological nomenclature scheme of binomial names, where the first name refers to the genus and the second, the specific epithet, to the species, e.g., *Homo sapiens* (modern humans) or *Papio hamadryas*. He also provided rules on how to name species, e.g., which language to use (Latin or Latinized Greek). The first edition of the "Systema Naturæ" was published in 1735 and already classified humans as members of the primate order. Of particular importance for zoology was the 10th edition from 1758 in which all listed animal species were given binomial names. The primate order in this edition contained four genera, namely *Homo* (humans), *Simia* (monkeys & apes), *Lemur* (lemurs & colugos) and *Vespertilio* (bats). Linnæus listed more than 20 species of primates, among them the ring-tailed lemur, the Philippine tarsier, the cotton-top tamarin, the lion-tailed macaque, and the mandrill, but he also wrongly included the colugo or Philippine flying lemur (*Cynocephalus volans*) and

Table 1 The descending ranks of the Linnaean hierarchy

Kingdom	Animalia	Animals
Phylum	Chordata	Vertebrates and relatives
Class	Mammalia	Mammals
Order	Primates	Primates
Family	Cercopithecidae	Old World monkeys
Genus	*Papio*	Baboons
Species	*Papio hamadryas*	Hamadryas baboon

The hierarchy starts with the kingdom and goes down to the species

The position of the hamadryas baboon within the system is shown here as an example. Additional (intermediate) ranks can be added, e.g., suborder, superfamily, subfamily, tribe, superspecies, subspecies. In case of hamadryas baboons additional ranks are Haplorrhini (Suborder), Cercopithecoidea (Superfamily), Cercopithecinae (Subfamily), Papionini (Tribe) and Papionina (Subtribe)

the bats, which are given their own mammalian orders today. Nevertheless, the work of Linnæus was a major progress in ordering and naming the living world and the binomial system is still in use. The use of Linnaean taxonomy is governed by the International Code of Zoological Nomenclature (ICZN).

During Linnæus' time, species were regarded as immutable and the idea that the perceived hierarchical and nested structure of the classification could be a result of common descent and hence of evolution was not yet conceivable. However, this changed in the nineteenth century with the work of *Charles R. Darwin* and *Alfred R. Wallace*. Within the evolutionary framework a hierarchical nested order made sense and graded similarities among groups of organisms could be explained by their descent from a common ancestor, thus by their phylogenetic relationships. After the recognition that species are not immutable but change over time and by adopting an evolutionary view, it became clear that a "natural order" of organisms has to be based on their phylogenetic relationship and not just on "similarities".

In many cases, similarity is indeed the result of a common heritage. For instance, members of two species of sportive lemurs (genus *Lepilemur*) are more similar to each other (e.g., genetically, morphologically, behaviorally) than either of them are to sifakas (genus *Propithecus*). Because they are closer related to each other than to the sifaka, their common ancestor lived not as long time ago as the common ancestor of *Lepilemur* and *Propithecus*. In other cases similarity is not due to common descent, but is a result of convergent evolution. Adaptation to certain environments or ecological niches produces traits that appear similar because they have the same function. For instance the multi-chambered stomachs of colobine monkeys and ruminants, only distantly related mammals, are both adaptations to digest leaves and grass with the help of microbes (Chivers and Hladik 1980). Therefore, not every similarity can be used to infer relationships and are not always useful in grouping

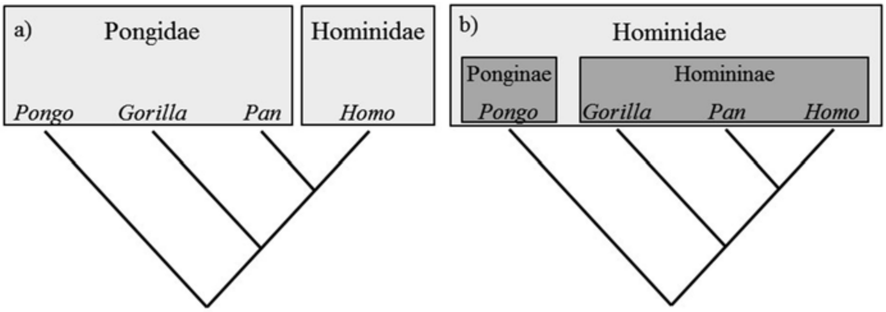

Fig. 1 Cladograms of great apes and humans. (**a**) The traditional paraphyletic taxonomy, where autapomorphic human traits, such as bipedalism, “naked skin,” or large brain size, have been used to separate humans (family Hominidae) from great apes (family Pongidae), resulting in paraphyletic relationships. (**b**) Evolutionary-based taxonomy, where genomic synapomorphies have been applied, resulting in the monophyly of the African great apes and humans (subfamily Homininae) separated from the sister subfamily Ponginae (modified from Groves 2004)

organisms in an evolutionary taxonomic framework. Along with traits shaped by convergent evolution, traits that occur in a number of groups are not usually useful to differentiate among groups. Taillessness is a character of all apes and humans (Hominoidea) and can thus not be used to group humans into the tribe Hominini (including, e.g., *Australopithecus*, *Homo*). Taillessness is a trait which was most likely already present in the common ancestor of the Hominoidea and as such is a “primitive” or symplesiomorphic character. To designate Hominini, we have to look for an evolutionary novelty, a derived or synapomorphic character only shared by the members of the Hominini, e.g., bipedalism, which most likely first occurred in their common ancestor. Groups defined by synapomorphies are called monophyletic (Hennig 1950, 1966). A monophyletic group of organisms, or a clade, contains an ancestral species and all its descendants (Fig. 1b). If a group does not include all the descendants of a common ancestor, i.e., one or a subset of its descendants is not included, the group is paraphyletic (Fig. 1a).

Within the hierarchical system each rank can be regarded as a monophyletic group containing one or more smaller monophyletic groups. Among Mammalia (mammals) the Placentalia (mammals with placenta) constitute a monophyletic group. Furthermore, within Placentalia the Archonta (primates, colugos, and treeshrews), within the Archonta, the order Primates, within Primates the Haplorrhini (primates with dry noses), within Haplorrhini the Catarrhini (Old World monkeys and apes), within Catarrhini the family Cercopithecidae (Old World monkeys), within Cercopithecidae the genus *Papio*, and within *Papio* the species *Papio hamadryas* all form monophyletic groups or clades nested within the respective higher level group. Although the species is the central unit in taxonomy and in biodiversity conservation, finding an all-encompassing definition of species is difficult and thus, the delimitation of units as species often remains controversial.

Species Concepts

Ever since Linnæus (1758) instructed taxonomists to use a hierarchical species classification, researchers have been unable to define a single all-inclusive species concept. More than 20 species concepts have been proposed (e.g., Mayden 1997; Mallet 2006; Wilkins 2009) and discussions about these concepts have filled volumes. For primates, the species concepts most frequently invoked in recent years are the Biological Species Concept (BSC, Mayr 1942), the Recognition Species Concept (RSC, Paterson 1986), and the Phylogenetic Species Concept (PSC, Eldredge and Cracraft 1980; Cracraft 1997). Essentially, the BSC tends to lump groups into few species, whereas the PSC tends to split groups into more species. For instance, the number of recognized primate species increased from 180 in 1967 (Napier and Napier 1967) to 480 in 2013 (Mittermeier et al. 2013) partly due to more thorough surveys, but mainly due to the application of the PSC. This increase invoked the question whether it is real or just "taxonomic inflation" (Isaac et al. 2004; Tattersall 2007; Markolf et al. 2011). Fierce controversy emerged and subsists on the higher or lower numbers of species that are delineated by the application of different species concepts and on the incidence that such numbers have on the practice of conservation biology (Morrison et al. 2009; Dubois 2010; Frankham et al. 2012; Gippoliti and Groves 2013; Groves 2013; Gutiérrez and Helgen 2013; Zachos and Lovari 2013; Zachos et al. 2013a, b; Cotterill et al. 2014; Frankham et al. 2014; Russello and Amato 2014; Wilmet et al. 2014; Zachos 2015).

Given that evolution and speciation is a process in time, placing cut-offs somewhere along the transition from populations to species, remains somehow arbitrary and discrepancies between species concepts may arise because they look at different stages of the speciation process. For instance, the sequence of events for two recently separated lineages may begin with the appearance of diagnostic differences (criterion of the PSC), then reciprocal monophyly will occur and finally the two lineages become reproductively isolated (criterion of the BSC) (de Queiroz 2007; Tobias et al. 2010) (Fig. 2).

Therefore, no species concept can fully capture what a species is (Hendry et al. 2000; Hey 2006; Wiens 2007; Tobias et al. 2010). In principle, we are still at the same point as Darwin 1859 (Chap. 2, p. 25) when he wrote about the pointless exercise of defining the nature of species: "No one definition has satisfied all naturalists, yet every naturalist knows vaguely what he means when he speaks of a species." Darwin simply preferred not to address the issue of species concepts at all, but instead referred to varieties.

Species can be regarded as taxonomic hypotheses and depending on the applied species concept and available data, units or taxa are split or lumped together. The dynamics in taxonomic knowledge affects biodiversity assessment and conservation strategies and decision makers in conservation politics may be alienated. Usually they prefer to work with more static taxonomies and species lists when setting conservation priorities, but there is no agreed-on official species list and there may never be.

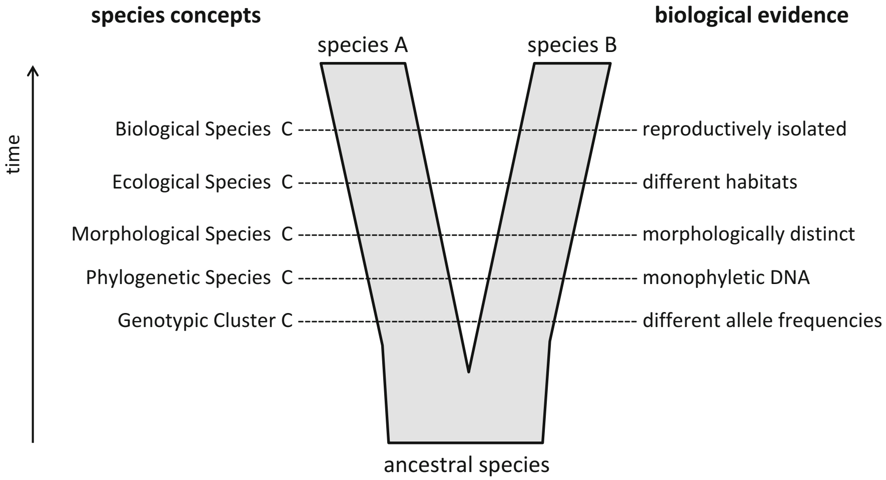

Fig. 2 Highly simplified diagram of speciation, possible sequence of species concepts, and corresponding biological properties of species (modified from de Queiroz 2007)

Species Delimitation

Since finding an all-encompassing definition of species is difficult, the delimitation of species remains controversial. However, we assume that species are real and that it is indeed possible to delimit them, because the process of speciation is most likely short compared to the long existence of the species, and that brief transitions between long-lasting and discrete entities (species) do not make those entities unreal (Coyne and Orr 2004). Christoffersen (1995), based on the PSC, provided some directions of how to delimit species on a more operational level. A species is "an irreducible cluster of sexual organisms within which there is a parental pattern of ancestry and descent and that is diagnosably distinct from other such clusters by a unique combination of fixed characters" (Christoffersen 1995, p. 448). Diagnosably distinct here means that they are 100 % diagnosable (given age/sex variation), they have fixed heritable differences between them, they are genetically isolated, though not necessarily reproductively isolated. A good example is the case of Northern and Southern white-cheeked gibbons (*Nomascus leucogenys* and *N. siki*). Both species are phylogenetically closely related (Thinh et al. 2010b) and females of both species are morphologically indistinguishable. However, males show a clear diagnosable character: while in *N. siki* the white cheeks extend just to the ears, in *N. leucogenys* they go well beyond the ears. Accordingly, both are classified as species and not just as subspecies of a single species.

Recently, molecular genetic methods have been applied to assist species delimitation. Molecular data can reveal the historical descent of lineages and the extent of gene flow between them. Such findings are relatively easy to interpret in the case of genera and families (Tobias et al. 2010), and phylogenetic analyses are therefore changing higher-level systematics in primates and other groups and improve the reliability of phylogenetic inferences. On the species level such approaches are not as easy to interpret, in particular since different genetic markers may provide different and contradicting phylogenies. When using molecular data, phenomena such as incomplete lineage sorting or (introgressive) hybridization can affect some genetic markers but not others, making groups diagnosable and reciprocally monophyletic for one set of markers and para- or polyphyletic for others.

For many taxa, differences in the mitochondrial genome have been used to diagnose species status (e.g., barcoding, http://www.barcodeoflife.org/). The barcoding approach is based on the assumption that by analyzing and comparing parts of the mitochondrial genome, taxon differences will be revealed, which can subsequently be used to delimit species (Tautz et al. 2003; Forsdyke 2013). This approach has been successfully applied to different taxonomic groups, including primates, and in many cases provided results that are congruent with results obtained by using other methods to delimit species (e.g., dissimilarities in morphology, behavior, or ecology). For instance, in several lemur groups many cryptic species have been discovered by the analysis of mitochondrial markers (e.g., *Microcebus*, Louis et al. 2006; Olivieri et al. 2007). Subsequently, for most taxa identified as potential species on mitochondrial differences species status was confirmed by using nuclear genetic data (Weisrock et al. 2010).

In other taxonomic groups the mitochondrial genetic approach failed to identity potential species. In baboons (*Papio*), mitochondrial clades mostly reflect the geographic provenance of the respective individual but not its taxonomic affiliation. No congruence was found between morphological characters used to delimit baboon taxa and their mitochondrial relationships (Zinner et al. 2009b, 2013b) (Fig. 3). Even more striking is the close relationship between the mitochondrial lineage of the southern yellow baboons and a population of kipunjis (*Rungwecebus kipunji*). If only the mitochondrial marker had been used, the kipunji would have been clearly delineated as a baboon. Zinner et al. (2009a), however, interpreted the close relationship as a result of introgressive hybridization.

The baboon example clearly shows that species delimitation based solely on one genetic marker (here mitochondrial sequence data) can result in a complete mess. Several authors have pointed to potential problems when using just one genetic marker to delineate species (Markolf et al. 2011, 2013; Stoeckle and Thaler 2014; Ermakov et al. 2015). We therefore agree that taxonomic decisions should be based on a number of characters. An ideal scenario would be an integrative approach involving a combination of genetic or even genomic, phenotypic, behavioral, and ecological data (e.g., Yoder et al. 2005; Padial et al. 2010; Wielstra et al. 2013; Dowton et al. 2014; Leaché et al. 2014).

The problem might even become more complicated if DNA information alone does not help to differentiate among species. In a population genomics study on carrion crows it was recently shown that small differences in gene expression (<1 %) is sufficient to maintain the phenotypic differences of carrion and hooded crows, although there is some gene flow between the two taxa (Poelstra et al. 2014). The results of the crow study stress the importance of using RNA-based information in addition to DNA, an approach, which most likely will also have to be applied in phylogenetic and phylogeographic studies on primate groups such as baboons.

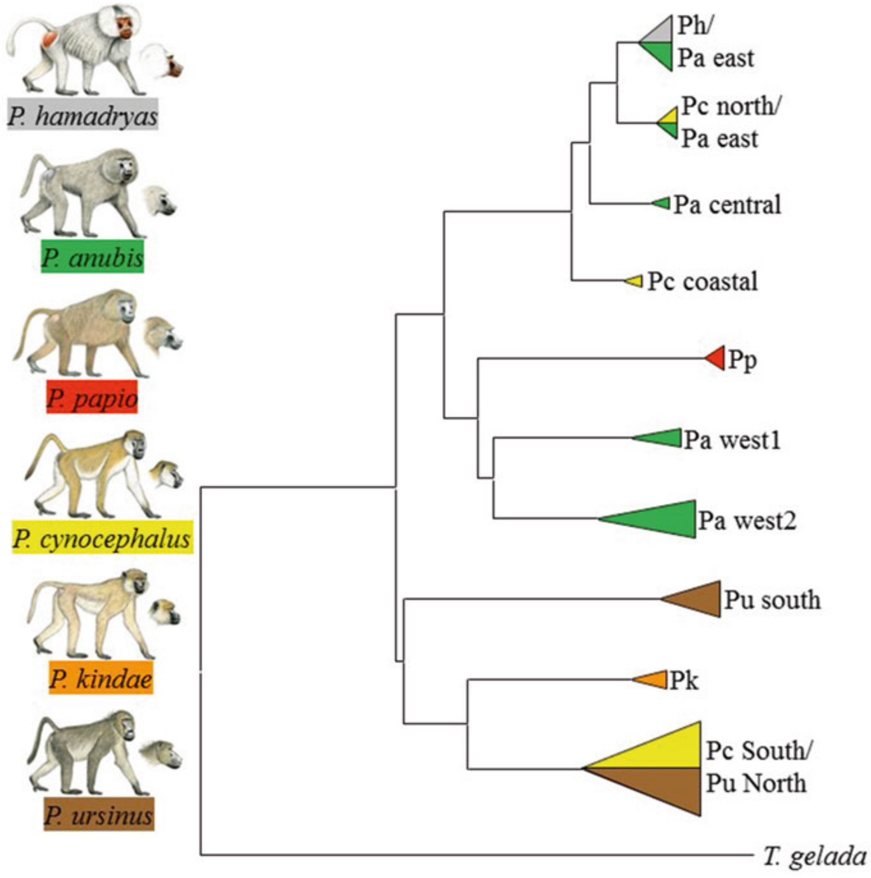

Fig. 3 Baboon phylogeny based on mitochondrial sequence data (Zinner et al. 2009b, 2013b). Para- and polyphyletic relationships are obvious among baboon species and almost no congruence between mitochondrial clades and morphologically classified species is indicated. Mitochondrial clades instead reflect the geographical provenance of the respective lineages. Introgressive hybridization was discussed here as a possible cause for the observed para- and polyphyletic relationships (baboon drawings by S. Nash)

Ranking of Taxa

Beside species delimitation, the ranking of taxa (assigning a taxon a rank in the hierarchical system) is another major problem in taxonomy. Even if species could be unambiguously delineated, the cut-offs for higher taxa would remain problematic (Fig. 4). One possible solution is to use genetic distance between sister taxa to delimit higher ranks and given that genetic differences accumulate by time, genetic distance correlates somehow with divergence ages (Goodman et al. 1998). By applying molecular clocks, divergence ages can be determined, but since molecular clocks run differently in different taxa a simple rule of thumb, such as if the

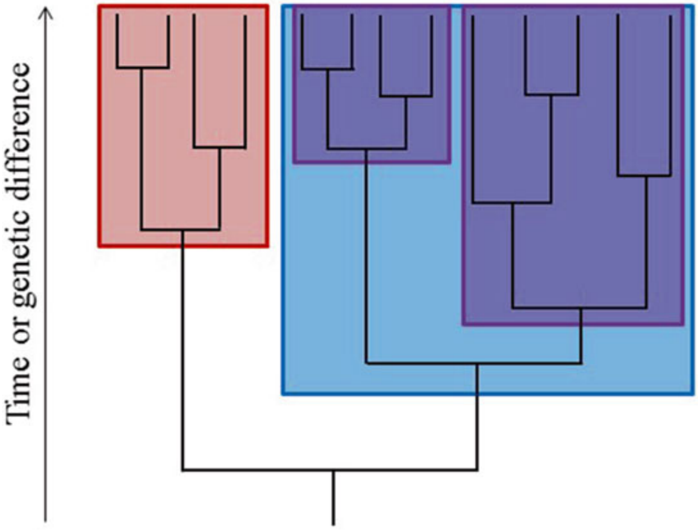

Fig. 4 A nested hierarchy and monophyly as species criteria. Hypothetical phylogenetic reconstruction with several alternative possibilities to delimit species according to monophyletic relationships. Since monophyletic clades are nested within monophyletic clades (e.g., *purple* nested within *blue*) the problem of how to decide at which level we will make the cut-off to delimit species and how to rank the monophyletic groups (taxa) arises. Should we delineate two *purple* and one *red* species or one *red* and one *blue* species or should we rank the *red* clade as a monotypic genus and the blue clade as a genus with two (*purple*) species?

divergence age between two taxa is two million years, we have two species, if it is four million years, we have two genera, and so on, is thus not applicable. Groves (2012) argues that ranking processes based on genetic distances are highly subjective and the same is true when evaluating the time of divergence (Alström and Mild 2003).

Primate Taxonomy

As mentioned the number of primate species increased dramatically over the last decades, mainly due to the application of the PSC (Groves 2011, 2012) and by routinely implementing molecular methods, but also due to surveys in remote areas and an increase in knowledge about species' ecology and behavior. Although several recently described primate species were indeed newly discovered in previously unexplored areas including the kipunji (*Rungwecebus kipunji*, Jones et al. 2005; Davenport et al. 2006), the lesula (*Cercopithecus lomamiensis*, Hart et al. 2012), and the Myanmar snub-nosed monkey (*Rhinopithecus strykeri*, Geissmann et al. 2011), most other recent species descriptions, however, rely on splitting a geographically widespread species into various locally restricted species or raising subspecies to species (e.g., *Microcebus*, *Lepilemur*, *Avahi*, *Callicebus*, *Piliocolobus*).

Molecular analyses provided fundamental insights into the evolutionary history of primates on all taxonomic levels and the taxonomic classification of primates on family or genus level changed accordingly. For example, New World monkeys originally contained only two families (Callithrichidae, Cebidae) (Napier and Napier 1967). Today we know that the original Cebidae family (comprising all non-callitrichid New World monkeys) is a paraphyletic group and thus should be divided into four families. This division is now widely accepted and there is consensus that the Pitheciidae split off first, followed by the Atelidae, before finally Cebidae (now containing only capuchin and squirrel monkeys), Aotidae and Callithrichidae diverged, while the relationships among the latter three families are still unresolved (e.g., Osterholz et al. 2009; Perelman et al. 2011; Finstermeier et al. 2013). Another good example for a misclassification of primates at the family level is provided above with the case of great apes and humans.

At the genus level, various changes and shifts occurred as well. For tarsiers it was recently shown that the lineages from the Philippines, the western Sundaland, and from Sulawesi diverged in the Miocene (Shekelle et al. 2010) and hence, these three are now classified as three genera (*Carlito*, *Cephalopachus*, *Tarsius*) (Groves and Shekelle 2010). Galagos originally contained only two genera (*Galago* and *Euoticus*) (Schwarz 1931), but today five genera are recognized (Mittermeier et al. 2013). For dwarf galagos (*Galagoides*) polyphyly was confirmed with the species from the African Eastern Arc forming a sister clade to *Galago*, while the more western species fall into a clade that is basal to *Otolemur*, *Sciurocheirus*, *Galago*, and the dwarf galagos from forests of the Indian Ocean catchment area in Africa (Pozzi et al. 2014, 2015). Accordingly, the dwarf galagos from the African Eastern Arc need a new genus name. Likewise, the African papionin clade originally contained only two genera, *Papio* subsuming the more robust morphotypes (baboons, gelada, drill, mandrill) and *Cercocebus* consisting of the more slender mangabeys (Napier and Napier 1967). Morphological and genetic investigations, however, have shown that the drill and mandrill cluster together with white-eyelid mangabeys, that the kipunji is the closest relative of baboons, and that the three lineages, the kipunji-baboon clade, the gelada, and the crested mangabeys diverged within a relatively short time period, although their phylogenetic relationships remain unresolved so far (Harris and Disotell 1998; Fleagle and McGraw 1999; Page and Goodman 2001; Finstermeier et al. 2013; Liedigk et al. 2014). Accordingly, the African papionins were divided into six genera: *Papio* (now containing only baboons), *Rungwecebus* (kipunji), *Theropithecus* (gelada), *Lophocebus* (crested mangabeys), *Mandrillus* (drill, mandrill), and *Cercocebus* (now containing only white-eyelid mangabeys) (Mittermeier et al. 2013). Similarly, the African genus *Cercopithecus* contained until recently the arboreal guenons, green monkeys, and terrestrial guenons, but it was shown that the latter two are closely related with patas monkeys (*Erythrocebus*) (Tosi et al. 2004), and hence, both were separated from *Cercopithecus* and classified in their own genera *Chlorocebus* (green monkeys) and *Allochrocebus* (terrestrial guenons) (Mittermeier et al. 2013). The lesser apes were originally divided into only two genera, *Symphalangus* with the siamang and *Hylobates* subsuming the remaining gibbon species (Napier and Napier 1967). However, today four major gibbon lineages are recognized which exhibit distinct diploid chromosome numbers and which diverged from each other roughly at the same time (Carbone et al. 2014). Accordingly, these four lineages are today recognized as four genera (*Symphalangus*, *Hylobates*, *Hoolock*, *Nomascus*) (Mittermeier et al. 2013). An example for shifting species from one into another genus is that of two langur species from the Indian subcontinent. While originally placed in the genus *Trachypithecus* (Napier and Napier 1967) the Nilgiri langur (*T. johnii*) and the purple-faced langur (*T. vetulus*) are today recognized as members of the genus *Semnopithecus* (Osterholz et al. 2008; Mittermeier et al. 2013). In other cases, new evidence suggests a return to an older classification, e.g., in the case of the woolly monkeys of the Neotropics. Groves (2001) separated the yellow-tailed woolly monkey *flavicauda* in its own genus *Oreonax* from other woolly monkey species (genus *Lagothrix*), but recent molecular investigations clearly showed that *flavicauda* and the other woolly monkey species are closely related thus suggesting the presence of only a single genus (*Lagothrix*) (Di Fiore et al. 2015).

The most extensive taxonomic changes in primates apply to the species level, with a general trend of an increasing number of species (from 180 in 1967 to >480 in 2013) in all families due to the application of the PSC and molecular techniques. A few examples are provided here. Most prominent are the nocturnal lemurs of Madagascar. Until the beginning of the 1990s, only two species of mouse lemurs have been recognized (*Microcebus murinus*, *M. rufus*). Today we list more than 15 *Microcebus* species (Mittermeier et al. 2013). Is this taxonomic inflation? Or does it reflect the evolutionary history and the existing number of cryptic species (Tattersall 2007)? Most of the recent mouse lemur species descriptions relied solely on sequence data of a mitochondrial DNA fragment, but multi-locus nuclear sequence data subsequently confirmed that most of these newly described species are indeed genetically distinct from each other (Weisrock et al. 2010). Further, with increasing knowledge of the behavioral ecology of these species, we see that they are indeed distinct from each other, in their ecological niche, behavior, vocalization, etc. Accordingly, despite being phenotypically cryptic species, they are likely valid species and the species richness of the genus *Microcebus* was underestimated. The same is true for most other Malagasy lemurs, e.g., the dwarf lemurs (*Cheirogaleus*), sportive lemurs (*Lepilemur*), or woolly lemurs (*Avahi*) for which numerous new species have been described in recent years (e.g., Rasoloarison et al. 2000; Andriaholinirina et al. 2006; Zaramody et al. 2006; Lei et al. 2014), or the sifakas (*Propithecus*) or "true" lemurs (*Eulemur*) for which many subspecies have been elevated to species (Mittermeier et al. 2013).

In the African and Asian cousins of the lemurs, the galagos, pottos, and lorises, the number of species increased due to new species descriptions and ranking subspecies as species (e.g., Grubb et al. 2003; Roos et al. 2007; Munds et al. 2013). This is mainly the result of improved knowledge about their biology and evolutionary history and with further information additional splitting can be expected for these primates. Tarsiers were recently not only divided into three genera, but also the number of species increased to a total of 11 (Mittermeier et al. 2013). For both, New World and Old World monkeys, the number of species increased dramatically over the last decades, mainly because taxa formally ranked as subspecies are now listed as species. This has occurred in howler monkeys (*Alouatta*), spider monkeys (*Ateles*), capuchin monkeys (*Cebus*, *Sapajus*), tamarins (*Saguinus*), baboons (*Papio*), green monkeys (*Chlorocebus*), red colobus monkeys (*Piliocolobus*), hanuman langurs (*Semnopithecus*), and doucs (*Pygathrix*). However, some New and Old World monkey species recognized today are indeed new to science. These include the Rondon's marmoset (*Mico rondoni*, Ferrari et al. 2010), the Hernández-Camacho's night monkey (*Aotus jorgehernandezi*, Defler and Bueno 2007), the Vieira's titi (*Callicebus vieirai*, Gualda-Barros et al. 2012), the kipunji (*Rungwecebus kipunji*, Jones et al. 2005; Davenport et al. 2006), the lesula (*Cercopithecus lomamiensis*, Hart et al. 2012), the Myanmar snub-nosed monkey (*Rhinopithecus strykeri*, Geissmann et al. 2011), or the white-cheeked macaque (*Macaca leucogenys*, Li et al. 2015). Finally, taxonomic changes in apes have also occurred, most prominently in the gibbons, where today 19 species are recognized (Mittermeier et al. 2013). One of these—*Nomascus annamensis*—was newly described in 2010 (Thinh et al. 2010a). The great ape genera *Pongo* (orangutans) and *Gorilla* (gorillas) formally contained only a single species with two and four subspecies, respectively, but today both orangutan subspecies were elevated to species and gorillas were divided into an eastern (*G. beringei*) and a western species (*G. gorilla*), each with two subspecies (Mittermeier et al. 2013).

Conclusion

Classifying and naming things seems to be a human universal, making communication about the environment possible which most likely had fitness advantages. In particular with respect to living things, humans everywhere think about plants and animals in highly structured ways, and rank organisms into lower- and higher-order groups. Interestingly, such folk-taxonomies show strong congruence with the Linnaean taxonomy, at least for vertebrates and higher plants. The basic entity of the indigenous classification systems is most often equivalent to species in the scientific taxonomy, providing additional arguments that biological species are real and not only a construct of taxonomists' imagination (Mayr 1982). Nevertheless, species definition and species delimitation remain controversial with subsequent consequences for biodiversity assessment and species preservation.

In our view, conservation biology, including primate conservation, is informed by taxonomy in two fields, and in light of limited resources for conservation, both are related to the "agony of choice" (Vane-Wright et al. 1991). (1) Assessing species diversity (How many species occur in a certain area?) and (2) in conservation priority setting (Which areas or species should be prioritized for conservation?). In both fields, the question of whether a taxon qualifies as species is essential. Beside the problem of species delimitation, the impact of taxonomy on primate conservation and conservation in general is affected by insufficient knowledge about diversity on inter- and intraspecific level and data deficiencies in species distribution. The identification and description of further primate taxa, either due to the discovery of truly new species in geographically so far unexplored areas or because of the application of molecular methods resulting in the splitting of formally widespread "species," would dramatically alter the vulnerability of these taxa to extinction, making an understanding of their taxonomy an area of urgent conservation action.

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Government and Community Based Primate Conservation Initiatives in Peru

Noga Shanee

Introduction

Peru is considered one of the most biodiverse countries on earth (Rodríguez and Young 2000; Pacheco et al. 2009; Schulenberg et al. 2010). In Latin America, Peru ranks third in both overall and endemic mammal diversity (Pacheco et al. 2009). Globally it ranks fourth in terms of primate species diversity (47), third in diversity of genera (12), and joint first in diversity of primate families (5 families, together with Brazil, Colombia, and Madagascar) (IUCN/PSG 2012).

Primates are widely distributed throughout Peru in the eastern Amazonian lowlands, Eastern Andean cloud forests, inter-Andean valleys, and the northern coastal forests bordering Ecuador (Aquino and Encarnación 1994). The eastern Andean mountain forest, or *Yungas*, forms part of the "Tropical Andes Biodiversity Hotspot," considered the most biodiverse area on earth and a global conservation priority (Myers 2003; Myers et al. 2000). Three of Peru's endemic primate species are restricted to the north of the country (Shanee 2011; Bóveda-Penalba et al. 2009; Shanee et al. 2011a; Mittermeier et al. 2009; Mittermeier et al. 2012a), two of them are considered "Critically Endangered," the yellow-tailed woolly monkey, (*Lagothrix flavicauda*) and the Rio Mayo titi monkey (*Callicebus oenanthe*) (Cornejo et al. 2008b; Veiga et al. 2013). Both of these species have repeatedly been listed among the world's 25 most threatened primate species (Mittermeier et al. 2012b), due to drastic population reductions caused by massive deforestation. The third endemic primate, the Peruvian night monkey (*Aotus miconax*), is one of the least known of all primates and would be better considered Endangered rather than Vulnerable in the IUCN Redlist of based on estimates of habitat loss and population decline (Shanee et al. 2015).

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An estimated 4.5 million people live in the Peruvian *Yungas* (CDC-UNALM and TNC 2006), many of them recent migrants from neighboring highland and lowland regions (INEI 2007). The subsistence and economic needs of this large human population places growing pressure on forests. By the year 2000 Peru had lost 7,172,953 ha (10.3 %) of its original forest cover. The regions with the highest deforestation rates were: San Martin with 1,327,736 ha (25.9 %) and Amazonas with 1,001,540 ha (25.5 %) of forest loss (PROCLIM/CONAM 2005). Both regions contain the main habitat for three of Peru's endemic primate species (Shanee 2011; Leo Luna 1980, 1987; Shanee et al. 2011a; Bóveda-Penalba et al. 2009; Cornejo et al. 2008a; Shanee et al. 2012). The steep slopes of the Andes can be a deterrent to agriculture, especially considering that soil erosion and leaching are severe problems for slash and burn and mechanized agriculture (Juo and Manu 1996; Soto et al. 1995; Rumpel et al. 2006; McDonald et al. 2002). Although many different crops are farmed in the Peruvian Andes, cattle ranching is the main cause of deforestation and biodiversity loss (Steinfeld et al. 2006; Kaimowitz 1996; Shanee 2012a). In the lowland rainforests, the main threats to primate species are subsistence hunting, hunting for the illegal pet trade, and habitat alteration related to deforestation for pasture, agriculture, road construction, gold mining, oil extraction, and timber extraction (Finer et al. 2008; Alvarez-Berríos and Aide 2015; Ministerio del Ambiente 2014a; Gutiérrez-Vélez and DeFries 2013).

As is the case in other parts of the world, NGOs influence the dynamics of conservation in Peru. However, this chapter does not specifically discuss NGOs as they are so diverse in their sizes, performances, and challenges that they could not be included in this scope. Government initiatives that directly protect primate species are mostly involved with the creation of protected areas and control measures to tackle the illegal wildlife trade and deforestation. Local communities protect primates and other wildlife through the creation of protected areas which they formally register with the relevant authorities and informal conservation initiatives such as placement of internal prohibitions on deforestation and hunting (Shanee et al. 2014b). This chapter aims to compare the potential and actual challenges and opportunities of both government and community based primate conservation initiatives focusing on the role of individuals within the implementation of these initiatives.

Methods

I employed a range of social science research methods to collect data from a variety of sources. Ethnographic methods are an effective tool for understanding complex, local, social situations (LeCompte and Schensul 1999). They engage the researcher in the lives and activities of the target population by utilizing the researcher's senses and working according to his/her intuition. The conservation initiatives reviewed in this article are from authorities, communities, associations, and individuals who are directly and indirectly involved in primate conservation in Peru.

Interviews with key informants—Individual, in-depth interviews are possibly the most widely used social research method (Fielding and Thomas 2001). They enable researchers to carry out a deep exploration of a wide variety of topics and discover new topics, as well as giving informants time and space to present and develop their ideas (Durand and Vázquez 2010; Schensul et al. 1999). Unplanned, informal interviews, in the form of spontaneous conversations arising from participant observation opportunities, were also chosen because of their non-standardized character, which is beneficial where the subject is complicated or sensitive (Fielding and Thomas 2001). Also, formal interviews, especially if they include recording devices are alien to rural people prove inefficient in generating valuable data. Short outline notes were sometimes taken during the conversation, but normally immediately afterwards. At the end of these interviews, the interviewees were asked if the information discussed could be used as part of the study and if they wished to remain anonymous.

Participant Observations—The extended field work period (approximately 8 years) and participative methodologies allowed prolonged exposure to social and environmental processes in addition to evidently increasing mutual understanding and trust between researcher and participants. Observations took place in a wide range of settings such as forest field trips, internal and public meetings organized by institutions or communities and participating in wildlife confiscations, as well as visiting field sites and conservation initiatives among many other planned and spontaneous observations or conversations. Through contact with authorities in different regions throughout Peru and in the central government, I gathered information about protected areas solicited and awarded, law enforcement strategies, the attitudes of the authorities and the challenges they face. I also reviewed relevant national and international laws. These enhanced the quantity and diversity of data collected through its validation.

Case studies—Case studies are an important and well-known anthropological methodology (Eckstein 1975; Stake 1995; Mitchell 2006; Flyvbjerg 2006). It is a strategy which seeks to understand the dynamics of single settings, extrapolating the insights gained to construct theories (Eisenhardt 1989).

This research was undertaken within one of the most biodiverse and threatened countries in the world using examples from the Tropical Andes Hotspot, which is referred to as the “Global Epicenter of biodiversity.” Conservation initiatives directed towards the protection of the yellow-tailed woolly monkey, one of the most endangered primate species on a global level, were also used. Many smaller case studies are embedded throughout the text. The study and its case studies were chosen as unique situations and dramatic events, or, as defined by Mitchell (2006) “atypical cases” chosen for their illuminating power and because they “may make theoretical connections apparent which were formally obscure” (Mitchell 2006). According to Eisenhardt (1989), because of their reliance on actual events case studies are particularly likely to lead to the creation of novel theories due to their ability to expose contradictions and paradoxes. They are also testable, and have high empirical validity. Hence, this methodology is "particularly well suited to new research areas or research areas for which existing theory seems inadequate." All data and quotes were gathered in Spanish and were translated to English by the author.

Data Analysis

The use of coding classification offered by the NVivo program facilitates systematic, careful handling of qualitative data, as similar themes and concepts are compared and contrasted with each other within a chronological framework (Fielding and Thomas 2001). The study is part of a long-term political ecology research of conservation initiatives in Peru. It took place during my time as a co-director of the Yellow-Tailed Woolly Monkey Project, run by UK non-governmental organization (NGO) "Neotropical Primate Conservation" (NPC). My personal engagement with conservation initiatives in the study area allowed for an intimate understanding of both degradation and conservation processes.

Protected Areas

Governmental Run Protected Areas

According to Article 68 of the Political Constitution of Peru "The state is obliged to promote the conservation of biodiversity and protected areas." Peru has 76 nationally protected areas totaling 19,518,146 ha in ten different protection categories, and 16 regional conservation areas protected by regional governments, covering an additional 2,407,966 ha (SERNANP 2015). These protected areas are made by the ministry of the environment in Lima through a supreme decree as a reserved zone, which passes through a lengthy process of adjustment to its geographical limits in coordination with communities in the surrounding area. The area is then categorized as one of the existing protected area categories. This process can take many years, the Alto Mayo Protected Forest was created in 1987, covering 182,000 ha and protecting Peru's three endemic species. It was not until 2000 that its first park management was established and park guards were employed (INRENA 2008). During the intervening years, protection of the reserve was not enforced, allowing mass inmigration across its boundaries resulting in the deforestation of large areas and hunting. There are an estimated 3000 families currently living inside the reserve and by 2009, 26,000 ha had already been deforested, equal to about 15 % of the area covered by the reserve (INRENA 2008; ICAM 2011). Another often used critique on the way protected areas are created in Peru is that despite the countries cultural and biogeographical diversity, protected areas all over the country are formed and function under the same model, no matter if the model is suitable or not for each area. A new law (Law No. 30230), signed by President Ollanta Humala in 2014, overrides the authority of the ministry of the environment in creating new protected areas and significantly reduces its authority in controlling environmental damage resulting from extraction projects such as mining and the exploitation of fossil fuel reserves. It also allows exploitation in any newly formed protected areas.

Although it is commonly agreed that the participation of local people is essential to successful conservation initiatives (Adams 2004; Hulme and Murphree 1999), it is recognized that opportunities offered by protected area management is often used as a “lip service” to support top-down practices allowing only passive cooperation and consultation (Durand and Vázquez 2010; Pimbert and Pretty 1997; Cooke and Kothari 2001; Few 2001). This study found in Northern Peru where local people are often discriminated against and ignored during conservation planning and implementation and are subject to prejudice and abusive discourses. It has been suggested that although local people in Northern Peru are attracted to the idea of conservation and initiate conservation projects themselves, they are opposed to the way conservation is often administrated by outsiders such as the government and NGOs (Shanee 2013). Therefore, local participation in government conservation initiatives is limited and there are even retaliatory actions such as the burning of parts of the Alto Mayo Protected Forest in 2010 as well as death threats and physical abuse toward park managers and guards. In another recent case the authorities in charge of the categorizing of the Rio Nieva Reserved Zone were prohibited from entering the area by several neighboring communities. They were taken hostage for a few hours during which time they received numerous death threats. They were later released after having signed an agreement not to enter the area again, an agreement that was canceled in a general meeting with the communities a few months later. The authorities believed the attack on them was a result of incitement against the reserve on the part of land traffickers and maybe also drug cultivators who use these lands for their illegal activities.

Community Run Protected Areas

Peru has two kinds of nongovernment protected areas, one, on privately owned lands, such as titled family plots or community lands, can be registered as a Private Conservation Area (ACP) for an unlimited period through application to the Ministry of the Environment. The other, on untitled state land, involves registration of the area with the respective Regional Government as a Conservation Concession (CC) renewable for up to 40 years. Ecotourism Concessions and Ecological Service Areas are other legal mechanisms under which land can be protected. Currently there are 75 ACPs in Peru, totaling 259,522 ha, 55 Conservation Concessions, totaling 1,041,626 ha, and 44 Ecotourism Concessions, totaling 100,195 ha (Lo and Monteferri 2014).

Local people’s rationales for conservation initiatives include an appreciation of nature’s intrinsic value, religious or spiritual value, aspirations for sustainability and a concern for future generations, and as an arena for the struggle for social justice and recognition (Shanee 2013). These communities often take pride and satisfaction in the return of, and increases in, populations of wildlife as a result of their initiatives. The main obstacles faced by local people who want to legally protect lands are the extensive legal requirements for registering the areas and lack of access to support from governmental and nongovernmental institutions, as well as the lack of economic resources to pay for the initial registration and to fund the area in the future (Shanee et al. 2014b).

In Northern Peru the social pressures related to gossip narratives can inspire very strong and even violent acts towards conservation promoters. The initiator of a Conservation Concession in San Martin Region was the victim of a social boycott and allegations that he later blamed for causing him depression, sickness, and other physical side effects. He was accused by his neighbors of selling the land he was protecting to mining companies, being paid by "the NGO," and becoming rich at the community's expense. In another community, which made a private conservation area that protects a population of *Lagothrix flavicauda*, the people threatened to burn the house of a local man who led the conservation process and banned the entrance of all NGOs to the area.

The "farmers for the Conservation of the Natural Forests of Simacache" is a small association of local farmers that took it upon itself to conserve a 41,000 ha Conservation Concession. Inside the area there are many land traffickers, land invaders, loggers, and hunters aided by an increasing number of roads constructed by nearby logging concessions. The association receives technical help from NGOs but does not receive substantial financial help and therefore the members invest much of their own money in many of the activities. Since 2012, the association has filed three complaints at the environmental public prosecutor's office against a group of land invaders, led by an engineer who provides them with false land property documentation. All three complaints were archived by the prosecutor's office without explanation. In December 2013, during a field trip to mark the limits of the concession, six of the association's members were assaulted and kidnapped by a group of land invaders living inside the concession. All their belongings were taken and they were threatened at gunpoint that if they did not cancel the reserve they would be killed. Among the things taken from them was a small digital camera that they used to document hunted wildlife they found in one of the invaders houses as proof of illegal hunting. The kidnappers then used these same photos to file a legal complaint at the environmental prosecutor, with the help of a lawyer, against the association, for poaching. This complaint was only archived after a lawyer hired by the association made a full report proving that the complaint had no factual base. However, in all cases reviewed during this study the gossip narratives and antagonist actions were drastically reduced approximately 1 year after beginning work on the reserves, with a growing number of local people joining the conservation initiators in their efforts. Despite the great social pressures, the initiators themselves sacrifice a great deal to assist their communities and promote conservation programs and the majority of locally run reserves do get registered despite the difficulties.

Another example of grassroots conservation is the work done by the Ronda Campesina, a network of autonomous civil organizations aimed at self-protection. They practice vigilance and civil justice in the rural Peruvian countryside where state control is insufficient (Langdon and Rodriguez 2007; Nuñez Palomino 1996; Rojas 1990; Gitlitz 1995; Yrigoyen 2002; Gallay 2002; Starn 1999). It is the largest and most influential grassroots movement in Peru. The Ronda supports many conservation initiatives run by other institutions but also initiate their own projects. Because of their extended network throughout the country, Rondas are able to reach a wide rural population. They run environmental education talks in rural areas, implement mechanisms for controlling deforestation and hunting within their traditional penalty system and protest against extractive industries. The size of the organization means that environmental messages transmitted through the Ronda are received by a large section of the rural community, including many of the most remote areas. In 2012 the Ronda launched a new conservation model: Ronda Conservation Areas (ARCAs). Reserves are set by signing an internal agreement in a Ronda assembly and are not officially registered with the government offices. These reserves have a double impact, most importantly they allow fast and effective conservation from local initiatives while focusing attention on state conservation systems that necessitate high economic investment and lengthy bureaucratic processes, excluding local people, and missing many opportunities for conservation by a population that does not have the means or academic expertise to follow traditional conservation routes. There are already hundreds of ARCAs throughout Peru that are autonomous initiatives of many different Ronda bases, ranging from tens to thousands of hectares each. Critically, many of these reserves were created autonomously before the launch of the ARCA model; however, these reserves are not georeferenced nor formally registered. Therefore although they have strong presence on the ground, quantifying their coverage and impact is difficult.

Wildlife Trafficking and Deforestation Control

State Law Enforcement Initiatives

Peru is in the process of updating its environmental legal framework and the authorities in charge of tackling deforestation and wildlife extraction were recently restructured and updated with a focus on decentralization (Sears and Pinedo-Vasquez 2011; Ravikumar et al. 2013). However, the authorities still face many problems dealing with wildlife trafficking related to outdated and complicated laws, lack of personnel (especially specialists in fauna), frequent changes in staff and institutional structure, lack of resources and equipment, excessive bureaucracy which hinders both confiscations and prosecution of wildlife crime, lack of rescue centers, the threat of personal lawsuits and physical aggression, and local politics that place extra obstacles in the way (Shanee 2012b).

The authorities are divided into various different offices, each with limited responsibilities and cooperation between them is necessary for all actions. It was repeatedly noticed that the connection between the offices is very lose, in many cases they did not even have each other's contact details. There are many disagreements and the passing of responsibilities between the offices is common. The environmental legal framework is also complex and divided between many different laws and institutional regulations. In several cases, the authorities expressed confusion over which animals should be confiscated or what constitutes an illegal activity or offense. Other doubts expressed by the authorities were observed during the interventions themselves, especially on species identification, handling, and technical information given to the perpetrators to explain the problems related to the maintenance of wildlife in captivity. It is clear that of the different types of environmental crime, such as timber trafficking and illegal gold mining, wildlife traffic receives significantly less attention.

Peruvian law also prohibits the burning or clear cutting of any type of forest without explicit authorization from the competent authorities. However, severely understaffed and underequipped authorities are unable to identify and intervene in many such cases, especially in areas further from roads, where healthy populations of primates are more likely to exist. At the Copenhagen Climate Conference in 2009, Peru announced targets to achieve zero deforestation by 2020, and in 2010 launched the National Program to Conserve Forests for the Mitigation of Climate Change, which aspires to conserve 54 million ha of forest.[1] Even so, deforestation levels are extremely high, rates varied from 123,200 ha/year between 2000 and 2009 to 105,975 ha/year between 2009 and 2011. A sharp increase in 2013 brought deforestation rates to the highest ever with 145,000 ha of rainforest cleared (Mongabay 2014; Ministerio del Ambiente 2014a, b).

Environmental authorities in Peru do not have incentives to take initiative and very often capitulate in front of threats and violence, under strong pressure from their coworkers and the threat of dismissal from their superiors not to act in certain cases, probably due to corruption. In many cases, employees that act against their superiors are dismissed and in others they leave their posts or give up hope of making changes. A common explanation given by authorities for the high level of corruption is that as everyone is corrupt, you either enjoy the bribe like everyone else or are killed by the traffickers, so there is no real choice.

The decentralization process that started in 2008 is still not complete (Ravikumar et al. 2013), some of the regional environmental authorities' responsibilities are still under the control of the ministry of agriculture but all the "Selva" regions, where most primate habitats and traffic exist already have regional environmental authorities run by the respective regional governments. The Forestry Service (SERFOR) of the central government has very little control over the regional authorities. The central government does not stipulate either a minimum budget for each regional government to invest in wildlife and deforestation control nor a minimum of activities the regional authorities are

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[1] Supreme Decree 008-2010-MINAM, 15.7.2010.

obliged to undertake. Therefore, the level of efficiency in controlling wildlife crime largely depends on local politics rather than national or international policies (Shanee 2012b).

It was observed that general, human, and economic resources in Peru are dramatically reduced as conservation initiatives get closer to implementation. Budgets descend from the international to local level whilst diminishing drastically (Shanee 2012a). Individuals constantly aspire to higher positions as those that stay at entry level posts, such as field biologists, park guards, and wildlife authorities in charge of interventions are either unmotivated, lack skills and social connections, or individuals motivated by ideology rather than self interest.

San Martin region is a region with comparatively good practices in wildlife trafficking control (Shanee 2012b). In fact San Martin has become known nationally for its unique progress in environmental policies especially in relation to its management of wild fauna. There is a very small group of people in charge of fauna control in the region that, with scarce resources, tackle all types of wildlife crime, organizing dozens of interventions a year to confiscate pets, seize meat from bushmeat markets, transportation companies, private houses, and illegal zoos, among others. They have legalized four rescue centers in the region that not only provide homes for rescued animals confiscated in San Martin, but also receive animals from the rest of the country. There has been a definite reduction in wildlife found illegally in captivity in San Martin since the beginning of the work of this group. Moreover, roadblocks on the main highway between the Amazonian and Coastal regions, which are organized by the regional government of San Martin, help reduce national trafficking levels. The future of this administration is however unclear. All existing staff may soon be placed by the new regional government in San Martin. Another example, an environmental public prosecutor working in Pucallpa, one of the most notorious wildlife trafficking centers in Peru, managed to confiscate hundreds of animals over the course of just a few weeks, including several interventions at the Bella Vista wildlife market, the biggest and one of the least controlled open markets in the country.

Communal Control of Hunting, Wildlife Trafficking, and Deforestation

As explained above local people find it hard to access the resources and expertise needed to officially register conservation areas. Informal conservation initiatives are different ways in which local people bypass these problems. Informal conservation initiatives can include voluntary agreements to control deforestation and/or hunting. These type of initiatives, although sparsely documented and hard to quantify, are very common in Peru and have significant importance for primate conservation (Shanee et al. 2014b).

As mentioned above, the Ronda Campesina is a great example of a grassroots organization controlling hunting and deforestation. In 2009 the Rondas of Amazonas region, and in 2013 the Rondas of San Martin region, decided unanimously to work towards the eradication of wildlife trafficking in these regions. Although they seldom confiscate wildlife themselves, they repeatedly talk about hunting and deforestation in their environmental education sessions in rural communities. They often use primates as examples of animals that should be respected and protected, repeating information they receive from outside conservation agents about primates' importance as seed dispersal agents and vulnerability to hunting. Local people that hunt, burn, and clear cut forest are often sentenced and punished by the Ronda assembly, paying fines, doing communal work, and/or nights of enforced physical exercise, depending on the severity of the infraction. The involvement of the Ronda Campesina is extremely important in rural areas that rarely receive visits from official environmental authorities. The Rondas are part of the communities they operate in; therefore, their ability to identify and capture environmental criminals is much greater than outside agents that arrive for short visits.

