Developments in Primatology: Progress and Prospects

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Nanda B. Grow
Sharon Gursky-Doyen
Alicia Krzton *Editors*

High Altitude Primates

Springer

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High Altitude Primates

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Introduction

Primates are remarkably flexible, resilient animals that have gone through multiple radiations during the Cenozoic era (Fleagle 1999). They have successfully colonized a wide range of habitats across four continents, a testament to their adaptable nature. Habitats found at high altitude provide particular challenges for their resident primate populations. As a rule, landscapes at high altitudes tend to be less productive than neighboring areas at lower elevations, exhibit decreased plant and animal density, and experience decreased temperature and atmospheric pressure combined with increased UV radiation (Grubb 1971; Körner 2007; Lomolino 2001; Vuilleumier and Monasterio 1986). Primates living at altitudes have been forced to adjust to these hardships, and the ways in which they have done so are instructive. We cannot fully appreciate the variability demonstrated by the primate order without paying them special attention. From the extreme lichenivory of snub-nosed monkeys to the tiny body size of pygmy tarsiers, some of the most unique and unexpected solutions to problems of survival are found in high-altitude primates.

From a comparative perspective, high-altitude populations of primates often serve as natural experiments, especially when nearby conspecifics or other close phylogenetic relatives persist in lower-lying areas nearby. Many of the trends that have been demonstrated to hold across latitudinal gradients, such as Bergmann's and Allen's rules, apply to altitudinal gradients as well. Despite their importance in ecological and evolutionary studies, primates living at altitudes have not received much attention until recent years. There are several reasons for this oversight. From a purely practical standpoint, high-altitude localities are more often than not inhospitable and difficult to access, making field studies of primates in these areas a difficult undertaking. In areas where the terrain is steep and rugged, a researcher may struggle to keep up with highly mobile subjects. Junichiro Itani remarked thus on his early studies on Japanese macaques: "Free as [the monkeys] were to run and leap wherever they chose on the ground or in the trees, their appearances and disappearances were bewilderingly sudden, as though they were forest sprites. On some days, even, they would outmaneuver us so successfully that we would walk from dawn to dusk without catching so much as a glimpse of them…" (quoted in

Knight 2011: 109). Anyone who has ever attempted to chase after unhabituated monkeys over heavily forested mountains can sympathize with Itani's frustration. When a species's distribution covers a range of altitudes, in particular, populations at lower altitudes are almost certain to be studied first.

This volume compiles the current research on a wide variety of primates that occupy higher altitudes than the majority of extant primates. Defining "high altitude" is complicated when environmental changes may occur at different elevations at different altitudes or regions of the world. Further, any data that take altitude into consideration will include both universal altitudinal phenomena and local ecological conditions (Körner 2002). In this volume, we use the term "high altitude" in the relative sense. All primate populations that live in relatively higher altitudes than their conspecifics or sister taxa are of interest to this volume. We divided this volume into three parts: High-Altitude Lemurs, High-Altitude Monkeys, and High-Altitude Apes.

The lemurs of Madagascar live in a broad range of altitudinal zones, particularly when compared to variation in the vertical range of monkey or ape clades. Lehman examines whether this phenomenon results from specialization on the vertical zone itself or whether it is a by-product of upward displacement from more desirable, low-altitude habitats. Using a nestedness model which can identify the degree of order and predictability of species assemblages at various altitudes, he found that in general, lemurs in Southeastern Madagascar do display nestedness along vertical gradients. A few species do exploit particular resource caches that are more easily monopolized at altitude, but they appear to be the exception. Thus, from the broader perspective of lemur conservation, enough species are susceptible to upward displacement that disturbance at lower altitudes is likely to impact lemur communities negatively.