A recent study in Amazonas reported increases in group (18.8 %) and individual (35.9 %) densities of the Critically Endangered yellow-tailed woolly monkey (*Lagothrix flavicauda*) as well as a reduction in deforestation rates after 5 years of informal conservation efforts by the Yambrasbamba community (Shanee and Shanee 2015). The same study also reported that after signing agreements to control hunting and deforestation in an ~80,000 ha area surrounding a 7174 ha Conservation Concession, villagers reported that the Endangered white-bellied spider monkey (*Ateles belzebuth*), which until recently were only found 4–5 h walk from villages, can now be found very near agricultural fields just 1 h walk from villages following 5 years of voluntary hunting controls (Shanee and Shanee 2015).

However, initiatives of this type are largely informal and therefore have no legal power against national and regional development plans such as mining and roads. They also struggle to control the constant in-migration of settlers to informally protected areas. The informality of these initiatives often leads to them being less respected by surrounding communities and, in the long term, even by the initiators themselves. A man in Yambrasbamba, Amazonas, complained that he wanted to conserve his forest but his neighbor often trespassed to hunt primates without his permission. In a meeting in Vista Alegre, a local man criticized local authorities for not respecting their own initiatives: "The authorities of the villages announce intangible zones, but after a few years they start dividing these areas between whoever wants them. Then they decide to conserve new areas."

Again, like in all other types of conservation initiatives, the individuals that promote them often find themselves threatened by litigation or violence, both if they are protecting lands and wildlife against private invaders or large extractive industry. Ronda leaders are often denounced to the public prosecutors by the people they have punished, opening legal processes that, because of the inefficiency of the justice system, may take years to be resolved. People fighting against mining, petrol or palm oil companies find themselves with even greater legal problem, often with false accusations. Edwin Chota, an indigenous leader, was murdered in 2014 together with three of his co-protesters who were fighting against illegal loggers invading their ancestral territory (Global Witness 2014).

Discussion

Many of Peru's primates are under severe threat of extinction and current conservation efforts are far from sufficient to offset the mounting pressures they face. This is especially true for the endemic, altitude restricted primates (Shanee 2012a, Shanee, S. this volume, Shanee et al. 2011b; Shanee and Shanee 2014; Shanee et al. 2014a). Although national laws offer protection to threatened species and forests, legal loopholes, as well as impoverished, untrained authorities, mean that the laws' impact "on the ground" is severely reduced and the system's corruption and ineffectiveness, results of complex legal and institutional frameworks, not only allow but also encourage black markets (Smith et al. 2006; Shanee 2012a, b). This confusion and the overlap of responsibilities regarding environmental issues between different government offices is, at least in part, a symptom of Peru's incomplete decentralization process, leading to the neglect of responsibilities (Dietsche et al. 2007; Ravikumar et al. 2013). These complexities are illustrated by the institutional structures created, allowing different processes to advance simultaneously in different directions, resulting in superficial conservation initiatives such as protected areas with petrol concessions inside or without park guards. This leaves wildlife authorities without resources to carry out investigations or confiscations.

Fortunately, there are individual agents who manage to operate under these conditions. Brockington and Duffy (2010) refer to this phenomenon of devoted people found within the neoliberal conservation system:

> "If there is a conservation proletariat then it is a tiny group of eager volunteers sacrificing time or underpaid staff forgoing better salaries elsewhere to serve a cause. These are social relations that are not well characterised by capitalist exploitation…. The volunteers and employees of the conservation movement are primarily motivated by their desire to make the world a better place" (Brockington and Duffy 2010).

Igoe et al. (2010) propose a theoretical framework to understand current conservation trends. They use Debord's (1995/1967) concept of Spectacle, where social life is replaced by images, as a result of influence from government, capitalism, and mass media. The spectacle promotes continuous consumption of commodities as the justification for people's existence, making people intellectually passive, validates existing ruling systems, and gives complex, conflicted situations a false appearance of unity. Igoe et al. (2010) compare Debord's Spectacle to the predominant current conservation discourses which conceal the contradictions and challenges of conservation interventions, presenting images of phenomenal successes which ordinary people can join only by consuming certain commodities such as T-shirts, mugs, or adopt a hectare schemes. This framework can be applied to the situation of Peru where governmental initiatives are deliberately ambiguous and superficial with little direct benefit to the survival of primates and other wildlife, but with much advertising and public relations. Local people's recognition of the pseudo participation and ineffectiveness of official conservation agents set them in search of their own ways to effectively execute these same agendas. These local actors and devoted individuals inside the governmental system which push governmental initiatives towards increased efficiency on the ground, thus making conservation paradigms in Peru more effective in protecting primates. However, these people must face excessive bureaucracy, severe pressure from inside and outside their own institution/society and risk to their lives, while receiving very little or no support and protection from the government or other institutions. It was recently recognized that Peru is the fourth most dangerous country in the world for conservationists, mainly due to the government's continual neglect of environmental conflicts (Global Witness 2014). Furthermore, law, no. 30151, was promulgated in 2014 granting legal immunity to security personnel who injure or kill environmental protesters. Therefore, it should be noted that in many cases their success in administrating efficient conservation is in spite of national governmental agendas and not because of them.

Igoe et al. (2010) believe that ethnographic research is essential to the understanding of the production and the possible transformation of current conservation trends. They also emphasize that people and processes that are excluded from mainstream conservation decision-making by choice or by segregation have the potential to contradict the dominating ideologies, but are constantly muted, disregarded, or degraded by armies of experts and groups of economic interest (Igoe et al. 2010).

Existing international, academic literature seldom describes small scale, low budget community run conservation projects (Horwich and Lyon 2007; Horwich et al. 2011). Even more so, conservation programs where rural dwellers are not passive respondents to external conservation agents are active proponents and executers of their own conservation initiatives. They also struggle against a system of which they are part of in order to implement real change.

In answer to Igoe et al.'s critique and the gap in the literature, this article, using ethnographic methods, carefully examined the case study of Peru, its primates and the Tropical Andes Hotspot as well as the diverse efforts to protect these global conservation priorities. Ethnography is designed to describe cultures and societies as well as to understand the sociocultural problems in communities or institutions and to use this research to positively change identified problems (LeCompte and Schensul 1999). Results of ethnographic studies, recognized scientifically, can become a base of evidence for drawing public and decision maker's attention to specific problems and possible solutions. Using this new angle and a novel way of framing the problem has the potential to establish new policy guidelines (Hess 1999).

Conclusions and Recommendations

Governmental initiatives, as described in this chapter, are often much bigger in physical size and in budget than locally run initiatives, but their top down nature limits their effectiveness on the ground. Locally run, grassroots initiatives are more socially adequate and are entirely focused on ground level implementation. However, their relatively small size and the lack of legal basis for informal initiatives such as internal hunting and deforestation control and the ARCAs put their sustainability at risk.

A tremendous amount of work is urgently needed in Peru in order to secure the future of its forests and primates. An amalgam of contradicting agendas, power struggles, superficial-spectacular solutions, and prejudices towards rural populations hinder the efficiency of conservation interventions in Peru. Actions to reduce corruption in state authorities and more transparency in conservation agencies are urgently needed.

Devoted individuals were recognized in this chapter as one of the main forces that turn ambiguous conservation agendas into conservation actions, which is likely the case in many other conservation settings around the globe. I recommend that whenever efficiency on conservation is desired, such individuals should be identified and supported. This support should probably not be monetary, to avoid corruption and dependency, but should ensure that these individuals receive recognition, equipment, information, and encouragement to be able to function within extremely limiting systems. The same is true in the case of local actors who are willing to invest their time and resources in the social and environmental improvement of their communities. This chapter shows that these individuals are under extreme social, economic, and legal pressures. Efforts should be made to compensate for these pressures through different means of non-monetary support.

Informal conservation initiatives as described above are rarely promoted by conservation agencies in Peru but were identified in this study as of high value for primate conservation and socially applicable. Rural environmental educators and representatives of grassroots movements such as the Ronda Campesina often complained that they do not get the support needed to transmit conservation agendas or internally control resource use. Usually, low cost, elementary requests were raised. These included updated ecological or legal information, simple equipment and help printing posters that they themselves had designed. Attentive, open door approaches can allow conservation agents to have a real impact with minimal economic investment. I challenge conservation practitioners to be far more attentive and responsive to the requests and requirements of local communities, providing them with real opportunities to conserve their own environment.

The methodology used in this chapter requires long-term involvement in the studied population and Sisyphean collection of data, and therefore it is not often used in conservation literature. However, it can be the key to understanding conservation problems worldwide. I have many reasons to believe that Peru is not an exception and the same challenges conservation initiators confront are similar in many of primate habitat countries around the world. This chapter describes an example of a country in which local and governmental conservationists, who try to protect wild and endangered primate populations in the twenty-first century, do not enjoy any of the great advances in technology available globally, nor the growing funds that are channelled into mainstream conservation in recent years, but however struggle with the most basic deficiencies and with insincere and limiting international and national agendas.

I call on academics anthropologists and scholars of conservation to use ethnographic studies to describe and assess the shortfalls and successes of local initiatives and devoted employees over the long term. With proper feedback to the initiating groups, this could help them greatly improve their interventions. Publishing in academic and popular journals will inform conservation practitioners and the general public about the potential of locally run conservation, and devoted individuals, a potential that might be deliberately obscured by mainstream conservation institutions. An informed public has the potential to provide funding to small, locally run projects as well as encouraging highly biodiverse countries to simplify the conservation policy processes. This would give local people equal opportunities to lead conservation initiatives and projects whilst insisting that international donation money be channelled to authorities in charge of on the ground implementation.

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Managing Human–Orangutan Relationships in Rehabilitation

Anne E. Russon, Joshua J. Smith, and Laura Adams

Introduction

Orangutans, like all great apes, are dangerously close to extinction in the wild. Recent estimates suggest as few as 60,000 survive in the wild and populations continue to decline (Meijaard et al. 2012). Human expansion and destruction of orangutan habitat are the main causes of this decline but hunting is a significant contributor (Marshall et al. 2006). In addition to killing adult orangutans, humans have orphaned thousands of immatures, removed them from their forest homes, and kept many illegally as captives (Rijksen 2001; Rijksen and Meijaard 1999; Russon 2009). To stem this problem, illegally held captives are confiscated and sent to projects that aim to rehabilitate and ultimately reintroduce them to free forest life. Because human captivity departs drastically from orangutans' developmental experience in the wild (Russon 2009; Snaith 1999), rehabilitation and reintroduction face very different challenges than other orangutan conservation programs. Protecting wild populations focuses on protecting habitat, whereas rehabilitation and reintroduction focus on enabling ex-captive orphans to resume free forest life. This entails helping

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them acquire the ecological and social expertise needed to survive in native forest within an orangutan community, i.e., the requisite knowledge and skills, and "dehumanizing" them, i.e., counteracting the human orientation caused by captivity. Failing to dehumanize them seriously undermines the success of rehabilitation and reintroduction, but achieving it has proven extremely difficult. In this chapter, we analyze humanization and dehumanization in orangutan rehabilitation from the perspective of human–animal relationships and use this analysis to develop recommendations for accomplishing dehumanization while at the same time achieving other rehabilitation goals.

Orangutan Rehabilitation, Reintroduction, and Humans

Reintroduction, the release of organisms into parts of their indigenous range from which they had disappeared, can make important contributions to conservation, individual welfare, and enforcement of nature protection laws when it is effective (Beck et al. 2007; IUCN/SSC 2013). It is especially important for great apes (henceforth "apes," for convenience), who are seriously threatened with extinction. The most extensive efforts at reintroducing apes have been devoted to orangutans. Projects that aim to return captive orangutans to free forest life have operated throughout the orangutan's modern range under the name of rehabilitation since Barbara Harrisson's pioneering efforts in Sarawak in the 1960s (Beck et al. 2007; Harrisson 1961, 1962). Twelve such projects have operated and eight remain active (Russon 2009). The number of rehabilitant orangutans awaiting return to free forest life probably exceeded 2500 by 2009 (Russon 2009) and has likely risen since. Rehabilitants now represent a significant proportion of the world's orangutan population in the modern range (Singleton et al. 2004), so ensuring their successful reintroduction stands to contribute substantially to orangutan conservation.

In orangutan circles, the terms "reintroduction" and "rehabilitation" have sometimes been used interchangeably or with nonstandard meanings (Russon 2009). Beck et al. (2007) define rehabilitation as the process by which captives are "treated for medical and physical disabilities until they regain health, are helped to acquire natural social and ecological skills, and are weaned from human contact and dependence, such that they can survive independently (or with greater independence) in the wild" (p. 5), and reintroduction as "an attempt to establish a species in an area which was once part of its historic range, but from which it has been extirpated or become extinct" (p. 4). For the vast majority of apes with captive backgrounds, return to forest life is inconceivable without some rehabilitation, so the two are intrinsically linked. We follow standard usage of "rehabilitation" and "reintroduction" when specific processes are involved but, for convenience, use "rehabilitation" for the enterprise as a whole.

Orangutan rehabilitation is a multifaceted process ranging from medical treatment and behavioral rehabilitation in sanctuary-like care facilities to release and assisted adjustment to independent forest life (see Fig. 1). Rijksen (1978) argued that behavioral rehabilitation has two essential dimensions, ecological and social:

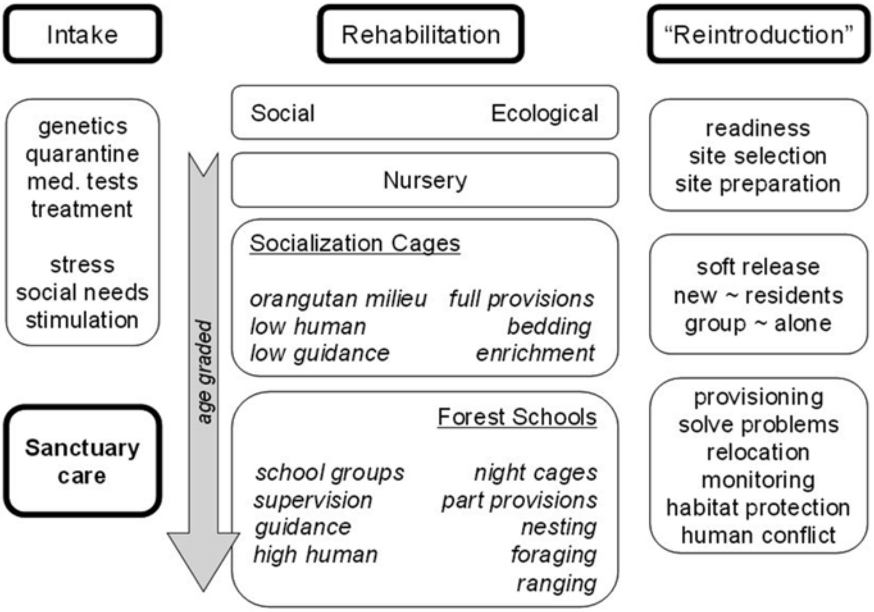

Fig. 1 Overview of orangutan rehabilitation and reintroduction. Boxes with bold borders represent major program phases. Boxes with regular borders represent components within each phase. Reintroduction components are ordered sequentially, top to bottom; components of other phases are not necessarily ordered

the first develops survival competencies for forest life (e.g., foraging, ranging, predator avoidance, nesting), the second fosters orangutan social competencies (e.g., relationships, social structures, communication) and discourages involvement with humans. We now know that social rehabilitation is also important because it establishes social learning opportunities with other orangutans, which may allow rehabilitants to gain essential knowledge and experience about forest life from knowledgeable conspecifics.

Behavioral rehabilitation is then critical to success. It is also the greatest and slowest of these rehabilitation processes because orangutans learn most of their ecological and social expertise. Like other primates, orangutans are lifelong learners whose most important learning is experience-based and socially mediated in apprentice-like fashion; primate learning is, however, concentrated in immaturity and subject to sensitive periods so that it meshes with species-typical ecological and social conditions (Parker and McKinney 1999; Russon 2003; van Schaik et al. 2003). Without the right kind of experience during the right period, individuals may have difficulty learning some expertise or never learn it at all (Lonsdorf et al. 2010; Russon 2003). For orangutans, learning adult-level expertise requires years of dedicated study. This is partly because their development is exceptionally slow and their bodies, brains, and cognitive abilities only mature well beyond infancy (Russon 2003; van Noordwijk et al. 2009) but also because many of their ecological and social challenges are complex: some require cumulative skills (i.e., complex skills that can be learned only after simpler ones are mastered) and/or age-appropriate social input. Orangutans can master basic expertise by late infancy, 4–6 years old, but may need many more years to refine it to adult levels (Russon 1998, 2003, 2006).

Wild orangutan biology and behavior have been studied for almost 50 years and orangutan rehabilitation projects have operated for almost as long, so lessons learned about the hurdles faced in rehabilitating orangutans are well substantiated (Russon and Susilo 2014). Important among these lessons are: (1) rehabilitation failures are often learning related, i.e., social and ecological experiences, (2) ecological rehabilitation is not easily achieved because the challenges are complex, fluctuating, and site-specific, (3) social rehabilitation is harder than ecological rehabilitation, especially dehumanization, and (4) human orientation is a major problem that can seriously undermine rehabilitation success. We sketch these major hurdles as a basis for understanding and managing the role of human–ape relationships in orangutan rehabilitation.

Why Dehumanize Rehabilitant Orangutans

Failing to dehumanize rehabilitants, i.e., reorient them away from humans, has resulted in serious problems that include the lack of fear, wariness, or avoidance of humans typical of over-habitation (Russon and Galdikas 1995; Setchell and Curtis 2011; Snaith 1999). It makes them more vulnerable to hunters and poachers and more liable to approach, attack, and steal from humans (Grundmann 2005; Lardeux-Gilloux 1995; Rijksen 1995, 2001; Russon 2009; Yeager 1997; Yuwono et al. 2007). It can also blur species boundaries by leading rehabilitants to treat humans as conspecifics; this has resulted in dangerous dominance interactions, sexual advances, and aggressive attacks on human strangers (Dellatore 2007; Dellatore et al. 2014; Lardeux-Gilloux 1995; Peters 1995; Riedler 2007; Rijksen 2001; Russon 1996; Russon and Susilo 2014). It keeps rehabilitants' interest away from orangutans and forests, which undermines their readjustment to both. It enhances their knowledge of and tendency to want human foods (e.g., cultivated fruits and vegetables, rice) and objects (e.g., boats, fire, locks), which encourages post-release "crop-raiding" and other forms of theft and thereby reinforces their dependence on humans (Dellatore 2007; Dellatore et al. 2014; Riedler 2007; Rijksen 1974). It tends to encourage terrestriality, which has been linked to increased vulnerability to predation, deficient nesting skills, poor arboreal travel, inefficient foraging, and greater proximity to humans (Peters 1995; Riedler 2007; Rijksen 1978; Russon 1996). All of these increase risks to orangutans from humans, ranging from injury and disease transmission to death.

Hopes that ex-captives will simply unlearn or forget human ways have proven unrealistic. An important reason may be that captivity establishes human-oriented early learning: since most rehabilitants were orphaned and captured as young infants, they typically develop strong attachments to and identify socially with humans and human ways of life (Rijksen and Meijaard 1999; Russon 1996, 2009). Learning early in life is especially important because it founds and orients later learning. Early human-focused learning can then delay, disrupt, or distort the developmental process, lead to counterproductive behavioral changes, and interfere with rehabilitation (Rijksen 1978, 1997, 2001; Rijksen and Meijaard 1999; Russon 2001; Russon and Galdikas 1993). Ex-captives have been found to grow more human-oriented the longer they remain in rehabilitation, not less, especially those who enter rehabilitation young (i.e., <5 years) (Smith 2009).

It appears that the goal should therefore be to encourage rehabilitants to learn alternatives appropriate for forest life with other orangutans and make these alternatives more prominent and valuable than human involvement. Accomplishing this entails gradually, firmly, and consistently discouraging human contact (i.e., reducing human bonds and the number of humans contacted, keeping ex-captives away from human facilities and objects), as early in life as possible, and simultaneously promoting and increasing involvement with forest and orangutan affairs.

Orangutan Rehabilitation: Ecological and Social Challenges of Wild Orangutan Life

What rehabilitation has to achieve is defined by the challenges that wild orangutans face in forest life and how they address them. Orangutans are very long-lived, large bodied, large brained, and primarily frugivorous primates who inhabit south-east Asian rainforests that provide relatively poor and irregular fruit supplies. Critical to rehabilitation is that they learn most of the knowledge and skills they need to succeed, this learning is developmentally constrained and scheduled, and it entails both experiential and social learning (Grundmann 2006; Russon 2006; Russon and Susilo 1999).

Major ecological challenges include identifying, locating, and obtaining a broad range of site-specific foods when the most important, fruits, are ephemeral and the fallback foods needed when fruits are unavailable can be difficult to process, as well as building and sleeping in tree nests, traveling arboreally through a discontinuous, compliant forest canopy, and navigating large expanses of forest habitat efficiently (Bebko 2013; Povinelli and Cant 1995; Prasetyo et al. 2009; Russon et al. 2009).

Social challenges are also substantial. While orangutans are habitually non-gregarious, solitary much of the time, and tend to social avoidance, they are considered to be organized in female kin clusters within spread out, loose communities (Knott et al. 2008; Singleton et al. 2009; Singleton and van Schaik 2001, 2002; van Schaik 1999; van Schaik et al. 2004). Both sexes disperse near adolescence but kin clusters suggest female philopatry (Delgado and van Schaik 2000; van Noordwijk et al. 2012). The primary social unit is an adult female and her dependent offspring (Galdikas 1984, 1985; Rijksen 1978). Beyond that, orangutans associate only occasionally even by weak criteria (partners <50 m apart: Morrogh-Bernard et al. 2003) although only flanged adult males are routinely solitary (Mitra Setia et al. 2009; van Schaik 1999). Associations are typically brief, in small parties, largely passive (e.g., aggregations in fruit trees), and more tolerant than affiliative (van Schaik 1999). The high costs of feeding competition are considered responsible (Delgado and van Schaik 2000). Active associations are rare and tend to serve social purposes including travel bands, nursery groups, immature social play, sex, and aggression (especially in males) (Galdikas 1985; Knott et al. 2008; Mitra Setia et al. 2009; van Noordwijk et al. 2012; van Schaik 1999).

Learning and Sociality

Learning in all apes is guided by interacting experiential and social influences within communities (Boesch and Tomasello 1998; Parker and McKinney 1999). Despite orangutans' spare social life, their learning is sufficiently socially mediated to generate and sustain local cultures (van Schaik et al. 2003). Social learning is important in acquiring ecological and social competencies from early infancy. It is important to infants' learning to identify foods, the locations of good food sources, and efficient travel routes to them plus mastering techniques for processing difficult foods, avoiding predators, and nest-building (Russon 2003; van Adrichem et al. 2006; van Noordwijk et al. 2009; van Noordwijk and van Schaik 2005).

Mothers are infants' first and primary social partners and models; they provide their infants' access to food, transportation, protection, assistance, and tutoring (Russon 2003, 2006; van Noordwijk et al. 2009). In apes, infants' social learning with their mothers has been likened to apprenticeship, in the sense of guided participation in shared activities (de Waal 2001; Matsuzawa 1996; Parker and Russon 1996). The importance of social learning extends far beyond infancy. In orangutans, immatures remain partly dependent on their mother for up to 11 years so they may continue to have her help in learning (van Adrichem et al. 2006; van Noordwijk et al. 2009; van Noordwijk and van Schaik 2005). Mothers are also their youngsters' gateway to and mediators of social contact beyond the natal unit. When adult females associate with female kin, their dependent young have the opportunity to observe, associate with, and learn from these conspecifics. Orangutans' loose communities and female kin clusters also favor immatures' associations with maternal kin, juvenile and adolescent peers, and sexual partners (Galdikas and Vasey 1992; van Noordwijk et al. 2012; van Schaik et al. 2004; van Schaik and van Hooff 1996). These associations further contribute to immatures' learning because the social tolerance involved facilitates information sharing (Coussi-Korbel and Fragaszy 1995; Russon 2003; Russon et al. 2007; van Noordwijk et al. 2012). They create the avenues for social transmission of knowledge and skills that generate and sustain local cultural traditions (van Schaik et al. 2003). Orangutan social life undoubtedly provides fewer opportunities for social learning than group-living primates do, both because of the low frequency of associations and the narrow range of social partners.

Learning and Development

Immatures' learning challenges change with age because of developmental changes in their ecological and social needs, their physical, cognitive, and social capabilities, and their social supports. Orangutan development typically progresses through four phases or stages: infant (pre-weaned immatures dependent on their mother for survival: 0-ca 4/6 years old), juvenile (weaned pre-pubertal immatures, still partially reliant on maternal support and guidance: ca 4/6–7/8 years old), adolescent (post-pubertal immatures, not yet fertile, 7/8 to ca 15 years old), and adult (reproductively mature individuals: females at first birth, ca 15.8 years old, males probably a bit older when they assume adult reproductive roles) (Pereira 1993; Pereira and Altmann 1985; van Adrichem et al. 2006; van Schaik and van Hooff 1996).

Experientially, infants are capable of learning only basic expertise (i.e., knowledge and skills) for both ecological (foraging, nesting, predator avoidance, travel) and social tasks (communicative signals, relationships) because their physical and cognitive capabilities are minimal. Juveniles are strong learners because they have sophisticated cognitive abilities, but their small bodies and low strength limit what they can master to only semi-independent expertise. Adolescents have the cognitive and physical abilities for full independence.

Socially, learning avenues change with age due to variation in the nature and strength of benefits and costs of sociability (van Schaik 1999). Broadly, adults are highly solitary, especially flanged males and females with dependent infants, immatures are actively social and adolescents have been described as gregarious (Delgado and van Schaik 2000). We sketch age-related changes for immatures that are likely to affect their opportunities for social learning.

1. Infant life is mother-centered. Maternal tolerance for their offspring is at its highest for infants and maternal influence on infant learning is substantial. Infants' encounters with other orangutans are rare and typically limited to an older sibling or their mother's associates. When their mother associates with her older offspring, or with other mother–offspring pairs, infants have opportunities to learn from other immatures. Immatures spend up to half their time playing with one another during these associations (van Noordwijk et al. 2009).
2. Juveniles travel and feed semi-independently but within their mother's home range and still rely on some maternal assistance. Juveniles may associate with other immatures, especially when they travel with their mother and she associates with other mother–offspring pairs (Galdikas 1985; van Noordwijk et al. 2009). Maternal tolerance wanes and peer tolerance increases (Galdikas 1984; van Noordwijk et al. 2009). Older juveniles rely less and less on their mother and spend more time with unrelated conspecifics, so they are increasingly exposed to complex skills beyond their mother's (Russon 2003; van Noordwijk et al. 2009).
3. Adolescents of both sexes disperse from their mother's range and become gregarious, sexually active, and increasingly competitive with same-sex conspecifics (Galdikas 1995; Rijksen 1978; van Schaik and van Hooff 1996). Females establish their own range near their mother's, males move farther away. For ado-

lescents, social input increases from peers and sexual associates, for males, it probably decreases from maternal kin.

Rehabilitants face greater hurdles than wild orangutans in meeting these challenges because of their abnormal and often deprived rearing. Since most were wild-born then orphaned, captured, and rescued as infants (ca 2–6 years old, most <4 years old) (Swan and Warren 2001), the developmental scheduling and context for almost the whole of their learning is distorted (Russon 2003). They would have learned little or nothing about forest life or orangutan sociality and much about human life and sociality. Some forest living rehabilitants have continued to refine complex foraging skills well into adolescence yet maintained preferences for interacting with humans (Russon 1996, 2003, 2006). Because care in rehabilitation is often provided by humans, there is a risk of further promoting human-oriented social and learning patterns.

Managing Humans in Orangutan Rehabilitation

Dehumanization includes eliminating human-oriented behaviors learned in captivity, weaning rehabilitants from human dependence, and reorienting them socially to orangutans and away from humans. Eliminating human involvement with rehabilitants is not a viable means of doing so because rehabilitation is a human-dependent process. Humans manage and provide rehabilitants' health care, food, housing, and rehabilitation training and management. Human involvement is essential in part because most ex-captives in rehabilitation programs arrived as infants or young juveniles, immatures who are by definition fully or partially dependent on adult support. Most ex-captives then still need maternal quality care, emotional support, and guidance during rehabilitation. Biological mothers are not available, so this care must be provided by humans. Since human involvement is essential to orangutan rehabilitation, it must be managed so as to achieve balance between human support and human withdrawal. This balance is delicate and difficult to achieve, and one that shifts over time.

Social Relationships: A Basis for Understanding and Managing Human–Orangutan Contact

Social relationships offer a useful framework for understanding and developing recommendations for managing human–orangutan involvement in rehabilitation. Relationships, here, refer to interaction patterns (expectations, behaviors) generated by participants' interaction history (Hinde 1976a, b). Social relationships are likely to play important roles in orangutans' decision-making and action choices because their social systems, like those of other primates, are characterized by long-term interindividual relationships (e.g., parent–offspring, kin, mating partners, dominance, allies) (Kappeler and van Schaik 2002; Meder 2007; van Schaik et al. 2004). Social relationships have been shown to guide social learning in rehabilitants (Russon and Galdikas 1995).

Hinde (1976a, b) further distinguished two kinds of relationships, individualized and generalized. Individualized relationships are defined by the interaction history between specific individuals (e.g., mother–infant, kin, dominant-subordinate, friend, mating partner, ally) and generalized relationships by the interaction history with a given "class" of individuals but not specific individuals (e.g., outsiders such as members of other groups or unfamiliar individuals of a given age-sex class).

A critical individualized relationship for orangutans is the mother–infant one. This relationship, often termed attachment, is defined as the social bond between an infant and its primary caregiver (a more capable and protective individual, normally the biological mother) and is understood to have evolved to promote infant survival (Bowlby 1969, 1982). Attachment is fundamental to normal infant development in primates and other mammals, and deprivation can cause severe and irreversible abnormalities (Bowlby 1969, 1982; Harlow 1961; Harlow and Harlow 1962; Maestripieri 2003). Dependent as primate infants are on their primary caregiver, however, they must gain independence and weaning is an important landmark (van Noordwijk et al. 2012). As a normal matter of course, both partners in attachment relationships progress gradually towards and ultimately achieve weaning.

Attachment is of central importance to orangutan rehabilitation because of the high numbers of orphaned infants involved. Attachment behaviors are similar across primate species, especially so between apes and humans (Bard 1995; Bard and Nadler 1983; Codner and Nadler 1984, Hoff et al. 1994, Maestripieri 2003; Nadler and Codner 1983; Nadler and Green 1975; van Ijzendoorn et al. 2009), so they may then offer useful models for rehabilitation practices that provide human support yet encourage independence from it.

In addition to infant–mother attachment relationships, the associations reported in wild orangutan communities are likely to generate other relationships. Immatures probably establish individualized relationships with maternal kin and other area residents whose home ranges overlap with theirs. These could take the form of traveling companions (tolerant-affiliative, often immatures or unflanged males) and, later, short-term consortships (Codner and Nadler 1984; Singleton and van Schaik 2001; 2002; van Noordwijk et al. 2009; van Schaik 1999). Associations might lead to generalized relationships with play partners (affiliative) and with transients (e.g., adolescent or unflanged males passing through their home range, neutral to intolerant). These potential relationships may serve as useful models for rehabilitation in terms of promoting resocialization to other orangutans and conspecific social learning.

Orangutan–Human Relationships in Rehabilitation/Reintroduction

Common orangutan rehabilitation practices include providing human (or when possible, orangutan) mother surrogates for infants in recognition of the fact that infants require intensive care and social support, caring for ex-captives in groups (to resocialize them to orangutans and reintegrate them into orangutan social life), providing human guards to control their behavior, and veterinary staff to manage their health (Russon 2009). Rehabilitant orangutans then tend to form similar types of relationships with humans and with one another: attachments between infants and their surrogate mothers, individualized relationships with orangutan group-mates and familiar humans (e.g., veterinary staff, other surrogate mothers, guards, regular researchers), and generalized relationships with newcomers (e.g., newly rescued orangutans, orangutans from other groups, new staff) or visitors (e.g., media, tourists, office staff). The issue we address is how to best manage orangutan–human relationships during rehabilitation to best achieve dehumanization. We first outline where rehabilitation practices have gone wrong, then suggest better practices for each type of orangutan–human relationship.

Early orangutan rehabilitation practices were based on informal "forest schools" where human staff took ex-captives into areas of protected native forest, encouraged them to learn ecological and orangutan social skills, and provided other supports as needed (supervision, supplemental provisions, protective housing) (Harrisson 1960, 1962; Rijksen and Meijaard 1999; Russon 2009). As practiced, they promoted direct human–orangutan interactions and strong human social and ecological support. They have been widely criticized because of the drawbacks of human–orangutan contact, including transmission of human diseases, failure to promote species-specific feral skills acquisition, lack of species-appropriate socialization, and failure to dehumanize ex-captives (Aveling and Mitchell 1982; Lardeux-Gilloux 1995; Rijksen 1995, 1997; Rijksen and Meijaard 1999; Smits et al. 1995; Yeager 1997). The tourism that some rehabilitation programs have promoted seriously exacerbates these problems (Russell 1995; Russon 2009; Yeager 1997). It is contrary to one of the main principles of reintroduction, reducing human contact, and it intensifies all of the problems caused by human contact mentioned above (Dellatore et al. 2014; Russell 1995; Russon 2009; Yeager 1997).

In response to these problems, the "socialization cage" approach was introduced in the 1990s (Smits et al. 1995). Socialization cages are large cages that house rehabilitants in groups, typically age-graded, and limit human care to food delivery, cleaning, and essential medical care (e.g., Rijksen and Meijaard 1999; Smits et al. 1995). Social caging aimed to induce rehabilitants to re-orient to and build strong relationships with other orangutans, learn the requisite forest expertise from each other, and lose their ties with humans. This approach has proven ineffective for ecological rehabilitation and problematic for social rehabilitation. Ex-captives with only socialization cage rehabilitation have shown poor ecological and social competencies once released (Peters 1995; Russon 1996, 2002). Several factors probably underpin these problems. For acquiring forest expertise, cage life precludes experiential learning and fails to foster socially mediated learning, since most ex-captives have minimal forest expertise to share and cages cannot provide the abundance of materials (e.g., trees, foliage, forest foods) needed to enable them to share whatever forest expertise they may have. For acquiring orangutan social expertise, group caging distorts orangutan interactions. Groups of immature rehabilitants in socialization cages have developed social problems including food competition, aggression, bullying, and rape (Russon 2009). Many rehabilitants need at least partial maternal-quality care because they enter rehabilitation as infants or young juveniles, but cagemates are largely unsuitable as caregivers and there are few alternatives other than humans. Finally, socialization caging may undermine rather than foster dehumanization because it makes orangutans entirely human-dependent; it focuses their attention on humans and intensifies the association between humans and food. Even partially provisioning free-ranging wild primates for tourism has this effect (Knight 2009).

Attachment

We consider attachment necessary for infant orangutans, with the understanding that secure attachment is probably as essential to their healthy development as it appears to be in humans (Ainsworth et al. 1978; Bowlby 1990) and in other apes (Bard 1995; Bard and Nadler 1983; Clay et al. 2015; Codner and Nadler 1984; Hoff et al. 1994; van Ijzendoorn et al. 2009). Rehabilitation projects have provided companions that serve as ex-captives' surrogate mothers, deliberately or not, in two forms: human (typically, local young women) and compatible orangutan age-mates. Although there are exceptions (see Fig. 2), such humans are probably better than other rehabilitants as mother surrogates because they are more competent individuals who can provide protection and mediate the infant's interaction with the environment (provide food, interpret and manage situations, emotions, and reactions, support learning); they are poor, however, as teachers for much of what ex-captives need to learn about forest life largely because they rarely have the relevant knowledge, skills, or physical capabilities (e.g., climbing). In contrast, rehabilitant peers may be the better helpers for exploring forest life, sharing forest expertise, and fostering orangutan social skills and relationships. Since humans and orangutan peers offer relatively complementary advantages, the best solution may be to provide a balanced combination of the two.

Other Individualized Human Relationships

Other individualized ape–human relationships have not been studied in rehabilitation projects but have been in zoos between apes and their keepers. These relationships may offer insight into individualized relationships other than attachment that rehabilitant orangutans form with familiar humans who have worked directly with them for relatively long periods (e.g., Chelluri et al. 2013; Smith 2014, 2016). For example, rehabilitants may form relationships with staff who regularly guard, provision, clean cages or conduct health checks, or affiliates such as long-term researchers.

Fig. 2 Humans versus orangutan peers as teachers. Orangutans are generally better than humans in helping ex-captives learn forest knowledge and skills, but occasionally the reverse is true. *Upper* photo: a knowledgeable human caregiver shows two juvenile female rehabilitants how to crack termite nests to get the termites inside. *Lower* photo: an older infant rehabilitant (ca 4 years old) shows a younger one (ca 2 years old) how to drink water from a stone

Most of these individualized relationships are essential to effective, cooperative work with rehabilitant orangutans. Maintained too long, however, then can promote rather than reduce human orientation (Smith 2009). The question is then how to manage them so as to dehumanize rehabilitants. Relative to this goal, the humans involved are typically orangutan-experienced, their presence is regular, their interest long term, and their agenda in interacting with orangutans strongly defined by their rehabilitation responsibilities. Their interactions with orangutans are therefore guided by the relationship, familiarity, and their rehabilitation responsibilities more than novelty. They also experience the consequences of these interactions, so their behavior tends to be skilled, attentive, and rehabilitation appropriate. They are often, however, frontline workers whose knowledge of orangutans tends to be limited to whatever practical, on the job training they receive. Their work with orangutans tends to concentrate on pre-release rehabilitation, so their knowledge of what orangutans need and experience in forest life is weak. Consequentially, their choices and actions are influenced by their personal experiences and views, the fact that their involvement with orangutans is just a job, and the fact that they can and do go home (see Fig. 3).

Generalized Human Relationships

In zoos, orangutans develop generalized relationships with humans on the basis of repeated encounters with common "classes" of unfamiliar individuals (Smith 2014, 2016). At rehabilitation projects, this type of relationship is well known with the veterinary team (feared). More problematic are generalized relationships with visitors (e.g., media, volunteers, students, tourists) and probably nonessential project staff. The kinds of interactions these relationships generate have been studied in zoos in terms of visitor effects (for review see Davey 2007; Fernandez et al. 2009; Hosey 2000) and recently in terms of human–animal relationships (Hosey and Melfi 2014; Smith 2014, 2016). They have also been studied in free-ranging primates in terms of ethnoprimatology including human-primate conflict, human-primate commensalism, and primate tourism (e.g., Fuentes 2010; Knight 2005, 2009; Russon and Wallis 2014a and references therein).

Generalized human–orangutan relationships differ from individualized ones in their impacts on dehumanizing rehabilitants. The humans involved, especially visitors, are typically orangutan-naïve, their presence and interest are transient, and their actions are strongly guided by personal agendas (Russell 1995; Russon and Susilo 2014). Accordingly, their interactions with rehabilitants tend to be guided by curiosity plus ignorance of or disregard for the consequences to orangutans, and their behavior tends to be poorly informed, inattentive, careless, and inappropriate relative to rehabilitation goals. Notable examples are visitors luring orangutans into close encounters by enticing them with food and other human goods. Rehabilitant orangutans also lure visitors into interactions wherein the orangutans act according to relationship parameters unknown to the visitors. Typical consequences are best known from studies of tourism at orangutan rehabilitation sites where tourists encounter free-ranging rehabilitants. Tourist–rehabilitant interactions typically result in orangutans getting tourists' foods or other goods, which leads to their associating tourists with food and increasing their attraction to tourists. Results for rehabilitants include improving their skills for engaging and manipulating

Fig. 3 Inappropriate staff behavior with rehabilitants. *Upper left photo*: an adult female has items she could only have gotten from staff (burning insect coil, page from a notebook), she has used the coil like a pencil to write on the paper (she often saw staff doing this) and is blowing on its burning tip (which will darken its marks on the paper). *Upper right photo*: an adult female and her young infant take supplementary provisions from the basket that staff left unguarded and accessible on the ground. *Lower photo*: an adult female and her infant sit on a bench used by tourists to view daily provisioning, overly close to an inattentive local guide.

tourists; examples include getting tourists to carry them to feeding sites (Russell 1995; Snaith 1999), soliciting and stealing tourists' foods and objects (Dellatore 2007; Donaghy 2002; Russon and Susilo 2014), and occasionally bartering with them to ransom back pilfered goods (Russon pers. obs., Russell pers. comm.). This can in turn lead to increased contact, aggression, wounds, and infectious disease transfer (e.g., Dellatore 2007; Dellatore et al. 2014; Muehlenbein and Wallis 2014; Rijksen 1997; Russon and Susilo 2014). Importantly, this progression correlates with the volume and frequency of these types of human encounters (Russon and Wallis 2014b).

Recommendations for Dehumanizing in Orangutan Rehabilitation

This relationship analysis offers a basis for weighing the pros and cons of individualized and generalized human–orangutan interactions in rehabilitation. It is also instrumental for developing recommendations to foster dehumanization. Human–orangutan interactions within generalized relationships do not, for the most part, help the rehabilitation process; they tend to generate major problems and are difficult to predict and manage. The sensible solution is to minimize them: prohibit them with rehabilitants eligible for reintroduction to forest life and allow them only with rehabilitants ineligible for release and then only under very tight control. Human–orangutan interactions within individualized relationships are essential to orangutans' welfare and rehabilitation; they also generate problems but are relatively more predictable and manageable because most involve project staff. Sensible solutions are limiting them to essential interactions with a few dedicated staff who are well trained and well supervised and programming the gradual "weaning" of orangutans from caregivers as their biological mothers would do.

Instituting these recommendations entails adjusting existing practices, especially for behavioral rehabilitation where most learning and social interaction occurs. We focus on forest schools as the most common approach to behavioral rehabilitation and, well-managed, the best means of achieving behavioral rehabilitation goals (Fernando 2001; Lardeux-Gilloux 1995; Russon 2009). Rehabilitant orangutans are known for weak forest competencies (foraging, nesting, arboreal travel, forest navigation) (Bowden 1980; Kaplan and Rogers 1994; Rijksen and Rijksen-Graatsma 1975) and forest schools offer them the forest experience vital to learning them, opportunities for learning with and from other orangutans, and age-appropriate support. In juvenile forest school groups, rehabilitants' social learning opportunities were frequent, with observing (watching, peering) or food transmission (stealing, scrounging) occurring on average approximately once every 45 min (Adams 2005). Forest schools also foster orangutan socialization and dehumanization by providing a more species-normal context for conspecific interactions and resolving social problems, better supervisory control, and favoring forest- and orangutan-oriented activities over human-oriented ones.

Some existing forest schools function reasonably well but problems have arisen, pitfalls are known, and practices have not been standardized. Ex-captives in island forest schools have escaped or drowned, forest schools near villages have generated human–orangutan conflict, and overcrowded forest schools have facilitated contagious disease spread (pers. obs.). Forest schools for infants and young juveniles are also susceptible to intensifying human involvement, which may be problematic later. We offer recommendations for forest school practices that best foster the learning needed to enable ex-captives to resume free forest life and dehumanize them (see also Russon et al., 2009).

Guiding Principles: Behavioral Rehabilitation in Forest Schools

1. *Aims*. Aims are to enable healthy, immature ex-captives' successful return to free forest life. Priorities are then nurturing and protecting them while they grow, maintaining their health, helping them learn the knowledge and skills for semi-independent forest life, and orienting them away from human life styles.
2. *Simulate normality*. The more closely behavioral rehabilitation simulates species-normal rearing and learning processes and the more flexible and individualized it is, the more effective it is likely to be in preparing rehabilitants for free forest life (Fernando 2001; Peters 1995; Pratje and Singleton 2006; Rijksen and Meijaard 1999; Russon 2002; Smits et al. 1995). Forest schools should have better chances of success if they prepare ex-captives to assume semi-independent forest life as juveniles, when they are normally ready for this experience in the wild: their learning potential is optimal, they are generally well tolerated socially, and they are still relatively easy to manage.
3. *Learning*. The program focus is learning: acquiring knowledge and skills for forest survival (foraging, predator avoidance, nesting, arboreal travel, navigation) and orangutan social life (communication, social organization, cultures), and extinguishing (to the degree possible) human orientation. Forest schools should foster individual (experiential) and social learning because orangutans use both: in the wild, learning foraging skills likely involves both in combination (Grundmann 2006; Russon 2006).
4. *Development*. Developmental accommodation is essential because changes in orangutans' needs, preferences, and learning are developmentally paced biologically, experientially, and socially (Russon 2003). Human contact and supports must be adjusted for these changes, especially in light of dehumanization aims.
5. *Captive residues*. Programs must be compensatory and individualized: captive experiences determine the problems ex-captives present and these vary case by case. Known patterns in captive orangutans are: wild birth, distorted attachment (orphaning early in infancy, varied or no human substitutes), distorted and variable care (abusive or deprived to pampered), variable length of captivity (days to years), and human-oriented learning (diet, terrestriality, human objects, depen-

dency on and some form of socialization to humans) (Aveling and Mitchell 1982; Grundmann 2005; Rijksen 1978, 1982; Rijksen and Meijaard 1999).

6. *Human–orangutan interaction*. Programs must manage human–orangutan interactions so that they further rehabilitation to forest life (support and guide ex-captives) and dehumanization. Human–orangutan interactions within individualized relationships are essential but need careful management. With the exception of veterinary staff, human–orangutan interactions within generalized relationships are generally counterproductive and should be eliminated or at least minimized.
7. *Limitations*. Forest school rehabilitation may not be possible for all ex-captives, especially older immatures and adults. Older immatures tend to disperse so their movements are hard to control; they are also quite large and can become aggressive and dangerous.
8. *Generality*. Principles may be relevant to other primates with adjustment for species-specific traits.

Forest School Design

1. *Scope*. Forest school designs for behavioral rehabilitation programs should address: the physical context (forest habitat, rehabilitation facilities), suitable orangutan residents, behavioral programming (learning ecological and social expertise, dehumanizing), human care (health and behavior, supports, controls), monitoring and evaluation, and transitioning to free forest life.
2. *Age-graded forest schools*. Age-graded schools are advisable because orangutan social life, learning, and behavior change greatly with age and similarly aged orangutans tend to have similar needs, abilities, and interests. Forest schools for each developmental phase provide programs, structures, and supports designed to suit age-related needs and abilities. Ex-captives are placed or moved into the forest school best suited to their needs and abilities. Several rehabilitation projects operate forest schools this way (e.g., Borneo Orangutan Survival Foundation 2012; Fernando 2001): nursery quality care in forest patches for young infants (ca 0–2 years old), protected and highly supportive forest life for older infants (2–4/5 years), and supervised semi-independent life in larger forest blocks for juveniles (4/6–7/8 years) and manageable adolescents (>7/8 years).
3. *As early as possible*. Rehabilitants should be placed in forest schools as early in life as possible because early learning and early relationships often have profound effects on later learning and orientation.
4. *Forest school sites*. Habitat used for forest schools should be suitable for resident orangutans, i.e., lowland forest areas that are large enough for the age level(s) of the orangutans who will use them and provide a suitable range of appropriate foods and good access to water. Candidate sites should be professionally surveyed to ensure they provide suitable and sufficient plant food sources and are as similar as possible to probable release sites. They should be safe from logging and hunting (preferably, with formal protected status) and safe for unskilled ex-

captives. They should be accessible to project services and far enough from human activity that orangutans will not encounter non-project humans.

5. *Forest school facilities*. Physical support facilities are needed at forest school sites but should be minimal (protective orangutan caging, post with secure and safe storage for provisions and waste, staff housing and work areas) and, other than orangutan caging, invisible and inaccessible to orangutan residents. Site preparation should include developing maps and field guides of orangutan resources for forest school staff, facilities for staff and their work, sanitary and inaccessible food storage and waste disposal systems, and orangutan caging for emergency/health/safety usage. Other than food provisions being delivered to orangutans, no human foods should be allowed anywhere in the forest school area where orangutans could access or even see them.
6. *Forest school staff*. To minimize the number of humans contacting rehabilitants, capitalize on individualized relationships, and ensure long-term familiarity with individual orangutans, each forest school should have its own small, stable, semi-autonomous, dedicated team comprised of staff who can fill age-appropriate social roles with orangutans (e.g., surrogate mother, tutor, guard, doctor) and supervisors. The team is responsible for helping resident ex-captives learn forest and orangutan social expertise (teaching, guiding, supervising) and dehumanizing (gradually but persistently withdrawing orangutans from humans). The team also provides age-appropriate socio-emotional care (maternal-like care for infants), orangutan social control (manage bullying, dominance, sexual aggression), and health monitoring/care. All team members should receive comprehensive, formal training on rehabilitation aims, wild orangutan behavior, and managing ex-captives to promote dehumanization.

   Small teams are recommended so that orangutans build relationships with a select group of humans and do not extend them to many humans or humans in general. In zoos, exposure to many keepers may impair development of positive human–animal relationships and may lead to negative outcomes, including attacks (Hosey and Melfi 2014). The team should be a closed, stable group of people who always work with the same orangutans, ideally though their entire rehabilitation. Each forest school team should be large enough to operate continuously (i.e., rotating staff *within* the team to handle holidays and shifts). Some staff continuity across forest school/age groups is also advisable to enable gradual transitions for individual orangutans.

   To profit from the relationship basis of orangutan sociality, in addition to employing stable teams, forest schools should remain strictly off limits to nonessential personnel. Orangutans will then always be exposed to the same humans, serving both to develop the relationships that enable effective teaching and management and to restrict the number of humans the orangutans meet. Stable teams promote trust and provide social and emotional support, especially to the youngest orangutans. Because they are familiar with resident orangutans, stable team members can serve as behavioral models and, in some cases, coach forest skills and adjudicate social life. They also offer the best opportunities for rapid detection of problems and intervention.

Caregivers should develop individualized relationships with specific infants to satisfy their attachment needs, meaning that forest school staff serving as primary caregivers should be responsive to "their" orangutans' needs while encouraging interaction with other orangutans and not with humans. Caregivers should gradually encourage infants' withdrawal from them so that, by ca 4–6 years of age, they can be "weaned" in the sense of reducing their dependence on human adults. Guards' roles are to maintain control and adjudicate conflicts. Each forest school team should have a dedicated supervisor who is trained and knowledgeable about orangutans (wild and rehabilitant) and the aims of rehabilitation, and who monitors, discusses, suggests, and corrects the team's work with resident orangutans.

7. *Program/Activities*. Forest school life should be immersive: orangutan residents live full time in the forest so that the forest and orangutans, not humans, are the norm for daily life. Exceptions are orangutans still in need of protective care (e.g., very young, cannot build or sleep in tree nests or otherwise insufficiently forest competent, ill, or injured). Human supervision should be provided as necessary to ensure orangutans' safety and well-being.

    (a) While free in the forest, rehabilitants should always be supervised and initially led by staff to encourage foraging, arboreality, travel, nesting, and orangutan sociality.
    (b) Human support in forest schools should promote the learning of forest and orangutan social competencies, interacting and building relationships with other orangutans, and weaning rehabilitants from humans. Staff should provide care that is responsive to immatures' needs but does not invite or encourage interaction with humans (van Ijzendoorn et al. 2009): in other words, to respond when and if needed but not encourage unnecessary interaction. Staff should work towards weaning in line with orangutan-typical development, adjusted for individual ex-captives' needs and captivity-induced problems.
    (c) Provisioning and protective housing should be provided to orangutans if needed, but never inside the forest. Orangutans unable to nest overnight in the forest or otherwise in need of protective care should be placed in secure cages when forest school staff cannot stay with them.
    (d) No visitors should be allowed in forest schools.
    (e) Forest school programs should be individualized in response to each rehabilitant's particular needs and abilities.
    (f) Forest school programs should be coordinated with early post-release programs to ensure newly released rehabilitants are provided with appropriate support.
    (g) Each rehabilitation project faces site-specific conditions, so forest school programs will also need to be customized to the orangutan, human, and habitat factors affecting it.

8. *Small groups*. Small forest school groups of age-mates (max 8–10, sex-balanced) are recommended over large ones because they are easier to manage, individualize and locate (smaller forest areas are needed), less competitive, and closer to

wild orangutan social patterns. They allow good orangutan socialization while remaining manageable for human caregivers. Caregivers may need to manage group membership and compatibility to improve group harmony and cohesion. Well-formed groups can enhance learning by increasing the likelihood that group members will travel, work, and play together, which in turn increases the likelihood that they will learn from each other. It can also be valuable to include, in each group, 1–2 orangutans with more advanced forest or social abilities, to guide the learning of less knowledgeable group members. Older females can sometimes be paired with younger individuals, but older males must be managed carefully to avoid aggression and raping if females cannot escape.

Conclusion

Forest schools with many of these features operate as essential components of most orangutan rehabilitation programs. They are not rehabilitation cure-alls and, as recommended, they are not easy to achieve. We know of no systematic evidence on the effectiveness of the measures recommended here for dehumanizing ex-captives, but when and where the key individualized relationships have been well managed in forest schools, ex-captives have made excellent progress in mastering forest knowledge and skills, establishing strong individualized relationships with orangutans and their particular human caregivers, and reducing their involvement with other humans. For example, in a study of older infant rehabilitants 6–12 months after their transfer from socialization cages to a protected forest setting, Riedler (2007) found that those who were forest-oriented and human avoidant were more forest capable than those who were less forest-oriented and human-bonded. Similarly, after 2 years in an East Bornean forest school for older infant and young juvenile rehabilitants, forest-oriented residents had learned more local forest foods than their human-oriented groupmates (Russon 2010). These forest school residents also tended to establish individualized relationships with similarly oriented rehabilitants, so peer social learning could hamper as well as enhance rehabilitation progress. The recommended measures are also well grounded theoretically and empirically with respect to normal orangutan development, sociality, and relationships and they do not entail depriving ex-captives of the care and supervision they need. Although imperfect, they should be better than other alternatives currently used. Carefully applied, they may provide a solution to the conflicting needs for human support and dehumanization during rehabilitation in a manner that improves success rates for reintroduction.

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The Little Fireface Project: Community Conservation of Asia's Slow Lorises via Ecology, Education, and Empowerment

K.A.I. Nekaris

Introduction

Since primate studies began to develop and escalate beginning in the 1960s, lorisid primates (pottos, angwantibos, and lorises) have remained amongst the least-studied (Nekaris and Starr 2015). Indeed, before the 1990s, knowledge of lorisids was based on a handful of observations conducted over the course of three field studies (one only lasting ten days), largely based on the difficulty of seeing wild lorisids or catching them in order to radio collar them (Petter and Hladik 1970; Charles-Dominique 1977; Barrett 1981). These studies led to some myths about lorisids regarding their diet, social behaviour, and habitat needs that have not only contributed to poor management in captivity (Fuller et al. 2013), but also to misunderstandings about their conservation status in the wild.

Of all the lorisids, the ones that began to gain the most notoriety were the Asian slow lorises (*Nycticebus* spp.). Over the last few decades, slow lorises have been regularly recorded in the open wildlife markets in the region (e.g. Shepherd 2010). The demand for lorises as pets, tourist attractions, medicine, and meat caused them in 2007 to be the first primates since 1986 to be transferred to CITES Appendix I to curtail international trade (Nekaris and Nijman 2007). Local trade can be more difficult to monitor and enforce; yet we know that lorises are regularly traded for domestic use despite their legal protection in the 14 range countries where they occur (Nekaris and Starr 2015). I began studying Asian lorises in 1993, and have continually witnessed a casual attitude towards the plight of these primates by both conservationists and primatologists. Some have called slow lorises 'unimportant primates'. Law enforcement officials have refused to raid a market because there were '…only lorises there'. Conservationists have believed that there were so many

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in markets, they could not possibly be threatened in the wild. Rescue centre workers have noted that they need to keep cage space for ‘real’ primates, resulting in hard releases into poor habitat.

In 2009, the plight of slow lorises reached an international audience when a YouTube video of a pygmy slow loris (*N. pygmaeus*) went viral. Counteracting this video with media attempts including a Wikipedia slow loris conservation page, newspaper interviews, scientific articles, and a major international documentary, an increase in public knowledge about the conservation issues facing slow lorises emerged (Nekaris and Campbell 2012). Such issues included illegal smuggling of wild slow lorises for the pet trade and then selling them with falsified CITES permits at pet shops (Musing et al. 2015). Fearing their painful and potentially poisonous bites (slow lorises are the only venomous primates), traders crudely cut out the teeth of slow lorises, usually with wire cutters or nail clippers. If the loris survives this practice without fatal infection (the most common result), the lack of its specialised toothcomb, necessary for feeding and grooming, means it can never be released to the wild (Moore et al. 2014).

Over the last 15 years, more data began to become available, but again without any animals monitored for a year continuously (Wiens 2002; Nandini et al. 2009; Starr et al. 2010; Das et al. 2009; Swapna et al. 2010). At this same time several rescue centres that were receiving increasingly large numbers of slow lorises began to monitor their releases (Moore et al. 2014; Kenyon et al. 2014). Working with International Animal Rescue, my Ph.D. student Richard Moore was the first person to monitor releases of Javan slow lorises systematically. Despite an increase in knowledge, most releases were unsuccessful, with up to 95 % of monitored slow lorises dying within weeks to months of being released (Moore et al. 2014).

Based on high numbers in trade, low numbers in the wild, and low reintroduction success, trade was clearly and intensely impacting the Javan slow loris (*N. javanicus*), leading to a change of its IUCN Red List status from Endangered to Critically Endangered. Additionally, the Javan slow loris has been listed four times as one of the Top 25 Most Endangered Primates in the World (Nekaris et al. 2014b). Less than 10 % of Java’s forests remain and surveys of Javan slow lorises in the protected area network have revealed low numbers (0–0.42 animals/km) (Nekaris et al. 2014a). Surprisingly, however, relatively larger numbers of slow lorises have been located in small pockets adjacent to agricultural areas (Voskamp et al. 2014). In a release study focussing on three Indonesian slow loris species, over 85 % of 180 animals rescued were unsuitable for release with 64 % having their teeth clipped; 55 % of these were *N. javanicus.* Interviews throughout Java, including with hunters, showed that much of the trade at its initial stage in the chain was done for minimal profit, as a secondary event to other activities such as agriculture (Nijman and Nekaris 2014a). Taking all of this into account, I decided in 2011 to launch the first long-term research project of Javan slow lorises. The complex conservation problems facing the Javan slow loris meant that the study had to be conducted in an anthropogenic landscape and that understanding the behavioural ecology of Javan slow lorises alone was not

Fig. 1 The images clockwise show how we study wild Javan slow lorises (**a**—A Walmsley) through ecological studies of their environment (**b**—A Walmsley), education of people locally and internationally (**c**—W Tarniwan) and through empowering officials and people around the world to identify slow loris threats and to not trade these primates. This image is from a law enforcement training workshop in Java (**d**—A Walmsley)

enough to protect this dwindling species. In this paper I describe the steps taken by my team and I to develop a research project comprising ecology, education, and empowerment (Fig. 1).

Choosing a Name

I wanted my project to have an identity from the outset, giving it a name with which local people could empathise. We conducted enthnozoological surveys throughout West Java and learned that the slow loris was deeply embedded in local myths and beliefs, from being considered a dangerous entity to a deity; its body parts could be used for good luck or to punish. More generally, however, it was considered shy, mysterious, or rarely seen (Nijman and Nekaris 2014a). Of the many names available for this primate, including the wind monkey, the shy-shy, or the moon face, we settled on the local name fire face. Because loris' eyes shine so brightly when exposed to torch light, this name not only represented aspects of our ecological work, but its general nature meant that 'little fireface' could also apply to any other nocturnal mammals we decided to later add to our study. Thus the name Projek Muka Geni or Little Fireface Project was conceived.

Selecting a Field Site

We worked with an ex-hunter to choose our field site, Cipaganti village, Garut District (S7°6′6–7°7′0 & E 107°46′0–107°46′5). We wanted to work in an area where we could make a difference, and we knew from the hunter that he and others had been catching lorises on a monthly basis. The site had been chosen by hunters based on accessibility to a village and a good road network to large cities such as Garut, Bandung, and Jakarta, making it also convenient as a research location. As research projects have been shown to play a positive impact on protecting species from hunting, we felt by selecting a high hunting site, we could not only make an immediate impact to protect Javan slow lorises, but that the community was a perfect potential recipient for education.

Cipaganti is certainly not a typical pristine forest where many might like to start a long-term project. The village lies in the foothills of Gunung Puntang, which is part of the mountain range containing the active volcano Gunung Papandayan. While Gunung Papandayan is recognised as a nature reserve (*cagar alam*), the agricultural areas surrounding the nature reserve rely wholly on local people for their protection. A contiguous forest lies approximately 2000 m from the edge of the village. The land in between reaches up to 1750 m asl and is covered with a mosaic of cultivated fields called *talun* by Sundanese people (e.g. tea, pumpkin, beans, chili, tomato, tobacco, potato, cabbage, onion, carrot), abandoned fields and bush patches, bamboo patches, tree plantations, and forest patches. The boundaries of fields comprise tree rows, many of which have proved vital to slow lorises, including fairy duster (*Calliandra calothyrsus*), string bamboo (*Gigantochloa apus*), green wattle (*Acacia decurrens*), and avocado (*Persea americana*).

Introducing the Project to Local People

The villagers of Cipaganti, numbering just over 3000, are ethnically Sundanese and are predominantly Muslim. The economy comes almost exclusively from farming (planting, picking, selling, and processing), although entrepreneurial activities in the form of small food shops, repair shops, mobile phone vendors, etc. also occur. Eighteen large mosques are found in the village, along with more than 50 small prayer houses. Six schools are within walking distance from or within the village and villagers estimate that the literacy rate is 90 %, with most children going to school until 16. From the beginning of the project, informing people about why we were working in Cipaganti and why the slow lorises are important was vital. Using primarily output indicators since 2012, we have reached 1000s of people in the village as well as in surrounding areas through a number of methods. A general rule to producing materials as qualitative output indicators is that they also have a function and will not simply be read and thrown away. For this reason, only once did we produce a brochure explaining the project. After that, we produced materials that can be used over and over again and contain the project's key messages. These are reviewed in Table 1.

Table 1 Examples of events run in Cipaganti area since 2012, including qualitative output indicators used to raise awareness of nocturnal mammals and their conservation. All numbers rounded up to the nearest 10

Event	Year	Number of participants	Output indicators
Community socialisation event	2012	120	Formal lecture and film; distribute laminated pictures of slow loris to all village shops; distribute 500 leaflets about the project
Petrol station socialisation	2012–2015	3000	Every 3 months, team and mascots stand at a busy petrol station and hand out loris and civet stickers that are adhered to 100s of passing vehicles
Community football tournament	2013–2015	$X=1600$	Renovate football pitch and provide new balls & nets; uniforms & trophies with slow loris and other nocturnal mammals
Live music and dancing festival	2013	550	'What makes you proud of Cipaganti photo booth'; I'm proud of slow loris t-shirts and badges, with associated film shown on local television
Talent competition	2014–2015	$X=340$	Badges with slow loris and civets; prizes (DVD player, tablet, mobile phone, children's games); Javan slow loris t-shirts; coffee tasting booth to show alternatives to civet coffee
Community photo/children's artwork exhibition	2014–2015	$X=270$	Slow loris scarves in regional batik style; printed photos handed out to individuals featuring in the photograph; selected photos featured on a community calendar; photo booth with team mascot; colouring books given to children who win artwork competition
Children's games competition	2014–2015	$X=80$	Pass the parcel with slow loris prizes (socks, scarves, t-shirts); small silver coins distributed as prizes; mascots hand out stickers
Calendar distribution	2012–2015	1500 per year	Calendars printed about the loris, the project and featuring people from the community
Cooking competition	2014–2015	250	Nasi goreng tasting competition, with rice cooker as prize; public lecture on slow lorises by a regional imam; distribute annual calendar featuring local people and environment and slow loris school notebooks
Tree nursery	2015	80	Run through Nature Club, with children collecting and nurturing saplings, using all recycled materials
Farmer's empowerment	2015	180	Lectures by Forestry Department & Wildlife Department on erosion, replanting, etc.; distribute umbrellas with loris-friendly messages

Ecology

Before we started our field project, virtually nothing was known about the behaviour of Javan slow lorises, with scant ecological data coming from interviews with local people (Winarti 2011; Wirdateti 2012). Since our project began in earnest in 2011, we have published 28 papers in international scientific journals and produced 41 published abstracts for international conferences in 13 countries. Our first efforts were simply to describe the ethogram of Javan slow lorises, their basic social organisation, and the types of trees they were using in our area (Nekaris 2014; Rode-Margono and Nekaris 2014; Rode-Margono et al. 2014; Rode-Margono et al. 2015). In an attempt to use ecological data to thwart the trade in slow lorises as pets, we also began a long-term study to determine why slow lorises are venomous (Rode-Margono and Nekaris 2015). We discovered that a major function of their venom is for use in intraspecific competition (Nekaris et al. 2013b), but that slow loris venom also impairs and kills ectoparasites (Grow et al. 2015), of which slow lorises have few (Rode-Margono et al. 2015). We were even able to collect medical evidence to show that slow loris venom can severely impact human health (Madani and Nekaris 2014). Other mini projects have included ecology of sleep sites; how human sound affects loris behaviour; how agroforestry affects loris behaviour; comparison of wild and captive activity budgets; slow loris social behaviour; botanical aspects of exudate feeding; ecology of noxious arthropods; developing a connecting classrooms programme; and analysis of movie nights.

Another area of interest has been to determine how many slow lorises are left in Java. This included concerted efforts in key national parks (Nekaris et al. 2014a) and examining slow loris distribution across Java (Voskamp et al. 2014). Indeed, in the latter study, we were able to increase the known range of Javan slow lorises substantially to include East Java. We also examined how slow lorises use the range around the disturbed areas of Garut using occupancy modelling (unpublished data), as well as the extent that slow lorises are able to move across open ground in such disturbed areas (Nekaris et al. in press).

Current work includes analysing dietary intake of slow lorises (Cabana and Nekaris 2015). Not only will such information be valuable to zoos and rescue centres keeping slow lorises, but it will also help with management decisions regarding protected area forest management. For example, slow lorises rely heavily on the nectar of *Calliandra calothyrsus*. One last stronghold of wild slow lorises, the Gunung Halimun National Park, had plans to remove this plant from the park, but we hope that our data can be used to keep populations of this beneficial albeit invasive species. The plant also has vital properties for soil richness and stability and we plan to use it in agroforestry projects with District farmers. Along the same lines, we are examining the impact of climate on slow lorises. We know that Javan slow lorises go into torpor, and we want to examine how and when this happens (Reinhardt et al. 2014). We will also use climate change projections to predict how slow lorises in the future may cope with habitat loss and the need to live at higher altitudes. Finally, slow lorises are highly exudativorous and it seems they use the same gum trees in a predictable pattern. We are currently examining cognitive mental maps in slow lorises using gum trees in a cognitive point change model; we hope that understanding how slow lorises navigate their environment will help improve reintroduction projects (Poindexter et al. 2014).

Education

LFP engages in many types of education activities and strives to develop quantitative output indicators for long-term assessment. As a loris-focused project, we wanted to examine knowledge of slow lorises over a period of time through a number of evaluated techniques, including free listing, cultural consensus analysis, behavioural engagement, and ability to express independent thought. Some of the activities in which we have engaged in since 2012 include weekly Nature Club in Cipaganti village with 20–59 children; biweekly Drama Club and Book Club with 15–20 children; construction of a village school for national curriculum and nature teaching; and region-wide assessment of a children's book about slow lorises. Children in our area enjoy drawing and colouring, and we wanted to develop a protocol to test children's knowledge in a fun way rather than traditional and often biased questionnaires. As an example, I present data collected from children's drawings.

From July 2013 to February 2015 we visited one primary school in Tasik Malaya District and 11 schools in Garut District, in three of which we taught two separate classes, yielding a total of 15 classes. For 12 of these schools, we were able to do an initial visit and a second visit approximately 6 months later. As part of a larger education programme regarding the importance of slow lorises to the ecosystem, children were asked to draw a picture of their perception of nature including slow lorises before teaching began, both for the initial and final sessions. We reached a total of 1209 children, including 636 boys and 573 girls (the proportions of which were statistically equal). The majority of children reached in the classes who wrote down their age were 9–11 years old ($n=856$) with only 28 children recording their ages as 8 or 12.

We analysed drawings for several features. First, for both the initial and final classes, children were told that we were going to teach them about slow lorises and they were asked to draw their idea of a slow loris. Some children drew scenes just of nature, but many drew animals. In total 46 animals other than slow lorises were drawn. Animals drawn by ten or more children included human ($n=100$), bird ($n=69$), cat ($n=64$), rodent ($n=29$), rabbit ($n=22$), fish ($n=21$), panda ($n=14$), cow ($n=13$), monkey ($n=12$), dinosaur ($n=12$), sheep ($n=11$), bear ($n=11$), shrew ($n=10$), and dog ($n=10$). Six hundred and eighty-seven children drew lorises across the two phases. In the initial phase, only 33.5 % of children included one or more lorises in their drawing. During the second visit, 89.8 % drew a loris, which was statistically significant ($\chi^2=372.26$, df $=5$, $p=0.0001$). We also wanted to know if children drew a loris that was 'accurate' including a face mask, dorsal stripe, five fingers and toes, or other distinguishing features, rather than a loris-like rendition. Of the children who drew a loris, only 21.5 % drew it accurately before with 78.5 % drawing accurately after ($\chi^2 = 150.65$, df = 2, $p = 0.0001$) (Fig. 2).

During the lessons, children were taught about the many reasons why slow lorises are important to the forest, including that they pollinate flowers and eat farmers' pests. They were also told that slow lorises are venomous and that they need their toothcomb not only to bite, but also to gouge for gum and to groom other slow lorises. For us this was a vital lesson to teach, since the greatest threat to pet slow lorises is having their toothcomb cruelly clipped or yanked out. Before any teaching began, 31 children included one of these elements in their drawings alongside a slow loris, whereas after 55 did so, which was significantly more ($\chi^2 = 20.71$, df = 3, $p = 0.0001$). In particular, before only 4.2 % of children drew lorises showing their teeth, whereas after 10 % did so; most children who drew teeth were boys ($n = 57$ boys vs. 24 girls); ($\chi^2 = 20.69$, df = 6, $p = 0.002$). In the initial drawings, a slow loris was more likely to feature on its own, whereas in the post session, more children drew lorises in the context of trees, bamboo, grass, mountains, or night time features such as moon or stars ($\chi^2 = 22.16$, df = 6, $p = 0.001$).

Our drawing data revealed that children could learn about the ecology of an animal and retain the information up to 6 months later. We were particularly keen to see that children could remember what a slow loris looked like in order to draw it accurately 6 months later and to add, without being told to do so, elements of its environment.

Fig. 2 Children's drawings featuring a less recognisable loris with fewer diagnostic features before any teaching, drawn in no nature context (*left*) and a more realistic loris (*right*) in a context with nature at the start of the second teaching session 6 months later

As all hunters we have met are men, we were particularly interested that boys drew lorises with teeth. We hope that the idea that lorises 'need' their teeth may stay with these children throughout their lives and that they would hesitate to clip teeth if they ever caught or were given a slow loris.

Empowerment

A major goal of LFP is to empower people to not keep slow lorises as pets, to understand the importance of slow lorises in the ecosystem, and to be able to identify slow lorises rescued from the illegal wildlife trade. We have done this through training on site, through social networking, and through various work with illegal wildlife traders. Since 2012, at our field site in Cipaganti we have worked with four Indonesian scientific counterparts; employed 12 local people; trained and employed 9 aspiring conservationists as Project Coordinators; provided services to 9 visiting researchers; were the subject of research for 6 Indonesian B.Sc. students, 12 foreign and Indonesian M.Sc. students, 6 Ph.D. students, and 2 postdoctoral assistants; and provided training for 26 international volunteers and placement year students. Our full team at any one time is about ten people.

We use social networking for news about our research, to announce events, to provide petitions and information on how to report illegal Internet activity regarding slow lorises, and to collect information about illegal wildlife trade. For example, in 2013 we published a major study on the impact of a single YouTube video on public attitudes towards slow loris conservation and showed that the Internet can be used to increase awareness over time that a slow loris is not a suitable pet (Nekaris et al. 2013a). LFP social networks are subscribed to widely, with numbers of people as of August 2015: Facebook ($n=9329$); Twitter ($n=2268$); and YouTube ($n=385$ subscribers; $n=54{,}914$ views). We also produce a newsletter three times a year with 1462 subscribers. We were instrumental in developing a Slow Loris Conservation page on Wikipedia, and have had our research featured by outlets such as Huffington Post, New Scientist, National Geographic, the Guardian, the Radio Times, BBC, Al Jazeera, Mongabay, and many more. Since 2012, we have been involved in several international television documentaries including major networks such as Animal Planet (world), Discovery Channel (Canada), History Channel (world), BBC (UK and world), ABC (USA), Al Jazeera (world), Trans7 (Indonesia), NHK (Japan), and EBS (Korea).

We have developed a set of law enforcement training materials on how to identify slow lorises in the illegal trade. So far we have performed training in several Asian countries: Indonesia; Malaysia (peninsular, Sarawak); Brunei; Thailand; Vietnam; Singapore; and Japan. We also perform monthly surveys of illegal animal markets in Indonesia, where we also collect data on nocturnal mammals, primates, and other protected species. Some published studies include examination of the trade in civets (Nijman et al. 2015), barbirusa (Nijman and Nekaris 2014b), and slow lorises (Nijman et al. 2014; Osterberg and Nekaris 2015).

As a main goal of our study was to stop trade locally, since 2012 we have followed 47 Javan slow lorises for various durations, including 9 observed continuously since 2012. Only a single one of these individuals disappeared in 'mysterious' circumstances, where a villager was found in possession of her collar, but claimed that a dog had attacked her. One animal was found drowned when dispersing into the village, and another was found dead after dispersing into the village (probably electrocuted). One animal was found dead of natural causes in the forest. Any other animals that were 'lost' were due to their dispersal out of the study area. We also took records of 13 slow lorises brought to us by villagers (Table 2). The number of slow lorises brought to us slowly increased over time, with 2 in 2012, 3 in 2013, 7 in 2014, and only 1 so far in 2015. With only three exceptions, all slow lorises were sub-adults, and found in seemingly peculiar places in the village (just outside villagers' houses). From radio-tracked animals that we have followed during dispersal, a common route of connectivity to another forest patch is through the village. After the peak of hand-overs in 2014, we did more awareness work and told people to leave the lorises if they saw them. Interestingly, in 2014 and 2015, two cases were from further afield in our district suggesting that information about our presence and our project had spread.

The Future

We have been asked why we want to study slow lorises in a human-modified landscape. It has been suggested that the behaviour of lorises might not be 'normal' and the fact that they eat some cultivated foods or exotic species means it is not their 'natural' diet. We feel the opposite. In a world with more and more humans and less and less space for other animals, knowing the intricacies about how humans and other animals can live side by side is vital. In the case of a Critically Endangered species that occurs in few protected places, where humans are the stewards of that species, such projects are even more important. As natural places become more and more humanised, it is imperative to know which of those aspects can in some way regain their nature; in which places animals can still thrive; and how they manage to do so. We also found that the days are quickly coming to pass where a researcher can sit in his or her tent, watching the animals all day, and never making contact with local people. In our project, we are members of the village and active members of the community. It has been vital to gain their trust and to incorporate their needs into our conservation strategy. At the same time, it is important to connect the small community where we are working with the rest of the world, to allow them to gain pride and empathy for the special species that share their farms, fields, and remnant forests with them. Through social media, the world can observe our efforts and join us through their online participation or active volunteering. For us, this is the way forward in twenty-first century conservation and we hope our project can inspire and persist over the next years to truly realise the impact of our actions.

Table 2 Animals ($n = 13$) brought to the LFP field station by villagers/officials, their health conditions and what happened to them

Date	Age/sex	Weight/name	Origin	Health	Consequence
11/05/12	Subadult female	903 g (Robinson)	Found by a villager in a tree near his house	Fluffy subadult with no wounds	Released to the bamboo near villager's house; radio tracked until dispersal
11/09/12	Subadult female	733 g (Cookie)	Found by kids walking in the village in the day	Subadult female with seeming cataracts on eyes	Brought to IAR for rehabilitation; was later released to Mt. Salak
05/10/13	Adult male	924 g (Honey)	Cipaganti: found in the village and brought to LFP	Healthy but very small testes for body weight; adult fur	Released to forest closest to spot where villager found him
06/11/13	Subadult female	550 g (Cuneng)	Cipaganti: found in the village and brought to LFP	Very stressed but healthy	Released to forest closest to spot where villager found her
21/11/13	Adult male	1140 g (Jack)	Cipaganti: found in the road gutter	healthy	Released in forest closest to the gutter
05/03/14	Subadult female	810 g (Angel)	Cipaganti: found her in a tree too close to people's houses	Very frightened, but healthy	Released her to the forest behind where she was found
17/05/14	Subadult female	762 g (Risa)	Cipaganti: found in tree next to house in village; called & asked to relocate her	Very calm and healthy	Released her to the forest behind where she was found
29/05/14	Subadult male	830 g (Tai)	Cipaganti: Villager saw him on the roof then found him curled up in his house	Very healthy	Released to Bamboo surat behind the area where he was found

(continued)

Table 2 (continued)

Date	Age/sex	Weight/name	Origin	Health	Consequence
24/06/14	Subadult female	860 g (Kiara)	Kiara, Cisurupan: Found by farmer when cutting bamboo; saw her walking on the ground; was afraid dogs would get her	Very beautiful loris; possibly pregnant	Released to same area; much bamboo was being cut there; we later found only her collar
14/07/14	Subadult male	? g (Poe)	Near Bandung: children took it from forest and gave it to a friend who called LFP	Eye cloudy, right arm chewed, wounds on feet	Taken to Aspinall then to IAR, where he died
27/08/14	Adult Female	837 g (Cinta)	Sumedang; seen by Cipaganti resident; he brought back to LFP	Tips of teeth clipped but no infection; underweight	Sent to PPSC for rehabilitation; plan to release in August 2015
02/12/14	Subadult female	719 g (Billy K)	Cisurupan: found walking on the road by local police man	Tip of canine broken leading to eye infection	Sent to PPSC for rehabilitation; due for release in Aug 2015
01/08/15	Subadult female	620 g (Listrika)	Garut city: found in an electricity box disturbing the circuits; Perhutani phoned LFP	Very healthy but very stressed leading to burst brachial gland	Sent to PPSC for health check, and returned almost immediately for release near the Cagar Alama

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The Many Facets of Human Disturbances at the Tonkolili Chimpanzee Site

Andrew R. Halloran

Introduction

As deforestation continues unabated across Africa (Hansen et al. 2013), animals such as chimpanzees find themselves facing an increasing reality of living in extreme anthropogenic habitats—frequently incorporating cultivated fields and villages into their core area. Such effects have led to an increasing number of interactions between chimpanzees and humans, the consequences of which have historically been negative for both species. It has, therefore, become crucial to the long-term survival of chimpanzees to understand their ecology in anthropogenic landscapes, and to look for ways to mitigate human–chimpanzee conflicts in order to protect chimpanzees living in such circumstances.

At this point, it can become tempting to search for universal variables that define human impacts, and explore solutions to anthropogenic conservation issues with chimpanzees based on these variables. However, factors within anthropogenic chimpanzee habitats, as well as human–chimpanzee interactions, can be unique and specific to the ecological, historical, social, and economic attributes of an area. Conversely, conservation initiatives targeting chimpanzees in these habitats, including mitigating the conflicts between humans and chimpanzees, require site-specific approaches to conservation that incorporate an exhaustive knowledge of all factors present within an area.

The effects of deforestation have been shown to push chimpanzees into isolated forest fragments, oftentimes sequestering a population within (Beck and Chapman 2008). Thus, the specific features of these fragments are the inescapable ecology of the chimpanzees within. Distinct fragment features have been shown to affect critical aspects of chimpanzee ecology specific to these ecosystems. These include

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forest attributes (Reynolds et al. 2003), parasitology (Gillespie and Chapman 2006), and interactions with local human communities (McLennan 2008). Any conservation initiatives for chimpanzees in fragmented areas must take into account the fact that the variables within can be unique. Failure to explore these factors, especially those related to the human component, can render a strategy unsuccessful (Webber et al. 2007).

A small group of chimpanzees in Sierra Leone live in a forest fragment surrounded by six human villages. This population shows how specific an anthropogenic ecology can be. This site, known as the Tonkolili Chimpanzee Site, carries with it particular dynamics endemic to it. These qualities illustrate that the variables defining human impacts are multifaceted and highly complex, and that any conservation initiative must incorporate a methodology tailored to the situation. In 2012, an initiative, "The Tonkolili Chimpanzee Project," was founded to address the conservation issues in the area (Halloran et al. 2014). The successes and challenges that the project has faced exemplify the intricacies of anthropogenic chimpanzee ecology.

Location

The Tonkolili Chimpanzee Site (Fig. 1) incorporates a forest fragment located on the banks of the Pampana River in Central Sierra Leone (Halloran et al. 2013). The fragment extends 7 km^2 from the river's riparian growth. The riparian forest connects this area to other fragments in Central Sierra Leone. Thus, there are forested

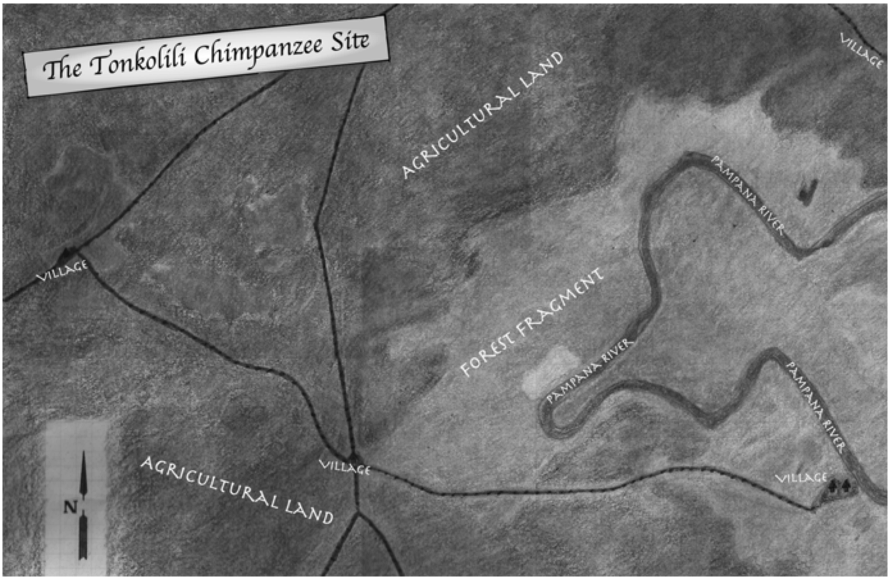

Fig. 1 A map of the Tonkolili Site showing four of the six villages

corridors in and out of the site. The site is also surrounded by agricultural fields that are cultivated and shared by the six local villages that surround the site. The crops in these fields vary; however, most of the land is used for oil palm (*Elaeis guineensis*). The edges of the fragment are fallow areas, cut down and cultivated at random times, then allowed to regrow once the harvest season has ended.

The six villages that surround the site belong to two different chiefdoms. The land and forest are shared unequally, with property rights shifting based on the political climate between the communities, which may favor some villages over others. In some cases, a village may be completely excluded from using the land by the others. The agricultural fields and villages are interspersed with several smaller forested patches. The chimpanzees, showing an ability and propensity to cross through domestic areas, frequently use these patches. The patches, and the cultivated areas between them, occupy 18 km^2. This, plus the 7-km^2 fragment, equals a 25-km^2 core area for the Tonkolili chimpanzees.

Background

The forest fragment contains a relatively high density of chimpanzees. A standing crop nest count (SCNC) census of chimpanzees reveals a density of two chimpanzees per km^2 (unpublished raw data). A survey of the wild food resources being consumed by the chimpanzees—primarily black velvet tamarind (*Dialium indum*), rubber tree fruit (*Funtumia* sp.), and tamarind (*Tamarindus indica*)—reveals an abundancy that may not support such a high density (unpublished raw data). However, the chimpanzees make up for these deficiencies by raiding and consuming cultivated crops—primarily the oil palm (both fruits and petiole), as well as the non-native mango (*Mangifera indica*) and pineapple (*Ananas comosus*). Crop raids are the most frequently reported interactions between the chimpanzees and humans.

A surprising by-product of crop raiding is that the seeds of the non-native cultivars are now being dispersed throughout the primary forest fragment. Mango saplings appear along chimpanzee created trails. In some places, deep in the forest, fully grown fruiting mango trees exist as part of the forest canopy. In addition, groundnut, guava, and pineapple can be found along the chimpanzee trails. These non-native food resources, imported by humans and introduced into the fragment presumably by chimpanzees, have altered the forest. Because of this, the chimpanzees have food preferences within the forests based on the presence of the human communities. This has modified their feeding ecology and, potentially (based on the presence of a uniquely introduced food availability), their social strategies, reproductive strategies, and territoriality; thus, giving a new facet of how humans can impact a landscape and the organisms within.

Interviews with the villages show a long history of human–chimpanzee interactions in the area. However, these interactions have changed over the course of several decades. The community also reports that encounters with chimpanzees have continually increased. Reports of interactions that occurred prior to the

Sierra Leone civil war consist mostly of chimpanzee attacks on livestock, pets, and humans. Reports since the civil war consist mostly of crop raiding by the chimpanzees. The community also reports that the killing of chimpanzees by humans has "always occurred", but has increased since the war as a method of crop defense and also due to the increasing number of encounters. The villagers claim to not eat the chimpanzees.

The primary reason for the present high density of chimpanzees in the fragment, as well as the increasing number of encounter with humans, stems from an exponential deforestation rate that has continually increased across Sierra Leone (Jallow 2014). This has resulted in high-density fragments such as the one occupied by the Tonkolili chimpanzees. The increasing density of chimpanzees within the fragment has necessitated their need for cultivated crops, resulting in the increased frequency of chimpanzees entering the agricultural fields.

Village economics has been a huge determinant on the nature of human–chimpanzee interactions at the site. Prior to the civil war, the communities relied on rearing livestock and cultivating honey (through bee keeping) as their primary sources of economy. In addition, they maintained crop fields of cassava and rice. During the war, rebel soldiers occupied the villages and many villagers fled into the forest. By the end of the occupation, the rebels had killed their livestock, destroyed their bee keeping boxes, and burnt their crop fields. When the villagers returned, they found they were left with no economic means. Since then, they have relied on obtaining loans for oil palm seeds. The oil palms can be harvested for kernels (which are used to make soap) and palm oil. However, because the chimpanzees frequently raid the palms and use the trees as nesting sites, the crops are often destroyed. The palms, therefore, do not produce a viable yield, leaving the villages in debt.

These factors have created a perception of chimpanzees as dangerous pests. Because of this, chimpanzees have been killed in the forest fragment out of both fear and as a method of resource defense. In addition, a dead chimpanzee can yield a relatively high price when sold to various societies for ritual practices. Combined, these variables point to a highly unsustainable coexistence between humans and chimpanzees at the site.

The Project

The Tonkolili Chimpanzee project began in 2012. While in Sierra Leone, we drove beside an agricultural field where several chimpanzee nests were visible from the road. We ventured on to the nearest village where the chief met us. When we asked him if there were chimpanzees in the area, he replied that, yes, they had "many" chimpanzees in the forest. In fact, he exclaimed, they had just killed two very recently. At this point, we were introduced to the hunter who had been killing the chimpanzees. He agreed to show us around the forest.

When we explored the forest, we were excited to find signs of chimpanzees throughout the fragment. Therefore, we made the decision to stay in the area for the next several weeks. Over the course of our first trip, we were able to explore the forest extensively. Of note was the fact that, though we were able to visually spot the chimpanzees and were in very close proximity to them, we never heard them vocalize. It is possible that this was because they were being regularly hunted.

Also during this initial trip, we were able to discuss the chimpanzees with members of the different villages. From this we learned that the chimpanzees were viewed as pests due to the economic problems caused by crop raiding. Based on this understanding, we began to design a conservation initiative that would reduce the villages' reliance on the crops that were being raided, while protecting the chimpanzees from being killed.

At the end of the summer, with the Conservation Society of Sierra Leone (our partner NGO), we proposed an agreement with the villages. It stated that we would seek out funds to rebuild prewar economic activities. In return, the villages would not hunt the chimpanzees in the fragment. The Conservation Society would monitor the agreement. The villages, and the governing chiefdoms, agreed and the project was commenced.

Upon returning to the USA, we began to look for funds. We approached a company that operated primate field schools and proposed a course whereby students learned about chimpanzee ecology in anthropogenic areas. We could then use a portion of the tuition to fund the project. They agreed. In addition, we approached Lynn University with an idea to construct bee keeping boxes as a student project. The university agreed to fund the materials and the shipment of the boxes, which we could set up the following summer.

The following summer, we returned to the site with funds to build livestock pens, purchase livestock, and plant a community garden with crops that we believed the chimpanzees were less likely to raid (okra, green beans, cassava, etc.). We also brought 10 bee keeping boxes. Together, the boxes would yield approximately 130 kg of honey per harvest—enough to be shared between the villages.

To monitor the chimpanzees, we set up camera traps (Fig. 2) throughout the forest. They revealed new chimpanzee births and a population that was larger than originally suspected. These photos, combined with the fact that the chimpanzees were now highly vocal, provided evidence that the villages had been true to their word and no chimpanzees had been killed. We began working on other community initiatives: building more livestock pens, purchasing more livestock, and having wells dug for two of the villages that had no access to adequate drinking water. We returned home that season feeling surprised at how well the project was doing. However, this feeling was not to last much longer.

The following winter, a fire swept through one of the villages (this was the village we had initially approached, stayed with, and had the closest ties to). The fire had spread from the agricultural fields into the village. The thatched roof huts were quickly consumed. In the end, all but three huts were destroyed. Luckily, no one had been hurt, but almost everything within the village was destroyed. We were able to raise enough funds to rebuild the huts. In an attempt to prevent future fires of this sort, we rebuilt the thatched roofs with metal roofs.

Fig. 2 A photo from one of the camera traps showing a female chimpanzee with an infant on her chest

With the village rebuilt, and no injuries from the fire, the project seemed poised to resume. However, when we returned the next summer, we found the chimpanzees silent again. After repeated inquiry, it was revealed that one of the villages had hosted a visiting hunter in the spring. The hunter had killed two adult male chimpanzees and sold them to secret societies. This village had apparently taken offense to the fact that the burnt village now had metal roofs instead of thatching (a more significant mark of status than we had realized). They hosted the hunter because, according to conversations with members of the village, they no longer felt the project had any value for them and wanted to end it.

The hunter, himself, was arrested—not for killing the chimpanzees, but for using an illegal riffle (both are illegal; killing a chimpanzee carries a fine of roughly $4, while using an illegal firearm can be punishable by years in prison). He had been turned in by the old hunter, who had initially taken us through the forest on our initial village and was now solidly behind the project.

The events of that year were symptomatic of a general short sightedness and oversimplification that was hindering the project. We were concentrating entirely on the fact that the chimpanzees were being perceived as an economic threat, while ignoring other factors at the site. Intervillage politics, land disputes, historical encounters with chimpanzees, and even mythic perceptions of the chimpanzees were having as much of an impact of the sustainability of the chimpanzee population as the perceived economic threat. Before that summer, we had begun to address some of the project's shortcomings. Most significantly, a cultural anthropologist joined the project as a collaborator. Through her expertise, we were able to collect more extensive ethnographic data on the local community. Most of this has centered on community perceptions of chimpanzees, chimpanzee conservation, and human survival. Through this, we will be better able to address community needs while simultaneously working to conserve the chimpanzee population.

We also initiated the process of training and hiring local community members from each village to act as both researchers and patrols. The researchers are trained to collect ecological data via GPS, as well as check, monitor, and maintain the camera traps. The goal of this initiative is to create a conservation enterprise. At the end of the summer, we held a meeting with members of all six villages together. The aim of the meeting was to clarify the project to all of the villages and to begin a more open dialogue with the community. At the end of the meeting, one of the elders from the largest village stood up and told a story that had occurred before the war. A woman, he recounted, was walking out to one of the fields with her infant strapped to her back. On the road, she encountered three large chimpanzees. The chimpanzees attacked the woman, took the baby from her back, and killed the baby in front of her. When he finished his story, he asked us a question. Why, he asked, would they want to keep these animals in the forest? The story and the question highlighted the extremely complex nature of the situation, not just at the Tonkolili site, but in all anthropogenic chimpanzee habitats. As human impacts have depleted chimpanzee habitats and increased the densities in small fragments, encounters with humans have increased. Each specific encounter adds an element to an ever-growing collective perception of chimpanzees held by a local human community. The negative consequences of these encounters, whether they are economic consequences or violent consequences, increase the collective community animosity and fear towards chimpanzees. It is the burden of the conservation strategy to find an optimality, a value, of living wild chimpanzees for the humans that live among them. The value must exceed the heavy detriments incurred by human–chimpanzee interactions. If not, the strategy will fail.

Towards a Sustainable Anthropogenic Landscape

The dynamics at the Tonkolili Site were forged element by element. Alter, or take away, any one element, and the dynamics can change drastically. Each ecological variable, each encounter between a human and a chimpanzee, each economic circumstance faced by the local human community, each aspect of the political and social landscape within the local human community, and each facet of history occurring at (or around) the site have all created these dynamics. The Tonkolili Site is shaped as much by the types of crops that the community has grown, as it is by chimpanzees dispersing cultivated seeds throughout the forest. The dynamics of the site are determined as much by the economic realities of the community, as they are by the brutal civil war that created these realities. The dynamics specifically identify

Fig. 3 The Pampana River cuts through the forest fragment

the Tonkolili Site, dictating the health of the ecosystem and the sustainability of the chimpanzees. Humans haven't just influenced the chimpanzee habitat, they have defined it (Fig. 3).

In order to create sustainability at the Tonkolili Site, the unique dynamics must be explored, understood, and addressed. Together, these dynamics can be viewed as a causal nexus where each variable creates a ripple effect. The ripples influence other variables, culminating in the present state of the site. The most obvious variable is the ecology of the chimpanzees in the forest fragment. As we have seen, they live with an unusually high population density. This was brought on by large-scale deforestation across the region. The deforestation represents human impacts that are not necessarily immediate. In fact, through deforestation, the chimpanzees are being impacted not just by the humans in their immediate vicinity, but by the actions of humans across the region and, in the sense that the forces of deforestation exist in the global demand for resources in West Africa, across the globe.

The high density has several consequences. Most significantly is the fact that the increased density equals more frequent encounters with humans. Because these encounters have been violent in the past, where livestock, pets, and even humans are injured or killed, each encounter builds a highly negative perception of chimpanzees among the community. This negative perception creates a massive barrier to any perception of value that the community could have of living chimpanzees. The high density also carries the consequence that the forest fragment alone cannot sustain the population of chimpanzees. The chimpanzees have adapted to this by feeding off the crops cultivated by the community. This creates a severe economic adversity for the villages because of what occurred during a war, they are economically reliant on cultivating crops that chimpanzees frequently raid. This, in turn, adds to the already negative perception of chimpanzees. Not only are chimpanzees potentially lethal, they also destroy the economic viability of an already highly impoverished community.

The result is the focal conservation issue: chimpanzees being shot in the forest. However, as this causal nexus shows, the killing of chimpanzees is merely a symptom of a much larger operation. When we initiated the Tonkolili Chimpanzee Project, we were only treating this symptom and its most obvious causes. However, as we worked to rectify the problem, the other ripples in the causal nexus were supplanting what we attempting to fix. As we treated the economic situation, we failed to address the perceptions. Had this understanding been the initial foundation of the Tonkolili Chimpanzee Project, we may have avoided some of the challenges we experienced. It is from this understanding that the project has proceeded ever since.

The final consequence of this causal nexus is the inadvertent seed dispersal by the chimpanzees. Through this phenomenon, we see a grand ecological adaptation to human impacts. The forest is becoming sustainable for the chimpanzees, while at the same time, reducing the chimpanzees' need to go into the crop fields. The forest has been altered in a way that benefits both species. It serves as a reminder that coexistence between the two species is possible, and perhaps there are ecological mechanisms that allow chimpanzees to survive in an anthropogenic landscape.

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How Living Near Humans Affects Singapore's Urban Macaques

Crystal M. Riley, Alexander S. DuVall-Lash, Srikantan L. Jayasri, Bryan L. Koenig, Amy R. Klegarth, and Michael D. Gumert

Introduction

There are currently 23 recognized species in the genus *Macaca*, the most widely distributed primate genus following *Homo* (Li et al. 2015; Thierry 2007). Their wide geographic range is a testament to their adaptability to different environments, including human-altered ones. While not all macaques are adapted to anthropogenic landscapes (i.e., lion-tailed macaques, see Singh et al. 2002), species such as long-tailed macaques (*M. fascicularis*), rhesus macaques (*M. mulatta*), toque macaques (*M. sinica*), and bonnet macaques (*M. radiata*) live in urban areas (Richard et al. 1989) and are often referred to as "weed macaques." As human populations and economic development continue to increase, more natural habitats will be converted

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into anthropogenic landscapes, causing more macaques to face the challenges associated with urban settings. In this chapter, we briefly summarize the human–macaque urban interface and focus on the time budgets, ranging, and group size of long-tailed macaques living in Singapore. We then discuss our perspective on nonlethal management strategies for urban macaques.

The Urbanization of Macaques

Most macaque species reside in South Asia, which is growing and developing rapidly. For instance, the percentage of the human population living in urban areas in Cambodia is expected to increase from 17 % in the year 2000 to 44 % in 2050 (Sheng 2012). Similarly, Singapore is projected to grow from 5.5 to 6.9 million people by 2030, a 25 % increase (National Population and Talent Division 2013). As this growth occurs, it is reasonable to think that the frequency of human and macaque encounters will increase. To better prepare for this increase, it is important to grasp the manner in which humans and macaques regard each other in urban settings. Farmland areas (Peterson and Riley 2013; Riley and Priston 2010), temple complexes (Fuentes 2013; Mallapur 2013; Wheatley 1999), and cities (Sha et al. 2009) are only a few of the areas where the human–macaque interface has been studied. The results of these studies suggest that humans impact macaques in several ways. For example, humans can transmit infectious agents to macaques (Epstein and Price 2009; Muehlenbein et al. 2010). Additionally, people can physically harm macaques. Intentional killings may include culling as a management strategy, pest control near crops, or hunting for food (Nahallage et al. 2008; Nahallage and Huffman 2013). Humans can also unintentionally affect macaque population levels by hitting them with cars or allowing pet dogs to kill them (Gumert et al. 2013; Riley et al. 2015a).

Studies have also found that the anthropogenic landscape alters several macaque behaviors including those associated with substrate use (Aggimarangsee 1992; Seth et al. 2001), ranging patterns (Berman et al. 2014; Klegarth in press), activity budgets (Chauhan and Pirta 2010; Chopra et al. 1992; Jaman and Huffman 2013), social structures (Chapman and Rothman 2009; Kamilar and Baden 2014; Lane-deGraaf et al. 2014; Sinha 2005; Sinha et al. 2005), aggression levels (Southwick 1972), and diets (Gumert et al. 2013; Klegarth in press; Singh et al. 2001; Sinha and Mukhopadhyay 2013). Additionally, obesity has been found to threaten the health of urban macaques (Aggimarangsee 1992; Knight 2011; Lane et al. 2010).

Many of the changes listed above are due to differences in food availability near humans when compared to “wild” habitats, as urban areas tend to be food rich. For example, people provision macaques for recreational pleasure, bait them out for viewing, or indirectly provide them with discarded refuse. Direct provisioning is especially common from tourists at monkey parks (Berman et al. 2014; Fa 1992; Knight 2011) and temples (Aggimarangsee 1992; Wheatley and Putra 1994a).

Provisioning is generally encouraged at these sites so that food vendors can gain profits (Gumert 2011; Wheatley and Putra 1994b). Direct provisioning can also occur in other urban areas, but is generally less organized than at tourist sites. Provisioning in this manner may decrease reliance on natural food sources. In Shimla, India for example, rhesus macaques derived only 9 % of their diet from natural sources, with scavenging and human feeding accounting for 77 % of their diet, snatching/stealing for 9 %, and crop raiding for 5 % (Chauhan and Pirta 2010). Humans can also indirectly affect food availability and diets with food that macaques scavenge from garbage bins, take from homes, or snatch from passersby. Such food snatching is especially common where macaques are highly habituated and do not fear people.

When macaques snatch food, people sometimes respond with aggression, such as chasing or attempting to strike the macaques, or with fear, such as fleeing or screaming. Thus, food snatching is typically a negative experience for people. For example, at Shou-Shan Nature Park in Taiwan, Formosan macaques (*M. cyclopis*) displayed aggression towards tourists nearly five times more frequently during food provisioning than during times of non-provisioning (Hsu et al. 2009). In Dehradun, India, humans engaged in aggression towards macaques six times more frequently than the macaques were aggressive towards humans, and aggression was often triggered in response to macaques attempting to steal food. Furthermore, macaque aggression was usually counter to the human-initiated aggression (Beisner et al. 2014).

Macaque Impacts on Humans

Although humans have many impacts on macaques, the human–macaque interface is bidirectional and macaques have harmful and beneficial impacts on people too. For example, macaques can transmit infectious agents to humans (Jones-Engel et al. 2005, 2006), damage people's property, raid crops, and cause other economic losses (Riley and Priston 2010). Macaques can also physically harm humans, typically during conflicts over food access (Fa 1992; Fuentes 2006; Fuentes and Gamerl 2005; Imam and Yahya 2001). Very rarely, macaques have killed people (BBC News 2010; Southwick and Siddiqi 2011; Zhao and Deng 1992).

Macaques can also benefit humans. For example, macaques provide substantial economic gains in the form of revenues from tourism (Fuentes 2006, 2010; Gumert 2011; Knight 2011) and are sacred symbols for millions of people (Aggimarangsee 1992; Fuentes 2006; Fuentes et al. 2005; Wheatley 1999). Macaques may also benefit the local environment as seed dispersers, helping to maintain the health of ecosystems (Dudgeon and Corlett 1994). Additionally, some people simply enjoy watching macaques (Malaivijitnond and Hamada 2008). In Singapore specifically, macaques add to urban biodiversity because they are among the only medium sized mammals that live in the urban environment (Lucas and Corlett 1998).

The Human–Macaque Interface in Singapore

Singapore is a densely populated city-state located at the southern tip of peninsular Malaysia. The 718-km^2 island is home to 5.5 million people (Singapore Department of Statistics 2015) and approximately 1900 macaques, according to a census in 2012 (Riley et al. 2015b). The majority of the macaque population is concentrated in the protected areas of the Central Catchment Nature Reserves and adjacent Bukit Timah Nature Reserve, which constitutes 4 % of Singapore's land area (National Parks Board of Singapore 2009, Riley et al. 2015b). The human–macaque interface in Singapore is relatively mild compared to other countries with human–macaque conflict problems (Fuentes et al. 2008; Sha et al. 2009). For example, direct physical contact between humans and macaques is less frequent than elsewhere in Southeast Asia (Fuentes et al. 2008), in part because Singapore does not have monkey temples and has strict regulations about macaque feeding. The mild nature of conflict can be partially attributed to proactive strategies of Singaporean government agencies. For example, they periodically conduct public service campaigns to educate people regarding how to live and act near macaques and they actively manage portions of the macaque population through culling when they reach high levels of overlap and conflict (Lee and Chan 2011). Despite these programs, Singapore still faces considerable challenges in managing their macaque population and limiting human–macaque conflict. Macaques take food, raid garbage bins, damage property, and injure people, albeit rarely (Feng 2011; Sha et al. 2009). Humans also continue to feed macaques in spite of the feeding ban, threaten or chase macaques, and unintentionally kill macaques with their cars.