Blanco and Godfrey propose that obligate hibernation evolved in dwarf lemurs (genus *Cheirogaleus*) as an adaptation to a cold, moist, high-altitude environment. Sibrey's dwarf lemurs (*C. sibreei*) living above 1400 m at Tsinjoarivo provide a paradigm for this lifestyle. Data collected at this site on the sympatric *C. crossleyi* indicate that body size increases with increasing environmental productivity (using rainfall as a proxy measure), but the variation is inconsistent with Bergmann's rule. This is consistent with a greater role for food availability than temperature regulation in determining the body size of hibernating dwarf lemurs. The Authors suggest that obligate hibernation will only evolve in situations where the environment permits energy savings through heterothermy and encourage additional research on the oxygen usage of dwarf lemurs in a variety of environments to more precisely identify the role of altitude.

Grow compares the ranging behavior of the pygmy tarsier (*Tarsius pumilus*), the only tarsier species found at elevations above 1500 m, with that of its congeners on the island of Sulawesi, Indonesia. These parapatric tarsier species provide an opportunity to test competing hypotheses about differences in vertical ranging patterns depending on the altitude at which primates live. Based on surveys conducted at Mt. Rore Katimbu, Grow found no pygmy tarsiers below 2000 m. Thus, this species has no vertical range overlap with any other tarsier species. The narrow range of elevation occupied by pygmy tarsiers, their relatively larger home ranges, and their unique morphology indicate that they are high-altitude specialists.

Shifting focus to the New World monkeys, Shanee et al. review the biogeography of primates inhabiting the Peruvian Andes. Peru is home to over 30 primate species, making it one of the most species-rich countries in the world with respect to the order. They found that many species considered to be ‘lowland’ primates also occur at higher elevations, including the montane cloud forests. High-altitude habitats constitute a marginal environment for these primates with the notable exception of the three endemic Peruvian primates: the yellow-tailed woolly monkey (*Oreonax flavicauda*), the Peruvian night monkey (*Aotus miconax*), and the Andean titi monkey (*Callicebus oenanthe*). These species are the most compromised by increasing levels of human disturbance in their habitats. Increasing fragmentation of the already patchy cloud forest negatively impacts populations by limiting gene flow, increasing parasite load, and reducing the carrying capacity, as well as worsening vulnerability to hunting. Shanee et al. conclude by warning that climate change may result in upslope displacement of species from lower altitudes, leaving these high-altitude endemics with nowhere to go.

Vargas et al. investigate the population density and feeding ecology of critically endangered Colombian woolly monkeys (*Lagothrix lagotricha lugens*) in Cueva de los Guacharos National Park, Colombia. This is the first study of its kind on this population, which ranges above 2000 m up to a maximum of 2400 m in elevation. The Authors sought to understand whether this large-bodied primate copes with the reduced productivity at altitude by broadening its diet. They found that this population lives at relatively high density, although it is never found in certain habitat types, and that only four species make up half of the total productivity within the suitable habitat. Perhaps most surprisingly, these monkeys consume arthropods as frequently as they consume fruit, which increases their reliance on environments that support heavy epiphyte growth. This suggests that conservation plans for this population must take the availability of epiphytes, and the arthropods they harbor, into account as an important resource.

Woolly monkeys also serve an important community function as seed dispersers. Using another dataset from Cueva de los Guacharos, Ramirez et al. compare seed dispersal by *Lagothrix lagotricha lugens* in montane versus lowland populations to determine how altitude may affect this behavior. The highland monkeys were found to disperse large amounts of seeds from a wide variety of plant species. Differences in the maximum size of seeds dispersed by adults versus juveniles suggest that carrier body size plays a role in whether larger seeds will be dispersed, indicating that high-altitude populations may be able to disperse more massive seeds if Bergmann’s rule holds for woolly monkeys.

Among the Old World monkeys, many of the species which occupy high altitudes are Asian colobines. Nijman reviews the ecology of ebony langurs (*Trachypithecus auratus*) living on the island of Java, which experience conditions different from other Asian colobines living at altitude owing to their proximity to the equator. Nijman found that high-altitude populations of ebony langurs are permanent residents, not vertical migrants, and that these monkeys can live at any altitude provided there is sufficient forest habitat (i.e., not above the treeline). Group size and population density tend to increase with the seasonality and decrease with the altitude of the habitat. Ebony langurs living at high altitude tend to be more folivorous and form one-male family units only, in contrast to the occasional formation of two-male units in lowland groups. Paradoxically, increases in altitude tend to reduce the level of seasonal variability to which these primates are exposed.