Attitudes toward macaques in Singapore vary. Visitors to recreation parks tended to view macaques more positively than residents who live near recreation parks, as 37 % of visitors reported a positive attitude toward macaques compared to 21 % of residents (Sha et al. 2009). Resident attitudes are also reflected in frequent media coverage of macaques. Sha and colleagues (2009) found 47 macaque-related headlines in Singaporean newspapers between 2004 and 2008, showing that the issue is frequently discussed in the public. Wildlife authorities have hotlines for receiving complaints about macaques, and complaints about macaques are frequently received (Ee 2013; Feng 2013) with high levels of complaints associated with culling. In 2013, 570 macaques were culled (Khew 2014) after receiving 1860 complaints (Feng 2015). This is approximately 30 % of the estimated macaque population in Singapore (Riley et al. 2015b). Several years prior to the culling, a small survey found high levels of support for conserving macaques and only a small number of people supported culling efforts (Sha et al. 2009).

For this chapter, we analyzed data collected during a nationwide census of the long-tailed population of macaques in Singapore. In particular, we focused on how overlap with humans affects group size, substrate use, and behavioral time budgets. We used two variables as indicators of human overlap: presence of humans during observation and whether or not a group had ever been observed accessing human food. Based on prior research, we expected groups with greater exposure to humans and human food to be larger. We also expected macaques with such exposure to be more terrestrial, less arboreal, and have altered time budgets.

Methods

A nationwide census of Singapore's macaques was conducted between October 2011 and November 2012 (Riley et al. 2015b). We studied 67 groups and spent an average of 7 h and 45 min with each group of macaques. During our study, positional and behavioral data were collected. Upon encountering a macaque group, macaques were counted every 30 min until we were confident in the accuracy of our count. For additional details on how groups were determined, see Riley and colleagues (2015b). While with macaques, our GPS device was set to automatically generate track points at 30-s intervals (Fig. 1). We conducted scan samples (Altmann 1974) of each visible individual's behavior at 30-min intervals to obtain data on general time budgets. Each subject was scored into one of six behavioral categories: resting, socializing, traveling, natural feeding, human feeding, and human–macaque interaction (other than feeding). For feeding scans, we scored the type of food being consumed into one of 17 categories (e.g., fruits, insects). For social scans, we scored the type of social behavior as aggression, grooming, mounting/being mounted, or playing. We also scored the type of substrate (i.e., arboreal, terrestrial, or human-made structure) and distance to the nearest human other than the researcher(s) (no humans visible, less than 1 m, 1–3 m, 3–5 m, 5–10 m, or greater than 10 m).

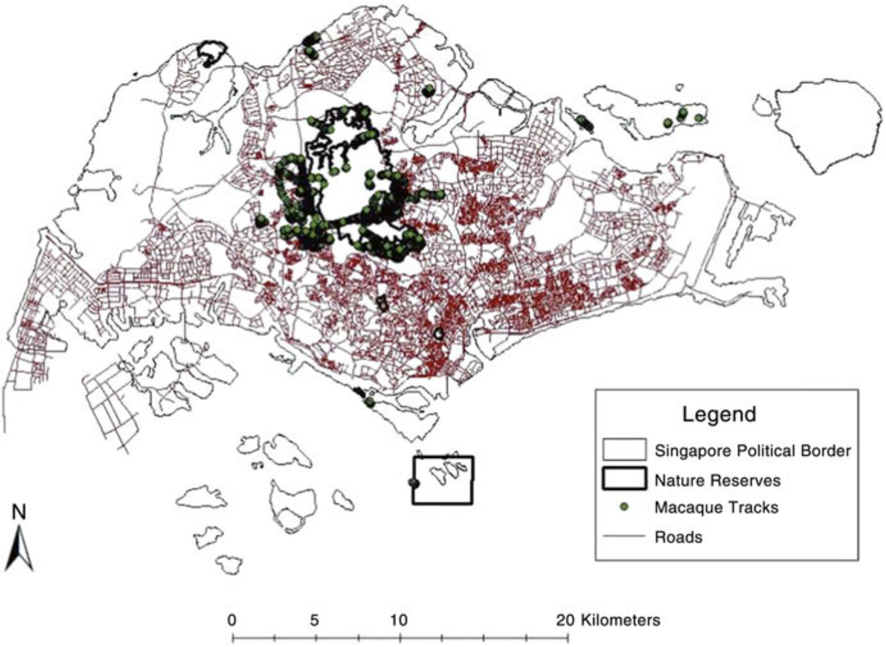

Fig. 1 This map shows the track points ($n = 64{,}666$) denoting the ranging patterns of Singapore's macaque groups ($n = 69$). Track points were collected at 30-s intervals during macaque follows

Although the presence of the researcher(s) likely did have some effect on the macaques, we attempted to mitigate those effects by maintaining a reasonable distance and avoiding direct eye contact, loud noises, and sudden movement.

Statistical Analyses

We coded macaques regarding whether they were in a group observed accessing human food at least one time or in a group never observed accessing human food. We examined differences in activity budgets and substrate use depending on human food access and presence or absence of humans other than the researcher(s). For count data, omnibus analyses were done using Pearson goodness-of-fit tests if sufficient observations were in each cell to meet assumptions (i.e., at least 80 % of cells have expected frequencies less than 5). If this assumption was not met, we instead report the likelihood ratio test. For post hoc analyses, the variable level of interest (e.g., arboreal) was separated from the others (e.g., structures and terrestrial) by coding the level of interest as a one and the other levels as zeroes. This process was repeated so that each level of the variable was designated as the level of interest and then compared with the other levels of the variable. Post hoc analyses used Pearson goodness-of-fit tests (or likelihood ratio tests if too many expected values were less than 5) unless analyses were of 2×2 tables, in which case we used Fisher's exact test. Alpha was set to $p < 0.05$ for all tests other than post hoc tests, which used Bonferroni-corrected alpha values to control for multiple comparisons. Throughout, any other statistical tests are explicitly mentioned. Statistical analyses were conducted in IBM SPSS Statistics version 22.

Spatial Analysis

In addition to behavioral data, we used ranging data to examine the extent of human–macaque overlap in Singapore. Spatial joins were conducted on each track point to determine the percentage of time macaques spent ranging within the boundaries of designated nature reserves and near anthropogenic areas such as residences or businesses. Five-meter buffers were placed around all roads to determine the amount of time macaques ranged on or within five meters of a road. Spatial analyses were conducted in ArcGIS version 10.3.1.

Results

Group Size

We studied 67 groups and found an average of 24.2 individuals per group (SD = 9.85, range 2–48). We also observed two lone males. Groups observed accessing human food ($M = 28.27$, SD = 11.50, 95 % CI: 23.17–33.37) were larger than those not observed accessing human food ($M = 21.36$, SD = 9.28, 95 % CI: 20.29–25.12), $t(31.35) = 2.04$, $p = .050$, $d = 0.57$ (using Welch two sample t-test due to unequal variances; Bartlett's K-squared = 4.03, df = 1, $p = 0.04$). For additional details on population characteristics (age-sex breakdown, population density by region, spatial distribution of groups), see Riley and colleagues (2015b).

Distance to Humans

Macaques spent 0.4 % of their time less than 1 m from a human, 1.7 % between 1 and 3 m, 4.4 % between 3 and 5 m, 4.8 % between 5 and 10 m, 31.5 % greater than 10 m from a human, and 57.2 % with no humans visible. Considering only whether humans were present or absent, 57.2 % of observations ($n = 6392$) occurred without a human present and 42.8 % of observations occurred in the presence of other humans. Given the low counts at some distances, and the fact that much of the variability in distance to humans can be accounted for by recoding distance as humans present or absent, subsequent analyses of activity budgets and substrate usage evaluated presence-versus-absence of humans rather than the distance to the nearest human.

Activity Budgets

Activity budgets differed for macaques in groups that had been observed accessing human food compared to those from groups never observed accessing food, χ^2 (3, $N = 6301$) = 9.36, $p = .025$ (Fig. 2). Observations of human–macaque interactions were excluded because there were too few observations for chi-square analysis. Post hoc analyses confirmed that the effect for food access held for traveling ($p = .001$), but not eating natural food ($p = .713$), resting ($p = .034$), or socializing ($p = .389$). Macaques from groups observed accessing human food traveled less.

Whether people were present or not (Fig. 3) was also related to activity budgets, χ^2 (4, $N = 6379$) = 90.79, $p < .001$. Post hoc analyses indicated this held for eating human food ($p < .001$), and traveling ($p < .001$), but not eating natural foods ($p = .496$), resting ($p = .488$), or socializing ($p = .947$). Thus, when humans were present the macaques were more likely to be eating human food and less likely to be traveling, but equally likely to be eating natural food, resting, or socializing.

Substrate Use

Whether an individual was in a group that had been observed accessing human food was related to the likelihood of using the three substrates χ^2 (2, $N = 6434$) = 136.42, $p < .001$. Post hoc analyses indicated differences for time spent arboreally ($p < .001$)

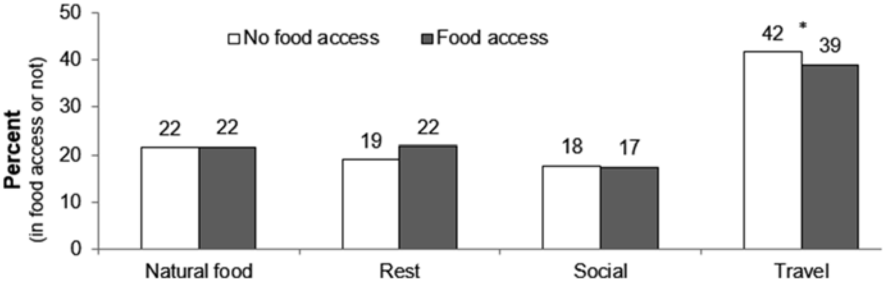

Fig. 2 Activity budgets of macaques with and without access to human food. An *asterisk* indicates a significant difference

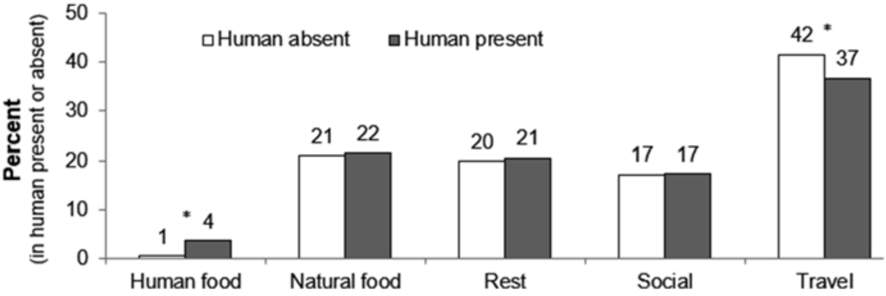

Fig. 3 Activity budget of macaques when humans were present versus absent. An *asterisk* indicates a significant difference

and on structures ($p < .001$), but not terrestrially ($p = .790$). The pattern of results (Fig. 4) indicates that individuals in groups that had been observed accessing human food were more likely to be on structures and less likely to be arboreal, as compared to individuals from groups never observed accessing human foods.

Human presence also had an effect on substrate use, χ^2 (2, $N = 6392$) = 77.49, $p < .001$. Post hoc analyses indicated that human presence was important for arboreal, structures, and terrestrial usage (ps < .001). When humans were present, the macaques were less likely to be in the trees and more likely to be terrestrial or on structures (Fig. 5).

Spatial Distribution

Our analysis showed that macaques spent much of their time within the boundaries of nature reserves. Of 64,666 track points that marked the position of the researcher every 30 s when following macaques, 43.2 % ($n = 27{,}910$) occurred within the boundaries of a nature reserve. Of the 69 social units (67 groups and two lone males) observed during the census, over half ($n = 35$) ranged in an anthropogenic area (near

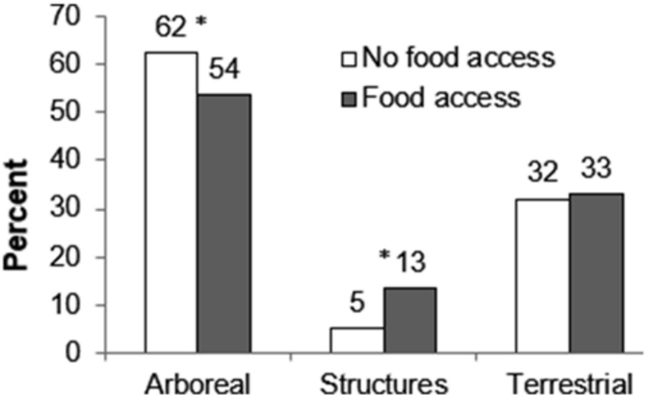

Fig. 4 Substrate use by macaques with and without access to human food. An *asterisk* indicates a significant difference

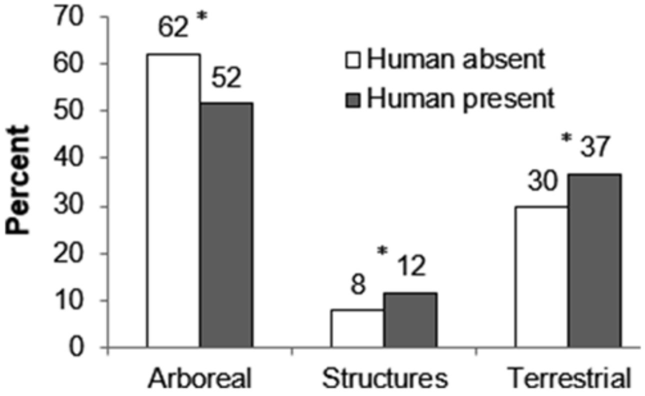

Fig. 5 Substrate use by macaques when humans were present versus absent. An *asterisk* indicates a significant difference

a road, residence, or business) at some point during our observations. Another 15.7 % ($n = 11$) ranged within 100 m of an anthropogenic area. Of the track points that marked macaque ranging, 17.5 % ($n = 11,337$) occurred on or within five meters of a road. A large portion of roadside track points, 14.6 % of observations ($n = 1658$), were accounted for by one road (Old Upper Thompson Road) which passed through home ranges of four groups of macaques.

Discussion

Our study found that for macaques in Singapore, human presence is associated with decreased traveling rates, decreased arboreality, increased terrestriality, and increased use of human-made substrates. A related variable, access to human food, correlates with larger macaque group sizes, decreased arboreality, and increased use of human-made structures. We also found that Singapore's macaques spent most of their time within the boundaries of the nature reserves.

These results highlight the differences related to exposure to humans and human food. Given that Singapore is highly urbanized and all macaque groups can reasonably be considered urban, substantial differences nonetheless exist among individuals and groups in the degree to which they overlap with humans and human food. Individuals in groups that accessed human food spent more time on human-made structures, consistent with results from Aggimarangsee (1992), less time in trees, consistent with Fooden (2000), and less time traveling. Surprisingly, individuals in groups that accessed human food did not spend significantly less time foraging for natural foods, which has been observed in other populations (Chauhan and Pirta 2010). Overall, macaque substrate use differed depending upon whether the group was observed accessing human food and whether or not a person was present. A clear pattern emerges across these analyses: human influence seems to bring the macaques out of the trees and onto the land and structures.

In the highly urbanized habitat of Singapore, it is perhaps surprising that macaques managed to avoid areas heavily populated by humans to some degree. Overall, 34 of 69 social units did not range in an anthropogenic habitat during our observations, and macaques spent 43 % of their time within the boundaries of nature reserves, even though protected parkland accounts for less than 5 % of Singapore's land area. Furthermore, 43 groups never accessed human food during our observations. However, simply because a group was not observed accessing human food or ranging in an anthropogenic area does not mean that those groups always avoid human food and human-inhabited areas. The finding that macaques spent 43 % of their time in nature reserves could be misinterpreted to mean that macaques spend a large proportion of their time away from humans. However, nature reserves in Singapore are heavily used for recreational purposes, so they are common areas of interface for macaques and humans, although they are typically less intense interfaces than anthropogenic areas such as residential complexes or roads.

Effects of Food Access

The macaque groups in our study differed on variables typically associated with urban versus nonurban living (including substrate use, behavioral time budgets, and group size), even though all the groups in our study could reasonably be considered urban. The reasons for such differences are not easy to determine. Jaman and Huffman (2013) found that human food access was responsible for the differences in activity budgets between urban and nonurban groups in their study. It seems likely that access to human food underlies activity budget differences in our study as well. Human food access may also result in larger groups, or larger groups may simply outcompete smaller groups for access to human food and to areas with human food access (Lane-deGraaf et al. 2014). If this is indeed the case, then human food access may be a feedback loop in which large groups outcompete smaller groups for access to human food; access to human food increases reproductive rates and groups get larger; and larger groups outcompete other groups for access to human food.

Management of Urban Macaques

In order to effectively manage human–macaque interfaces, officials need to address three key dimensions: the macaque dimension, the human dimension, and the environmental dimension (Jones-Engel et al. 2011). The macaque dimension focuses on understanding and changing the composition, distribution, and/or behavior of the macaque population. The human dimension involves understanding the changing composition, distribution, and/or behavior of the human population. Lastly, the environmental dimension deals with understanding, developing, and modifying the local conditions where humans and macaques interface, so as to reduce overlap and contact between humans and macaques. Although some conflict management approaches attend to all three of these dimensions, we briefly discuss the macaque dimension (to discourage culling) and then focus our recommendations on the human dimension, as human behavior is typically the main driver of human–macaque conflict (Lee and Chan 2011; Sha et al. 2009). Given our finding that humans can influence macaques by their presence and by the availability of food, it seems that management efforts should take greater effort to mitigate the influences that humans have on macaques. Below we provide a brief summary of several management ideas. For a more thorough review of management recommendations for long-tailed macaques, see Jones-Engel and colleagues (2011).

Focus on Preventive Measures Instead of Culling

Interventions to manage human–macaque conflict are often made based on two related assumptions. First, overpopulation of macaques drives conflict. Second, reducing the overcrowded population will cause conflict to subside. However, little to no research has examined these assumptions. The effects of culling on the structure of populations in Southeast Asia are poorly understood. Widespread culling on Ngeaur Island, Republic of Palau failed to achieve the desired result of eradicating the population (Wheatley 2011). In addition, macaque populations are a natural part of their habitat and serve important functions such as seed dispersal (Dudgeon and Corlett 1994). This is especially important in places like Singapore where large vertebrates have become scarce (Lucas and Corlett 1998). Nevertheless, Singapore has heavily employed culling as a macaque management strategy (Khew 2014). We recommend that culling should become better informed through research and there should be a managerial focus on nonlethal techniques, as described in the subsequent sections. If culling continues to be used as a management technique, we recommend careful data collection to determine whether culling achieves the intended goal of reducing human–macaque conflict. For example, Lee and Chan (2011) reported that macaques are trapped and culled in response to nuisance complaints from the public. However, little effort is made to ensure that the individual caught in the trap is in fact the individual responsible for the complaints. Thus, a juvenile female could be caught and culled in response to complaints about an aggressive adult male. This will not resolve the source of the complaints and it may sensitize the macaques to the trap resulting in greater difficulty catching the target macaque in the future. Officials investigating nuisance complaints should gather sufficient information from the public, including photographs when possible, to identify a target macaque before culling. A studbook of identification sheets (which contain photos and identifying marks) for 596 individual macaques was created as part of the 2012 macaque census (Riley et al. 2013), and could aid with identification of specific macaques.

Enforce the Feeding Ban

The undesirable effects associated with macaques accessing human food—especially aggression—suggest that preventing macaques from eating human food is critical to any management program. In fact, preventing macaques from eating human food could be the single most important step in reducing human–macaque conflict. Benefits include preventing aggression from macaques to humans, decreasing macaque population growth rates, reducing disease transmission, and maintaining a healthier macaque population. Singapore has already taken an important step by banning macaque feeding and imposing large fines. In 2008, NParks doubled the monkey feeding fine to SG$500 (about US$380; NParks 2008) and enforcement also increased during that time (Lee and Chan 2011). However, monkey feeding still frequently occurs without intervention by officials. By stepping up enforcement, Singapore could reduce undesirable macaque behavior through removing access to human food sources. Yet another benefit is that the revenue from macaque feeding fines could be used to fund other macaque management initiatives.

In addition to stopping direct feeding of macaques by people, it is critical that management also curb indirect access to foods. At residences near nature reserves, most residents receive monkey-proof trash bins or use bungee cords to secure the bins against monkeys. When trash bins are improperly secured, macaques gain access to the refuse. Imposing fines on residents that improperly secure their garbage could make residential areas less attractive to macaques, reducing the time macaques spend there and the messes they make while scavenging, thus alleviating some forms of human–macaque conflict. Effective litter control in areas that macaques inhabit is also important.

Employ "Macaque Security Guards" to Mitigate Conflict

"Macaque security guards" could be useful in Singapore for monitoring and directly managing human–macaque interfaces. Hong Kong has successfully used guards to patrol their areas of human–macaque interface and intervene in situations of potential conflict (Shek 2011). Because conflict often occurs near private residential condominiums, which typically employ private security guards, it would be practical and efficient for those guards to be trained in the mitigation and prevention of human–macaque conflict by appropriate wildlife authorities and experts. With some basic training, guards could assist people by helping them to navigate safely in areas with macaques, for example passing near macaques without having their grocery bags or food snatched. The guards would also be able to herd macaques away from residences, businesses, and busy streets. Furthermore, they could inform people in human–macaque interface zones how to best avoid interaction with macaques and what behaviors reduce the likelihood of conflict escalating. For example, guards can help ensure people keep food secure and out of sight, while also maintaining a safe distance from macaques. More professional guards associated with wildlife authorities could also be employed that could issue citations to those who engage in macaque feeding and the feeding fines could pay some of the salary for guards. If they were not empowered to issue citations, they could still remind violators that feeding macaques is illegal and call proper authorities. The nongovernmental organization Animal Concerns Research and Education Society (ACRES) has made some efforts to use macaque guards, but efforts could be increased (Khew 2014). Security guards could be especially helpful in urban areas, where human–macaque interfaces are more concentrated and thus easier to monitor than in rural areas, where interfaces are spread over larger areas.

Focus Efforts on Conflict Hotspots

Almost 15 % of our observations near roads occurred along a single road. This suggests the potential benefit of targeting macaque management efforts at particular hotspots that are especially likely to attract both macaques and people. Sha and colleagues (2009) identified six human–macaque interface hotspots in Singapore: Bukit Timah Nature Reserve, Upper Pierce Reservoir Park, Lower Pierce Reservoir Park, MacRitchie Reservoir Park, Upper Seletar Reservoir Park, and Rifle Range Road. This strategy would be most successful when paired with an ongoing macaque-monitoring program that can assist in identifying conflict areas.

Continue and Expand Current Educational Programs

NParks and other local agencies organize programs to educate the public about how to peacefully coexist with macaques (Lee and Chan 2011). Those programs include Monkey Walks, which are tours of nature parks that are led by a primatologist who explains macaque behavior and social structure to people while observing macaques (Ang 2010). Educational programs are valuable tools, but tailoring some programs specifically to residents who live near nature reserves could be useful, as these residents regularly engage with the local macaque population and are more likely to have negative attitudes toward macaques than park visitors (Sha et al. 2009).

Conclusion

Overall, Singapore has relatively mild human–macaque conflict when compared to human–macaque interfaces in other locations, especially considering that humans and macaques extensively overlap within a small, highly urbanized area. This relatively benign interface may be due in part to the fact that, compared to most other macaque habitat countries, Singapore is relatively affluent and has resources available for managing human–macaque conflict. In addition, the macaque feeding ban, although not one hundred percent effective, does reduce feeding to some degree and thus likely cuts down on conflicts and other issues (e.g., health problems such as obesity and disease transmission) that could arise from unregulated food access.

Our research showed that long-tailed macaques that access food in Singapore have larger group sizes, travel less, and use substrates differently from macaques that do not access human food. We made recommendations for decreasing macaques' access to human food and more effectively managing the urban interface between humans and macaques. Our management recommendations apply specifically to Singapore, but they could potentially be useful for the management of other urban human–macaque interfaces. However, the most successful management strategies will be tailored specifically to the species, the human population with which they interface, and the local environment.

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Risk-Taking in Samango Monkeys in Relation to Humans at Two Sites in South Africa

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Introduction

Prey animals have to constantly weigh the benefits of investing in maintenance activities such as feeding and socializing with avoiding risk of exposure to predators, including humans (Frid and Dill 2002; Willems and Hill 2009). Responses to predators in general vary from flight to freezing in direct encounters, and vigilance to selective and discerning microhabitat use when monitoring risk. Such responses

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to perceived risk, while improving chances of survival, are costly in terms of energy and time. Importantly, prey species do not modify their behavior solely in the direct presence of a predator but also show sensitivity to variation in the riskiness of distinct environments. Such sensitivity falls under the heading “non-lethal effects of predation risk” (Lima 1998).

According to the risk-disturbance hypothesis, animals respond to human disturbance in a way that is similar to their response to natural predators (i.e., flee, make alarm calls, become stressed; Frid and Dill 2002). Humans and human infrastructure can, however, pose both a threat and potential source of safety for wild animals, adding another layer of complexity to animals’ perception of risk. Some animals may indirectly benefit from human presence. For example, while both wolves (*Canis lupus*) and elk (*Cervus canadensis*) in two national parks in Canada avoid areas within 50 m of human trails, elk will approach at 50–400 m distances, which wolves continue to avoid (approaching human trails only at >400 m). As a result, these areas become elk predation refugia, altering underlying trophic interactions (Rogala et al. 2011). Similarly, when it is time for pregnant moose (*Alces alces*) to give birth in Yellowstone National Park, they move closer to paved roads to protect their newborns from bears (*Ursus arctos*) (Berger 2007). In the highlands of southern Ethiopia, mountain nyala (*Tragelaphus buxtoni*) overnight near human settlements to avoid predation by hyenas (*Crocuta crocuta*) (Atickem 2013), although there is some individual heterogeneity in their use of humans as shields (Atickem et al. 2014). Researchers working in Amboseli National Park, Kenya noticed that leopards (*Panthera pardus*) tended to prey on vervet monkeys (*Chlorocebus pygerythrus*) when people were away from the field site suggesting that researchers shield monkeys from terrestrial predators simply by being present (Isbell and Young 1993). These examples point at the differences in the ways predator and prey species respond to humans and their infrastructure (Leighton et al. 2010; Muhly et al. 2011).

Commensalism takes this relationship with humans to another level, where animals view humans as a source of food. Some troops of rhesus macaques (*Macaca mulatta*) in Nepal spend their time close to temples waiting for handouts from humans and forage in nearby homes and gardens (Jones-Engel et al. 2006). Chacma baboons (*Papio ursinus*) in Cape Town are notorious “pests” where in some areas they have become so bold and aggressive in their pursuit of human food that humans are fearful of baboons or aggressively retaliate (e.g., shoot them), with thousands of dollars spent annually by the city to mitigate this conflict (Beamish 2010; Swedell 2011; Kaplan 2013).

Still, wild animals perceive humans as a threat in the majority of cases and not as potential protectors or shields from danger. The simple need to habituate wild animals suggests that the default response to humans may not be de facto trust, although some human-naïve wildlife populations tolerate approach, capture, and even chasing by humans (e.g., marine iguanas *Amblyrhynchus cristatus* on the Galápagos Islands, Rödl et al. 2007). Red colobus (*Procolobus badius*) and black-and-white colobus (*Colobus guereza*), commonly hunted across Central Africa, are so well protected by impenetrable swamp forest, that they are naïve when encountered by humans (H. Rainey pers. obs.). Another such example includes naïve chimpanzees (*Pan troglodytes*) in the Goualougo Triangle, Republic of Congo (Morgan and Sanz

2003). Nevertheless, interactions with wildlife generally lead to flight (Stankowich 2008), alarm calls and threat displays (Soltis et al. 2014), active avoidance (Tadesse and Kotler 2012), and stress (Creel et al. 2002), which can negatively influence animals' reproduction and even survival. The goal of this chapter is to better understand the various ways in which primates react when sharing space with humans, using arboreal samango monkeys as a case study.

Animals' Perceptions of Risk

Whereas the perceived riskiness of any encounter with a potential threat can be quantified by describing the prey animal's direct response (physical and/or physiological) in that instance, it is much more challenging to determine how animals perceive variation in riskiness across space. The "Landscape of Fear" approach (Coleman and Hill 2014, Laundré et al. 2010; Willems and Hill 2009) allows us to quantify animals' behavioral responses to variable threats on a spatial level, not simply describe immediate responses to direct or potential threats, which, while useful, could be less reliable indicators of risk or disturbance (Beale 2007; Beale and Monaghan 2004). A clear sign that spatial variation in risk is a biologically salient phenomenon is the nonrandom way in which animals distribute themselves across, or use, a landscape. This sensitivity to risk is evident not only in larger scale distribution patterns, but becomes apparent on a fine-grained level where animals use their habitats in a more spatially complex way.

Arboreal taxa, including African guenons, experience risk in their environment along three-dimensional axes. This makes their landscape of fear more complex than that of terrestrial species. Social primates have evolved a variety of antipredator responses, notably alarm-calling, reactions to heterospecific alarm signals, formation of polyspecific associations, and strategic avoidance of canopy strata at which they may be more vulnerable to predation in multi-predator environments (Cheney and Wrangham 1987). Primates are known to exploit humans and their infrastructure for food and shelter, perceiving us as a potentially valuable resource. Primates also recognize the threat that humans may pose. Wooly monkeys have demonstrated the ability to distinguish hunters from nonhunters (Papworth et al. 2013). These examples highlight the complex factors many primates are forced to navigate and complicate the task of untangling the effects that humans may have on primates' antipredator and risk-taking decisions.

Samango Monkeys

Samango monkeys (*Cercopithecus albogularis* spp.; Dalton et al. 2015), related to Sykes's and blue monkeys (*Cercopithecus mitis*), are limited to Afro montane and coastal forests in South Africa (Lawes 1990). They coexist with a number of natural predators across their range including felids, leopards and caracals, and raptors such as crowned (*Stephanoaetus coronatus*) and Verreaux's eagles (*Aquila verreauxii*) (Fig. 1). Natural predation pressure varies across sites. For example, the Soutpansberg Mountains in northern South Africa have high leopard (Chase Grey et al. 2013) and crowned eagle predation pressure. In contrast, sites along the coast of the Indian Ocean are characterized by low natural predation risk and comparatively more human pressure due to higher human population densities.

In this study, we were interested in detecting differences in monkeys' behavior across sites as gauged by the trade-offs they make between food and safety. Specifically, we weighed the evidence for and against the risk-disturbance hypothesis in areas dominated by humans, or where monkeys and humans come into conflict. Throughout the study we took into account that humans may be perceived as either threats or resources. We used the method of "giving-up densities" (GUDs), which allowed us to measure the amount of food a forager gives up or leaves uneaten

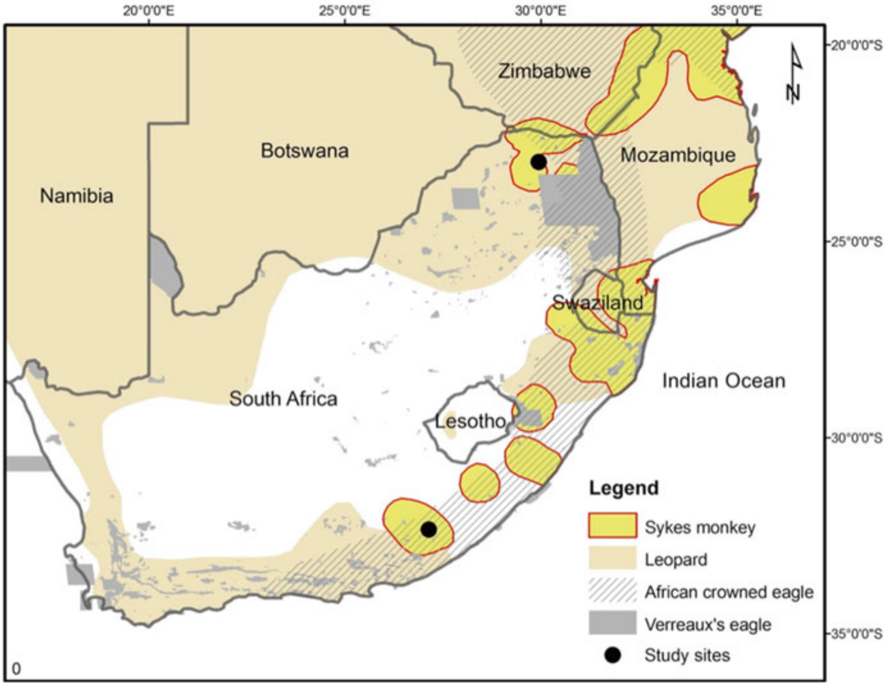

Fig. 1 The patchy forest-dependent distribution of samango monkeys and their major predators in South Africa. Shapefiles from the IUCN Red List. Lajuma is the northern, predator-rich study site in the Soutpansberg Mountains, and Hogsback is the southern, predator-poor study site in the Amathole Mountains

at artificial food patches as an indication of perceived risk (Emerson and Brown 2013; Emerson et al. 2011; Makin et al. 2012) to gauge monkeys' perceptions of risk at each site. Animals will deplete more food from an artificial patch where and when they feel safe (Brown 1988) providing an indirect measure of risk that can be employed in the absence of human observers and without the need for direct observation, thereby removing human effects on animals' behavior (Nowak et al. 2014; Williamson and Feistner 2011).

Methods

Sites and Groups

We studied samango monkeys at two montane sites, the Lajuma Research Centre in the northern Limpopo province and Hogsback, southern Eastern Cape province of South Africa (see Fig. 1). Lajuma lies in the western Soutpansberg Mountains (23°02′ S, 29°26′ E) and encompasses an area of natural vegetation including mist-belt forest, thicket, savannah, and grassland at between 1150 and 1750 m elevation (Willems and Hill 2009). In addition to an intact predator community, Lajuma has two diurnal primates, vervet monkeys and chacma baboons sympatric with the samango monkeys (*C. albogularis schwarzi*). Two samango monkey groups were studied at this site, Barn group (consisting of ~40 individuals) and House group (~60 individuals).

The second site, Hogsback, in the Amathole Mountains (32°35′ S, 26°56′ E), encompasses patches of indigenous forest (primarily mist-belt), plantations of pine (*Pinus* sp.), and the village of Hogsback where human gardens contain exotic trees such as oak (*Quercus robur* and *Q. palustris*) and black wattle (*Acacia mearnsii*). Samango monkeys (*C.a. labiatus*) use the whole matrix. We studied one group, the Village group (~30 individuals), whose home range encompassed both gardens and indigenous forest (Wimberger et al. in review; Nowak et al. in press).

Giving-Up-Density Experiments

We used artificial feeding patches established at random points generated within monkeys' home ranges, determined from existing data collected in previous years (by Kirsten Wimberger in Hogsback and by Russell Hill and the Primate Predator Project in Lajuma). Experiments were conducted at each site for 20 days, 4 consecutive days per week for 5 weeks, following an initial habituation phase of at least 1 week during which monkeys became accustomed to the experiment and learned the locations of patches. Artificial food patches consisted of four basins suspended at four heights: 0.1, 2.5, 5, and 7.5 m, and filled with 4 L of sawdust. Twenty-five raw peanut halves were mixed into the sawdust in each basin on each morning of the experiment and at 16:00, sawdust was sieved and peanuts counted. Sawdust was replaced if spilled, and data were excluded from analysis if >1 L of sawdust had been spilled from a basin (see Nowak et al. 2014 for further details on the methods).

When monkeys were in or near the area of the experimental patches in the mornings, we positioned ourselves at feeding stations to collect data on their visits. We attempted to observe and enumerate at least one group visit per each experimental patch during the 20-day experiment (eight patches in each of two groups' ranges in Lajuma, 16 patches in one group's range in Hogsback, number of observers = 2; typically, we did not observe at more than two experimental trees per morning as monkeys moved rapidly between patches). In addition, at Lajuma, but not in Hogsback, monkeys were regularly followed by researchers collecting behavioral data for other studies and independently of our experiment. These observers and followers (pooled into a single variable, "researchers") were not present every day of the experiment; therefore we could use this presence/absence of researchers as an independent factor to gauge the influence of human presence on monkeys' foraging behavior and perceived risk at experimental patches (as measured by GUDs, or peanuts left uneaten).

Analysis

Using R Statistics (v.3.0.2) (R Core Team 2012), we employed two different models on data on "visits" and data inclusive of "non-visits." "Visits" excluded data from experimental trees that the monkeys did not attend, thus offering a view of monkeys' risk-taking behavior only during their actual visits to experimental patches. Our analysis that included "non-visits" was indicative of visitation patterns overall and therefore suggestive of monkeys' preferences for certain locations of patches.

When looking at visits only, we fitted linear mixed-effect models to the GUDs data (peanuts left) examining the fixed effects of basin height, researcher presence, and habitat (garden/forest in Hogsback, forest only in Lajuma) and controlling for tree and experimental day (two random effects). We also looked at the interaction between basin height and researcher presence. Finally, we examined the possible fixed effect of a combined site-group-location ("SGL") factor/identifier on monkeys' GUDs and its interaction with researcher presence.

For analysis of data inclusive of "non-visits" we used a logit model to examine the probability that patches were visited. A non-visit could be viewed as a decision by monkeys to leave a patch uneaten; these data therefore highlight group decisions about which trees to visit and which to avoid. In the models that include non-visits, the initial model had habitat (garden or forest), group (Barn, House, Village), site (Lajuma or Hogsback), and experimental day as fixed effects. Our dependent variable was visit (yes/no) and therefore we defined the family as "binomial." All models were simplified by the stepwise exclusion of nonsignificant interactions and fixed effects. We removed those interactions where $p > 0.01$ and single effects where $p > 0.05$.

Results

There was no difference between sites (Lajuma/Hogsback) in overall GUDs (Kruskal–Wallis rank sum test on mean peanuts left by site: $\chi^2 = 1.052$, df = 1, $p = 0.31$). In our analysis of tree visits only, the effects of basin height, researchers, and the interaction between basin height and researchers on GUDs were significant (final model, Appendix 1; Fig. 2). Monkeys depleted more peanuts with increasing height (see Fig. 2). That they opted to forage high in the trees suggests that terrestrial risks may be greater than arboreal risks. The presence of researchers reduced perceived risk (lowered monkeys GUDs) at both sites and at all heights, particularly at the ground level. The combined site-group-habitat variable did not significantly predict GUDs; however, it did interact nonsignificantly with researcher presence

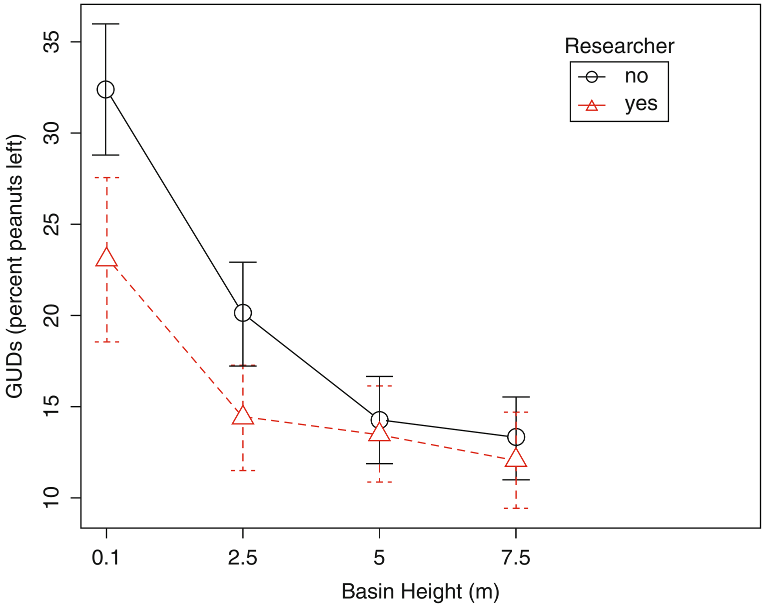

Fig. 2 Mean giving-up densities (GUDs) or percent peanuts left uneaten at four different heights and in the presence and absence of researchers. The effects of basin height and researchers on GUDs, and the interaction between height and researchers, were found to be significant. Non-visits to trees are excluded here. Monkeys left the most peanuts at the bottom (0.1 m) level, where the presence of people significantly decreased monkeys GUDs suggesting a shield effect. $N = 1970$, error bars = 95 % CI

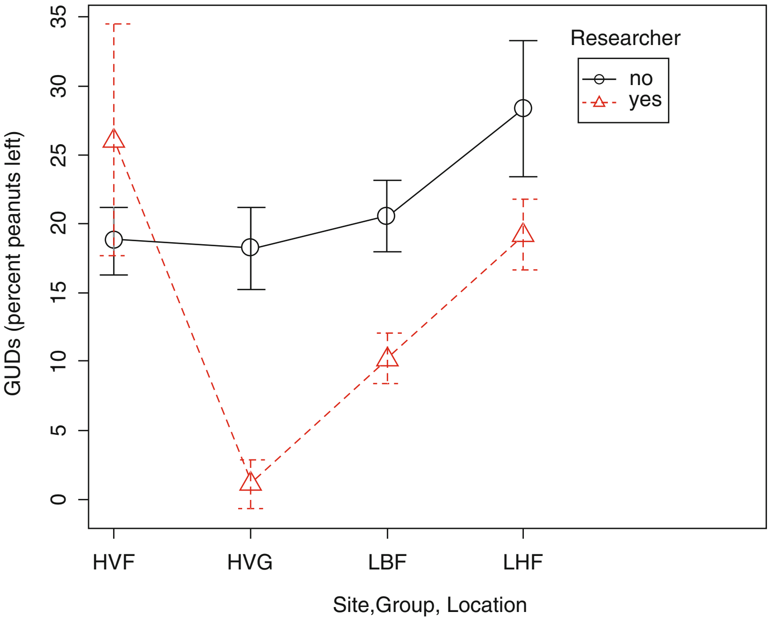

Fig. 3 Mean (+StDev) giving-up densities (GUDs) or percent peanuts left by site, group, location (SGL) and researcher presence (yes/no). GUDs were lower in the presence of humans in all conditions except in Hogsback forest (HVF). HVG = Hogsback Village gardens, LBF = Lajuma Barn forest, LHF = Lajuma House forest. Non-visits excluded. *N* = 1970

(Fig. 3). GUDs increased in the presence of humans in one condition—the Hogsback forest (Fig. 3). This trend suggests that experience with nonthreatening researchers in Lajuma (forest only) and expectation of humans in a specific habitat (gardens) in Hogsback may affect how monkeys perceive the relative riskiness or potentially shielding effect of humans. The slightly raised GUDs in Hogsback forest in the presence of researchers suggest that people may be perceived as a potential threat in this habitat rather than as a shield or may simply be less expected inside the forest than in the gardens. The lack of a notable effect of habitat (forest versus garden) suggests that once monkeys entered gardens (in Hogsback), they depleted experimental patches to a similar extent as those in the forest; overall, GUDs were actually slightly higher in the forest than in the gardens, but this may be the outcome of the differential effects that humans had on monkeys in the two habitats with researchers lowering monkeys' GUDs in gardens but not forest (Fig. 3).

In our analysis of non-visits, habitat (garden/forest), group (Barn, House, Village), and site (Lajuma/Hogsback) all had significant effects (Appendix 2) on visit probability with monkeys in Hogsback visiting more forest than garden patches (Fig. 4). Barn group visited patches every day of the experiment and therefore depleted more basins than the House group, which did not visit patches on 3 of the 20 experimental days. Like the Barn group, the Hogsback Village group visited patches everyday.

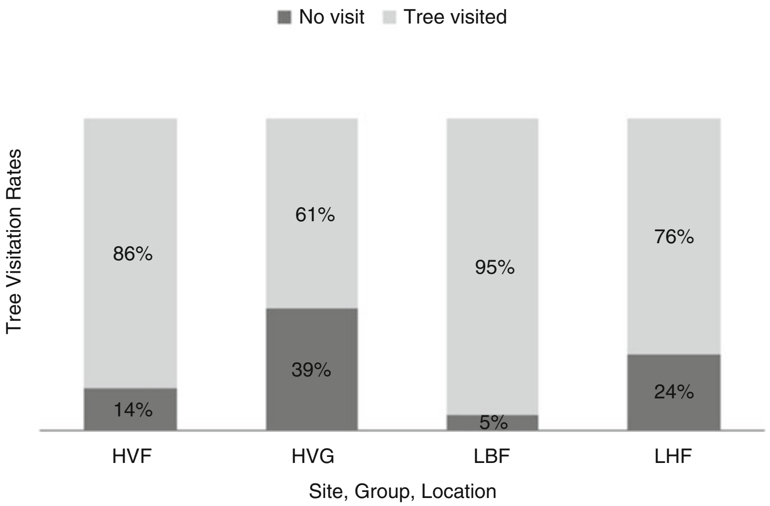

Fig. 4 Tree visitation patterns by site, group, and habitat. Forest patches were significantly more likely to be visited than garden patches in Hogsback. In Lajuma, House group did not visit experimental patches on 3 of the 20 experimental days (which explains the significant effect that "group" has on visit probability; Appendix 2). HVF = Hogsback Village forest, HVG = Hogsback Village gardens, LBF = Lajuma Barn forest, LHF = Lajuma House forest. Non-visits included. $N = 2484$

Discussion

We found that in both Lajuma and Hogsback, researchers were not a neutral element of the environment. The amount of food eaten by monkeys from experimental patches was not only affected by vertical height, but also by the presence of researchers at the feeding stations. At all experimental trees, samango monkeys depleted more food at canopy levels, with ground level feeding representing the most risky stratum (Nowak et al. 2014; Emerson et al. 2011). Human observers subtly altered this axis of fear. In Lajuma, monkeys ate more when observers were around with the most notable difference at the ground level, suggesting that they perceive us as shields against potential terrestrial predators (Nowak et al. 2014). In Hogsback, where there is some human–monkey conflict and monkeys have had mixed experiences with people, a slightly more complex picture emerged. Humans did not appear to be perceived as shields in the forest, but in gardens monkeys' perceived risk decreased (the amount of food they consumed increased) in our presence. This suggests a nuanced perception of human presence and human habitat alteration by the group in Hogsback. Likely, humans encountered by monkeys inside the forests tend to pose a threat to the small primates, and, indeed, camera traps deployed in the forest during this study indicated the presence of poachers in the forest. In contrast, humans in gardens may be less threatening and may even be perceived as shielding monkeys from threats such as dogs.

If non-visits to experimental trees are considered, then monkeys in Hogsback show a clear preference for feeding on artificial patches in the forest relative to gardens. Overall, the continuous forest habitat with dense cover facilitates avoidance of humans in a way that gardens do not (e.g., monkeys must use fences and electric power lines to navigate the patchy garden habitat). Considering visitation patterns or visits/non-visits to patches in a GUDs experiment may be useful when evaluating animals' preferences for particular locations or habitats.

Strong seasonality may be a further factor influencing monkeys' risk-taking in Hogsback, the southernmost extent of this taxon's range. Our study was conducted during winter (May–July), when monkeys spend more time on the ground and in people's gardens where they exploit abundant exotic foods including oak acorns (Wimberger et al. in review). However, while seasonal differences in food availability may help explain monkeys' use of gardens, they do not explain the varied human effects.

A short concurrent student-led study conducted at Hogsback suggests that samango monkeys interact with novel (non-food) objects for significantly longer periods in gardens compared to indigenous forest (Mathibane 2014), suggesting that neophilia can vary within the same group and population, increasing in human-altered habitats. This context-specific behavior attests to these monkeys' plasticity and the rapid way in which primates learn to exploit human habitats. In Hogsback and at sites such as Cape Vidal (KwaZulu Natal, South Africa), monkeys are drawn into human areas for foraging opportunities or commensal reasons. During winter months in Hogsback, monkeys forage predominantly on exotic plant species planted by humans as well as raid homes and rubbish for food (Wimberger et al. in review), whereas in Cape Vidal, monkeys steal food from campers and waste bins (Chapman et al. 1998). Even at Lajuma, one adult male (House group) began entering researchers' quarters and stealing food. Therefore, monkeys at both of our study sites and elsewhere in South Africa have come to associate humans and their infrastructure with feeding opportunities, even if exploiting these carries risks.

Samango monkeys appear to respond quickly and flexibly to new, negative interactions with humans and their tools. Following a live-trapping and ear-tagging event in Lajuma (that took place after the experiment described here: Nowak et al. 2016), less clear patterns in the ways that observers are perceived emerged: monkeys in House group raised their GUDs in the presence of observers (but not in the presence of the trap stimulus), while Barn group monkeys became more vigilant when researchers together with the trap stimulus were near. However, these responses to observers were temporary and the trends not statistically significant. In Hogsback, negative experiences with people, electrocution when using electric lines to navigate gardens, deadly attacks by dogs, road kills, and cutting of tall trees in gardens (with loud electric saws) are all real disturbances that pose distinct threats to monkeys and may explain why monkeys show a preference for foraging in indigenous forest, ideally in the tree canopy, when given the choice (i.e., “equal” feeding opportunities in the form of experimental food patches in both gardens and forest in winter months).

Rather than avoid people, monkeys may therefore come to associate with us or our infrastructure if these provide predator buffers (Muhly et al. 2011; Leighton et al. 2010) and only later, secondarily, the relationship may develop into a commensal one. Commensalism could be an offshoot of the human-predator refugia association (i.e., a trade-off between human proximity and disturbance with evasion of natural predators) or the eventual result of the habituation process. A fruitful direction of research would be to investigate ways in which primates do not adhere to the risk-disturbance hypothesis. We have presented evidence of a far more sophisticated and flexible response to humans and their infrastructure than the theory currently permits. It is likely that this plasticity in response to anthropogenic change is not restricted to primates, but numerous other species that come into regular contact with us.

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Appendix 1: Model 1

```
Linear mixed-effects model fit by REML
   AIC BIC logLik
   12701.97 12746.64 –6342.986
   Random effects: Formula: ~ExpDay | Tree
   Structure: General positive-definite, Log-Cholesky parametrization
   StdDev Corr
   (Intercept) 2.2702498 (Intr)
   ExpDay 0.1373389 –0.652
   Residual 5.9674331
   Fixed effects: PeanutsLeft ~ BasinHeight + Researchers + BasinHeight:Researchers
```

	Value	Std. error	DF	*t*-Value	*p*-Value
(Intercept)	7.702045	0.4870477	1947	15.813737	0.0000
BasinHeight	−0.637220	0.0599672	1947	−10.626151	0.0000
Researchers	−2.619970	0.4862516	1947	−5.388094	0.0000
BasinHeight:Researchers	0.1028469	1947	2.841911	0.0045	0.292282

Appendix 2: Model 2

glm (Visit ~ Location + Site + Group, family = “binomial”)
Deviance Residuals:
Min 1Q Median 3Q Max
−2.4478 0.3203 0.5323 0.7338 0.9669
Coefficients: (1 not defined because of singularities)

	Estimate	Std. error	*z* Value	Pr (>|*z*|)
(Intercept)	1.8827	0.2342	8.038	9.14e–16***
LocationG	−1.3651	0.2862	−4.770	1.84e–06***
SiteLajuma	1.0617	0.4318	2.459	0.0139*
GroupHouse	−1.7698	0.4074	−4.344	1.40e–05***

Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
(Dispersion parameter for binomial family taken to be 1)

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Predicting Future Effects of Multiple Drivers of Extinction Risk in Peru's Endemic Primate Fauna

Sam Shanee

Introduction

Conservation in the twenty-first century is predicted to be dominated by mitigation of the effects of man-made climate changes and the ramifications to natural systems and the species that depend on them (Bonan 2013; Laurance and Williamson 2001; Lewis 2006; Thomas et al. 2004; van Aalst 2006). Some changes are already being observed in temperatures, precipitation levels, cloud formation, and secondary impacts such as changes in plant phenologies that are predicted to have drastic consequences for ecosystems and species (Bertin 2008; Dore 2005; Lenoir et al. 2008; McCarty 2001; van Aalst 2006; Walther et al. 2002). Of the world's major biomes, tropical montane forests will be one of the most severely affected (Bubb et al. 2004; Foster 2001; Herzog 2011; Still et al. 1999), with many more localized climate changes seen in air temperatures, cloud formation, and cloud capture (Pielke et al. 2002). This will affect many primates and other species that have restricted distributions or specialized habitat requirements (Newbold et al. 2014). Currently, all but one primate species listed as Critically Endangered on the IUCN Redlist of Threatened Species have restricted distributions (IUCN 2013), 26 of which have distributions in Montane habitats, five of which are entirely restricted to montane and pre-montane areas (Shanee 2013).

Another major concern for conservationists is the continued expansion of agricultural frontiers to support a growing human population and its demand for food and other resources (Fearnside 1983; Garland 1995; Newbold et al. 2014; Perz et al. 2005; Sanchez-Cuervo and Aide 2013; Wyman and Stein 2009). As much of the

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worlds suitable lands have already been converted to agricultural production, new frontiers are opening up in areas less suited to clearance, including montane ecosystems (Cayuela et al. 2006; Hall et al. 2009). The clearance of montane areas for agriculture works in tandem with climate changes to intensify local scale effects, increasing air temperatures, which in turn slows cloud formation and lowers precipitation levels, slowing forest regeneration. Heavier downpours increase erosion on slopes, further limiting forest regeneration, lowering soil fertility, necessitating the clearance of more areas for cultivation, resulting in a dangerous cycle (Laurance and Williamson 2001; Pielke et al. 2002).

The montane and pre-montane forests of northern Peru lie at the heart of the Tropical Andes Biodiversity Hotspot and are among the most threatened forested areas in the world (Myers et al. 2000; Robles Gil et al. 2004). Peru's northern regions of Amazonas and San Martin suffer from the highest immigration and deforestation rates in the country (INEI 2008; PROCLIM/CONAM 2005; Reategui and Martinez 2007) accounting for approximately 18 % of Amazonian forest loss in Peru in the year 2000 (INRENA 2005). The tropical Andes are home to incredible levels of biodiversity with ~30,000 vascular plant species, 50 % of which are endemic, and the highest number of vertebrate species of any "Biodiversity Hotspot" (Myers et al. 2000). This includes 584 species and 69 genera of endemic birds. Diversity and endemism of mammals is similarly high with at least 75 species and five monotypic genera endemic to the area (Myers 2003; Myers et al. 2000).

Peru's cloud forests account for only 5 % of the country's 700,000 km^2 tropical forests (Bubb et al. 2004) but species diversity is comparable to that of the much more extensive eastern Amazonian lowlands (Pacheco et al. 2009). In particular, the area between the Marañón and Huallaga rivers, ~8000 km^2, has very high levels of endemism but is also severely threatened by logging, slash and burn and industrialized agriculture (Schjellerup 2000; Shanee 2012a), subsistence and commercial hunting (Shanee 2012b), and the cultivation of illicit crops such as coca (*Erythroxylum coca*) and opium poppies (*Papaver somniferum*). The production of these illicit crops is a double threat to the environment. The production causes habitat loss and contamination whilst the measures employed to control them, such as defoliant sprays and forced crop clearances, not only remove the crops but also affect neighboring forests and increase deforestation when producers relocate to new areas (Dourojeanni 1989; Fjeldså et al. 1999, 2005; Young 1996).

Three of Peru's eight endemic primates (Boubli et al. 2012; Alfaro et al. 2012a, b; Marsh et al. 2013; Matauschek et al. 2011; Wilson et al. 2013) have distributions restricted to the Marañón-Huallaga landscape (Shanee et al. 2013b). The yellow-tailed woolly monkey (*Lagothrix flavicauda*), the San Martin titi monkey (*Plecturocebus oenanthe*), and the Peruvian night monkey (*Aotus miconax*) are all considered threatened by the IUCN (2013), with *L. flavicauda* and *P. oenanthe* considered Critically Endangered and *A. miconax* considered Endangered. Until recently, very little was known about these species, but recent conservation-based research programs have provided basic data on the distribution and ecology of these species (For example, Bóveda-Penalba et al. 2009; Buckingham and Shanee 2009; deLuycker 2007a, b; Shanee 2011; Shanee et al. 2011, 2013a, 2015). This information has been vital in providing a better understanding of threats, conservation need, and population trends for these species. The very restricted distributions of the three species are probably a result of the high levels of habitat heterogeneity in the area which is almost completely surrounded by the Maranon and Huallaga river valley's (Fig. 1) divided by isolated areas of dry forests, high mountain ridges, and deep river valleys, impeding dispersion into new areas and creating localized bioclimatic zones (Shanee et al. 2013b, c, 2015).

Computer-based modeling of species distributions and ecological niches has become popular in recent years with better access to more powerful processors and dedicated software (Bocedi et al. 2014; Brown 2014; de Souza Muñoz et al. 2011; Goodchild et al. 1996; Guo and Liu 2010; Phillips et al. 2006; Skidmore 2004; Thuiller et al. 2009). Computer-based modeling is particularly useful when field surveys are made difficult by the physical impediments of the terrain or sociopolitical factors limiting researchers' access to some areas within a species distribution. Many different modeling techniques exist, each with its own advantages and disadvantages (Elith and Graham 2009; Elith et al. 2006; Guisan et al. 2007; Guo and Liu 2010; Thuiller et al. 2009), in recent years ecological niche modeling with Maxent program (Phillips et al. 2006) has proven to be a robust presence-only modeling technique that balances accuracy with limitations on data availability, time, and model complexity. In addition, many tools and recommendation on how best to use Maxent for modeling have been developed to further robustness of models (Brown 2014; Warren et al. 2010). Similarly, computer modeling provides the best option for predicting the effects of future climate changes. These predictions are constantly being refined with many models now freely available to researchers (Hijmans et al. 2005; Kriticos et al. 2012).

For this chapter, I aim to model the possible effects of future climate changes on the distributions of three of Peru's endemic and most endangered primate species. Building on this, I will model the effect of various simple thresholds as proxies to simulate expansion of the agricultural frontier and hunting pressure. This is done to highlight the challenges and opportunities climate changes may present for conservation for these species. Also, to examine the utility of GIS-based predicative modeling, balancing complexity with robustness.

Methods

Species and Distributions

Lagothrix flavicauda, *Plecturocebus oenanthe*, and *Aotus miconax* are endemic to a small area of northern Peru in the departments of Amazonas and San Martin (Shanee et al. 2015; Aquino and Encarnación 1994; Bóveda-Penalba et al. 2009; Shanee 2011). *Lagothrix flavicauda* and *A. miconax* are sympatric throughout the majority of their distributions (Fig. 2a, c) on the eastern slopes of the Andes in a thin band of montane cloud forest between approx. S78° 12′30″ and S75°24′55″ at altitudes

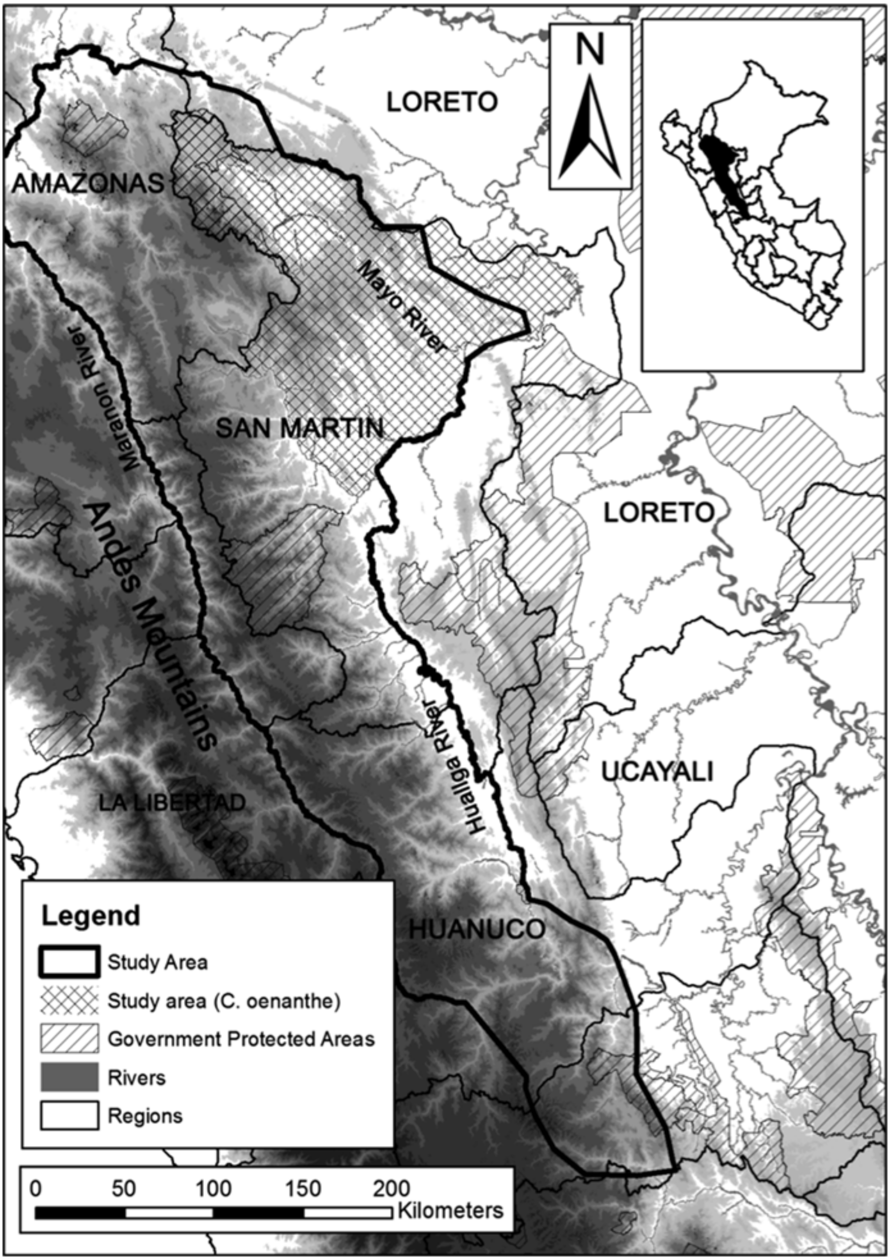


Fig. 1 Map of the study area showing major landmarks and the Maranon and Huallaga river systems and clipped area used in modeling, with inset showing location of study area in Peru

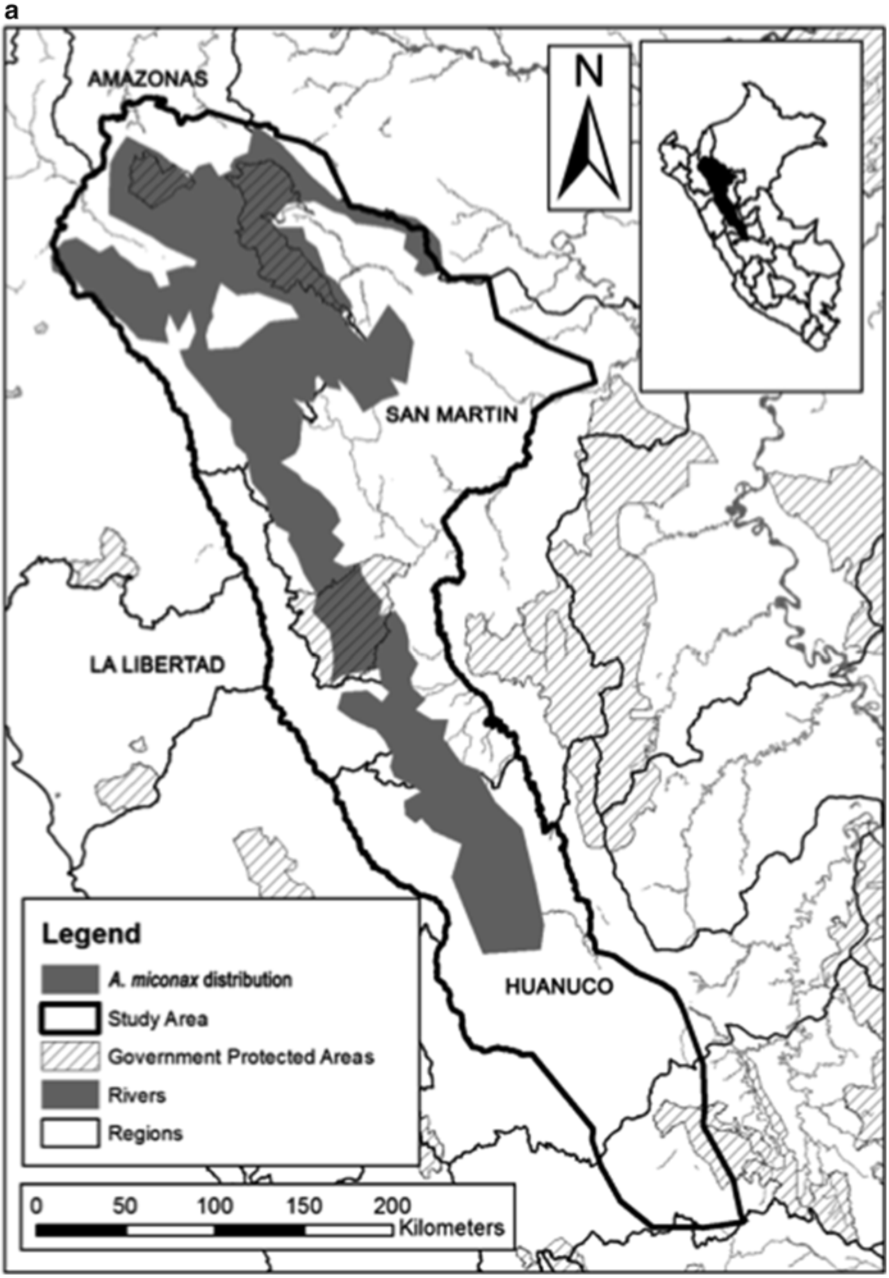


Fig. 2 Map showing the estimated distributions of the focal species in northern Peru, (**a**) *A. miconax*, (**b**) *P. oenanthe*, and (**c**) *L. flavicauda*, with insets showing location of study area. Distribution maps adapted from Rowe and Myers (2012)

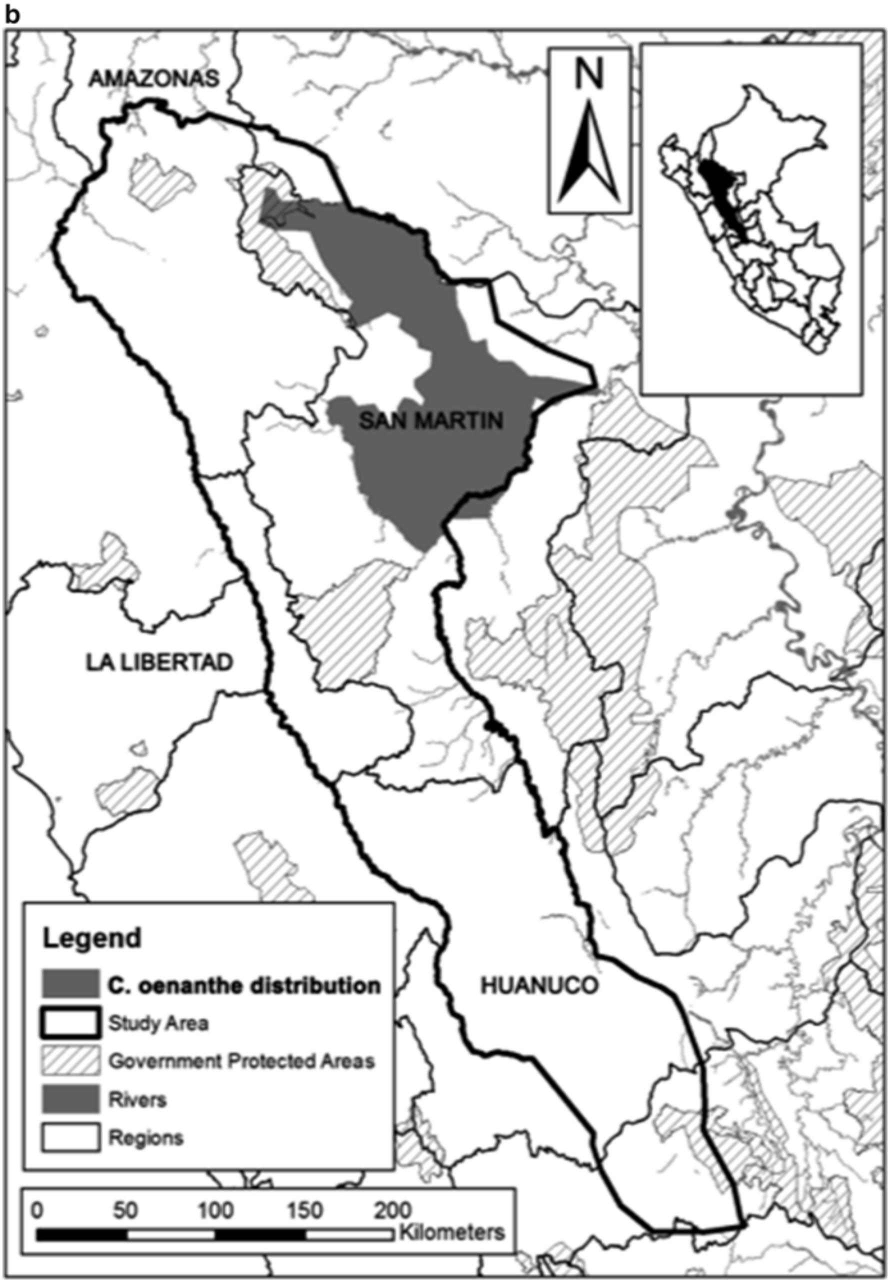


Fig. 2 (continued)

c

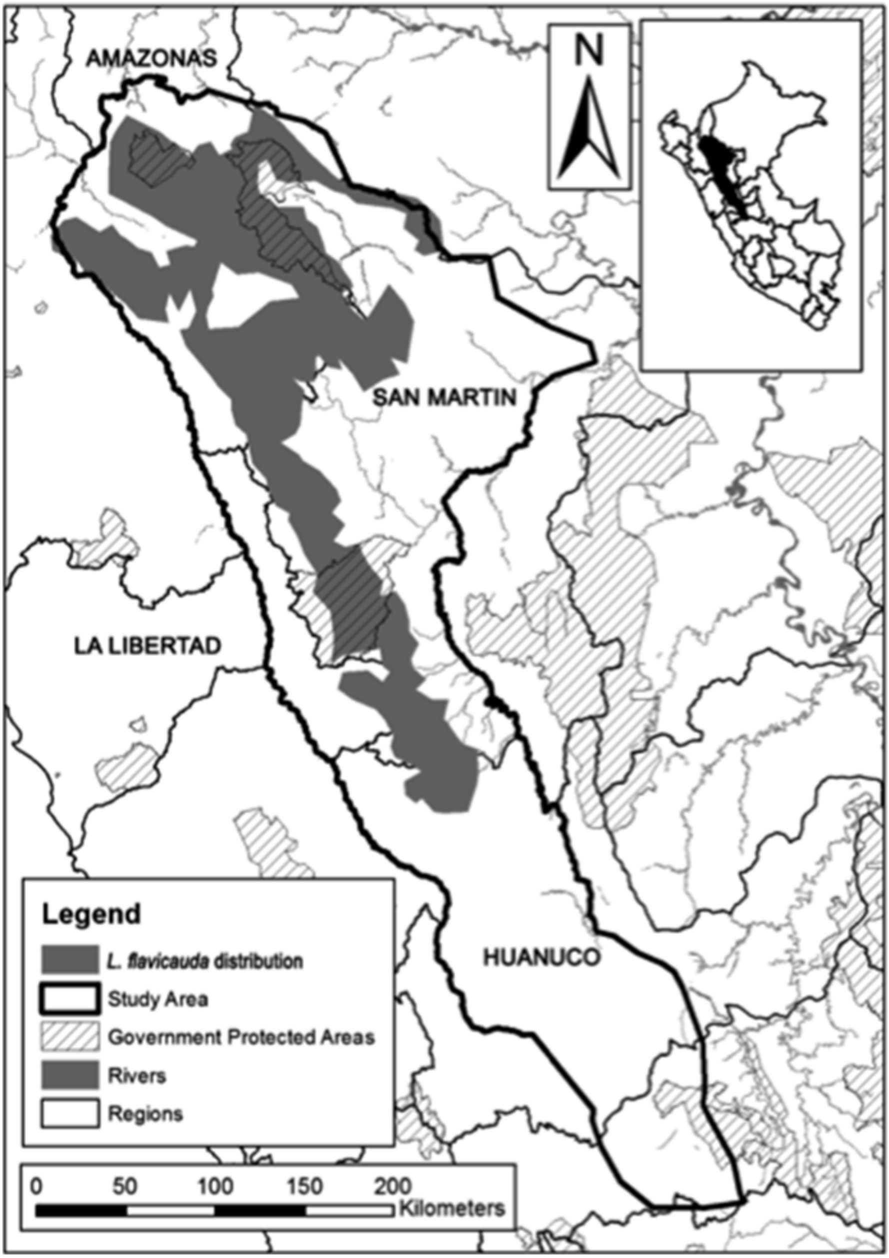


Fig. 2 (continued)

ranging from 1500 to 2800 m above sea level, (MSL) although in some areas they are found at slightly higher or lower altitudes (Allgas et al. 2014; Campbell 2011; Shanee et al. 2013b, c). *Plecturocebus oenanthe* is restricted to the pre-montane area of the *Rio Mayo* valley south to the west of the *Rio Huallaga* as far as the *Rio Huyallabamba* (Fig. 2b) in lowland *terra firme* and tropical dry forests at elevations between 200 and 1200 MSL (Bóveda-Penalba et al. 2009). This species has been also been reported in small areas outside of these boundaries (Bóveda-Penalba et al. 2009; Shanee et al. 2013b; Vermeer et al. 2011).

Data Collection and Preparation

I used point data for each species from confirmed presence localities in previously published studies and my own fieldwork (Shanee et al. 2015; Bóveda-Penalba et al. 2009; Shanee 2011). This gave a total of 48 points for *Lagothrix flavicauda*, 110 points for *Plecturocebus oenanthe*, and 73 points for *Aotus miconax*. To remove spatially non-independent localities and clusters of points, I spatially rarefied occurrence data using three natural breaks between 5 and 25 km^2. For bioclimatic variables layers, I used freely available data sets from Worldclim (Hijmans et al. 2005). This provided me with 19 bioclimatic layers representing different environmental variables (Table 1). All layers were clipped to the bounds of a polygon layer of Peru's national borders. I then carried out a principle component analysis (PCA) of climate heterogeneity, variable layers that showed high levels of homogeneity were then removed from subsequent analyses. I then made bias files for selection of locations for background and pseudo-absence points for use in predictions to limit errors of commission (e.g., overprediction of the model) (Anderson and Raza 2010; Phillips et al. 2009). Bias files were created using a minimum convex polygon (MCP) buffered to 200 km outside of sample presence points. I then carried out a spatial jackknife to evaluate which model performed best and used this for final modeling (Boria et al. 2014; Radosavljevic and Anderson 2014; Shcheglovitova and Anderson 2013).

For future predictions, I downloaded four sets of layers representing the same bioclimatic variables produced by the International Panel on Climate Change fifth assessment (Raper 2012; Rogelj et al. 2012). I chose the models from the NASA Goddard space institute, these layers are freely available from Worldclim (Hijmans et al. 2005). The future bioclimatic layers represented predictions of conditions under different greenhouse gas representative concentration pathways (RCP) in different years (Moss et al. 2010): RCP = 26 and 85 for 2050 and 2070. These layers had the same spatial resolution as the layers used in the initial analysis and were also clipped within the bounds of the Peru polygon. The final model, based on the results of spatial jackknifing, was then projected onto these climate scenarios. As standard, ROC (Receiver Operating Characteristic) curve and AUC (Area Under Curve) were used as measures of the predictive power and fit of the models (Peterson et al. 2007; Merckx et al. 2011).

Table 1 Data sets used in analyses

	Variable name/source	Variable value	Details	Used in analyses
Bioclim	Bio 1	Annual mean temperature	–	Yes
	Bio 2	Mean diurnal temperature range	Mean of monthly Max/Min	Yes
	Bio 3	Isothermality	Bio2/Bio7 × 100	Yes
	Bio 4	Temperature seasonality	Standard deviation × 100	Yes
	Bio 5	Max temperature of warmest month	–	No
	Bio 6	Min temperature of coldest month	–	No
	Bio 7	Annual temperature range	Max temperature-Min temperature	No
	Bio 8	Mean temperature of wettest quarter	–	No
	Bio 9	Mean temperature of driest quarter	–	No
	Bio 10	Mean temperature of warmest quarter	–	No
	Bio 11	Mean temperature of coldest quarter	–	No
	Bio 12	Annual precipitation	–	Yes
	Bio 13	Precipitation of wettest month		No
	Bio 14	Precipitation of driest month		No
	Bio 15	Precipitation seasonality	Coefficient of variation	Yes
	Bio 16	Precipitation of wettest quarter	–	No
	Bio 17	Precipitation of driest quarter	–	No
	Bio 18	Precipitation of warmest quarter	–	Yes
	Bio 19	Precipitation of coldest quarter	–	Yes
Forest cover	Forest cover year 2000	–	–	Yes
	Forest gain (2000–2010)	–	–	Yes
	Forest loss (2000–2010)	–	–	No
Cities	Ministry of Education	–	–	Yes
Towns	Ministry of Education	–	–	Yes

(continued)

Table 1 (continued)

	Variable name/source	Variable value	Details	Used in analyses
Roads	Ministry of transport and communications	–	–	Yes
A. miconax	Shanee et al. (2015) and Unpublished data	–	–	Yes
C. oenanthe	Bóveda-Penalba et al. (2009), Shanee et al. (2013b, c) and Unpublished data	–	–	Yes
L. flavicauda	Shanee (2011), Shanee et al. (2013b, c) and Unpublished data	–	–	Yes

Final Modeling

Even using bias files to limit the possible extent of niche predictions the Maxent models can over predict possible niche area when compared to known geographical barriers limiting the species' distributions, often including areas outside of a species' actual or historical distribution. To rectify this all model outputs for *A. miconax* and *L. flavicauda* were clipped to areas within the bounds of a polygon, representing the area between the Maranon and Huallaga rivers (Fig. 1). Similarly, outputs for *P. oenanthe* were clipped within a polygon representing the area between the Maranon and Huallaga rivers north of the Huyllabamba River and south of the eastern cordillera that forms the margin of the Mayo River Valley (Fig. 1). I then divided model predictions into ten equally sized classes representing different probability levels of species presence, the two lowest classes (0–9.9 and 10–19.9 %) were then removed to reduce errors of commision. The remaining eight classes were then divided into two subclasses representing two levels of probability (Good and Very Good). I then calculated the area of each subclass and overall as a measure of original habitat extension for each species (Table 2). To calculate the current area of occupancy of each species, I overlaid a forest cover layer (Hansen et al. 2013) to the outputs, removing areas with less than 50 % forest cover from predictions as areas without suitable habitat (Shanee et al. 2015; Wyman et al. 2011) and calculated the area in km^2 of each subclass and overall to estimate the current distribution of the species. I repeated this for the four future climate scenario predictions. To predict the effect of future expansion of the agricultural frontier and the effect of hunting on the species, I created two thresholds of moderate and high hunting pressure/possibility of deforestation within the 35- and 55-year time frames used in the climate change analysis. Thresholds were set at areas <1 km (high pressure) and <5 km (moderate pressure) away from human settlement and infrastructure for high and moderate pressure, respectively. Additionally, I remodeled these thresholds

Table 2 Results of ecological niche modeling and future threat analyses, all results are in km^2

	Original niche area	Good	Very good	Habitat availability	Good	Very good	Area outside 1 km	Good	Very good	Area outside 5 km	Good	Very good	<1 km excluding PAs	<5 km excluding PAs
A. miconax	37,220	22,640	14,580	29,990	17,930	12,060	–	–	–	–	–	–	–	–
Future	–	–	–	27,370	17,140	10,230	22,657	14,800	7857	11,536	8,803	2,733	22,978	14,114
P. oenanthe	6,992	4,335	2,657	5,547	3,628	1,919	–	–	–	–	–	–	–	–
Future	–	–	–	6,873	2,930	3,943	5,233	2,619	2,614	1,565	1,071	494	5,452	2,772
L. flavicauda	57,910	37,150	20,760	39,060	22,460	16,600	–	–	–	–	–	–	–	–
Future	–	–	–	36,340	18,600	17,740	30,180	16,380	13,800	15,416	9,691	5,725	31,640	18,489
Change (+/−)														
A. miconax	–	–	–	−2,620	−790	−1,830	−4,713	−2,340	−2,373	−15,834	−8,337	−7,497	−4,392	−13,256
P. oenanthe	–	–	–	+1,326	−698	+2,024	−314	−1,009	+695	−3,982	−2,557	−3,449	−1,421	−2,775
L. flavicauda	–	–	–	−2,720	−3,860	+1,140	−6,160	−2,220	−3,940	−20,924	−8,909	−12,015	−4,700	−17,851

including only habitat outside of protected areas to see if the current protected area system will be sufficient to support viable populations of the three species taking into account possible changes in niche occurrence with future climate changes.

Results

After multi-distance spatial rarefying of the original species occurrence points (48 for *Lagothrix flavicauda*, 110 for *Plecturocebus oenanthe*, and 73 points for *Aotus miconax*) to remove spatially non-independent localities and clusters, the number of data points for *L. flavicauda*, *P. oenanthe*, and *A. miconax* used in subsequent analyses were 34, 45, and 39, respectively. The PCA for climatic heterogeneity showed high autocorrelation of variables in 11 of the 19 bioclimatic layers; therefore, I used only eight in the final model, Annual Mean Temperature, Mean Diurnal Range, Isothermality, Temperature Seasonality, Annual Precipitation, Precipitation Seasonality, Precipitation of Warmest Quarter, and Precipitation of Coldest Quarter.

Model Results

The results from models projected onto the future bioclimatic layers showed no significant differences between predictions for years or RCP levels (All $p>0.001$); therefore, results presented here are averages across the four different year/RCP combinations for each species.

Aotus miconax

The final ecological niche model for *Aotus miconax* gave an ROC curve AUC of 0.913 for training data. Minimum training presence was 0.473. Results of the jackknife test showed the environmental variable with highest gain when used alone was annual precipitation. The environmental variable that decreased gain the most when omitted was annual mean temperature.

When clipped to within known geographical boundaries and excluding cells in the lowest two probability levels, the total original possible extent of occurrence of *A. miconax* was ~37,220 km^2. After reclassification into two subclasses representing Good and Very Good probabilities of species presence (20–59.9 and 60–100 %), estimated original niche sizes were 22,640 and 14,580 km^2 for each subclass. After deforested areas were removed from these predications (areas <50 % forest cover) the current maximum possible extent of occurrence is ~29,990 km^2 of which 17,930 km^2 was classed as Good and 12,060 km^2 was classed as Very Good. Future climate changes are predicted to reduce niche availability for *A. miconax* by a further 9 %, the most affected probability subclass is predicted Very Good category with a further 16 % loss. Including the 1 and 5 km future deforestation/hunting pressure buffers there is a 16 and 53 % loss of niche availability. This is reduced to 15 and 44 % for the two respective buffer thresholds when assuming no future habitat loss or hunting within protected areas.

Plecturocebus oenanthe

The final ecological niche model for *Callicebus oenanthe* gave an ROC curve AUC of 0.951 for training data. Minimum training presence was 0.370. Results of the jackknife test showed the environmental variable with highest gain when used alone was precipitation of the coldest quarter. The environmental variable that decreased gain the most when omitted was annual mean temperature.

When clipped to within known geographical boundaries and excluding cells in the lowest two probability levels, the total original possible extent of occurrence of *C. oenanthe* was ~6,992 km^2. After reclassification into two subclasses representing Good and Very Good probabilities of species presence (20–59.9 and 60–100 %), estimated original niche sizes were 4,335 and 2,657 km^2 for each subclass. After deforested areas were removed from these predications (areas <50 % forest cover), the current maximum possible extent of occurrence is ~5,547 km^2 of which 3,628 km^2 was classed as Good and only 1,919 km^2 was classed as Very Good. Future climate changes are predicted to increase niche availability for *C. oenanthe* by almost 24 %, the largest increase is predicted to be in the Very Good category with an increase of over 100 % in niche availability. Including the 1 and 5 km future deforestation/hunting pressure buffers there is a loss of 6 and 72 % of niche availability. This was reduced to 26 and 50 % for each respective buffer threshold when assuming no future habitat loss or hunting within protected areas.

Lagothrix flavicauda

The final ecological niche model for *Lagothrix flavicauda* gave an ROC curve AUC of 0.910 for training data. Minimum training presence was 0.387. Results of the jackknife test showed the environmental variable with highest gain when used alone was precipitation of the warmest quarter. The environmental variable that decreased gain the most when omitted was precipitation seasonality.

When clipped to within known geographical boundaries, and excluding cells in the lowest two probability levels, the total original possible extent of occurrence of *L. flavicauda* was ~57,910 km^2. After reclassification into two subclasses representing Good and Very Good probabilities of species presence (20–59.9 and 60–100 %), estimated original niche sizes were 37,150 and 20,760 km^2 for each subclass. After deforested areas were removed from these predications (areas <50 % forest cover), the current maximum possible extent of occurrence is ~39,060 km^2 of which 22,460 km^2 was classed as Good and 16,600 km^2 was classed as Very Good. Future climate changes are predicted to reduce niche availability for *L. flavicauda* by a further 7 %, the most affected of the probability subclasses is predicted Good category with a further 18 % loss, the Very Good category is predicted to increase by 7 %. Including the 1 and 5 km future deforestation/hunting pressure buffers there is an additional predicted 16 and 54 % loss of niche availability. This is reduced to 12 and 46 % for each respective buffer threshold when assuming no future habitat loss or hunting within protected areas.

Discussion

The areas of the original ecological niches modeled here for *A. miconax* and *L. flavicauda* are similar to those from previous GIS-based studies (Shanee et al. 2015; Buckingham and Shanee 2009). The largest difference found was in the estimated original niche size for *P. oenanthe*, which is much smaller than previous studies have estimated (Ayres and Clutton-Brock 1992; Shanee et al. 2011). Similarly, future climate changes are predicted to reduce the available niche area for *A. miconax* and *L. flavicauda*, whereas niche area for *C. oenanthe* is actually predicted to increase with future climate changes, even when taking into account expansion of the agricultural frontier. Actual levels of habitat loss for all three species are estimated here to be much lower than previous predictions (Buckingham and Shanee 2009; Shanee et al. 2011). The use of a 50 % forest cover threshold for species habitat does not include the effect of hunting pressure, which is high for all three species, particularly *L. flavicauda* (Shanee 2012b), nor does it take into account the effect of habitat fragmentation on the species' dispersal ability. Using the <1 and <5 km thresholds may give a truer picture of actual presence of species, as many available areas which have the correct bioclimatic conditions may not currently hold populations of these species.

As with all modeling, the predictions presented here are only as good as the data available. I am confident that I have used the most complete data sets for species presence points, including results from several recently published exhaustive field studies (Shanee et al. 2013b, 2015; Bóveda-Penalba et al. 2009; Shanee 2011). By using only published data and localities from my own recent field surveys and those of researchers whose methods are known, I have avoided problems of unreliability of data downloaded from internet databases, museum collections, and other sources where accuracy of species data points is uncertain (Chan et al. 2011; Graham et al. 2008).

The resolution of data layers used in modeling effect the robustness of results, with finer resolutions generally producing better results (Vale et al. 2014). The bioclimatic data sets I used have a resolution of ~1 km which allow for the models to include all but micro-scale gradients in niche presence (Elith and Graham 2009). Comparing the Maxent outputs and the distribution maps for *A. miconax* and *L. flavicauda* given by Rowe and Myers (2012) (Fig. 2a, c), this limitation can be seen clearly in central Amazonas, where the species are not present (Shanee et al. 2015; Shanee 2011) but the correct bioclimatic conditions exist (Figs. 3, 4, and 5). Even so, when the deforestation layer was applied to models the corresponding area a

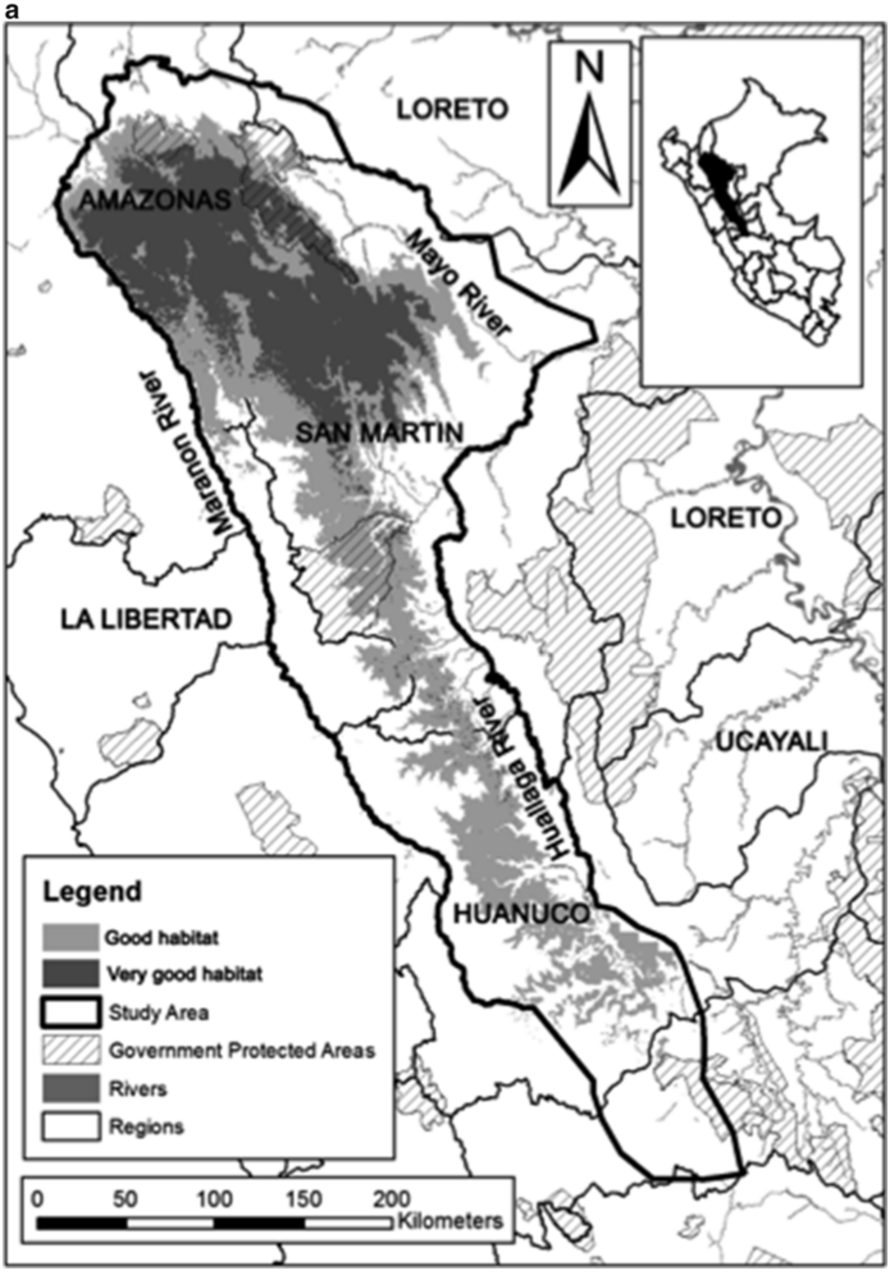
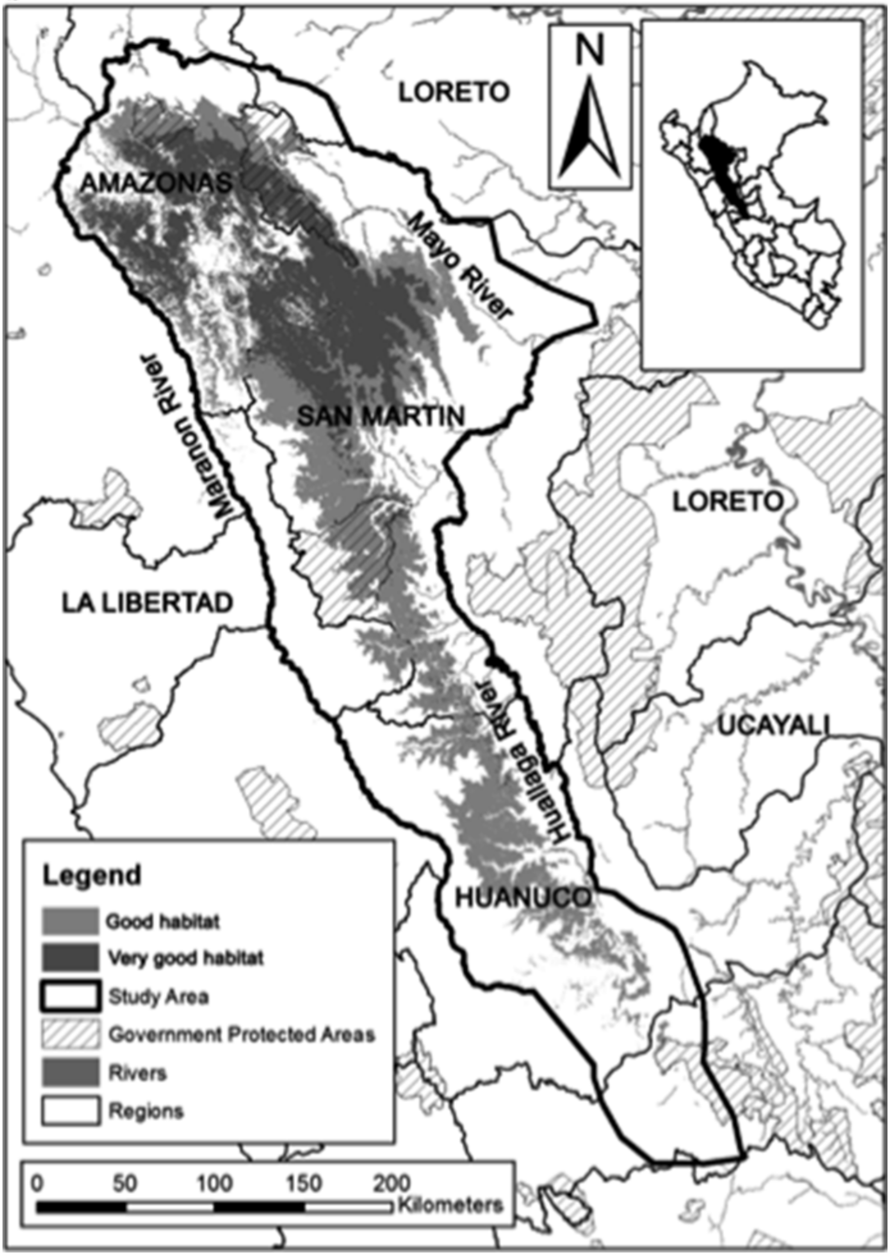


Fig. 3 (**a**) Prediction of the original ecological niche area of *A. miconax*, (**b**) Current habitat availability for *A. miconax,* original niche area minus current deforestation, (**c**) Predicted future habitat availability for *A. miconax* based on modeling results, with areas of current deforestation removed, and (**d**) Predicted future habitat availability for *A. miconax*, including 1 and 5 km thresholds of predicted deforestation and hunting

b



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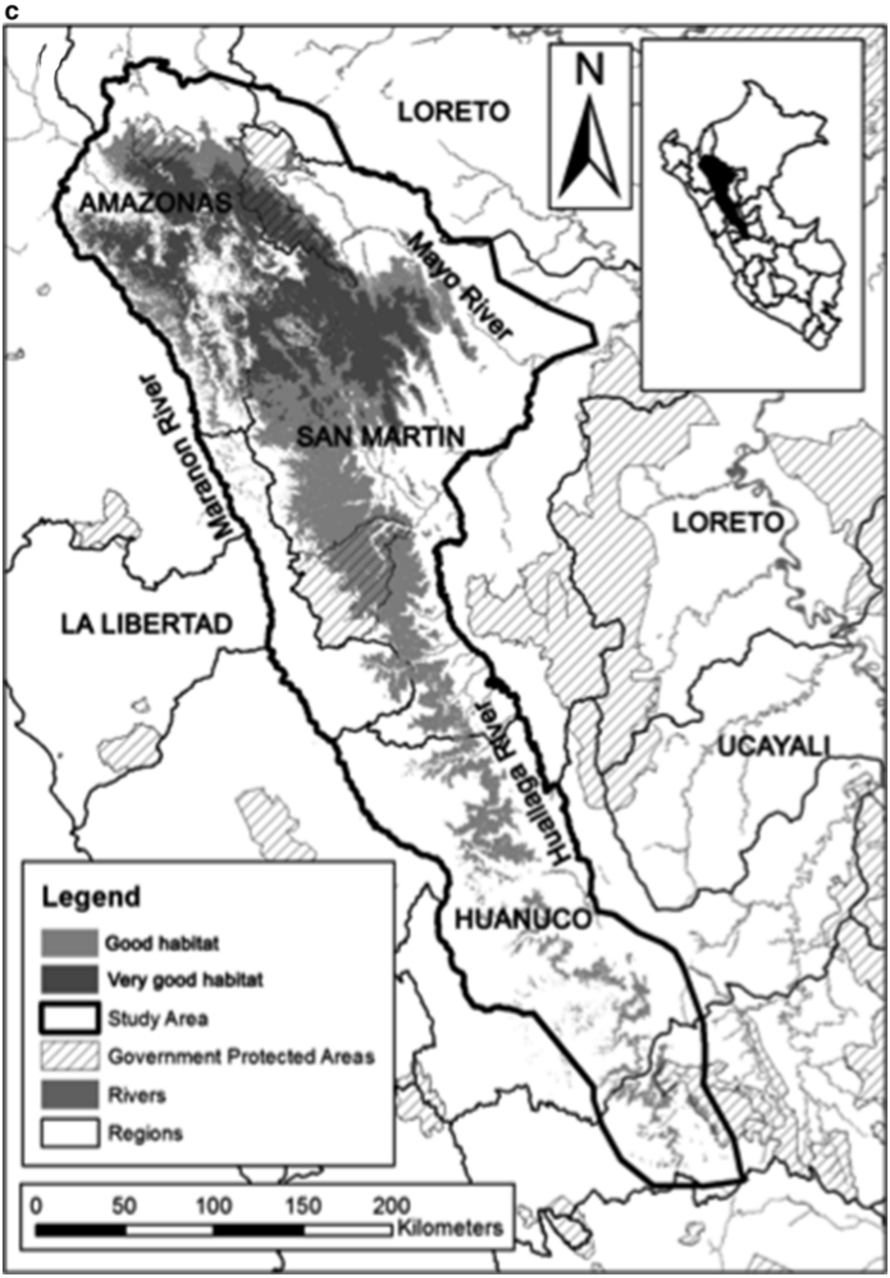

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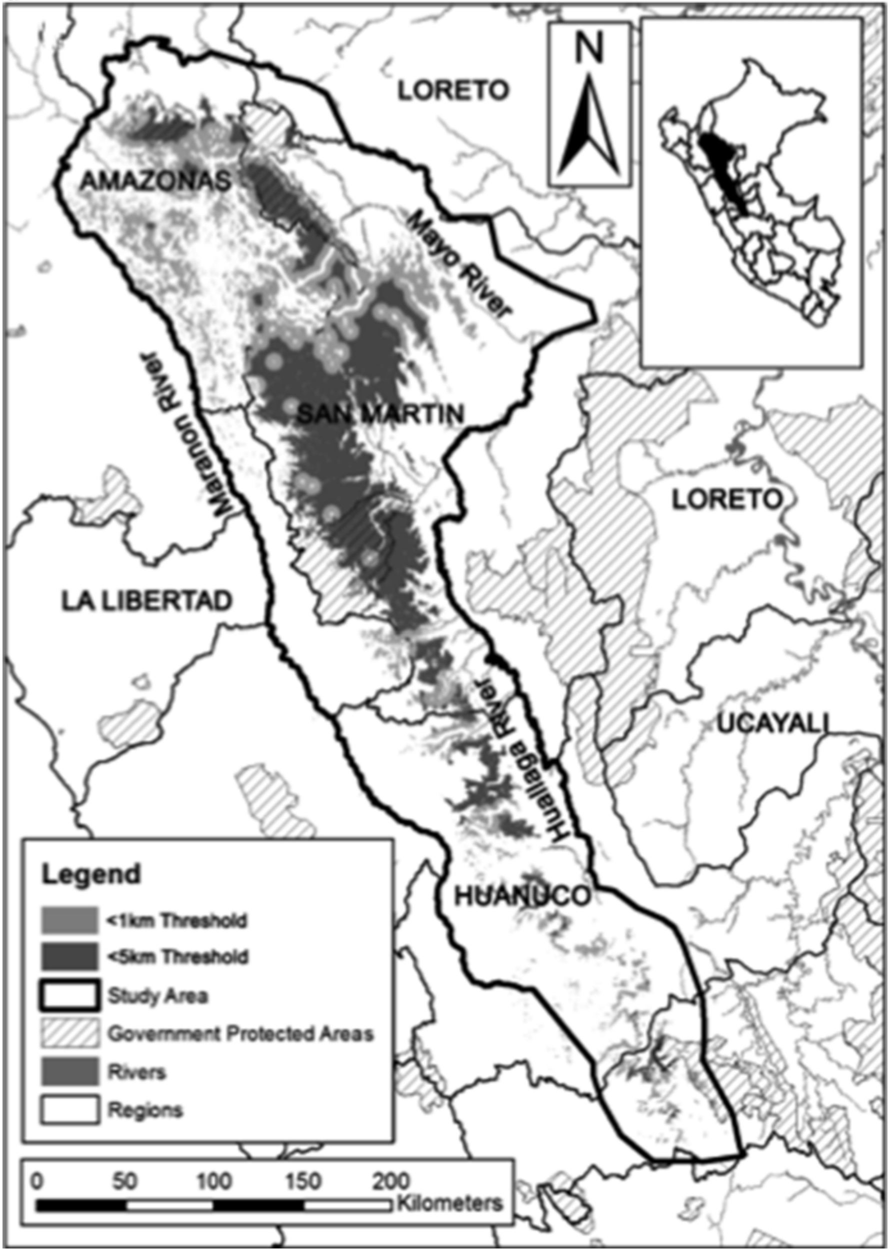

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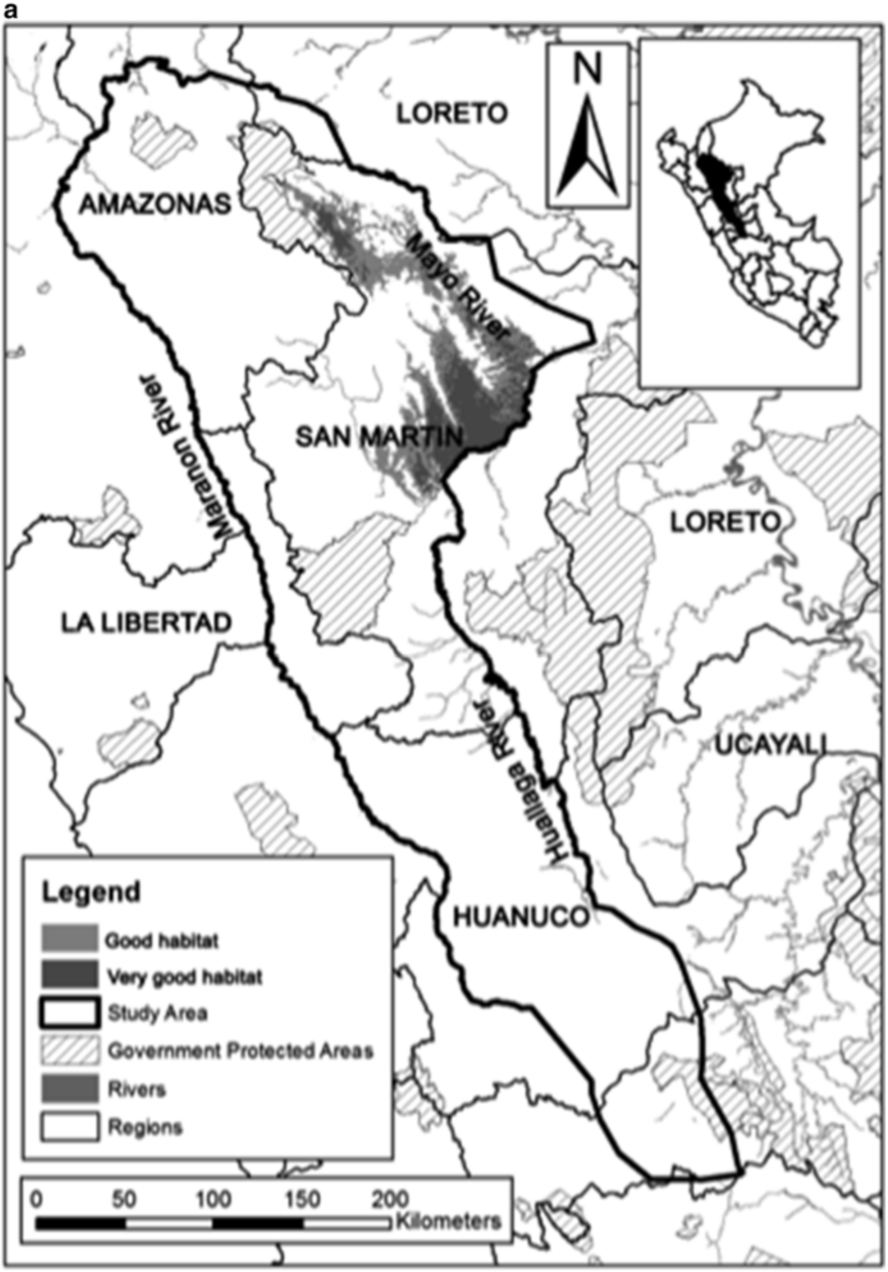
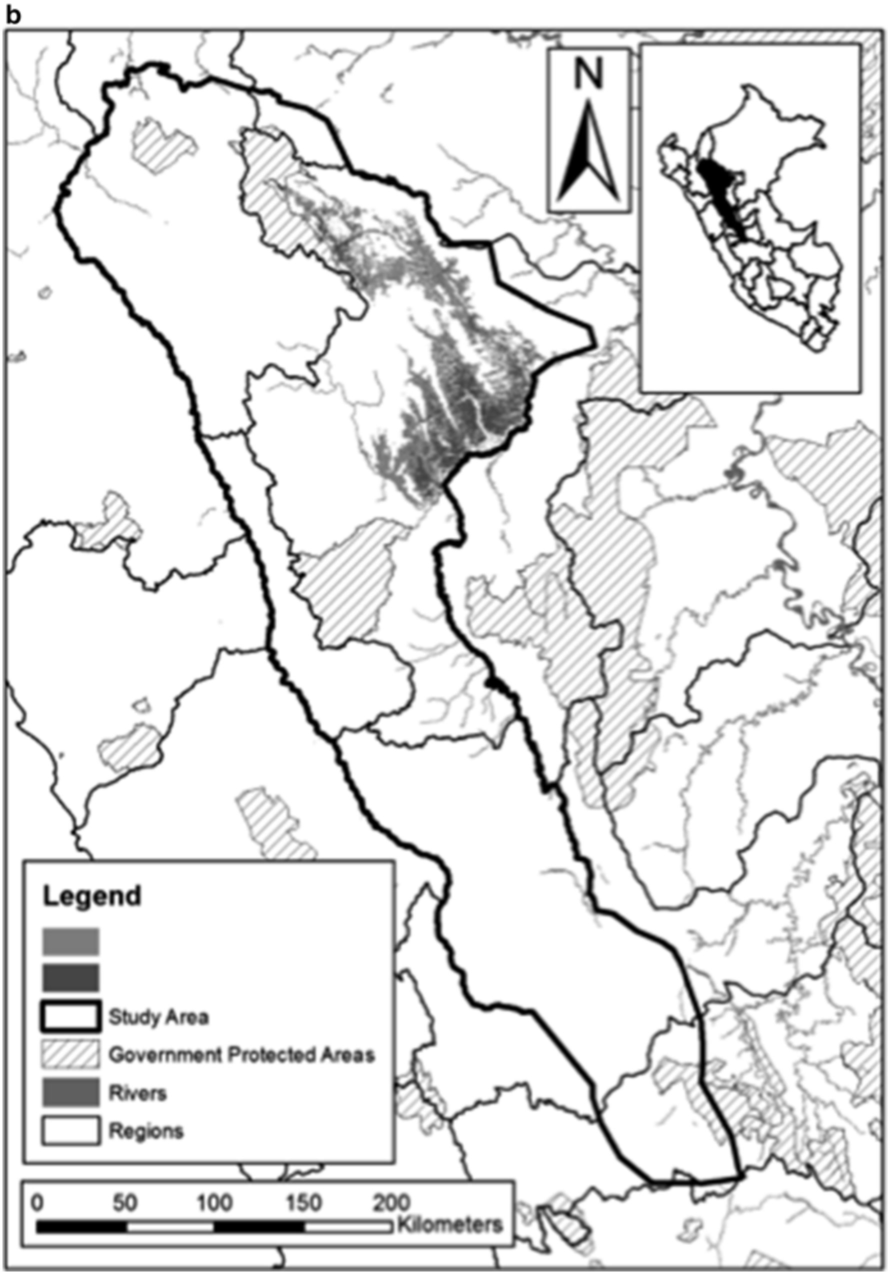


Fig. 4 (**a**) Prediction of the original ecological niche area of *P. oenanthe*, (**b**) Current habitat availability for *P. oenanthe,* original niche area minus current deforestation, (**c**) Predicted future habitat availability for *P. oenanthe* based on modeling results, with areas of current deforestation removed, and (**d**) Predicted future habitat availability for *P. oenanthe*, including 1 and 5 km thresholds of predicted deforestation and hunting



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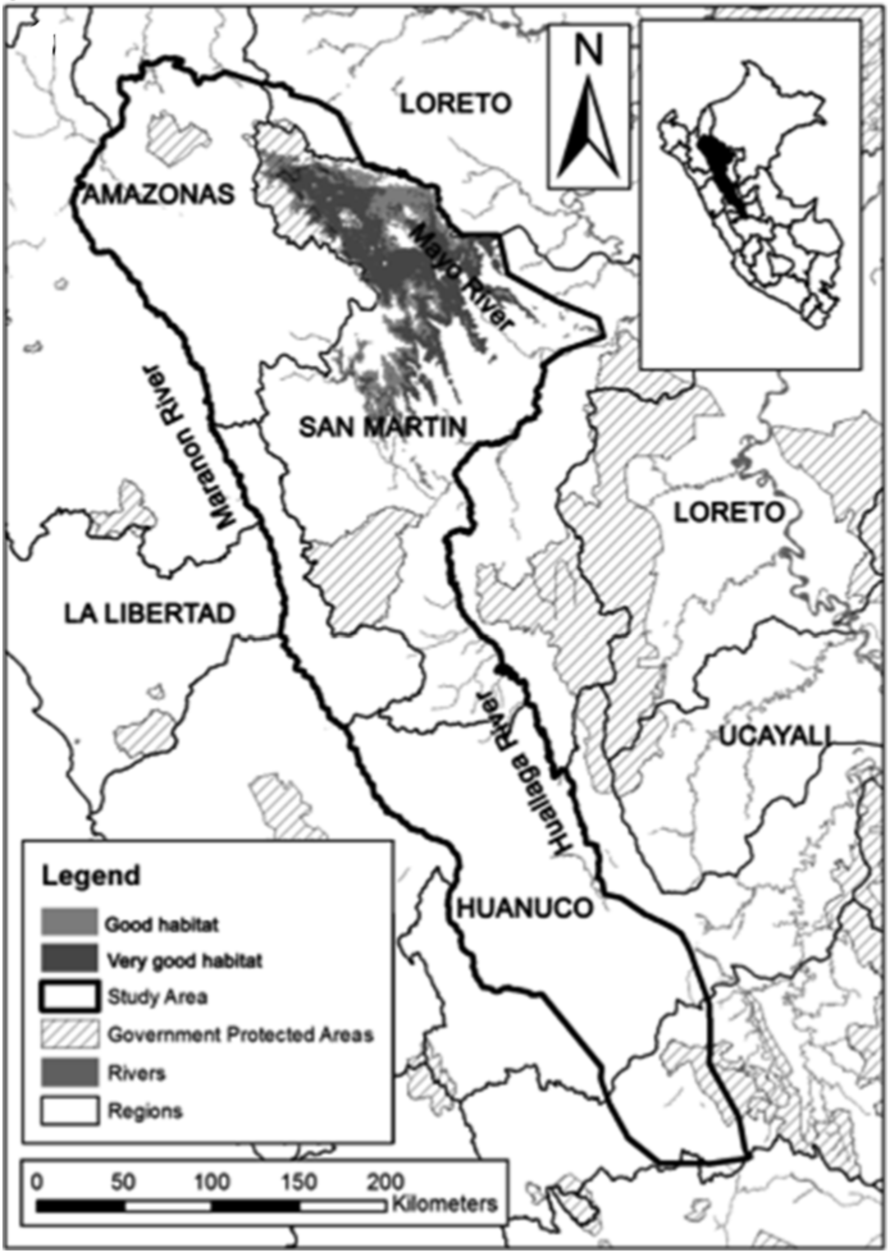

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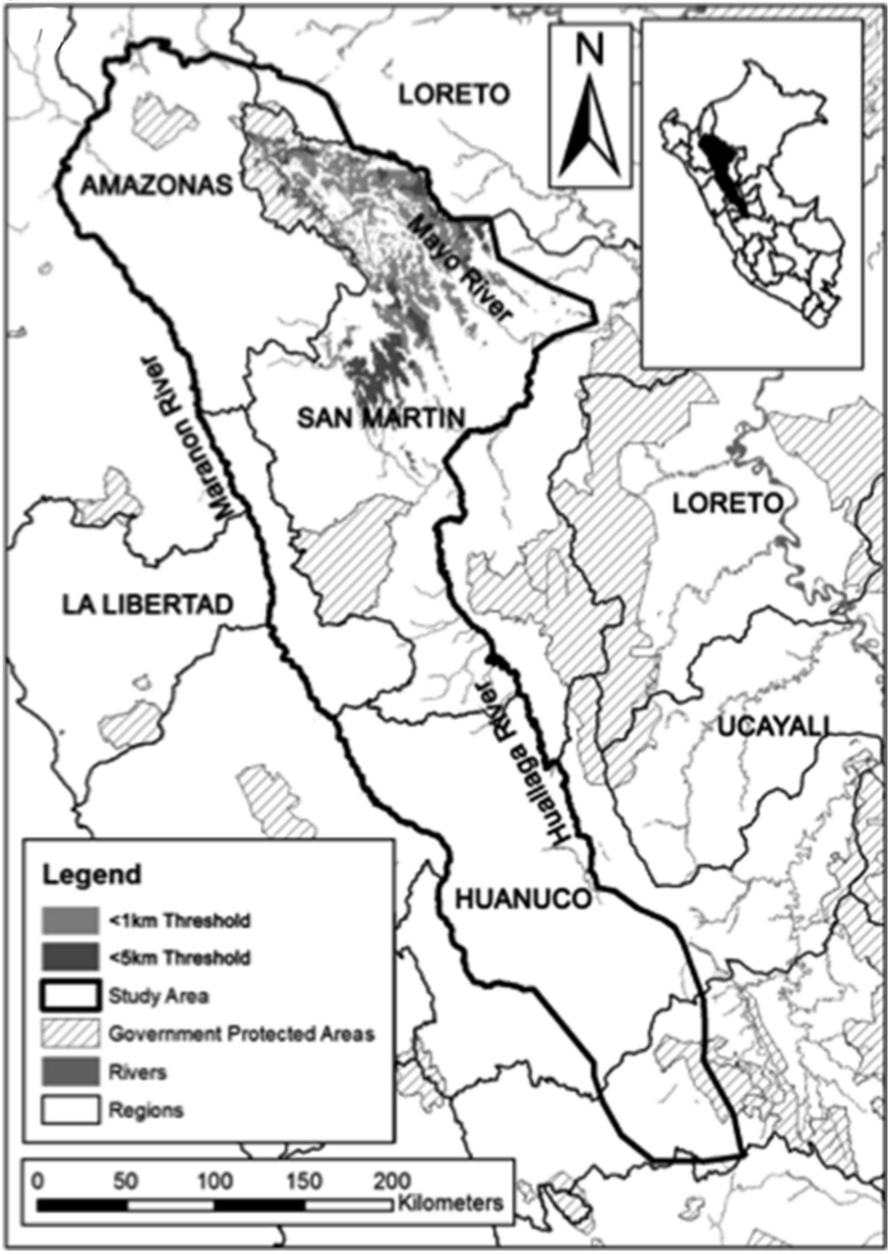

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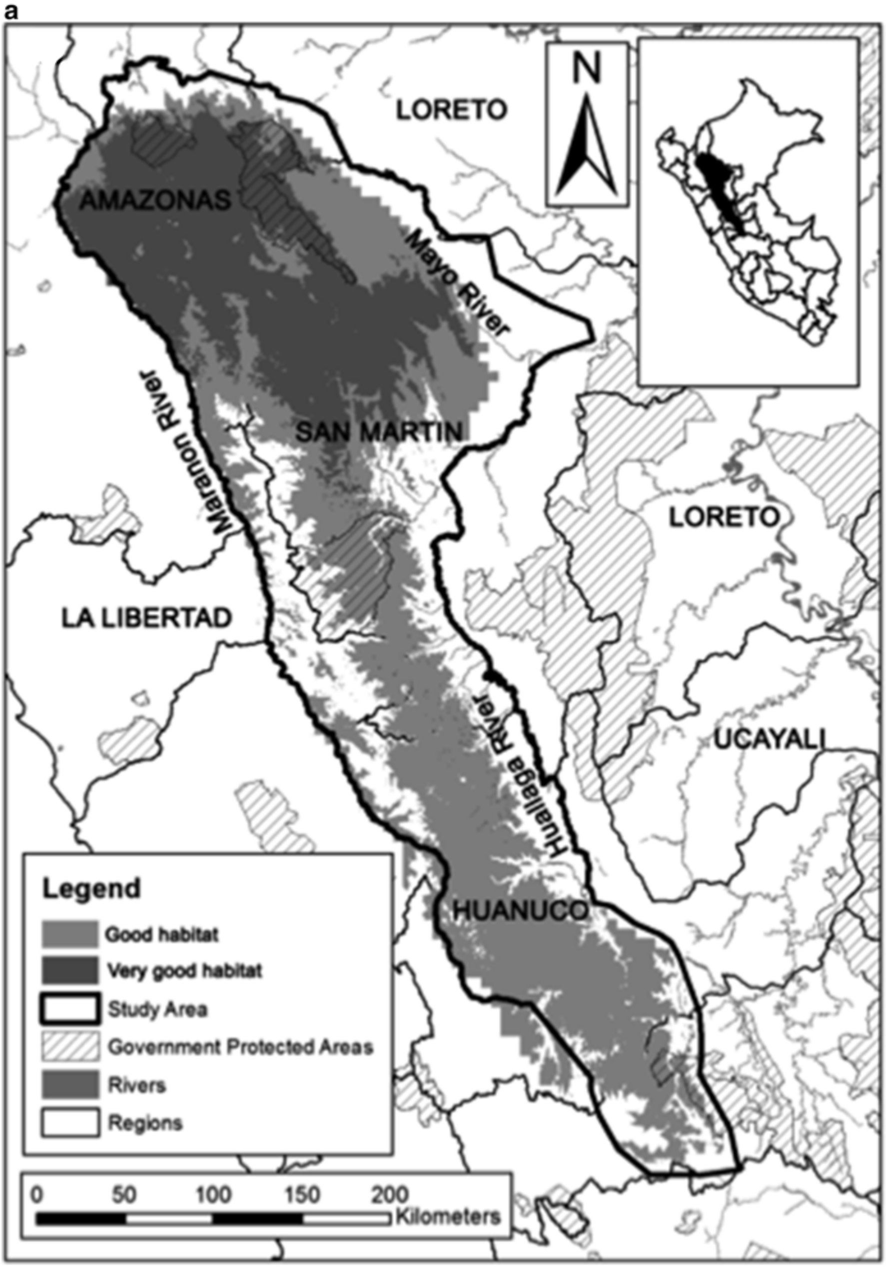
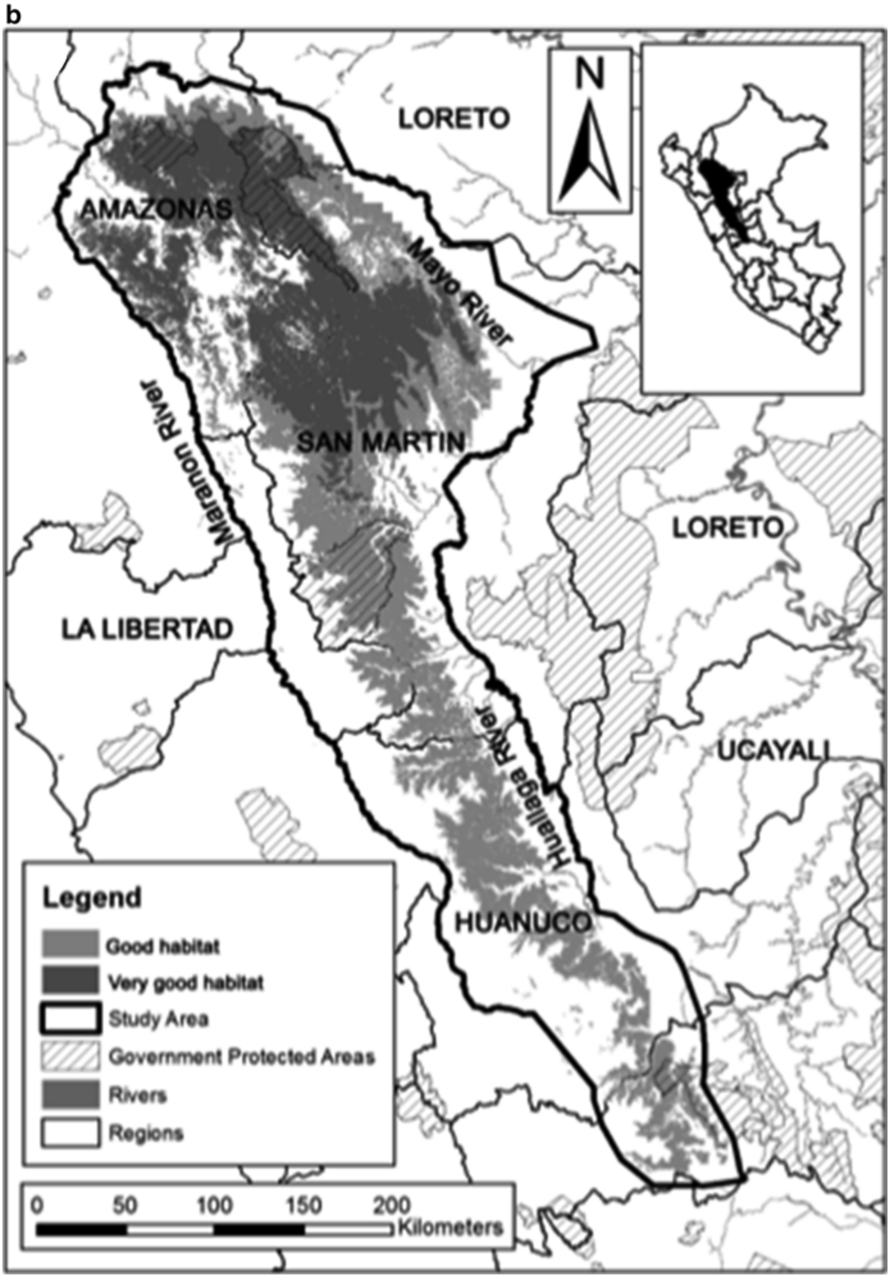


Fig. 5 (**a**) Prediction of the original ecological niche area of *L. flavicauda*, (**b**) Current habitat availability for *L. flavicauda,* original niche area minus current deforestation, (**c**) Predicted future habitat availability for *L. flavicauda* based on modeling results, with areas of current deforestation removed, and (**d**) Predicted future habitat availability for *L. flavicauda*, including 1 and 5 km thresholds of predicted deforestation and hunting



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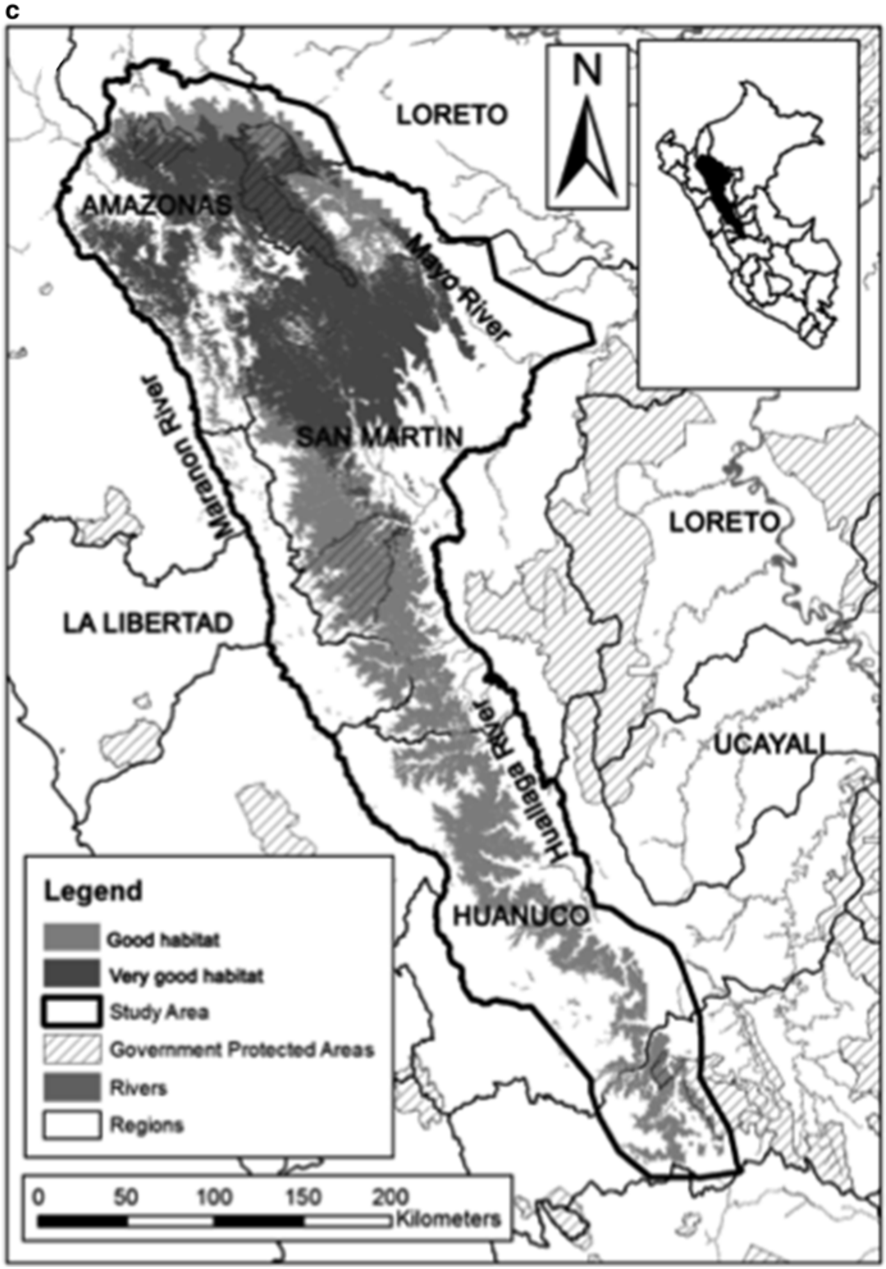

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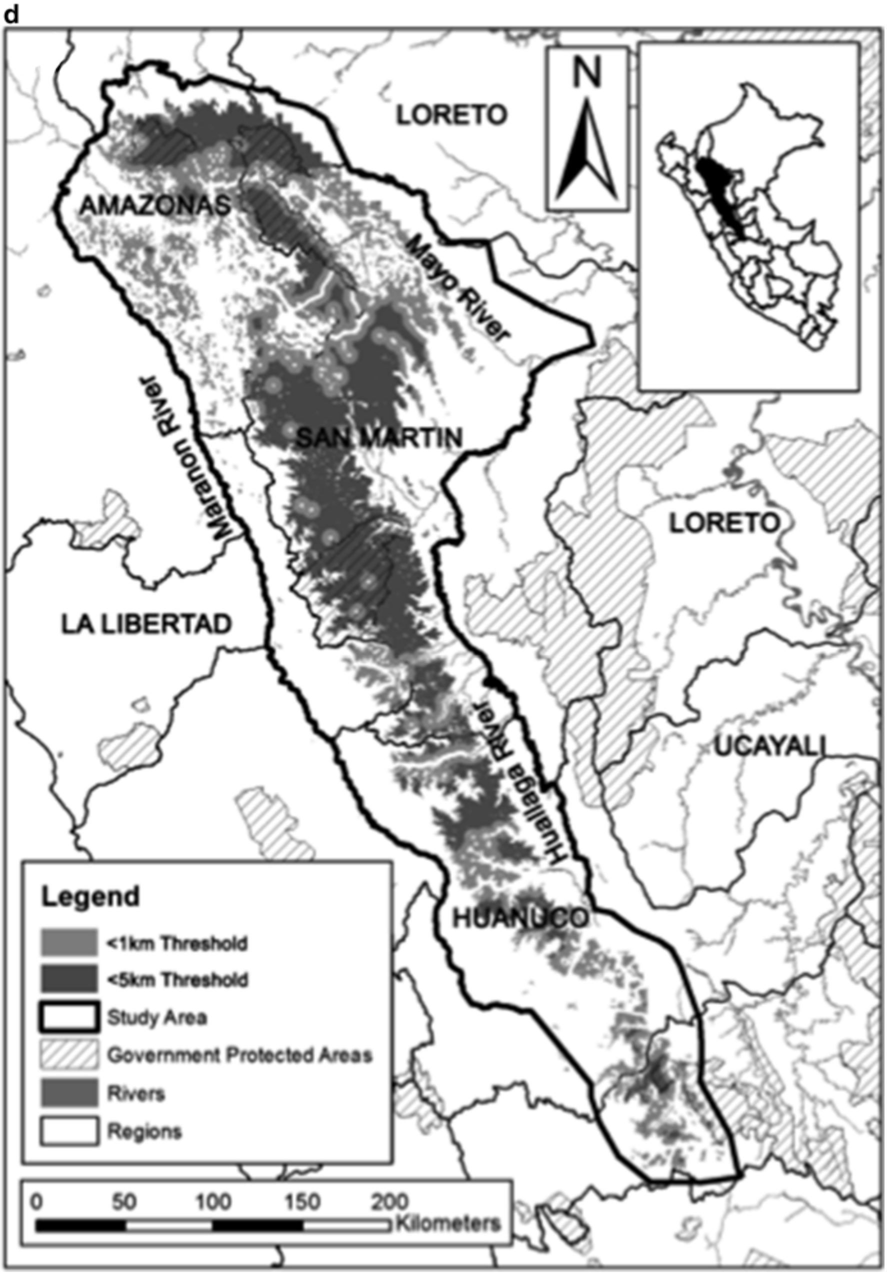

Fig. 5 (continued)

is largely removed from the resulting distribution predictions. Scale is another factor that can influence applicability of models (Guisan and Thuiller 2005; Suárez-Seoane et al. 2014). By using bias files to limit gain and results of commission models were improved (Guisan and Thuiller 2005). I corrected problems of over prediction by clipping model outputs to known geographic barriers. Other problems in accuracy of modeling can occur from spatial autocorrelation of point data, inflating measures of accuracy (Veloz 2009), and spatial heterogeneity of bioclimatic layers. By carrying out a PCA of climate variables and spatially rarefying locality data, I was able to limit the possible effect of these problems on model results (Boria et al. 2014; Veloz 2009).

As expected future climate changes are predicted to reduce niche availability for *A. miconax* and *L. flavicauda*. This is because of general and localized changes in temperatures, precipitation levels, and cloud formations, all of which will in turn have drastic consequences on plant phenologies affecting habitat availability and quality (Bubb et al. 2004; Foster 2001; Herzog 2011; Pielke et al. 2002; Still et al. 1999). Interestingly, my models predicted a large increase in niche availability for *P. oenanthe* with future climate changes. These very different results could stem from the different habitat requirements of the species. *Aotus miconax* and *L. flavicauda* are restricted to higher elevation montane forests, which are predicted to be very sensitive to climate changes (Bubb et al. 2004; Herzog 2011; Still et al. 1999), whereas *C. oenanthe* is restricted to lower elevation pre-montane and tropical dry forests. Increased temperatures and reduced precipitation may account for the predicted increase in niche availability, particularly in dry forest areas. These differences in the predicted effects of future climate changes on niche availability for these species demonstrates the complexities involved in modeling such changes (Newbold et al. 2014). Caution needs to be used when interpreting this result as the increase in area is mainly outside of the species current distribution. In this case the species, or habitat, may not be able to adapt quickly enough to the geographic shift in niche location (Feeley and Silman 2010), and this could therefore constitute a significant decrease in the actual niche availability. When I applied the two thresholds of predicted future land use change and anthropogenic hunting pressure, the models all predicted reductions in niche availability for all species.

Natural inaccessibility and socioeconomic instability played major roles in protecting *A. miconax* and *L. flavicauda,* and to a lesser extent *P. oenanthe,* from anthropogenic pressures for many years (deLuycker 2007b; Ellenbogen 1999; Kent 1993; Shanee 2011; Young 1996). Since the paving of the main highway from Peru's Pacific coast to the Amazonian lowlands, increased immigration from the high mountain sierras of Peru's interior has caused widespread deforestation and substantial increases in hunting rates (deLuycker 2007b; Dreyfus 1999; Morales 1986; Shanee 2012a). From remote, unsettled regions, this area now has the highest immigration and deforestation rates in Peru (INEI 2008; PROCLIM/CONAM 2005; Reategui and Martinez 2007). This has caused severe fragmentation of habitat for all three species (Shanee et al. 2011, 2015; Bóveda-Penalba et al. 2009; Leo Luna 1987; Shanee 2011). As in all areas, deforestation, fragmentation, and the presence of livestock and waste products have many negative impacts on populations of wildlife (Newbold et al. 2014) including, increased competition for resources (Andrén 1994; Estrada and Coates-Estrada 1996), increased hunting pressure (Jerozolimski and Peres 2003; Michalski and Peres 2005; Peres 2001), increased zoonotic infections (Chapman et al. 2006; Fahrig 2003; Gillespie et al. 2005; Goldberg et al. 2008; Sanchez-Larranega and Shanee 2012), and reduced connectivity between populations, reducing genetic fitness (Bergl et al. 2008; Brenneman et al. 2012; Marsh et al. 2013).

Protected area networks have been a mainstay of conservation for many years but have been criticized for shortfalls in effectiveness in protecting species (Cantú-Salazar et al. 2013; Geldmann et al. 2013; Rodrigues et al. 2003; Seiferling et al. 2012), increasing the need for landscape level solutions that include local communities in gap areas (Gálvez et al. 2013; Porter-Bolland et al. 2012). Community-managed forests provide a solution for conservation in highly populated areas and often perform better then protected areas (Porter-Bolland et al. 2012). The inclusion of conservation programs in gap areas is of particular importance as levels of land development around protected areas has a direct influence on their effectiveness as conservation units (Durán et al. 2013; Leroux and Kerr 2013). In northern Peru, the inclusion of communities is of particular importance as human populations are relatively high and increasing (PROCLIM/CONAM 2005; Shanee et al. 2014). The protected area network in northern Peru covers a fairly large area of forests including areas of current and future habitat for *A. miconax* and *L. flavicauda* but provides little protection for *P. oenanthe*. As with other areas in the Andes, protected areas in northern Peru may not be enough to safeguard these species from anthropogenic development activities (Swenson et al. 2012). Including the predicted increase in niche area for *P. oenanthe*, anthropogenic activities will still reduce total available area for the species, even assuming no more habitat loss within protected areas.

The results presented here show that multiple drivers of extinction risk combine to threaten species (Newbold et al. 2014) and that future man-made climate changes will have variable effects depending on a species' habitat and ecological needs (Newbold et al. 2014). Although climate change is predicted to dominate conservation during this century (Bonan 2013; Laurance and Williamson 2001; Lewis 2006; Lewis et al. 2011; van Aalst 2006; Veech and Crist 2007), other anthropogenic activities are still and, in many cases, will continue to be the major drivers of extinctions (Feeley and Silman 2010; Hurtt et al. 2011; Krausmann et al. 2013; Newbold et al. 2014; Peres et al. 2010; Tilman et al. 2001). Future conservation actions should not only concentrate on mitigating the effects of climate change but should also concentrate on reducing other anthropogenic pressures which are driving species to extinction. This is particularly true for species with limited geographic ranges and habitat specializations (Newbold et al. 2014) that are intrinsically more at risk of extinction (Cardillo et al. 2005; Purvis et al. 2000a, b) but that also may not be able to adapt to changing climates and habitats in the near future.

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Protecting Nonhuman Primates in Peri-Urban Environments: A Case Study of Neotropical Monkeys, Corridor Ecology, and Coastal Economy in the Caribe Sur of Costa Rica

Stacy M. Lindshield

Introduction

Peri-urban environments present an unusual set of challenges for non-human primates (NHP) due to habitat loss, habitat fragmentation, and competition with humans for resources (Jaman and Huffman 2013; Printes et al. 2010, but see Cunha et al. 2006). Although the drivers of habitat loss and fragmentation in these landscapes are numerous, some contributing factors include industrialized agriculture (see chapter "The Threat of Industrial Oil Palm Expansion to Primates and Their Habitats" this volume), urbanization, roads, and electricity and telephone grids (Lokschin et al. 2007; Maibeche et al. 2015; Meijaard et al. 2012; Printes et al. 2010; Vickers et al. 2015). These developments can negatively impact the survival rates of NHP populations (Lokschin et al. 2007; Meijaard et al. 2012, but see Jaman and Huffman 2013). Although protected areas remain a vital part of species conservation strategies, a stark reality is that all primate habitats cannot be strictly protected (Meijaard et al. 2012). In these unprotected areas, community-based conservation (Horwich and Lyon 2007) and ethnoprimatology (Fuentes and Hockings 2010) are essential for effectively managing and preserving NHP populations.

The anthropogenic matrix that is characteristic of peri-urban landscapes may introduce a range of problems for NHPs. This matrix includes areas unsuitable for most primates to occupy aside from brief forays usually associated with traveling or foraging. Examples of the anthropogenic matrix include urban zones, cropland, and roads (Meijaard et al. 2012; Pozo-Montuy et al. 2011; Printes et al. 2010). Furthermore, dog depredation on NHPs is a substantial risk in such areas, especially near human settlements (Anderson 1986; Printes et al. 2010). Wildlife managers,

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road developers, and local communities are increasingly incorporating wildlife corridors into species and population conservation strategies in areas, where habitat loss and fragmentation have created serious barriers to animal movement (Paige 2015). In general terms, wildlife corridors are strips of habitat that link larger habitat fragments. In addition to promoting wildlife movement, such corridors aim to decrease mortality rates associated with ranging in the anthropogenic matrix and to offset the high economic costs of animal-vehicle collisions (AVCs) (Hilty et al. 2006; Paige 2015). While wildlife corridor ecology has undergone tremendous growth in recent years (Bissonette and Cramer 2008; Gilbert-Norton et al. 2009; Haddad et al. 2003; Hilty et al. 2006; Proctor et al. 2015; Silveira et al. 2014; van der Ree et al. 2009; van der Ree et al. 2015; Vickers et al. 2015), few studies have examined primate corridors (Donaldson and Cunneyworth 2015; Lokschin et al. 2007; Teixeira et al. 2013; Valladares-Padua et al. 1995).

Ethnoprimatological approaches are well positioned to contribute to the study of primate corridor ecology. Provided that human land use is often a core issue of corridor ecology (Hilty et al. 2006) and that ethnoprimatology in general seeks to understand the multidimensional relationships between human and nonhuman primates (Fuentes and Wolfe 2002), practitioners will certainly benefit from exploring how such interactions, including the localized socioeconomic and cultural factors, impact the primate populations targeted for conservation. This chapter addresses the gap on primate corridor ecology using a case study of three New World monkey species living in a spatially and culturally complex, peri-urban landscape in and near the Refugio de Gandoca-Manzanillo, Jairo Mora Sandoval (REGAMA) on the coast of southeastern Costa Rica. Specifically, this study deconstructs the multi-causal drivers of primate habitat loss and fragmentation, examines the sources of primate mortality, measures the effectiveness of corridors, and evaluates wildlife barriers aimed at reducing fatalities associated with power lines. Lastly, this chapter outlines management recommendations and identifies the challenges facing NHPs living in peri-urban environments.

Location and Study Period

REGAMA (9° 37′04″ N, 82° 38′13″ W) is a 9449 ha marine and terrestrial (terrestrial: 5013 ha; marine area: 4436 ha) refuge located along the southeastern coast of Costa Rica. REGAMA is located within the Districts of Sixaola and Cahuita, Canton of Talamanca, and Province of Limon. In 2013, REGAMA was renamed in honor of Jairo Mora Sandoval, a local conservationist from Gandoca that was murdered while patrolling a beach in Moín to protect sea turtle eggs from poachers (Fendt 2015). The vegetation includes a narrow strip of coastal forest as well as premontane moist and swamp forest (Holdridge et al. 1971). The coastal forest is dominated by woody plant species such as *Terminalia catappa*, *Coccoloba uvifera*,

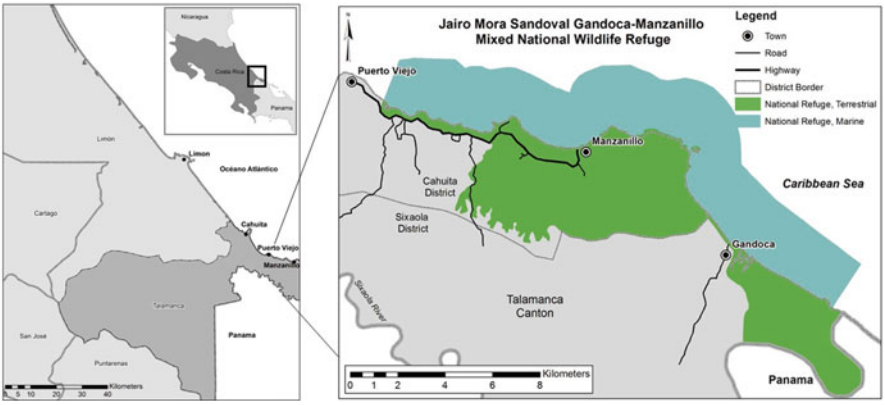

Fig. 1 Location of the study site in southeastern Costa Rica

Cocos nucifera, *Laguncularia racemosa*, and *Rhizophora mangle*. The premontane moist forest is characterized by pioneer species such as *Cecropia obtusifolia*, *Ochroma pyramidale*, *Castilla elastica*, *Genipa americana*, and large trees such as *Ficus werckleana*, *Luehea seemannii*, *Dipteryx panamensis*, *Hura crepitans*, and *Spondias mombin*. The data for this study were collected at REGAMA as well as at public roads near the refuge (Fig. 1) in December 2005, June 2006, May–July 2007, June–July 2008, June–July 2009, January 2010, August 2010, May 2012, and January–August 2015.

Nonhuman Primates of the Caribe Sur

Three NHPs occupy REGAMA: the endangered black-handed spider monkey (*Ateles geoffroyi*) (IUCN Red List A2c ver 3.1, Cuarón et al. 2008), the mantled howler monkey (*Alouatta palliata*), and the white-faced capuchin (*Cebus imitator*). Spider monkeys are the largest of these three species (body weight male average = 8.2 kg; female average = 7.7 kg) and are generally distinguished by their large home ranges, highly frugivorous diet, and fission–fusion social system (reviewed in Di Fiore et al. 2011). The much smaller capuchin monkey (body weight male average = 3.7 kg, female average = 2.7 kg) also ranges widely but tends to socialize in larger, more cohesive groups and displays a greater breadth of dietary items, notably animal prey (reviewed in Jack 2011). The howler monkey is another relatively large New World monkey (body weight male average = 7.2 kg, female average = 5.4 kg). Howler monkey groups have relatively smaller home range areas and usually incorporate a larger proportion of leafy material in the diet relative to *Ateles* and *Cebus* (Di Fiore et al. 2011).

The Peri-Urban Landscape Near REGAMA

REGAMA is located near the towns of Puerto Viejo, Manzanillo, and Gandoca. Most of the peri-urban landscape is located between Manzanillo and Puerto Viejo in the northwestern section of REGAMA, and deforestation is widespread from Puerto Viejo to Playa Chiquita outside of the borders of the refuge. Puerto Viejo, the larger of the two communities, draws thousands of tourists each year due to its beachfront blend of surfing, Afro-Caribbean culture, and ecotourism. Manzanillo also draws many tourists but it is smaller, less urbanized, and has more primate habitat near the town's borders. The Gandoca community situated in the southeastern section of the refuge is considerably smaller than Puerto Viejo and Manzanillo and has the least number of tourists. A highway, the main economic vein along this coast, connects Puerto Viejo to Manzanillo, and also bisects the refuge into coastal and inland sections. This highway does not directly connect to Gandoca. Thus, travelers must take a significant detour around the refuge on highways and unpaved roads to reach this community. The additional effort needed to travel to Gandoca may be related to their smaller ecotourism economy. Further inland, where there are fewer tourists, agriculture (e.g., cattle, banana plantation) is the primary contributor to deforestation outside of REGAMA.

REGAMA is a mixed refuge, meaning that a portion of the land is owned by the State (20 %), and the remaining 80 % consists of privately owned properties (Universidad de Costa Rica 1996). Many property owners have kept their land within their respective families for generations but increasing foreign interest in coastal development and tourism has led several owners to sell their lands at a premium to foreign investors or immigrants from developed countries such as the United States, Canada, Italy, Argentina, and Spain. Private property owners are allowed to use the natural resources and live on their lands, but they must also follow strict environmental laws regulated by the Ministerio de Ambiente y Energía (MINAE) that are aimed at environmental protection and conservation, primarily through minimizing urban development. These laws prohibit draining wetlands, destroying coral reefs, or building structures higher than 9 m, to name a few (Law 34946-MINAE). However, violations of these laws are numerous. Community vigilance is sometimes used to aid in law enforcement (Quesada 2014, P. Vangoidsenhoven, personal communication). In one prominent case, the owners of two large hotels situated within the refuge were charged with breaking numerous environmental laws. The proceeding legal case unfolded over 18 years and, ultimately, led to the closing and demolition of these hotels, but not without significant local opposition, including political protests (Williams 2011).

Immediately outside of the borders of REGAMA, where environmental restrictions aimed at sustainability and conservation are significantly relaxed, the municipality of Talamanca oversees and enforces legal matters of land use. The impact of these management differences in land zoning and natural resource use are easily visible to the naked eye, with more abundant primate habitat located within REGAMA.

The anthropogenic matrix also includes utility grids. Electric power and telephone lines present life-and-death challenges to NHPs and other arboreal wildlife.

The most serious and obvious problem is the risk of electrocution when individuals directly contact the electric current through non-insulated cables or transformers. A further complication concerning this grid is that telephone lines, which are positioned below the electric cables in REGAMA, offer no risk of electrocution as long as individuals completely avoid the electrified components that are situated overhead. However, it may be the case that primates using telephone lines as corridors are also more likely to perceive electrified cables as safe and, thus, be at risk of electrocution at a later time.

Roads are also dangerous for NHPs and other animals, and these structures are often situated parallel to power and telephone lines at REGAMA. A two-lane highway with asphalt and numerous secondary, unpaved roads are located within and around REGAMA (see Fig. 1). As a consequence, NHPs must either remain on one side of the road, cross the road using a forest canopy corridor, or cross the road by traveling on the ground. The number of AVCs is greatest along the highway because of the higher number of vehicles traveling at higher speeds. Conversely, it is easier for drivers on the gravel and dirt secondary roads to decelerate and avoid animals. High-speed driving is also a public safety issue for pedestrians and bicyclists in the region, and the area is rarely policed for speeding violations. It is within this complex peri-urban context, inside and outside of the refuge, that NHPs must navigate.

The Coastal Economy

The Caribbean coast of Costa Rica plays an important role in the production and shipment of agricultural products. The fertile soils of these lowlands principally support the production of bananas and pineapples (Food and Agricultural Organization of the United Nations 2014). Within this industrialized agricultural context is a network of roads linked to the key shipping port city of Límon. This port is ranked second in trade within the Caribbean, behind only Colon, Panama (World Bank 2015). While agricultural exports are vital to the Costa Rican economy, tourism is the primary source of income for many residents in the coastal areas of the Caribe Sur (Quesada 2014). Historically, the tourism economy here is centered on small-scale ecotourism, domestic tourism, and surfing (Associación Talamanqueña de Ecoturismo y Conservación 2009), in contrast to the large-scale marinas and resorts that populate parts of the Pacific coast. For example, Tortuguero National Park, Cahuita National Part, and the Puerto Viejo area attract a large number of ecotourists drawn to the Caribe Sur for a variety of reasons (Associación Talamanqueña de Ecoturismo y Conservación 2009). As visitor numbers increase, however, so too does the need for infrastructure expansion. Innovative solutions to this conflict are needed to ensure a bright future for both NHPs and the people dependent upon the ecotourism economy. In order to develop a well-informed primate conservation and management plan in this area, basic research on primate ranging and habitat use, corridor use, and mortality risks within the Caribe Sur peri-urban landscape is necessary.

Primate Ranging and Road Surveys

In this study, public roads were surveyed in order to gauge primate ranging within the peri-urban environment. Roadside areas were the focus of this study as habitat loss and fragmentation is strongly associated with road access (Nelson and Hellerstein 1997), and these environments play an important role in primate corridor ecology. Although surveying off-road habitat is essential for accurately estimating ranging behavior, it was not achievable during the study period due to the cultural landscape at REGAMA. Most NHPs ranged among several small properties, which resulted in the need to acquire landowner permission to use each property prior to conducting each survey. Moreover, many owners could not be located and dogs guarded several properties. For these reasons, private properties were avoided but should be included in future studies.

Roads were surveyed on 67 days between May and July 2007, January 2010, May 2012, and January–April 2015. Surveyors walked slowly (1–2 km/h) and searched for all three primate species (see Peres 1999). For each primate encounter, the species, location in geographic coordinates, minimum number of individuals, and the predominant activity (travel, feed, rest, socialize, other, out-of-view) of the group were noted. In addition, all observations of corridor use, road use, and dead animals were recorded.

All three NHP species occupied areas of the peri-urban landscape, inside and outside of the refuge (Fig. 2). Howler monkeys were occasionally encountered along the periphery of Puerto Viejo. Spider and capuchin monkeys were not observed near this densely populated area. All three species inhabited the peri-urban landscape between Puerto Viejo and Manzanillo. Howler monkeys were encountered most often and commonly occupied habitat on either side of the highway bisecting REGAMA into coastal and inland sections. Capuchin and spider monkeys were less often encountered. They usually occupied the inland roadside, although both species ranged within the coastal side in less disturbed areas of the refuge near Manzanillo.

Mortality Risks in the REGAMA Landscape

Monkey-vehicle collisions and electrocutions were assessed using road surveys in addition to anecdotal reports from local residents that were verified with photos whenever possible. During 45 surveys between January and April 2015, two mammal (1 %), 24 reptile (17 %), 34 crustacean (23 %), and 85 amphibian (59 %) roadkills were located. The mammal-vehicle collisions involved one kinkajou (*Potos flavus*) and one opossum (*Didelphis marsupialis*). No NHP roadkills were identified during pedestrian surveys but a local resident observed a collision involving one howler monkey near Cahuita in 2015 (C. Orr, personal communication).

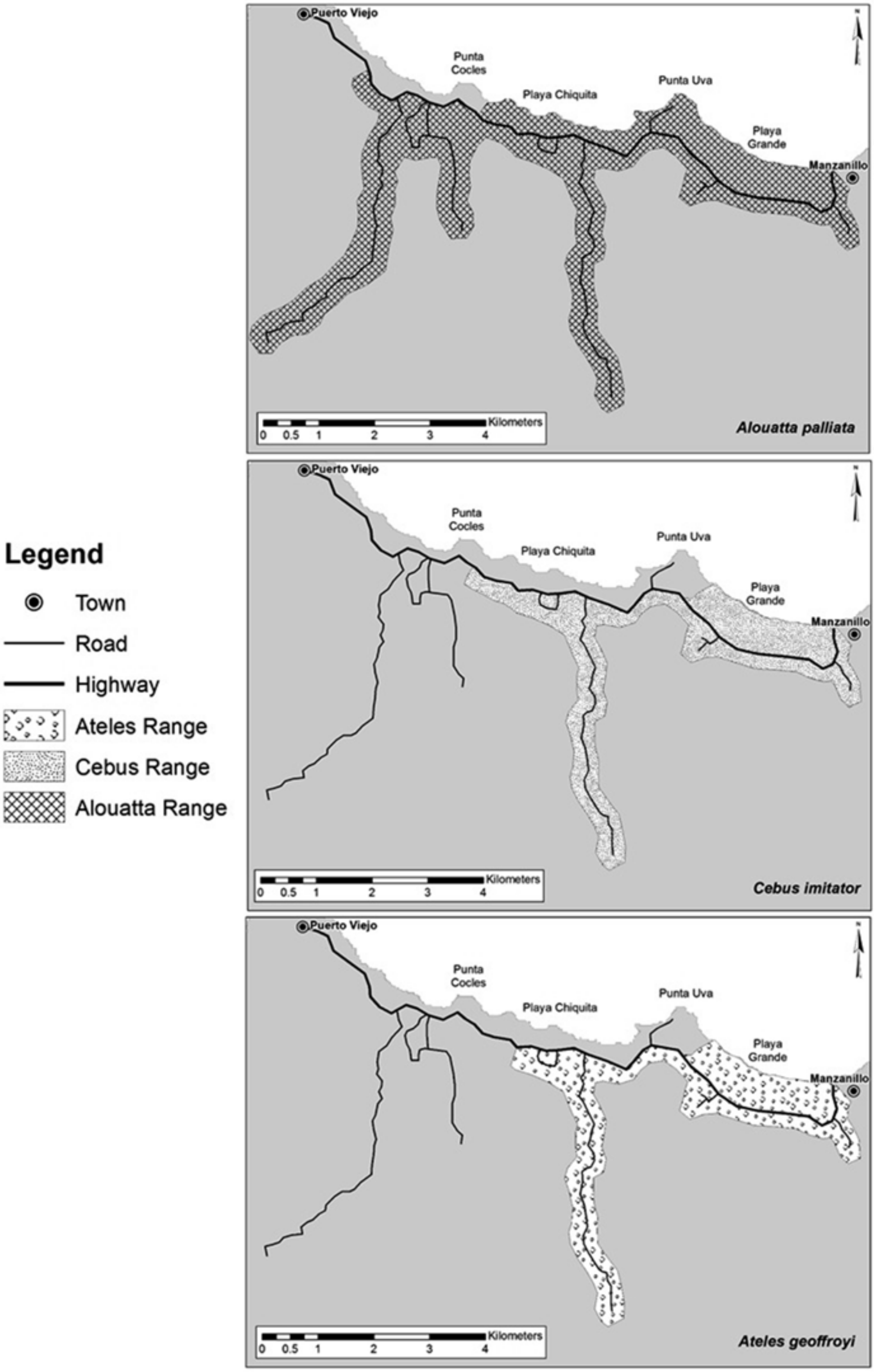

Fig. 2 Estimated ranges for nonhuman primate in the peri-urban landscape between Puerto Viejo and Manzanillo

Two factors complicating this assessment of primate-vehicle collisions include the underreporting of roadkill events and the potentially short interval between an AVC event and the removal of the carcass from the road. Although it is possible for mammal carcasses to mummify along the road, they may also rapidly disappear due to the high abundance of scavengers in REGAMA (e.g., domesticated dogs). For example, one resident witnessed dogs immediately removing a fresh howler monkey carcass. In this case, an adult female with an infant fell from a height of approximately 15 m onto the road while using a natural canopy bridge in 2014 (J. Jones, personal communication). According to the witness, a broken, leafy branch fell with her and she died on impact. Her infant survived the fall and was taken to a local wildlife rescue center. Shortly after her death, several dogs arrived at the site and carried her away. This canopy bridge was used by a group of howler monkeys for at least 2 years prior to her death, and following this incident a rope bridge was installed to reinforce the canopy bridge.

Four mammals were found dead from electrocution during the road surveys in May 2012, and January to April 2015, including three kinkajous and one opossum. In all of these cases, the carcasses were suspended from the electric cables. Although electrocuted primates were not observed during these surveys, two residents reported viewing mummified primates on the roadside in August 2014 that were likely electrocuted (P. Vangoidsenhoven and P. Venegas Vargas, personal communications). A total of three primates ($n=1$ *Ateles*, $n=2$ *Alouatta*) were found on the road in close proximity to several electric lines spanning across a dirt road in a heavily disturbed, forest-pasture matrix (Fig. 3). These events happened on different days, with all three individuals discovered at the same location. The remains were not recovered for analysis and thus the cause of death is not known for certain, but electrocution is inferred due to the proximity of the electric cables.

Forest fragmentation from roads, grids, and settlements in the peri-urban landscape create forest gaps that primates must either avoid or travel across. Although all three species exhibit some terrestrial behavior, this activity is generally rare and in REGAMA it appears to be risky due to the high abundance of dogs. Several residents have reported negative interactions between dogs and howler monkeys, where howler monkeys have dropped branches and feces above dogs, and dogs have barked and directed aggression towards howler monkeys (B. Walker, personal communication). These interactions can result in mortality events, as a resident reported that a dog attacked and killed a howler monkey that was on the ground in 2012 (C. Meeds, personal communication).

In summary, verified anthropogenic mortality risks include electrocutions, falls from the forest canopy, dog attacks, and AVCs. It is possible that monkeys are hunted, as one resident reported that spider monkeys have been targeted by hunters (J. Diaz Villalobos, personal communication) but no direct evidence of hunting has been found to date. In addition, crop raiding behavior could lead people to regard monkeys as pests and exterminate those that reside near plantations and gardens, but there was no evidence of this problem in REGAMA.

Fig. 3 Inferred electrocution events involving *Alouatta palliata* (*top right*) and *Ateles geoffroyi* (*bottom right*). Subsequently, wildlife barriers (*orange spheres*, *left photo*) were installed at this site. Photos by P. Vangoidsenhoven (*right*) and the author (*left*)

Natural Canopy Bridges and Artificial Crossing Structures

One approach to manage and conserve primates in fragmented, anthropogenic landscapes is to improve habitat connectivity with artificial crossings (Silva and Bicca-Marques 2013). These structures are strategically located between habitat patches to provide a relatively safe passageway amidst the surrounding anthropogenic matrix (Bissonette and Cramer 2008; Donaldson and Cunneyworth 2015; Haddad et al. 2003; Luckett et al. 2004; Teixeira et al. 2013; Valladares-Padua et al. 1995). Two corridor types are the focus of this study: (1) natural canopy bridges, where the tree crowns on each side of a road grow together to create a living corridor (Fig. 4), and (2) artificial crossing structures, such as a rope or ladder bridge (Figs. 5 and 6), that connect forest patches on either side of a road or gap. These corridors tend to be relatively small in length (e.g., 10–30 m) and vary in width from a few centimeters to a few meters.

While artificial crossings appear to be a creative solution to the conservation-development conflict, very little is understood about their effectiveness in promoting primate movement and reducing human-related mortality events. Furthermore, it appears that there is high interspecific variation in crossing structure use that may be related to body size, locomotor behavior, and degree of terrestrial versus arboreal

Fig. 4 Natural canopy bridge in use by a spider monkey (photo courtesy of Kelley Littlefield)

Fig. 5 Ladder bridge (photo by the author)

habit (Donaldson and Cunneyworth 2015). Therefore, this management strategy may be ineffective for some primate species. For instance, the relatively small and arboreal Samango (aka Sykes') monkey (*Cercopithecus albogularis*) frequently used monkey bridges ("Colobridges") at Diani Beach, Kenya, whereas the larger and more terrestrial yellow baboons (*Papio cynocephalus*) did not (Donaldson and Cunneyworth 2015). Similarly, the smaller red-backed squirrel monkey (*Saimiri*

Fig. 6 Rope bridge in use by a three-toed sloth (photo courtesy of Pablo Venegas Vargas)

oerstedii) and white-faced capuchin used monkey bridges in Manuel Antonio National Park, Costa Rica more often than the relatively large, mantled howler monkey (Martín 2012). In light of this interspecific variability and the growing interest in corridors within the wildlife conservation and management communities (Paige 2015), more research is urgently needed to improve our understanding of corridor ecology and behavior for primates.

In an attempt to better understand primate mobility near roads or other gaps, artificial crossings were constructed and natural canopy bridges were monitored at REGAMA. Two types of artificial crossing designs were implemented, a ladder model composed of PVC and rubber tubing threaded on wire cable and chain (see Fig. 4) and a rope model that involved one or two strands of thick rope tautly stretched between two or more anchoring trees (see Fig. 5). The ladder bridge model was developed by Colobus Conservation (www.colobusconservation.org) in Diani Beach, Kenya and is used by Samango monkeys, Angolan black-and-white colobus monkeys (*Colobus angolensis*), and vervets (*Chlorocebus pygerythrus*). Kids Saving the Rainforest (kidssavingtherainforest.org) in Quepos, Costa Rica developed a rope bridge model that is used by squirrel, capuchin, and howler monkeys (Martín 2012). In this study, ladder bridges were tested between 2006 and 2012, followed by rope bridges from 2008 to 2015. There was a shift in design from the ladder to the rope model because the Instituto Costarricense de Electricidad (ICE), a collaborating institution that installed and maintained these crossing structures, preferred the rope model as rope was less expensive, easier to purchase from local vendors, and easier to install. Moreover, this rope was nonconductive, which is a vital characteristic for wildlife bridges installed near electric cables. The shift to rope may also benefit wildlife as there were fewer instances of animals using the ladder bridges, reinforcing the notion that bridge design and bridge materials are important factors to consider (Lindshield 2013).

The location of artificial crossing sites was also important and involved an assessment of habitat structure (e.g., plant species composition, forest canopy height, forest gap width), NHP activity in the immediate vicinity, and the views of property owners towards wildlife. Several hectares of mature secondary or primary forest that included known feeding trees had to occupy both sides of the road. Sites that were located within or near gallery forest were preferred because this vegetation is nationally protected (Article 33 of Forestry Law 7575). In addition, these sites had to have large, hardwood trees (≥ 40 cm diameter at breast height) on each side of the road to anchor the artificial crossings. These anchoring trees had to be positioned no more than 25 m apart from one another or a support post would have been necessary to prevent bridge sagging. Although rare, sites where a landowner or occupant protested an installation were not pursued. Each location was field inspected by ICE for preliminary approval and determination of bridge height. Final approval from ICE required internal reporting and scheduling, as these installations required a work crew, basket crane, and coordinated power outages. Once installed, these bridges ($N=7$; Fig. 7) were monitored using pedestrian surveys, camera traps, and opportunistic sightings from project personnel and local residents. Nine species from six orders were found to use artificial crossings structures (Table 1). Howler monkeys rarely used these structures, while spider and capuchin monkeys were never observed on these bridges during the study period. Camera traps were particularly useful for capturing nocturnal mammal activity on these bridges.

Natural canopy bridges, where trees from opposite sides of the road connected above the road, were also evaluated. There were two natural canopy bridges between Cocles and Manzanillo during the first year of study in 2005, but by 2012, eight more of these bridges had developed within the same area due to natural canopy growth (Lindshield 2013). Altogether, 34 crossings ($n=27$ natural canopy bridges, $n=7$ artificial crossings) now exist around REGAMA. In contrast to the artificial crossings, camera traps were not used regularly at natural canopy bridges because of technical problems (e.g., high rate of device failure, high abundance of vegetation in the motion sensor detection field). Therefore, it is not yet possible to evaluate species' differences in artificial and natural canopy bridge use for nocturnal mammals. There were five independent cases of NHPs using natural canopies ($n=4$ *Alouatta palliata*, $n=1$ *Ateles geoffroyi*), however, suggesting that they are important for NHPs. In two of these cases, a group of howler monkeys used the natural bridges, while the remaining events involved lone individuals.

Preventing Primate Electrocutions

Given that electrocution is a mortality risk for NHPs and other arboreal mammals in REGAMA, several residents and institutions have taken steps to prevent these events from occurring. ICE, a local wildlife sanctuary known as the Centro de

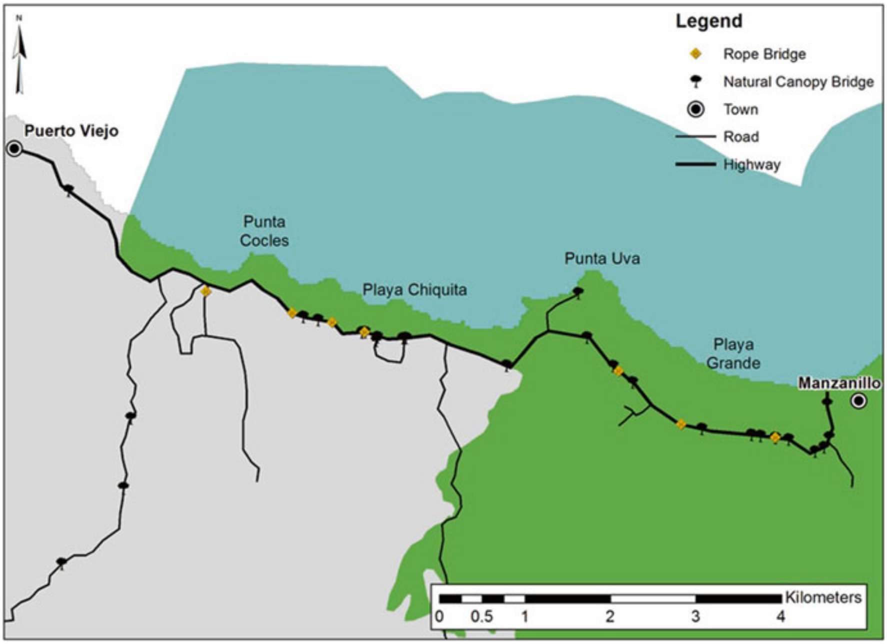

Fig. 7 Locations of the 34 crossing structures ($n = 27$ natural canopy and $n = 7$ rope bridges) in the peri-urban landscape between Puerto Viejo and Manzanillo

Rescate Jaguar, and this project, which is formally known as the nonprofit Monkey Bridge Project Inc., have implemented management techniques to prevent wildlife from contacting electrified cables. These include the trimming of tree branches to create buffer zones between forest canopies and power lines, insulating power lines, and placing physical barriers on cables to prevent animals from contacting power lines (see Fig. 3). Although there have been no studies to date on the impact of these management techniques on wildlife electrocution prevention in REGAMA, they will likely reduce the number of electrocution events.

One alternative management approach is to bury electric cables. Belowground power lines may effectively eliminate wildlife electrocutions in areas, where residents or organizations can afford the installation and management costs. However, buried cable grids must be several meters wider than many existing power line and road grids within the study area (B. Perez Chaves, personal communication), likely resulting in further deforestation in the refuge, wider forest canopy gaps, and fewer natural canopy bridges. For these reasons, it is not known at this time if burying cables will be a net gain for primate conservation at REGAMA.

Table 1 List of species known to use the artificial crossing structures

Class	Order	Species name	Common name	Mode of detection[a]	Relative use[b]
Mammalia	Primates	*Alouatta palliata*	Mantled howler monkey	OS	Rare
	Rodentia	*Sciurus variegotoides*	Variegated squirrel	CT, OS	Common
	Carnivora	*Potos flavus*	Kinkajou	CT, OS	Common
		Bassaricyon gabbii	Bushy-tailed olingo	CT	Common
	Didelphimorphia	*Didelphis marsupialis*	Common opossum	CT, OS	Intermediate
		Caluromys derbianus	Derby's woolly opossum	CT	Common
	Pilosa	*Bradypus variegatus*	Three-toed sloth	OS, PS	Intermediate
		Choloepus hoffmanni	Two-toed sloth	OS	Intermediate
Reptilia	Squamata	*Boa constrictor*	Boa	OS	Rare

[a] *CT* camera trap, *OS* opportunistic sighting, *PS* pedestrian survey

[b] Rare: <1 sighting per month, intermediate: 1–5 sightings per month, common: >5 sightings per month

Management Recommendations and Challenges

Due to significant population declines for all Costa Rican NHP species (Sherwood 2007), the management and preservation of these charismatic animals in unprotected areas is important. Because of the localized social and economic context of REGAMA, which is principally focused on ecotourism and its associated activities, such as wildlife viewing, supporting primate conservation efforts in the Caribe Sur is an important long-term economic investment for this community. Furthermore, REGAMA was designed to facilitate human–wildlife coexistence, rather than displace human communities with the creation of a national park. Such sympatric living ought to be sustainable provided that national law mandates low impact habitat disturbance and that this law is enforced through governmental and nongovernmental organizations as well as members of the local community acting autonomously. Equally important is the need for residents to maintain a pleasant standard of living within this ecotourism context. Upon considering all of these issues, it is apparent that the protection of NHPs in and near REGAMA requires community-based conservation (Horwich and Lyon 2007), protected areas, corridors, sustainable economies, and a deep understanding of the cultural dimensions shaping primate habitat. Notably, some property owners have strictly designated their land for rainforest conservation, thus there are numerous, small-scale (e.g., 4–100 ha) protected areas within REGAMA. However, these areas, if isolated from each other through deforestation, will result in NHP population declines and range retractions. Spider monkeys and capuchin monkeys will be particularly vulnerable under this scenario, as these populations need larger areas of forested habitat to thrive. One NGO working within the region, called the Asociación de Organizaciones del Corredor Biológico Talamanca Caribe (ACBTC), addresses the problem of forest fragmentation through collaborating with property owners to map, manage, and reforest private conservation areas (www.corredortalamanca.org). While continued support for projects like the ACBTC are essential to promoting and preserving biodiversity, this approach alone is insufficient for reducing the types of primate mortality events occurring in the REGAMA area, namely dog attacks, electrocutions, and AVCs.

Reconnecting primate habitat that has been fragmented by the peri-urban, anthropogenic matrix is also important and requires natural canopy bridges, artificial crossing structures, or both. This study found that primates used the natural canopy bridges more often than the rope bridges, but this result may be related to differences in sample size, as natural canopy bridges outnumber the other nearly four to one. For the moment, preserving the existing forest canopy over roads and promoting new natural canopy connections are important components of the conservation and management plan for the monkeys of the Caribe Sur. To do this, informing local residents as well as the institutions responsible for managing roads and power lines (e.g., MOPT, ICE) about the importance of natural canopy bridges must be a central component of any conservation tactic as natural canopy bridges are vulnerable, fragile, and dynamic. By Costa Rican law (Civil Code Article 403), large trees may be rooted no less than 5 m from the right-of-way boundary of the roads and branches must be at least three meters from electric cables. Many potential natural canopy bridges may be cut down due to this law, which was designed to protect people from accidental electrocution while working near the electric grid. Care should be used to limit damage to natural canopy crossings while at the same time removing vegetation near power lines in order to reduce the risk of electrocution for animals and people.

The formation of new natural canopy connections is a multi-year process and may require decades of investment. In some cases, artificial crossing structures may be the only option for the rapid connection of forest canopies. Although this study shows that REGAMA monkeys do not frequently use these structures (but see Donaldson and Cunneyworth 2015; Martín 2012), several other mammal species did travel using artificial crossings. Thus, rope bridges are important for the conservation and management of biodiversity in the area. Furthermore, it may be the case that the primate bridge designs, or the height of these bridges, are not well suited for *Alouatta palliata, Ateles geoffroyi,* and *Cebus imitator*. Perhaps these species would be more likely to use structures designed in a different way. Alternative crossing designs should be investigated.

While improving habitat connectivity for primates is an important step to preventing roadkill and dog attack events, natural canopy bridges, and artificial crossings are unlikely to prevent all AVCs (Paige 2015). Taking measures to reduce the probability of an AVC via driver behavior, rather than rely exclusively on reforest-ing roadside habitat and installing road crossing structures, is another important strategy. In REGAMA, the highway and smaller roads serve as important transportation routes for pedestrians and bicyclists. Furthermore, schools, homes, and businesses are located along these roads. For these reasons, many members of the local community are concerned by speeding motorists and have taken steps to reduce high-speed traffic, such as installing speed bumps and posting signs notifying motorists of the importance of driving slowly. Conservationists should support and promote these community efforts because drivers are more likely to avoid hitting animals while traveling at slower velocities.

Reducing the frequency of dog attacks also requires strong community support. There are no leash laws or animal control agencies in this peri-urban environment. In recent years, a veterinary clinic opened and financial support was provided to encourage owners to spade or neuter their companion animals. These are important steps towards managing the large population of domesticated dogs but, ultimately, strong community support for leash laws and mechanisms to manage stray dogs are needed to reduce the dog-related mortality events.

Preserving the population of NHPs in the Caribe Sur requires a multilayered approach that effectively addresses the problems of deforestation, habitat fragmentation, and mortality events caused by human activity. Central to this strategy is the premise that adequate habitat is preserved for the NHP populations. Moreover, innovative strategies are necessary to protect primates living within the anthropogenic matrix. This chapter has shown how small-scale projects that aim to prevent accidental deaths and encourage migrations via natural and artificial corridors are instrumental for protecting wildlife in a changing landscape. It also shows that a deep understanding of the economics and cultural landscape is equally important, and that an ethnoprimatological approach improves our understanding of the primate conservation challenges that lie ahead in southeastern Costa Rica.

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Primates and People in the Zoo: Implications of Human–Animal Interactions and Relationships

Joshua J. Smith

Why a Chapter on Zoos

At first glance, a chapter on human–primate interactions in zoos may seem out of place in a book with a strong primate conservation focus. Yet conservation is a central component to the mission of responsibly managed, internationally accredited zoos (AZA 2015; BIAZA 2011; EAZA 2012; Patrick et al. 2007). Funding for field conservation and education/awareness campaigns for visitors may be among zoos' most visible efforts to contribute to wildlife conservation, but zoos also contribute to conservation through research. A substantial proportion of zoo-based research is conducted with primates (for a review see Hosey et al. 2013). A survey of research conducted in zoos in the USA and the UK found that more than 70 % of published research with primates had a conservation connection (Melfi 2005). In keeping with this trend, this chapter discusses how research on zoo-housed great apes' interactions and relationships with humans may provide valuable insights for conservation efforts with their wild counterparts.

Human population expansion and destruction of primate habitats increasingly bring humans and other primates into close proximity and contact and result in their vying for the same space and resources, increasing the chances of interaction and the potential for conflict (Fuentes 2012; Fuentes and Hockings 2010; Hockings and Humle 2009). Understanding of how and why humans and other primates interact and influence each other is a key element of effective conservation (Fuentes 2012; Fuentes and Hockings 2010). Ethnoprimatology is the study of the interconnections between humans and other primates, the spaces in which they come together to interact and influence one another have been referred to collectively as the human–primate interface (Fuentes 2012; Fuentes and Hockings 2010). Fuentes and

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colleagues have recently argued that ethnoprimatology, and the human–primate interface, may be among the most important focus areas for primate conservation in the twenty-first century (e.g., Fuentes 2012; Fuentes and Hockings 2010). The fact that a full symposium at the 2014 meeting of the American Society of Primatologists was devoted to explorations of human–primate interfaces, including conservation, supports this assertion (Smith 2014b).

Zoos are one type of human–primate interface. In this chapter, I examine human–animal interactions (HAIs) and human–animal relationships (HARs) in the zoo using findings from recent research. In this chapter, I (1) provide a brief history of HAI studies in zoos (with a focus on primates), (2) present recent findings from my own and other research on zoo-housed great apes' interactions and relationships with humans, (3) examine the implications of these findings within the zoo setting (i.e., for zoo ape welfare and zoo-based research), and finally (4) explore how the findings from zoo-based studies may improve our understanding of HAIs in other contexts (i.e., other human–primate interfaces) that are tied to great ape conservation but share common features with the zoo environment, specifically primate rehabilitation and reintroduction projects (afterward, for convenience, simply rehabilitation) and tourism. I focus on great apes because this is my area of expertise. However, much of what is discussed here is applicable to non-ape primates and non-primate species.

Humans in the Zoo: Chronic Human Presence

Modern zoo environments are partly defined by the chronic presence of humans and their interactions with zoo animals (Hosey 2000, 2005). However, a recent review of the literature reported a dearth of HAI studies in zoos, particularly studies of interactions with humans other than unfamiliar visitors (Hosey and Melfi 2014). This is changing as researchers recognize the importance of understanding zoo animals' interactions with a wider range of humans and the resultant relationships that may develop (Chelluri et al. 2013; Hosey and Melfi 2012, 2014; Smith 2014a). Primates are among the most frequently studied zoo animals (Hosey et al. 2013; Melfi 2005) and account for the majority of HAI studies in zoos in the form of visitor impact studies (Davey 2007; Fernandez et al. 2009; Hosey 2000). This makes studies of HAIs in zoo primates particularly useful for exploring how HAIs impact other aspects of the zoo environment.

The zoo environment and the HAIs that occur in zoos have been claimed to be, to some degree, unique in comparison to other human–primate interfaces (e.g., the wild, primate laboratories), particularly in terms of the number and familiarity of humans encountered, the nature of the interactions that occur, and the relationships that develop (Hosey and Melfi 2015; Smith 2014a). Daily, zoo-housed primates encounter and interact with a range of humans in addition to unfamiliar visitors, including familiar keepers and other zoo personnel, familiar visitors, and occasionally researchers (who themselves span the range of familiarity). However, as I will discuss later, some of these "unique" characteristics may be present to some extent in other contexts such as primate rehabilitation and tourism, which have been connected with primate conservation. This makes studies of HAIs/HARs a valuable point of comparison for understanding similarities and differences in the human–primate interface across contexts. Further, zoo-based studies may provide valuable insights for understanding and managing HAIs/HARs in outside the zoo.

Early Studies of Human Influences on Zoo Animals: Visitor Effect Studies

Early theories of human impacts on zoo animals ranged from humans being inconsequential (i.e., no impact) (Snyder 1975) to targets of social interest (both positive and negative) (Hediger 1970) to novel sources of entertainment (i.e., enriching) (Morris 1964), but prior to the 1980s, human impacts were not systematically investigated and most researchers believed humans had little influence on zoo primates' behavior (for a review, see Hosey 2000). Systematic human impact studies have been more popular since the 1980s, typically as attempts to quantify the welfare impacts, if any, of humans in the zoo (Davey 2007; Hosey 2000, 2005). The majority of human impact studies have examined the impact of visitor's presence and behavior on zoo animals' behavior and welfare and have been labeled visitor effect studies (VES). While physiological measures have become more popular recently (e.g., cortisol levels, Clark et al. 2012; Davis et al. 2005), behavior remains the most common measure of environmental impacts in zoo animal studies, including VES (Hosey et al. 2013; Hosey 2008). Most VES have been undertaken with primates and have consistently reported negative effects on zoo primate welfare (Davey 2007; Fernandez et al. 2009; Hosey 2000, 2008).

VES have provided a number of valuable insights. They showed that humans are not a passive part of the zoo environment and highlighted humans' potential to impact zoo primates' behavior and welfare. They identified a number of important variables associated with visitors and visitor behaviors related to stress and negative welfare in zoo primates (e.g., crowd size, noise and activity level, inappropriate attempts to attract primates' attention or elicit action/interaction). Finally, they presented a clear problem and provided suggestions on how to improve enclosure design and visitor education programs to promote improved primate welfare. However, VES have also been, to a degree, incomplete. In the late 2000s, researchers began to recognize that VES do not capture the full range of primate–human interactions in the zoo (Hosey 2008; Kuhar 2008; Stoinski et al. 2011). VES have typically only assessed interactions with unfamiliar visitors or pooled all humans encountered into a single category without considering whether they were familiar or not. Most VES have only (or primarily) examined behavioral responses to visitors, measured by changes in activity budgets, rather than actual ape–human interactions. When human-directed behaviors have been considered, they have typically been considered a single variable, regardless of their individual nature or meaning.

For example, Hosey and Druck (1987) combined aggressive, submissive, and affiliative behaviors into the variable "audience-directed behaviors." Similar combinations are found in other VES (e.g., "attention to visitors" Chamove et al. 1988, "audience-directed behaviors" Mitchell et al. 1992). Finally, conclusions and welfare recommendations from VES have often been based on data pooled across primate species without consideration for potential species differences (e.g., Chamove et al. 1988; Hosey 2000; Hosey and Druck 1987; Mitchell et al. 1992).

Human–Ape Interactions: Beyond Visitor Effects

The Human–Animal Relationship Model

In 2008, Geoff Hosey proposed a model of HARs that may develop in zoos, and suggestions of how to characterize them behaviorally (Hosey 2008), based on research into conspecific relationships in humans and other primates (Hinde 1976a, b) and human–livestock relationships in farmed animals (Hemsworth 2003; Waiblinger et al. 2006). Hinde (1976a, b) defined relationships as a series of interactions over time, where interactions are behaviors directed by one individual to another, with or without a recipient response. Hinde classified relationships as individualized, based on shared social history between individuals, or generalized, based on and individuals' history of interactions with relevant classes of others. The HAR model further characterizes relationships as positive, neutral, or negative based on whether animals typically exhibit confidence, indifference, or fear and/or aggression in interactions with humans and whether they accept, ignore, or avoid human proximity or contact (Hosey 2008; Waiblinger et al. 2006). Positive relationships are characterized by behaviors that suggest comfort and confidence with humans, including proximity seeking and initiating close affiliative behaviors. Negative relationships are characterized by a lack of affiliation and close proximity, high levels of visual monitoring, aggression, and hiding. Neutral relationships are consistent with habituation and are characterized by a lack of positive and negative behaviors. By systematically comparing great apes' interactions with familiar and unfamiliar humans, we can draw inferences about the nature of the underlying relationships.

Ape–Human Interactions: The Effects of Human Familiarity

Background and Study Goals

In 2014, I conducted the first systematic test of Hosey's (2008) HAR model with nonhuman primates (for full details, see Smith 2014a). Previously, the model had only been tested in non-primate species (Carlstead 2009). I examined whether zoo-housed great apes' used human familiarity to guide their social initiatives to humans and whether their human-directed behaviors (HDBs) were consistent with familiarity-based differences in their relationships with humans. I hypothesized that ape-initiated HDBs would be consistent with positive relationships with familiar zoo personnel and neutral or negative relationships with unfamiliar visitors. I predicted that with familiar humans (zoo staff), apes would initiate more and longer affiliative behaviors and fewer behaviors indicative of fear or aggression, whereas with unfamiliar humans (zoo visitors) they would initiate fewer and shorter affiliative behaviors, more fear and/or aggression related behaviors, and high levels of visual monitoring.

Subjects and Methods

Subjects were seven (four adult, three immature) Sumatran orangutans (*Pongo abelii*) aged 4–43 years and seven (four adult, three immature) western lowland gorillas (*Gorilla gorilla gorilla*) aged 5–39 years housed at the Toronto Zoo in Toronto, Canada. Observations were made from visitor areas in apes' indoor enclosures. All visitors were considered unfamiliar to apes unless identifiable as repeat visitors by the author or zoo personnel. All zoo staff (keepers, maintenance and support staff, volunteer docents) were considered familiar. All occurrence sampling (Altmann 1974; Martin and Bateson 2007) was used to collect data on all observed ape-initiated HDBs, which were classified as visual, aggressive, hiding, or affiliative. Affiliative behaviors were further designated as close (<3 m) or distant (>3 m). Raw data were corrected for the proportion of time that humans of each familiarity class were present and analyzed using repeated measures MANOVAs. Predictors were human familiarity and ape species. Outcomes were hourly rates and average durations (in seconds) for each HDB type. Reliability was established during live observations with a second observer using intraclass correlation coefficients and was high across all variables (ICC 0.855–1.000 for individual behaviors).

Study Findings

I observed 715 HDBs (405 to unfamiliar humans, 310 to familiar humans). Visitors were present at enclosures more frequently than staff (visitors: 92 % of observations, staff: 14 % for orangutans, 25 % for gorillas). Aggression, hiding, and distant affiliative behaviors could not be analyzed statistically because they were too infrequent, directed primarily to one category of humans, or exhibited by only one species, but, in general, patterns were consistent with study predictions. Only close affiliative and visual HDBs could be assessed statistically. In addition to planned analyses (unfamiliar visitors vs. familiar staff), I was also able to explore differences in patterns of close affiliative and visual behaviors directed to unfamiliar versus identifiably familiar visitors.

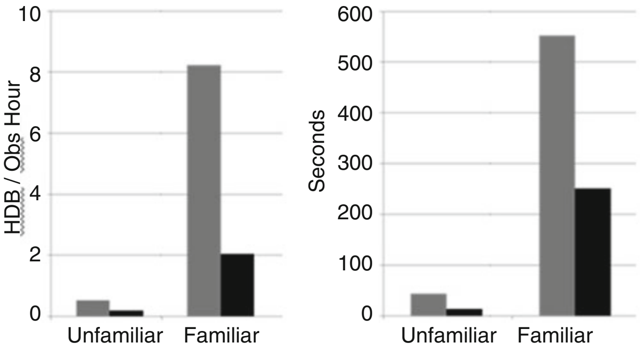

Fig. 1 Rate and average duration of great apes' close affiliative HDBs to unfamiliar and familiar humans. Orangutans are represented by *gray bars* and gorillas by *black bars*

Table 1 Significant MANOVA results for close affiliative HDBs and descriptive statistics

Significant effects					
	Pillai's trace	*F*	df	*p*	*p*η2
Human familiarity	0.72	13.85	2.11	0.001	0.72
Species	0.47	4.79	2.11	0.032	0.47
Familiarity * species	0.45	4.52	2.11	0.037	0.45
Descriptive statistics					
	N	Rate (*X*±SE)	Average duration		
To familiar humans					
Orangutans	7	8.22±4.65	552.14±449.77		
Gorillas	7	2.05±2.09	250.86±209.37		
Across species	14	5.14±0.96	400.50±93.76		
To unfamiliar humans					
Orangutans	7	0.53±0.55	43.57±37.82		
Gorillas	7	0.19±0.21	13.14±13.98		
Across species	14	0.36±0.11	28.36±7.62		

Notes: Rate=HDB/h, Average Duration is reported in seconds/HDB, *p*η2=partial eta squared (a measure of effect size for individual predictors, can sum to more than 1), * Familiarity by species interaction

Close Affiliative Behaviors

I observed 255 close affiliative HDBs, which were, on average, approximately 14 times more frequent and 14 times longer with zoo staff than with unfamiliar visitors. I found significant main effects of human familiarity and ape species and a significant familiarity by species interaction (see Fig. 1, Table 1). Consistent with predictions, all apes initiated more and longer close affiliative behaviors with familiar staff compared to unfamiliar visitors. Regardless of human familiarity, orangutans initiated more and longer close affiliative HDBs than gorillas. The familiarity by species interaction is best explained as a species difference in the strength of the familiarity effect, which was much stronger in orangutans than gorillas.

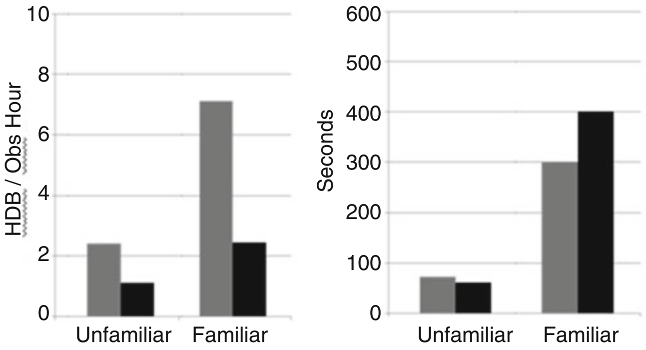

Fig. 2 Rate and average duration of great apes' close affiliative HDBs to unfamiliar and familiar humans. Orangutans are represented by *gray bars* and gorillas by *black bars*

Table 2 Significant MANOVA results for visual HDBs and descriptive statistics

Significant effects					
	Pillai's Trace	*F*	df	*p*	*p*η2
Human familiarity	0.78	20.01	2.11	<0.001	0.78
Species	0.44	4.25	2.11	0.043	0.44
Familiarity * species	0.49	5.35	2.11	0.024	0.49
Descriptive statistics					
	N	Rate (X ± SE)	Average duration		
To familiar humans					
Orangutans	7	7.11 ± 3.56	301.14 ± 420.56		
Gorillas	7	2.45 ± 0.81	401.00 ± 266.84		
Across species	14	4.78 ± 0.69	351 ± 94.13		
To unfamiliar humans					
Orangutans	7	2.42 ± 1.92	72.86 ± 19.43		
Gorillas	7	1.11 ± 0.80	2.45 ± 0.81		
Across species	14	1.77 ± 0.39	66.86 ± 7.22		

Notes: Rate = HDB/h, Average Duration is reported in seconds/HDB, pη2 = partial eta squared (a measure of effect size for individual predictors, can sum to more than 1), * Familiarity by species interaction

Visual Behaviors

Visual behaviors were the most common HDBs (543 observed). I found significant main effects of human familiarity and ape species, as well as a significant familiarity by species interaction (see Fig. 2, Table 2). Visual HDBs were the only behaviors to diverge from predicted patterns. Contrary to the prediction that apes would direct more visual monitoring to unfamiliar than familiar humans, across species, rates, and average durations of visual HDBs were greater for zoo staff versus unfamiliar visitors. Across levels of human familiarity, orangutans initiated visual behaviors at higher rates than gorillas. Orangutans also initiated longer duration visual monitoring of unfamiliar visitors than gorillas did, but gorillas initiated longer duration visual monitoring of staff than orangutans. The familiarity by species interaction is best explained as a result of species difference in this pattern of rates and durations, particularly with zoo staff.

Aggression, Hiding, and Distant Affiliative HDBs

Overall, patterns of aggression, hiding, and distant affiliative behaviors were consistent with predicted directions (i.e., more hiding and aggression with unfamiliar visitors, more affiliative behaviors with familiar staff). Sixty-two behaviors were coded as aggressive (orangutans 7, gorillas 55). Rates of HDBs coded as aggressive were approximately three times greater when directed to unfamiliar visitors versus zoo staff. Adult males initiated 15 clearly aggressive HDBs (orangutan 7, gorilla 8, yawn threats both species, charge glass—gorilla) which were only directed to unfamiliar visitors. Orangutan adult females and immatures never initiated aggressive HDBs, and adult female gorillas did so only rarely (2 instances). Most behaviors coded as aggressive were initiated by immature gorillas (45/62 cases), 30 directed to unfamiliar visitors and 15 to familiar staff. These were the most difficult to identify observationally because aggressive bids for attention or play behaviors were difficult to differentiate from actual aggression (i.e., threat of violence). More than half (24/55) of immature gorillas' behaviors that were coded as aggressive were similar to behaviors used by immature gorillas in play or to gain attention, (e.g., drumming on walls/glass Genty and Byrne 2009).

Hiding (55 instances) was observed only in orangutans and only when unfamiliar humans were present. Orangutans used enclosure features or manipulable objects to fully or partially place themselves out of human sight, consistent with avoiding human interaction. Hiding only when unfamiliar visitors were present and never when familiar staff were present was consistent with more negative relationships with unfamiliar visitors and more positive relationships with familiar staff.

HDBs to Familiar Visitors

Familiar visitors were excluded from planned analyses because they were difficult to identify systematically and from a theoretical perspective their inclusion in visitor versus staff analyses would have confounded analyses of familiarity effects. During this study, a small number of visitors were identifiably familiar (11 visitors: 8 for orangutans, 3 for gorillas) and were present at enclosures only rarely (~7 % of total observation time). Although data for familiar visitors did not support statistical analyses, familiar visitors represent an important extension of VES, particularly for testing visitor effects hypotheses, which are likely biased toward unfamiliar visitors who comprise the majority of zoo visitors. Therefore, I compared patterns of ape-initiated HDBs to familiar visitors with HDBs to both unfamiliar visitors and zoo personnel. Data were pooled across ape species because data for familiar

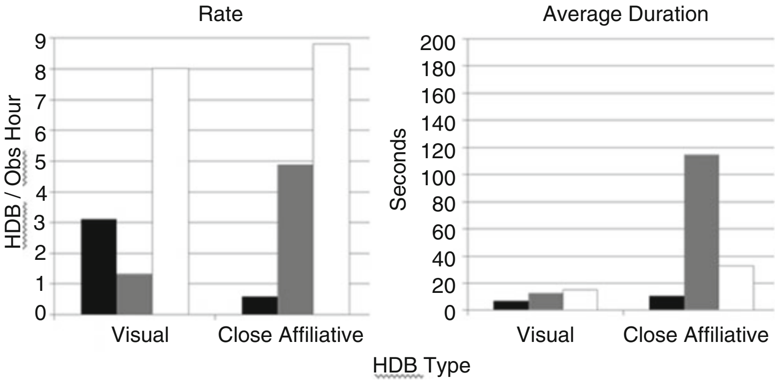

Fig. 3 Great apes' visual and close affiliative HDBs to unfamiliar visitor (*black*), familiar visitors (*gray*), and familiar zoo personnel (*white*), pooled across ape species

visitors was limited and previous analyses of unpooled data indicated that both species showed similar familiarity-based HDB patterns with unfamiliar visitors and zoo staff.

Apes initiated close affiliative behaviors to familiar visitors at rates higher than those to unfamiliar visitors, but lower than those to zoo personnel. The average duration of close affiliative behaviors to familiar visitors was longer than those to either unfamiliar visitors or zoo personnel. The rate of visual behaviors to familiar visitors was lower compared to both unfamiliar visitors and zoo personnel. The average duration of visual behaviors to familiar visitors was higher than to unfamiliar visitors but lower to zoo personnel. Hiding and aggression were never observed with familiar visitors. Overall, patterns of behaviors to familiar visitors suggested positive relationships and were more similar to interactions with zoo staff than with unfamiliar visitors (Fig. 3). This indicates that not all visitors influence zoo apes negatively and that human familiarity is important when assessing visitor effects.

Summary

This study examined previously uninvestigated aspects of zoo-housed great apes' interactions with humans: interactions with humans beyond unfamiliar visitors, ape initiatives to humans rather than responses, and species differences in interactions. Human familiarity successfully predicted differences in ape-initiated interactions humans. Behavior patterns were consistent with model-based predictions of individualized (familiar) and generalized (unfamiliar) relationships with zoo staff and (most) zoo visitors, respectively, and consistent with more positive relationships with zoo personnel and familiar visitors and more negative relationships with unfamiliar visitors. Apes sought proximity to and engaged in affiliative behaviors with familiar humans, whereas they avoided proximity, hid, and were potentially aggressive with unfamiliar humans. Visual behaviors were the only exception to predicted patterns. I suggest that rather than indicating fear or stress-based vigilance (Birke 2002; Carder and Semple 2008; Hosey 2000), visual behaviors may simply indicate attention. Visual attention to unfamiliar humans may be consistent with vigilance. However, visual attention to familiar humans may reflect interest in humans rather than fear or stress (Farrand 2007; Hosey 2000) and may be associated with tracking individuals and relationships of interest (Edwards and Snowdon 1980).

Additionally, this study revealed important methodological issues with a priori data pooling. Differences in behaviors to familiar and unfamiliar visitors strongly suggest that pooling visitors into a single category may bias or obscure research findings, conclusions, and recommendations. Apes initiated quantitatively and qualitatively different interactions with visitors based on their familiarity and interactions with familiar visitors (and their attendant effects/impacts) may be missed if visitor data were pooled without considering familiarity. Pooling human-directed behaviors appears similarly problematic. Pooling behaviors to humans without regard for their individual meanings may hinder our understanding of what they reveal. Additionally, as with visual behaviors in my study, the meaning of specific behaviors may change when directed to different humans or used in different contexts (e.g., visual behaviors). In cases such as these, combining all instances of behavior X to all humans may obscure important contextual differences in their use and meaning. Finally, a priori pooling of species data may obscure important species differences. Important species-based similarities and differences reported here may have been overlooked had species data been pooled from the outset.

Based on these findings, I conclude that the HAR model is useful as both a theoretical and research framework for studying ape–human interactions. Using a relationship-based approach, I was able to explore aspects of ape–human interactions not typically considered in VES, specifically apes' use of relationships to guide their social behavior with humans. I was able to identify quantitative and qualitative differences in ape-initiated interactions with humans as a function of human familiarity that differentiated between visitors and zoo staff as well as between familiar and unfamiliar visitors. Finally, I was able make qualitative inferences about what those differences mean and gain insight, from the ape-perspective, into whether they experience humans and human interactions as positive, neutral, or negative by identifying with humans they choose to interact with or avoid. These findings are based on a small sample, but have implications for extending ape–human interaction studies and for improving zoo ape welfare, designing zoo-based studies, and may offer useful insights into interactions and relationships with humans in other contexts such as primate rehabilitation and tourism.

Additional Considerations

Here, I briefly discuss a few considerations that affect the interpretation of study data: behavioral reinforcement, food, and species differences in social organization (for a fuller discussion, see Smith 2014a). A history of reinforcement very likely influences zoo apes' choice of HDBs as well as their social targets. This cannot be avoided. However, reinforcing interactions are part of forging relationships (Davis and Balfour 1992; Hosey 2008; Waiblinger et al. 2006) and, while arguably more common, reinforcement is not unique to zoo animals' interactions with familiar zoo staff. Although certain behaviors and interactions with humans may be reinforced, they remain part of the interaction history from which relationships are constructed and thus reflect the underlying relationship.

Food is another important consideration. Food may serve as both a driving force for specific interactions and as a reward. For example, zoo keepers may reward apes' begging for food. Visitors also feed zoo apes in attempts to engage their attention or provoke interactions (e.g., Cook and Hosey 1995; Fa 1989; Hosey 2000). Thus, one would expect apes to direct begging to zoo keepers and visitors, yet I noted begging to zoo personnel 27 times, but only once to unfamiliar visitors. In terms of study predictions and outcomes, food-related behaviors made up only a small portion of HDBs (28 of 715) and likely had small, if any, impact on findings related to familiarity. Furthermore HDB patterns to familiar visitors, which never included food as a factor, were very similar to those for zoo personnel. However, differences in food begging between orangutans (28 instances), whose keepers regularly provided food during interpretive talks, and gorillas (1 instance), whose keepers did not, support the argument that some differences in HDBs may reflect knowledge of food availability and thus food as a motivating factor cannot be ignored. This may become particularly important in contexts where great apes can and do regularly obtain food from unfamiliar individuals.

A final factor to consider, particularly in light of the species differences reported here, is species specific social organization. In all conditions, orangutans initiated more HDBs than gorillas did and exhibited a larger familiarity effect, particularly for close affiliative behaviors. In part, this likely reflects differences in the zoo environment. For example, with fewer conspecific social partners, orangutans may have been more prone than gorillas to seek out and interact with humans. Species-specific social structure and behavior are also likely sources of variation. Wild gorillas live in established, cohesive, and relatively stable social groups characterized by close proximity (approx. 5 m) (Harcourt and Stewart 2007; Robbins 2007). Encounters with outsiders often involve agonism (e.g., aggression, avoidance, flight), particularly when encountering unfamiliar groups (e.g., Bermejo 2004; Harcourt and Stewart 2007). Therefore, the majority of gorillas' social interactions may be more likely to be directed within their group than without. On the other hand, orangutans have a more dispersed social system with social "groups" that appear more fluid and are not typically defined by close proximity or even presence (Setia et al. 2009; Singleton et al. 2009). Wild orangutans within 50 m of one another are considered (Setia et al. 2009) and are known to affiliate with orangutans whose home ranges border theirs (Setia et al. 2009; Singleton et al. 2009; Utami Atmoko et al. 1997). Compared to gorillas, wild orangutans may be more to show interest in and interact with individuals at a distance. Additionally, orangutans' may be more likely than gorillas to maintain familiar relationships with conspecifics outside of their immediate proximity and whom they may encounter less frequently. These patterns appear consistent with species differences in apes' interest in and interactions with humans reported here. However, the most likely explanation is that these differences are the result of an interaction between aspects of the zoo environment and species-typical social organization.

Implications for Zoo Ape Welfare

Traditional VES conclusions and recommendations consider only unfamiliar, and thus unpredictable, humans (Hosey 2000, 2008). Welfare recommendations based on VES regularly include limiting the number of visitors at exhibits or regulating crowd noise or behavior (Fernandez et al. 2009; Hosey 2008). While scientifically sound, these recommendations may be practically difficult. Large bodied species, including primates, are popular with zoo visitors (Moss and Esson 2010); great apes are especially popular (Cantin and Prescott 1980; Hosey et al. 2013; Kawata and Hendry 1978). This can result in high visitor densities as well as increased activity and noise; all have been linked with negative visitor effects (Davey 2007; Fernandez et al. 2009; Hosey 2008). Here, I suggest three ways in which knowledge of ape–human interactions and relationships may inform efforts to improve zoo ape welfare. First, if negative human interactions result in negative ape welfare (consistent with most VES findings), positive interactions with humans should be associated with positive welfare outcomes. Second, positive outcomes associated with positive interactions and relationships with familiar visitors and zoo personnel may offset the impacts of negative interactions with unfamiliar visitors. Third, zoos will likely benefit from implementing practices to promote positive ape–visitor interactions.

Positive HAIs/HARs Promote Positive Welfare

Zoos may be able to capitalize on positive interactions and relationships with familiar zoo staff and visitors to promote positive welfare. While systematic exploration of interactions with familiar visitors is still needed, recent studies provide evidence that positive ape–keeper (caretaker) interactions and relationships may improve ape welfare outcomes. A 2012 survey of zoo professionals' perception of human–animal bonds suggested that positive animal–keeper interactions and relationships may result in a number of potential benefits (Hosey and Melfi 2012). In addition to staff benefits (e.g., easier animal handling, improved job satisfaction, enjoyment of being with the animals), the study suggested numerous perceived animal welfare benefits: keepers more familiar with animals are better able to recognize animal needs, identify problems, and respond more quickly, reduced fear and stress related to routine husbandry and veterinary procedures, easier handling/management and reduced potential for problems/injuries, animals appear to enjoy interactions, seek attention and contact, and appear to anticipate interactions.

Recent research with zoo-housed great apes supports many of these perceived benefits and suggests additional benefits. For example, positive interactions with keepers/caretakers is associated with increased affiliation and cooperation with keepers/caretakers, decreased stereotypies and other abnormal behaviors suggesting reduced stress and anxiety, increased social cohesion (increased affiliation and play, decreased agonism), and decreased interest in or aggression toward visitors (Carrasco et al. 2009; Chelluri et al. 2013; Jensvold 2008; Jensvold et al. 2010; Pizzutto et al. 2007). Similar positive findings (e.g., increased conspecific affiliation, reduced agonism, and abnormal behaviors) have been reported for laboratory chimpanzees (e.g., Baker 2004). However, not all studies report unilaterally beneficial outcomes. For example, while Chelluri et al. (2013) reported generally positive outcomes for gorillas and chimpanzees, they reported a low-level increase in conspecific agonism in chimpanzees, but not gorillas, during and following interactions with keepers, possibly associated with competition for keeper attention and/or keeper-provided foods/objects. Similar competition effects have been observed in laboratory chimpanzees (Baker 2004). It should be noted that these competition effects result in *temporary*, low-level increases in agonism that may be preventable and are probably outweighed by larger, long-lasting welfare benefits associated with positive ape-keeper/caretaker relationships such as increased predictability of keepers, reduced stress related to routine husbandry, lower incidence of self-directed and abnormal behaviors, and buffering negative visitor impacts. These findings illustrate the importance of examining HAIs in all forms, even for positively intended interactions. A recent review of zoo-animal attacks makes a similar conclusion, indicating that even in cases of animals with a history of positive interactions, changes in circumstances or routines could elicit unexpected, negative consequences (Hosey and Melfi 2015).

Positive HAIs/HARs May Offset or Ameliorate Negative Ones

This suggestion has been offered previously based on predictions from the HAR model (Claxton 2011; Hosey 2008), more recently based on reconsideration of how zoo animals perceive humans (i.e., as enemies, aspects of the inanimate environment, or as conspecifics) (Hosey 2013), and again based on a review of zoo animals' attacks on humans (Hosey and Melfi 2015). It is supported by empirical evidence in gorillas (Carrasco et al. 2009; Pizzutto et al. 2007) and non-ape primates (Melfi and Thomas 2005). Following positive interactions with keepers, gorillas have been found to direct less aggression toward visitors (Pizzutto et al. 2007) and were less agitated by visitors' presence (Carrasco et al. 2009) than before keeper interactions. In Abyssinian colobus monkeys, primate–keeper interactions have been associated with similar reductions in visitor-directed aggression and generally reduced interest in visitors (Melfi and Thomas 2005). While limited, the available data indicate that positive interactions with keepers may reduce negative visitor impacts. Whether positive interactions with familiar visitors may offset negative interactions with others requires study and testing. However, based on my findings, when familiar visitors are presents (as with zoo staff), apes appear to focus their attention and interactions on these individuals and to ignore unfamiliar individuals and thus may not experience or register concurrent negative behaviors from unfamiliar visitors. More research is needed, but based on the available data, zoos may benefit from initiating practices to capitalize on this possibility, such as having familiar humans stationed at ape exhibits or acting as guides for visitors.

Changing Visitor Behaviors and Promoting Positive Ape–Visitor Interactions

This may be among the most important and difficult challenges faced by zoos. Zoo visitors have their own agendas (e.g., socializing, entertainment), which may align zoo agendas (e.g., education, animal welfare) (e.g., Fernandez et al. 2009; Maple and Perdue 2013). Because the majority of humans in zoos are visitors (primarily unfamiliar), reducing negative visitor impacts remains critically important for promoting positive zoo animal welfare. Zoo apes appear sensitive to crowd size (e.g., large crowds are associated with more negative outcomes than small crowds), large crowds that are simultaneously loud and active are associated with particularly negative visitor effects (e.g., Birke 2002; Wells 2005). Visitor behavior (e.g., noise and activity vs. crowd size) is perhaps the most consistent predictor of negative visitor effects (Davey 2007; Fernandez et al. 2009; Hosey 2000). However, relatively simple changes in visitor presence, such as relative primate-visitor height (Chamove et al. 1988), visibility (Blaney and Wells 2004), and visitor behavior (e.g., noise) (Birke 2002) have been associated with behavior changes indicative of positive welfare in zoo-housed apes. While these do not specifically address ape–visitor interactions, they indicate that visitor impacts can be remediated.

Cook and Hosey (1995) reported that some chimpanzee interactions with visitors appeared positive and potentially enriching. Similarly, in my study, apes initiated some close affiliative interactions even with unfamiliar visitors, indicating the potential for positive ape–visitor interactions. Additionally, apes clearly engaged positively with familiar visitors. Together these indicate that some aspect(s) of visitors' presence or behavior are at times attractive to great apes. Given proper information, visitors may be encouraged to engage in behaviors that promote positive ape–visitor interactions.

As suggested above, stationing zoo personnel at ape enclosures may be one method of changing visitors' behavior. In addition to possibly reducing the impact of unfamiliar visitors, zoo personnel may help moderate visitor behavior. While untested, my personal experience supports this suggestion. During my study, visitors frequently assumed I was a zoo employee and parents repeatedly acted to control their children's behavior. Loud, highly active visitors regularly became quiet and sedate when they noted my presence. I suggest that zoo personnel might influence visitors in three ways. First, they might prevent visitor behaviors that might otherwise occur in unobserved visitors such as pounding on walls and viewing glass or attempts to attract apes' attention. Second, zoo personnel might offer visitors an alternative to engaging apes. Based on my experience, at least some visitors want information about apes' biology, behavior, and conservation status and will ask if there is an available "official" (even a graduate student with no actual zoo affiliation). Importantly, visitors who asked questions during my research were simultaneously quiet, interested in learning about apes, and actively engaged in managing children (preventing them from yelling, climbing, or pounding the viewing glass), often commenting on the importance of not disturbing my research. Third, zoo personnel may demonstrate proper behavior for visitors (i.e., how to or *not* to engage, interact with, or respond to apes). If the presence of familiar zoo staff already improves ape welfare, then any changes in visitor behavior would represent an essentially twofold welfare benefit.

Implications for Research in Zoos

Important as they are for welfare, ape–human interactions and relationships also have potential implications for research, in terms of study design and implementation and for interpreting data. In addition to illustrating the need to expand the scope of HAI studies and revealing problems with a priori data pooling, information presented in the previously discussed studies may be useful for planning and executing future zoo-based studies. The implications of HAIs and HARs, if any, depend on the nature of the research undertaken, whether apes actually encounter humans during that research, and who those humans are. Barring studies where humans are not present (e.g., video studies of animals in holding), humans and the potential to interact with them probably affect all other aspects of zoo apes' environment and behavior (e.g., Claxton 2011; Hosey 2005). Therefore, studies that ignore humans and human impacts may be flawed from the outset.

Beyond human impacts in welfare-related research (e.g., visitor effects, enclosure design studies), I am unaware of any systematic studies of how interactions and relationships with humans impact zoo-based research. As such, what follows here is theoretical and is based on my own experience and inferences drawn from the HAI literature. Given the range of research undertaken with zoo-housed great apes, a full discussion of the research impacts of ape–human interactions and relationships is beyond the scope of this chapter. Here, I discuss a few examples of how humans' presence and ape–human interactions and relationships might influence zoo research, particularly for studies *not* focused on HAIs or human impacts. Although my suggestions are based on behavioral research with great apes, they are relevant to a broader range of zoo-housed species and research areas.

Implications for Research Design and Implementation

Human–animal interactions and relationships in zoos are potentially unrecognized or unacknowledged sources of variation in zoo-based studies and may result in inadvertent and unaddressed influences on study findings. Interactions and relationships with humans influence zoo-housed great apes' behaviors. By extension they influence behavioral research conducted in zoos, including the nature of data collected, its validity and reliability, and its interpretation. In terms of data collection, I will consider, generically, observational studies of behavior and experimental studies. In observational studies, the data available depends primarily on researchers' ability to predict the circumstances under which target behaviors are likely to occur, which probably depend, at a minimum, on the nature of the behavior, its frequency, and how visible or conspicuous it is (Altmann 1974; Martin and Bateson 1986, 2007). While visitor effect studies do not specifically address ape–human relationships, they do provide a basis for making predictions about the impacts of humans on observed ape behaviors. For example, activity budgets for zoo apes are of concern for a variety of reasons: assessments of group formation or composition changes, new enclosures or enclosure design components, enrichment devices, husbandry procedures, and behavioral training to name a few. Reviews of the visitor effect literature routinely associate zoo visitors' presence and behavior with changes in zoo apes' behavior profiles (Davey 2007; Fernandez et al. 2009; Hosey 2000). However, outside of VES, I have rarely seen studies that utilize activity budgets report whether humans were present during observation periods, whether and how humans affected apes' behaviors, or whether or how considerations of humans and/or ape–human interactions might affect data interpretation or study conclusions. Knowing that visitors influence zoo apes' behavior and not addressing those impacts in behavior studies is problematic enough. Yet, as the recent research discussed in this chapter indicates, human impacts in the zoo go beyond visitor effects and visitor effects are probably more complicated than previously believed. It is not merely the presence and behavior of humans in the zoo that affect zoo-ape behavior, but the nature of the ape–human relationships and resultant reactions as well. This makes it all the more important for studies that draw conclusions based on observed ape behavior to consider the impacts humans may have on the apes and/or behaviors of interest.

Experimental studies of laboratory-housed great apes' behavior and cognition have been criticized for not attending to ape–experimenter relationships (e.g., Boesch 2007). Similar studies in zoos may be subject to similar criticisms, particularly when humans are part of the research, for example, as interaction participants or communicative partners. Experimental researchers working with zoo apes should consider whether and how HAIs and HARs might influence the design, implementation, and interpretation of their studies. Researchers may be able to capitalize on familiarity effects and researcher–subject relationships to improve experimental paradigms, for example to improve subjects' participation or experimenters' understanding and interpretation of behavior.

Apes who know researchers with whom they work may be more likely to take and understand task directions, remain on task longer, and engage in unfamiliar (and, to apes, sometimes meaningless or irrelevant) tasks, than apes tested with relative strangers. Zoo apes' interactions with familiar keepers seems to support this suggestion. I found orangutans and gorillas were more likely to approach, seek interaction with, and interact longer with familiar keepers. Jensvold et al. (2008,

2010) reported that chimpanzees were more likely to affiliate and cooperate with (familiar) research staff who engaged them in positive interactions using species-specific social behaviors. Finally, Carrasco et al. (2009) found gorillas appeared more comfortable and were more willing to participate in behavioral training as they became more familiar with researchers during the course of their study.

Familiar researchers who have positive individualized relationships with their subjects, based on shared experience and knowledge, are probably better able to interpret ape behavior (e.g., Matsuzawa 2006; Pedersen and Fields 2009). Three potential benefits suggest themselves here. First, researchers who share a relationship with their subjects may better understand what motivates them, furthering subject participation. Second, they probably recognize smaller changes in subject behavior than unfamiliar researchers do and can then recognize them sooner. This is important for identifying changes in study-related behaviors, but also for changes related to subjects' health and welfare (which can also compromise research progress and outcomes).

Human–Animal Interactions and Relationships as Potential Research Confounds

So far I have suggested potential problems with not considering HAIs and HARs in observational studies and highlighted potential benefits of positive ape–human relationships in experimental studies. However, the types of interactions and relationships considered and promoted/avoided must be considered in terms of study goals. What is important or appropriate in one study may be meaningless or highly problematic in another. Here, I discuss a few (potential) additional confounds that may result from zoo apes' interactions and relationships with humans.

While researchers who interact regularly and develop positive relationships with their subjects may be better able to understand them and interpret their behavior, there is also a risk of biasing data collection or interpretations. Therefore, consideration of potential observer influences or biases on study variables becomes critical during study design, a second observer or coder to assess reliability may be especially important. However, if the subjects' relationships with observers/coders differ, there may be a risk of conflicting interpretations which may require additional consideration prior to analyzing data and drawing conclusions. However, these potential problems can be predicted and addressed if the ape–human interactions and relationships are known and considered.

Finally, I offer one last potential confound, as a series of considerations. First, consider the situation where you are familiar to your subjects and have positive relationships with at least some of them. As a result, certain subjects may seek to establish proximity or initiate interactions. Depending on the nature of your research, the effects of these researcher-induced changes in apes' behavior may range from little/no effect to substantial. In a study of conspecific gestural communication (or other conspecific social behavior), time engaging with researchers implies time spent *not* engaging with conspecifics. Yet, study impacts may be minor beyond more time collecting data. In this case, time-based assessments (e.g., hourly behavior rates) can be adjusted for time engaged with researchers, so long as those data are recorded.

Now consider the possible impacts of a similar set of ape–researcher relationships and interactions on studies assessing enclosure location use (e.g., to assess changes in enclosure design). Here, time spent in specific utilized areas is an important variable. If apes spend time in proximity to and interacting with researchers, important study variables may be compromised. In such cases, familiar observers may be undesirable. However, this is still a manageable case, so long as it is considered during the design of the study.

Ape–human interactions and relationships become especially problematic when they are not recognized and/or predicted during study design or implementation, such as when the potentially influential interactions and relationships are not ape–researcher relationships, but with another human. During my study at the Toronto Zoo, many unfamiliar undergraduate students were collecting data for a project on general behavior (e.g., locomote, socialize, rest) and location (e.g., terrestrial, on climbing structures) simultaneously with my own visits. For my own study, the apes did not treat these students differently than other visitors. However, over time, the apes became more familiar with me. Some came to the viewing glass on my arrival, watched me unpack my supplies, and eventually moved on. Occasionally, certain apes spent as much as 10 min in close proximity to me, thus changing their enclosure use depending on where I was. For my study, this was not problematic. However, data collected on enclosure use during these periods was clearly biased. Fortunately these, now biased, data were for an undergraduate educational project on *how* to observe animals and did not adversely affect any ongoing scientific study. Yet this demonstrates the potential problems that may result when ape–human interactions and relationships are not considered.

As can be seen, the impacts of ape–human interactions and relationships can range from irrelevant to substantial. Therefore, any research conducted in zoos should consider the potential for human–animal interactions or relationships and consider whether and how they might influence the proposed research in the early stages of research design and, if necessary, again during the collection, analysis, and interpretation of study data.

Beyond the Zoo: Implications for Rehabilitation/Reintroduction and Tourism

To this point I have discussed great apes' HAIs and HARs only as they pertain to the zoo environment. Now I shift focus to discuss insights from zoo studies for understanding and managing great apes' HAIs/HARs in other human–primate interfaces.

Detailed discussions of primate tourism (e.g., Macfie and Williamson 2010; Russon and Wallis 2014a and chapters therein) and rehabilitation (e.g., Beck et al. 2007; Humle et al. 2011; IUCN/SSC 2013; Pearson et al. 2007; Russon et al. 2009) are available elsewhere and will not be reviewed here. Both are regularly employed as conservation tools (Beck et al. 2007; IUCN/SSC 2013; Macfie and Williamson 2010; Russon and Wallis 2014a). Because humans are central components of great ape rehabilitation and tourism, managing ape–human interactions and relationships is critical to their success.

Rehabilitation and reintroduction are terms for related and complementary processes, in some cases they are conflated or used interchangeably (Hannah and McGrew 1991; Russon 2009). Rehabilitation entails remediation of physical or medical problems (e.g., from captivity) and the promotion of species-typical social and forest expertise necessary for survival, whereas reintroduction refers to the process of releasing individuals into parts of their species' indigenous range but from which wild populations have disappeared (Beck et al. 2007). For convenience, in this section I use "rehabilitation" to refer to the enterprise as a whole. A primary issue related to HAIs and HARs in rehabilitation is human orientation (i.e., interest in humans, human objects, and human events), which may result from captivity (Rijksen and Meijaard 1999; Russon 1996, 2009) or close human contact during rehabilitation (Farmer and Courage 2007; King and Chamberlan 2007; Smith 2009). Human orientation can delay, disrupt or distort rehabilitants' developmental process, produce counterproductive behavioral changes, and interfere with rehabilitation (Farmer and Courage 2007; King and Chamberlan 2007; Rijksen 1978, 1997, 2001; Rijksen and Meijaard 1999; Russon 2001; Russon and Galdikas 1993) and increases the potential for disastrous future conflicts with humans in rehabilitation and beyond (Beck et al. 2007; Beck 2010; Dellatore 2007; Hockings and Humle 2009; King and Chamberlan 2007; Rijksen and Meijaard 1999; Russon 1996, 2009; Russon et al. this volume).

Great ape tourism refers (primarily) to visits to habitat countries to view apes in their "natural" habitats (Macfie and Williamson 2010; Russon and Wallis 2014b). I use "natural" in quotes because recreational viewing by human groups is not really natural for any ape species. Here, it refers to tourism with apes in the wild (habituated to human viewing or not) or with apes undergoing rehabilitation or living in protected forests following reintroduction. The primary HAI/HAR concern for ape tourism is overhabituation, characterized by a lack of fear, wariness, or avoidance of humans (Russon and Galdikas 1995; Setchell and Curtis 2011; Snaith 1999). This may lead primates' to seek interactions with tourists and other humans (Williamson and Feistner 2011), making them more vulnerable to zoonotic diseases and risks from hunters and poachers and more liable to engage in dangerous contacts with humans such as inappropriate social/sexual interactions, attacks, stealing foods/objects from tourists (Dellatore 2007; Dellatore et al. 2014; Grundmann 2005; Lardeux-Gilloux 1995; Peters 1995; Riedler 2007; Rijksen 1995, 2001; Russon 1996, 2009; Russon and Susilo 2014; Williamson and Feistner 2011; Yeager 1997; Yuwono et al. 2007). Tourism with rehabilitant apes exacerbates these risks because of problems with preexisting human orientation (see above) (Dellatore 2007;

Dellatore et al. 2014; Russon et al. this volume; Russon and Susilo 2014). A final concern related to HAIs/HARs, particularly with unfamiliar humans, in both rehabilitation and tourism is ape welfare, which is probably best assessed in terms of behavioral changes.

Rehabilitation and tourism share a number of features with the zoo environment, including exposure to large numbers of humans who span the range of familiarity, a potential for close ape–human proximity, and a history of ape–human interactions (Beck et al. 2007; Macfie and Williamson 2010; Russon 2009; Russon et al. this volume; Russon and Wallis 2014a). Studies of zoo apes' interactions and relationships with humans may provide valuable insights into similar issues in these other contexts. Because human-directed behaviors can be successfully predicted for specific types of human–animal relationships (Smith 2014a), the HAR model should provide valuable insights for managing potentially problematic ape–human interactions before they occur. Here, I outline the types of relationships likely to occur in great ape rehabilitation and tourism and offer insights from zoo studies for understanding managing them.

Human–Ape Interactions and Relationships in Rehabilitation and Tourism

As in zoos, great ape rehabilitation and tourism expose apes to both familiar and unfamiliar humans. In rehabilitation, familiar humans include caregivers and technicians (i.e., surrogates and others responsible for apes' daily care), some veterinary staff, and regular researchers, unfamiliar humans include other project staff (e.g., office staff, new employees), media, project visitors (e.g., government officials, short-term researchers and volunteers), and in some cases tourists. In ape tourism, familiar humans likely include rangers, tour guides, some veterinary staff, and regular researchers (in some projects), unfamiliar humans are primarily tourists but may also include media and other project visitors (as above). As in zoos, apes in rehabilitation and tourism probably develop individualized relationships with familiar humans and generalized relationships with classes of unfamiliar humans. These relationships may be positive, neutral, or negative depending on individual apes' history of human interactions.

Individualized relationships in rehabilitation, when effectively managed in a manner that mimics apes' species-typical conspecific relationships and is consistent with rehabilitants' developmental needs, should promote project goals, specifically acquisition of necessary social and ecological survival expertise and gradual distancing from and dependence on human support. These types of relationships should provide the necessary social and emotional support that rehabilitants need and guide them toward appropriate social and learning activities (i.e., forest activities, resocialization toward conspecifics).

In tourism, apes do not need the same support and guidance provided by individualized ape–human relationships in rehabilitation. Where tourism projects use food to habituate/attract apes, rangers/guides may serve a role similar to zookeepers in provisioning. Unfortunately, this reinforces the human-food association and may cause more problems. Perhaps the most appropriate relationship is a guard-like relationship, where humans maintain control and adjudicate conflicts (Russon et al. this volume). Where ape-tourism groups are species-typical social groups, human guards may still be necessary to prevent interaction between apes and tourists (although this may be difficult in the case of adult or older adolescent apes). In the case of rehabilitant tourism, human guards may be especially necessary because species-typical social controls may not be present (e.g., no adults to control group members), social groups may be atypical (e.g., orangutans in large groups, groups comprised of immatures only), and because rehabilitants (if not dehumanized) may be predisposed to initiate contact with tourists.

In both rehabilitation and tourism, the most problematic relationships are probably the generalized ones. These typically include humans who are relatively naïve regarding great ape behavior and biology and/or project/conservation goals (vs. key project staff), and whose interests in great apes are typically personal and related to immediate entertainment (at least during visits to rehabilitation/tourism projects). These relationships, and their attendant interactions, promote a generalized orientation to humans (i.e., overhabituation) and promote rather than reduce the potential for negative ape–human contacts and conflicts. Generalized relationships in rehabilitation are best avoided, in most cases they do not promote rehabilitation goals and may actively interfere with them. Generalized relationships with tourists are probably unavoidable, but outcomes of these relationships are predictable based on whether individual apes relationships with tourists are generally negative (may be poor candidates for tourism, avoid tourists, risk for aggressive encounters if avoidance is impossible) or generally positive (risk overhabituation, approach and initiate interactions, seek contact, food stealing). In either case, apes relationships with tourists as a group should be considered when planning and conducting tourism visits.

Managing Ape–Human Interactions in Rehabilitation and Tourism: Insights from Zoo Studies

Zoo studies show that great apes' human-directed behaviors can be predicted for different ape–human relationships. I argue that this is equally possible in ape rehabilitation and tourism. Further, these predictions provide a basis for developing and implementing practices to effectively eliminate, limit, and manage various HAIs and HARs in line with project goals in these contexts. Specifically, knowledge of potential HAIs/HARs should allow projects to capitalize on positive relationship-based outcomes, particularly positive relationships between apes and familiar project staff, and to avoid or reduce problematic outcomes associated with generalized human relationships (i.e., generalized human orientation, overhabituation).

Positive ape–keeper relationships appear to promote ape welfare, may offset negative impacts of unfamiliar visitors, and may serve to direct apes attention away from visitors. In rehabilitation, small, stable, dedicated teams may be able to capitalize on relationships in a manner that mirrors developmentally appropriate conspecific relationships (e.g., infant–mother, peer) (Cox et al. 2000; Russon et al. 2009, this volume). Additionally, positive ape–caretaker relationships may promote positive welfare by providing a sense of safety and security, may help ameliorate the negative effects of previous human interactions and relationships in captivity, and may help to direct apes attention toward rehabilitation-appropriate activities and away from other human-oriented activities. In ape tourism, positive relationships between apes and rangers and/or tour guides (as the primary project staff) may offset potentially negative impacts related to tourist presence and behavior and may serve to divert apes' attention from tourists. Additionally, as in zoos, informed tourism staff should be able to encourage tourist behaviors that simultaneously reduce ape stress and the potential for ape–tourists interactions.

Generalized relationships between zoo apes and unfamiliar visitors appear to compromise ape welfare and may promote negative human-directed behaviors, including hiding but also aggression (Hosey and Melfi 2015; Smith 2014a). Hiding from and avoiding unfamiliar humans in rehabilitation and or tourism do not, in themselves, pose tremendous problems and may in fact be beneficial (at least to the nonhuman primates). However, overhabituation in rehabilitation and tourism may preclude these responses and instead promote interaction which could prove disastrous. For apes with negative generalized relationships with unfamiliar humans this could result in dangerously aggressive and potentially deadly encounters, especially where there are no physical barriers to ape–human contact as in many programs that allow visitors/tourists. However, even if apes intentions are not aggressive, contacts with unfamiliar humans can be dangerous because visitors are probably unaware of how their actions will affect the apes involved and are likely unaware of how to respond to apes' initiatives or how to effectively terminate or de-escalate interactions once they begin. Additionally, because apes are much stronger than humans, even behaviors that are innocuous to apes can be unintentionally dangerous to humans.

Therefore, ape rehabilitation and tourism projects are likely best served by adopting or strengthening practices that prevent overhabituation. Ideally, rehabilitation projects should be off-limits to all but essential personal, thus minimizing the potential for generalized human orientation and reducing the possibility of negative HAIs in rehabilitation and beyond. Because human visitors define ape tourism, encounters with unfamiliar humans cannot be avoided. However, as in zoos, regulations may be implemented or better enforced to reduce the negative consequences of the presence and behavior of tourists. Stricter enforcement of minimum viewing distances and regulations prohibiting the availability of food in the presence of apes are a starting point. Educating tourists about the consequences of HAIs and proper behavior during ape visits may help reduce/prevent problems. Finally, findings from visitor effect studies (e.g., crowd size, noise, and activity, relative visibility of visitors) should be especially beneficial for planning and implementing tourist visits.

Conclusion

Humans are defining components of zoos, but also of other human–primate interfaces such as rehabilitation and tourism. Zoo studies with great apes reveal different relationships with different humans as a function of human familiarity. Importantly, specific behavior patterns, particularly for human-directed behaviors, can be accurately predicted within specific ape–human relationships. These predictions should help zoos to design and implement programs to reduce negative visitor impacts and improve ape welfare. Additionally, considering possible ape–human interactions and relationships should help to improve other studies of zoo-housed apes. Finally, because rehabilitation and tourism share common features with zoos, particularly in terms of exposure to humans, insights from zoo-based studies may be helpful in understanding and managing ape–human relationships and interactions in a manner that promotes project goals and reduces or avoids counterproductive outcomes in these contexts.

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Conservation: New Potential for Stable Isotope Analysis?

James E. Loudon and Matt Sponheimer

Introduction

Humans and nonhuman primates live in complicated networks and characterizing their interactions is, at best, difficult. Nonhuman primates have lived among humans (*Homo sapiens*) for thousands of years, and alongside our ancestors (early *Homo* and *Australopithecus*) for millions of years. It is well known that humans possess an evolutionary continuity with our nonhuman primate kin, and we recognize our shared biology and behavior as “primate-wide trends.” Primatologists also acknowledge that humans play a large ecological role in the lives of nonhuman primates and recognize our direct and indirect impacts on nonhuman primate habitats.

In this chapter, we discuss stable isotope analysis, which within the past two decades has provided significant insights into the behavioral ecology of nonhuman primates (Ambrose and DeNiro 1986; Lee-Thorp et al. 1989; Thackeray et al. 1996; Schoeninger et al. 1997, 1998, 1999; Schoeninger 2010, also see Crowley 2012; Sandberg et al. 2012 for thorough reviews). In particular, we examine the potential of this technique for complementing traditional approaches to primate conservation. To do so, we provide some background on stable isotope ecology and highlight a few applications of stable isotope analysis in primatology and other closely related disciplines.

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Stable Isotope Background

Isotopes of an element differ from one another in the number of neutrons in their atomic nuclei. Isotopes with more neutrons (^{13}C and ^{15}N) are heavier than their lighter counterparts (^{12}C and ^{14}N). As a result of these differences in mass, the heavier isotopes react differently in physical and chemical processes. The differential isotope behavior in these processes results in different amounts of light and heavy isotopes in a material, known as fractionation (Fry 2006). Without fractionation, materials would have uniform distributions of isotopes.

The differences in the ratios of isotopes are incorporated into biogeochemical cycles, and these can be read in the plants that constitute the foundation of terrestrial food webs. The carbon and nitrogen isotope compositions of these plants are reflected in the tissues of the animals that eat them with varying degrees of isotopic fractionation (Ambrose and Norr 1993; Lee-Thorp et al. 1989; Tieszen and Fagre 1993; Tieszen et al. 1983). Thus, it is sometimes avowed, “you are what you eat, plus or minus a few permil” (DeNiro and Epstein 1976).

By convention, stable isotope ratios are expressed as δ values relative to an international standard in parts per thousand (permil), as in the following example for carbon isotopes: $\delta^{13}C\ (‰) = (R_{sample}/R_{standard} - 1) \times 1000$, where $R = {}^{13}C/{}^{12}C$. The carbon isotope standard was the PeeDee Belemnite (PDB), a Cretaceous marine fossil (*Belemnitella americana*). PBD consisted of more ^{13}C than most organisms in the terrestrial biosphere, resulting in plants with negative $\delta^{13}C$ values. Today, the standard is the Vienna-PDB (V-PDB) because the original PBD has been exhausted. For nitrogen ($^{15}N/^{14}N$), the standard is atmospheric nitrogen, which is sometimes referred to as the ambient inhalable reservoir (AIR) (Fry 2006).

Stable Isotopes in Nature

Carbon

The carbon isotope compositions of foods consumed by primates are faithfully incorporated into their tissues and excreta, and since nonhuman primates predominantly consume plants, understanding the isotopic variation in plants is essential. Most plants (dicot trees, shrubs, temperate grasses) follow the C_3 photosynthetic pathway, named for the three-carbon molecule into which CO_2 is initially fixed by the enzyme RuBisCo. CO_2 fixation by RuBisCo discriminates against atmospheric $^{13}CO_2$, producing tissues with $\delta^{13}C$ values averaging about −27 ‰ and ranging between −23 and −31.5 ‰ (O’Leary 1981, 1988; Kohn 2010). Most tropical grasses and some sedges possess a cellular structure that allows them to concentrate CO_2 around RuBisCo to reduce photorespiration and increase photosynthetic efficiency. These plants use the C_4 photosynthetic pathway, referring to the four-carbon molecule into which CO_2 is initially fixed by the enzyme phosphoenolpyruvate carboxylase (PEP carboxylase). CO_2 fixation by PEP carboxylase discriminates less strongly against ^{13}C and the subsequent fixation by RuBisCo does not further discriminate against ^{13}C because all the delivered CO_2 is converted. This results in tissue $\delta^{13}C$ values between −11 and −14‰ (O'Leary 1988). A third photosynthetic pathway, crassulacean acid metabolism (CAM), is utilized by many succulents (Kluge and Ting 1978). The $\delta^{13}C$ values of CAM plants often resemble the values of C_4 plants (O'Leary 1981, 1988; Winter 1979). However, some plants use the CAM pathway facultatively, using C_3 photosynthesis when conditions are favorable and switching to CAM when droughts occur (Marshall et al. 2007). As a result, facultative-CAM plants may have $\delta^{13}C$ values between those of C_3 plants and C_4 plants.

Variation in the Carbon Isotope Compositions of Plants

Among C_3 plants there exists a considerable degree of carbon isotopic variation. Plants growing under dense canopy cover have lower $\delta^{13}C$ values than those growing in more open areas due to the incorporation of ^{13}C-depleted CO_2 produced by decaying leaves (Medina and Minchin 1980) and lower light intensities, which affect the rate of carbon fixation during photosynthesis (Ehleringer et al. 1986). Plant organs also vary in carbon isotope composition with the non-photosynthetic organs (i.e., bark, fruit, seeds, stems) typically exhibiting higher $\delta^{13}C$ values than leaves (Codron et al. 2005). Variation can also exist among leaves of the same plant, with young leaves being ^{13}C-enriched relative to mature leaves (Cernusak et al. 2009).

Humans have cultivated a variety of C_3, C_4, and CAM plants throughout the world and their $\delta^{13}C$ values are often atypical for the regions in which they are grown. This is best illustrated by our widespread cultivation of the C_4 grass, corn or maize, which is sometimes planted in temperate landscapes dominated by naturally occurring C_3 plants. Humans and other animals consuming corn and corn products reflect the high $\delta^{13}C$ values of the C_4 plants they consume, and this may appear as an isotopic mismatch for those populations living in temperate environments.

Nitrogen

Understanding nitrogen isotopic variation is not as straightforward as carbon. Global patterns of $\delta^{15}N$ values in soils, and hence plants, are determined by the nitrogen cycle (rates and types of nitrogen inputs and outputs) and tend to loosely follow precipitation and temperature gradients (Amundson et al. 2003; Craine et al. 2009). The $\delta^{15}N$ values of plants are usually higher than those of atmospheric N_2 (0‰) because ^{14}N is preferentially lost from soil by ammonia volatilization and denitrification (Sandberg et al. 2012). At a global scale, plant $\delta^{15}N$ values generally increase with decreasing precipitation and increasing temperature (Amundson et al.

2003; Handley et al. 1999; Craine et al. 2009). Among plants, legumes tend to have lower $\delta^{15}N$ values than non-legumes because they derive nitrogen from symbiotic bacteria that directly fix atmospheric nitrogen with no modification of the $^{15}N/^{14}N$ ratio in air (0‰) (Virginia and Delwiche 1982; Schmidt and Stewart 2003).

The nitrogen isotope compositions of animals reflect those of their diets, and like plants, there is a tendency for herbivore $\delta^{15}N$ values to correlate negatively with rainfall (Sealy et al. 1987; Cormie and Schwarcz 1996), but this relationship is non-linear and driven largely by animals living in arid climates (Pate and Anson 2008). Animal tissues are ^{15}N-enriched relative to diet, and a stepwise ^{15}N-enrichment of 3–5‰ with trophic level is well documented (DeNiro and Epstein 1981; Schoeninger and DeNiro 1984). There are also differences in the nitrogen isotope compositions of organic and synthetic crop fertilizers used by humans. Organic and synthetic fertilizers often exhibit $\delta^{15}N$ values different from those of the local habitat. In general, synthetic fertilizers have lower $\delta^{15}N$ values, and narrower ranges, than their organic counterparts (Bateman and Kelly 2007). Knowledge of a habitat's $\delta^{15}N$ values can be useful for examining the consumption of human crops and processed foods by populations of wild animals.

Applications of Stable Isotope Analysis

Given that the stable isotope values of a primate are permanently recorded in its tissues (i.e., bone apatite and collagen, hair, dental enamel) and excreta, this technique is particularly useful for understanding the diets and habitats utilized by primates. For some of these tissues, there is a fair bit known regarding their growth patterns and isotopic turnover rates (Bearhop et al. 2004). This allows for serial sampling which can reveal changes in the habitat use patterns of animals as well as their dietary shifts over time (i.e., over the length of a hair strand, whisker, nail, or tooth or across the circumference of a tusk or bone). Samples can also be collected which are linked to seasonal changes including molted feathers or skin, or shed hairs.

Understanding an animal's diet and habitat use is fundamental for developing durable conservation strategies (Cowlishaw and Dunbar 2000), and stable isotope analysis provides insight into the behavior of nonhuman primates that other techniques cannot. For example, stable isotope analysis can detect cryptic or secretive feeding patterns such as crop raiding by nonhuman primates. Stable isotope analysis can also be used to estimate the contributions of particular foods to a population's (or species) diet between field seasons when the study population is not observed. Dietary data can also be gauged for nocturnal nonhuman primates who are difficult or dangerous to observe at night. These dietary and habitat use data can also be compared to historic populations or fossil relatives allowing insights in behavioral ecology over time. Below we discuss some of the uses of stable isotope analysis in more detail with an aim at improving our understanding primate behavioral ecology with respect to conservation.

Diet and Habitat Utilization

Diet is fundamental to an animal's behavior, biology, and persistence. There is a rich history of studies concentrating on the diets of a broad suite of animals, as feeding patterns can reveal the ways in which species are connected to their environments and their distributions on landscapes through time and space. Thus, diet is crucial for understanding niches and ranging patterns and is considered of the utmost importance for developing conservation programs.

At the simplest level, stable isotope analysis can be used to estimate the degree to which grazing ungulates rely on C_4 grass, browsing ungulates rely on C_3 browse, and mixed feeding ungulates rely on both types of vegetation without lengthy field observations (Cerling et al. 2003; Sponheimer et al. 2003; Codron et al. 2006a). For specialist grazers and browsers, this technique provides very clear data regarding their dietary strategies, but some of the most interesting applications have been on animals that use both C_3 and C_4 vegetation. For instance, impala (*Aepyceros melampus*) are well-known mixed feeders and Codron et al. (2006a) were able to show massive swings in their consumption of grass from month to month on the granites of Kruger National Park. These dietary shifts appear to be driven by a preference for grasses of high quality linked to where and when they become available. Similarly, Cerling et al. (2006) sequentially sampled tail hairs of African elephants (*Loxodonta africana*) to examine the degree to which migrants switched from C_3 to C_4 foods, which provided insights into elephant feeding ecology, migratory patterns, and crop raiding behavior, all of which are elements critical for establishing suitable conservation programs.

Among nonhuman primates, the stable carbon and nitrogen isotope compositions of chacma baboons (*Papio ursinus*) have revealed temporal and spatial dietary shifts (Codron et al. 2006b, 2008). These studies showed dietary differences between baboons inhabiting the savanna sites in the Waterberg region and those living in the Kruger National Park in South Africa (Codron et al. 2006b). The Kruger baboon diets consisted of 10–20 % C_4 resources. $\delta^{13}C$ values of the baboons from the Waterberg suggested diets of 30–50 % C_4 grasses. In a similar vein, serial sampling of hair strands and molars from two other South African baboon populations at Blydepoort and Welgevonden, revealed month to month dietary variations (Codron et al. 2008). Dietary shifts of 12–32 % (C_3 vs. C_4) and 10–36 % (C_3 vs. C_4) were observed in hair and teeth, respectively (Codron et al. 2008). These data align reasonably well with observations of chacma baboon feeding patterns which note strong seasonal preferences in the plants that are consumed (Byrne et al. 1993).

Another application of stable isotopes is the investigation of the behavioral patterns of nocturnal primates who are difficult to watch. Variation in the $\delta^{13}C$ values of hair from captured sympatric galagos (*Galago zanzibaricus* and *G. garnettii*) from Kenya suggested the two species were vertically partitioning their habitats, and $\delta^{15}N$ values supported behavioral observations that *G. zanzibaricus* relied more heavily on invertebrates (Schoeninger et al. 1998). The $\delta^{15}N$ values also revealed that both species of galagos consumed more invertebrates than Malagasy lepilemurs (*Lepilemur leucopus*), which are strict folivores and are also active at night (Nash 1998). Intra-population variation in $\delta^{13}C$ values among the lepilemurs demonstrated a greater reliance on CAM plants for those animals inhabiting the driest portions of the reserve, and $\delta^{15}N$ values also elucidated differences in the consumption of leguminous plants (Schoeninger et al. 1998). Stable isotope analysis has also provided substantial gains in our understanding of the behavioral ecology of the smallest and perhaps most elusive primates, the mouse lemurs (*Microcebus* sp.). This work has examined feeding strategies (Dammhahn and Kappeler 2010), seasonal variations in diet (Rakotondranary et al. 2011), trophic positions within a lemur community (Dammhahn and Kappeler 2014), and geographic variation across Madagascar (Crowley et al. 2011). Taken together, these studies highlight the utility of stable isotope analyses to bolster behavioral observations of cryptic primates.

Niche and Community Ecology

Since isotope values represent true dietary signals, stable isotope analysis is a useful tool for testing conventional models of community ecology (Hutchinson 1957, 1978). This technique has proven very helpful for understanding feeding niches and trophic positions of species in aquatic communities, where behavior is often impossible (or extremely burdensome) to observe. Wada et al. (1987) were among the first researchers to use carbon and nitrogen stable isotope analyses to investigate a pelagic food web and situate the trophic position of some of the marine species within in the web. Today, stable isotope analysis is a conventional means for understanding these relationships (Michener and Kaufman 2007). For terrestrial ecosystems, carbon and nitrogen isotopes have also been used to understand trophic niches (Bearhop et al. 2004; Newsome et al. 2007).

While there have been several stable isotope studies that have examined the behavioral ecology of nonhuman primates, only a handful of primatologists have used the technique to address questions regarding community ecology despite the numerous studies that have focused on habitat partitioning (Gautier-Hion et al. 1980; Ganzhorn 1988; Fleagle et al. 1999). At the western Malagasy site of Kirindy, Dammhahn and Kappeler (2014) examined the stable carbon and nitrogen isotope compositions of eight species of lemurs exhibiting a range of sizes, dietary preferences, and substrate use. Placing the eight species on a $\delta^{13}C$ and $\delta^{15}N$ biplot revealed isotopic differences linked to diet, with the smaller and insectivorous dwarf (*Cheirogaleus medius*) and mouse lemurs (*Microcebus murinus* and *M. berthae*) having higher $\delta^{15}N$ values than the larger folivorous lemurs (*Lepilemur ruficaudatus* and *Propithecus verreauxi*) in the community. The feeding niches of Kibale anthropoids and other mammals have been explored using carbon and oxygen isotopes with an eye towards understanding the dietary patterns and habitat use of Miocene and Pliocene hominoids (Nelson 2013). Of the modern Kibale mammalian community, L'Hoest monkeys (*Cercopithecus* *l'hoesti*) and sitatungas (*Tragelaphus spekii*) had low $\delta^{13}C$ values indicating the consumption of foods in a closed canopy, while warthogs (*Phacochoerus aethiopicus*) exhibited the highest $\delta^{13}C$ values indicating the consumption of grasses in more open environments. The $\delta^{18}O$ values of the Kibale mammalian community showed clear differences related to feeding height (arboreal vs. canopy) and the degree to which an anthropoid was folivorous or frugivorous.

Migration and Dispersal

Stable isotope analysis is also useful for tracking animal migrations. Tracking animals over long distances using collars, leg tags, or radio or satellite transmitters is difficult, expensive, and requires capturing (and may require recapturing) (Hobson et al. 2010). As an alternative, stable isotope analysis is a relatively cheap method that can track changes in diet over large geographic regions.

To date, stable isotopes of several elements (carbon, hydrogen, nitrogen, oxygen, strontium, and sulfur) have been used to track the movements of animals including insects, fish, birds, and mammals (Hobson 1999). Some of the first applications of stable isotopes to understand migratory patterns among marine animals included analyzing the $\delta^{13}C$ and $\delta^{18}O$ values of barnacles attached to gray whales (*Eschrichtius robustus*) and loggerhead turtles (*Caretta caretta*) (Killingley 1980; Killingley and Lutcavage 1983). Across the barnacle shells $\delta^{18}O$ values record differences in temperature and salinity and $\delta^{13}C$ values indicate growth in coastal or estuarine waters used by whales, turtles, or other migratory marine species onto which the barnacles are affixed (Hobson 1999). The ratios of carbon and nitrogen isotopes have also been sampled across the baleen of right whales (*Eubalaena australis*) which migrate from the coastal waters of South Africa to the Subtropical Convergence (STC) (Best and Schell 1996). The waters of the STC are more enriched in ^{13}C and ^{15}N compared to the waters of South Africa, and oscillations in the $\delta^{13}C$ and $\delta^{15}N$ values across the baleen reveal differences in feeding and migratory patterns in this whale population.

Isoscapes are also of great interest to track the migratory patterns of birds which may fly thousands of kilometers between wintering sites and breeding sites (Hobson et al. 2010). Hydrogen and oxygen isoscapes can be paired with the $\delta^{13}C$ values of birds feeding from agricultural fields to provide a rich understanding of migratory routes, as well as the mode and tempo of their movements. For example, the migratory routes of snow geese (*Chen caerulescens*) were better understood by examining their reliance on rice (C_3 crop), corn (C_4 crop), and their use of marine and freshwater habitats (Alisauskas and Hobson 1993).

At a much smaller scale, group transfer was detected in two ring-tailed lemurs (*Lemur catta*) inhabiting the Beza Mahafaly Special Reserve (BMSR) in southwest Madagascar (Loudon et al. 2007). The BMSR lemurs have been continuously studied for decades (Sussman et al. 2012), and much is known regarding their diet, health, and life history since most the adults in the study groups are collared with a personal identification tag (Cuozzo and Sauther 2006; Sauther and Cuozzo 2009). Identification of group transfers among the BMSR ring-tailed lemurs was accomplished by using discriminant function analysis (DFA) of the $\delta^{13}C$ and $\delta^{15}N$ values from hair taken from tagged lemurs with known group affiliations. The two transferring lemurs were considered isotopic outliers, and the DFA misclassified each of their group memberships. Since the life histories of the collared lemurs were known, it was possible to determine that both lemurs left the group they were collared in, and subsequently joined another group that ranged to the west (Loudon et al. 2007).

Detecting Environmental Change Though Time

Stable isotopes are especially useful for recovering information about individuals or populations that are no longer living. So long as some tissues are preserved, such as hair or enamel, one can still learn much about their behavior, biology, and ecology. For instance, among the first stable isotope studies of primates focused on early hominins and were able to show that they did not have diets dominated by C_3 plants like chimpanzees (*Pan*), indicating that they were either eating C_4 (or less likely CAM) plants or animals eating those plants (Lee-Thorp et al. 1994; Sponheimer and Lee-Thorp 1999).

Many of our insights into hominin dietary ecology are derived from stable isotope work on chimpanzees. Schoeninger et al.'s (1999) pioneering work on the isotope ecology of two "savanna" chimpanzee communities (Ugalla, Tanzania; Ishasha, Democratic Republic of the Congo) demonstrated clear differences in the dietary patterns between *Pan* and early hominins. This work was followed by an examination of the isotope ecology of a third "savanna" chimpanzee community at Fongoli, Senegal (Sponheimer et al. 2006). Taken together, these studies demonstrated a difference in the dietary patterns of early hominins and savanna-dwelling chimpanzees. These studies also suggested that baboons are perhaps a more suitable ecological analog (Jolly 1970, 2001) for early hominins given their omnivorous diets (often including C_4 plants) and savanna habitat use.

Stable isotope analysis an especially powerful tool for the study of extinct nonhuman primates since we have so few sources of knowledge about their behavioral ecology. However, stable isotope analysis can also provide insights into species for which we know a fair bit about their behavior when we have collections of recent populations on hand at museums. For example, O'Regan et al. (2008) examined the stable carbon and nitrogen isotope compositions of hair and bone taken from museum curated rhesus macaques (*Macaca mulatta*) dating from 1913 to 1927 from six Southeast Asian populations spanning from western India to northern Vietnam. Stable isotope analysis has also been used to examine the dietary patterns of a now extinct population of chimpanzees (*Pan troglodytes*) which inhabited Liberia in the 1940s (Smith et al. 2010). More recently, museum specimens of extirpated gorilla

(*Gorilla gorilla*) and chimpanzee (*P. troglodytes*) populations collected from 1927 to 1935 from central Cameroon have been analyzed to investigate dietary niches and life history traits (Macho and Lee-Thorp 2014).

To date, much of the isotope work examining how nonhuman primates respond to ecological change through time have focused on long time spans (tens to millions of years). In contrast, Loudon et al. (2014a, b) were able to show increased variability in both $\delta^{13}C$ and $\delta^{15}N$ values associated with climatic variables among 11 groups of BMSR ring-tailed lemurs over a short time period (2003–2006). BMSR is situated in a region characterized as “hypervariable” given its unreliable, acute, and dramatic shifts in rainfall and temperature (Dewar and Richard 2007). Based on climate data collected at the site, the researchers were able to compare carbon and nitrogen isotope compositions during a “normal” year of rainfall (2003), two drought years (2004 and 2006), and a cyclone year (2005). In January of 2005, Cyclone Ernest moved across portions of southwest Madagascar, and as a result, BMSR received above average rainfall and high winds (~130 km/h) uprooting many trees and defoliating many others. In the aftermath, the BMSR ring-tailed lemurs consumed alternative food sources including an invasive herb (*Argemone mexicana*) and human crops, particularly sweet potato leaves (*Ipomoea batatas*) planted in open fields located adjacent to the reserve (LaFleur and Gould 2009). These dietary changes manifested themselves in the $\delta^{13}C$ values of the BMSR lemurs, which exhibited the greatest degree of $\delta^{13}C$ variability during the 2005 cyclone year. In contrast, 2004 and 2006 were periods of low rainfall. Extended periods of drought often result in abscission of fruits, flowers, and seeds (Borchert et al. 2002), and observations of the forest in 2006 are consistent with these patterns. In the past, the BMSR lemurs have mitigated food shortages by changing their ranging patterns (Sussman 1992), and it is likely they “fell back” on alternative foods when their preferred resources were hard to come by (Sauther and Cuozzo 2009). The two drought years combined revealed the greatest variability in $\delta^{15}N$ values, which may reflect the consumption of alternative foods (Loudon et al. 2014a, b).

Stable Isotope Analysis and Nonhuman Primate Conservation

We believe that stable isotope analysis holds much promise as a technique to inform conservation pursuits. Because stable isotope ratios reveal feeding data which are permanently recorded in an animal’s tissue, they provide researchers with the opportunity to study a population or species rather seamlessly through time (Koch et al. 2009). Towards this end, stable isotope analysis can be used to estimate the ecological flexibility of a species and assess its ability to respond to human influences (i.e., habitat loss, hunting). Among North American fauna, $\delta^{13}C$ and $\delta^{15}N$ values of California condors (*Gymnogyps californianus*) inhabiting the Pacific Coast demonstrated this population’s dietary flexibility compared to other populations in the USA that were less flexible and, possibly as a result, went extinct (Fox-Dobbs et al. 2006). The stable isotope compositions of these coastal condors indicate the consumption of terrestrial and marine foods. However, during the late Pleistocene, a period marked by terrestrial megafauna extinctions, they began to consume principally marine resources. They subsequently shifted back to terrestrial carrion when humans began harvesting marine mammals commercially and developing cattle ranching, which provided these condors with a new land-based food resource (Chamberlain et al. 2005).

Feeding preferences linked to anthropogenic disturbance have also been detected in urban kit foxes (*Vulpes mutica*) living in Bakersfield, CA. The foxes exhibited $\delta^{13}C$ values that were similar to those of their human counterparts and had $\delta^{15}N$ values that were lower than those of free-ranging foxes (Newsome et al. 2010). These urban foxes relied heavily on anthropogenic foods and probably scavenged commercial meat that typically has higher $\delta^{13}C$ values (due to the consumption of corn products) and lower $\delta^{15}N$ values (Newsome et al. 2010). Human foods are often completely digested and cannot be observed in the feces of free-ranging scavengers, leaving no trace of their consumption. However, human foods frequently have isotopic compositions that are different than those of naturally occurring foods in a specific area; thus, stable isotope analysis can be a useful tool for substantiating the consumption of these foods.

At present, a handful of stable isotopes studies have noted the impact of humans on the diets and habitat use of nonhuman primates. The stable isotope values of three BMSR lemur groups revealed that the group that lived exclusively within a protected parcel of forest exhibited lower $\delta^{13}C$ values due, in part, to a continuous canopy. The same group had low $\delta^{15}N$ values which probably indicated the consumption of kily (*Tamarindus indica*) fruit, a nitrogen-fixing legume (Loudon et al. 2007). The two groups that utilized the anthropogenically disturbed habitats surrounding the parcel had higher $\delta^{13}C$ values indicative of consuming plants from open environments (i.e., deforested regions and fields). Moreover, the group that regularly ate human leftovers (including C_4 and CAM plants) from the BMSR camp had the highest $\delta^{13}C$ values.

Hair $\delta^{13}C$ and $\delta^{15}N$ values were also combined with behavioral observations of eight free-ranging groups of South African vervet monkeys (*Chlorocebus pygerythrus*). This study was among the first to combine stable isotope analyses with ethnoprimatological methods (Loudon et al. 2014a, b). These eight groups were placed into three categories of anthropogenic disturbance (low, mid, high) based on preliminary behavioral observations. Two of the three groups in the high category lived in urban regions and the remaining group in this category lived at a resort. All three groups had more access to human processed foods than the groups in the mid and low category. However, the $\delta^{13}C$ values revealed that two groups with perceived mid levels of interaction with humans were consuming more C_4 foods than those groups with high levels of human contact. Both of these groups inhabited small nature reserves and sporadically interacted with tourists and the reserve employees. However, further observations revealed that these groups were secretly consuming C_4 crops (maize and sugar cane) by swimming across rivers and/or raiding fields without the knowledge of the local people. The $\delta^{15}N$ values were more difficult to interpret; however, one population exhibited extremely high values, which may be linked to the consumption of human foods enriched in ^{15}N. High δ^{15}N values were also found among the ring-tailed lemur group that ate at the BMSR camp and among free-ranging South African chacma baboons that were suspected of consuming human foods from campsites (Codron et al. 2006b). Similarly, Schillaci et al. (2014) compared the hair δ^{15}N values from seven groups of free-ranging long-tailed macaques (*Macaca fascicularis*) from Singapore to previously published values (O'Regan et al. 2008; Schurr et al. 2012) and found that populations with the highest δ^{15}N values had been provisioned.

In the most severe (and saddening) cases, humans are guilty of causing local extinction events. The interplay between human behavior and subfossil lemur extinctions was illuminated by Crowley et al. (2012) using δ^{13}C and δ^{15}N values to measure the dietary breadth of extant species in lemur communities in the Spiny Thicket Ecoregion of southwestern Madagascar. These values were compared to those of seven species of extinct subfossil lemurs. Stable isotope data suggested that humans modified Malagasy habitats shortly after their arrival, and that after the subsequent extinction of the large subfossil lemurs, smaller (and extant) species began using some of the newly unoccupied niches.

Conclusions

In the space above, we have discussed a handful of studies that have used stable isotope analysis to enhance our understanding of nonhuman primate diet and ecology. We have also attempted to highlight the strengths of such applications. It is certainly possible that stable isotope analyses can be used to address a litany of conservation concerns surrounding nonhuman primates. While in the field, primatologists can easily collect feces and plant samples for future stable isotope analyses. Nonhuman primate isotope compositions from present-day populations can be compared to historic collections in museums and provide data to illustrate shifts in feeding behaviors, habitat utilization, and changes in ecosystems due to human disturbance.

Using stable isotope analysis to address questions regarding conservation remains in its infancy. To date, carbon and nitrogen compositions have been used to identify the consumption of human foods or crop raiding (Loudon et al. 2007, 2014a, b; Schurr et al. 2012; Schillaci et al. 2014). Researchers are now looking at isotopes of other elements to provide further clues about the diets and behavior of free-ranging animals. For example, magnesium stable isotopes (δ^{26}Mg) have been used estimate the degree to which species are omnivorous and faunivorous (Martin et al. 2015). One could envision comparing the δ^{26}Mg values of populations of nonhuman primates living with no access to humans to those that live alongside people to examine their consumption of higher trophic level foods (i.e., meats, eggs, cheeses, milk). Strontium isotope analysis (^{87}Sr/^{86}Sr) may also be useful for sourcing nonhuman primate remains from museums and tracing the movement patterns of existing populations (Copeland et al. 2011). This may make it easier to source translocated nonhuman primates for sale in illegal bazaars, or the carcasses of deceased individuals in bushmeat markets. But like all methods, isotopic methods have strengths and weaknesses. It is only by harnessing multiple techniques that we will develop synergistic and durable approaches to conservation by more fully documenting anthropogenic effects on nonhuman primate behavior.

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