The invasion of novel, marginal habitats by generalist species serves as one model for how primates can colonize high-altitude areas. Enari summarizes the ways in which Japanese macaques (*Macaca fuscata*) cope with the unique challenges of environments that receive heavy snowfall. Macaques in snowy localities are constrained by cold conditions, the difficulty of moving in the snow, and a scarcity of food during winter. They respond by consuming more fallback foods, such as bark and buds, but also by adopting risky foraging strategies such as exploring steep slopes for high-value items. They have also been found to use conifer plantations, normally considered to be an undesirable habitat, as refugia. These macaque populations, having been decimated in the past by hunting, are now poised to grow and may serve as sources for the recolonization of suitable habitats which macaques occupied historically.

An alternative strategy is to use high-altitude habitats only when there is no snow on the ground. Izumiyama examines seasonal migration patterns of Japanese macaques in the Northern Japan Alps, with an emphasis on vertical range use. When multiple local populations are compared, only macaques that do not forage in cultivated areas ascend to higher altitudes. This occurs primarily in June and July, which corresponds with the availability of seasonal resource patches in the alpine areas. Local population densities observed in this species are strongly dependent upon habitat quality (specifically food availability); thus, troops living at higher altitudes on average also have larger home ranges and display more pronounced seasonal migration. Despite their ability to exploit high-altitude resources during the summer, these troops are highly dependent on the availability of suitable habitat at lower altitudes during the winter, which may be more vulnerable to anthropogenic disturbance.

Xiang reflects on adaptive responses to high-altitude habitats in light of the ecology of the black and white snub-nosed monkey (*Rhinopithecus bieti*), one of the few primates to habitually range above 4000 m. He reviews data he has collected continuously since 2003 from groups residing at Xiaochangdu, the northernmost locality in which this species can be found. When compared with other populations residing in less marginal habitats South of this site, the monkeys of Xiaochangdu display a greater reliance on lichen, a fallback food, as a staple. They also exhibit seasonal trends in daily travel, range use, and reproduction, notably a birth peak that occurs earlier than the one described in more southerly populations. With regard to conservation, Xiaochangdu is an example of how high-altitude sites can become refugia for species under pressure from habitat loss at lower elevations.

Adaptations that allow primates to subsist in high-altitude environments may also be costly. Bissell outlines the physiological processes that permit *Rhinopithecus bieti* to rely so heavily on lichen in their diets. Due to this species' identity as a colobine with foregut fermentation, comparative data from ruminant animals such as reindeer become relevant. These monkeys display a remarkable ability to survive utilizing a staple food that is both toxic and contains insufficient protein to meet bodily requirements. However, lichen is in many respects a fragile resource, a fact which puts the most lichen-dependent populations of this species in jeopardy. Future research concerning the effects of climate change, pollution, and local depletion on lichen availability is necessary for a thorough understanding of the vulnerability of black and white snub-nosed monkeys.

Shifting to a multi-species focus, Barelli et al. examine the effect of an altitudinal gradient on the relative abundance of four diurnal monkeys living in the Mwanihana forest of the Udzungwa Mountains in Southern Tanzania. Mwanihana is an ideal natural laboratory because its large, intact forest covers elevations ranging from 300 to 2300 m.a.s.l and is known as a biodiversity hotspot. Barelli et al. found a significant negative relationship between elevation and relative abundance for Sykes's monkey, Udzungwa red colobus, and Angolan colobus, although patterns of correlation varied between species. This results from the monkeys' preference for forest with a greater mean basal area (MBA) per tree, especially marked in the two colobine species. They also found that their fourth study species, the Sanje mangabey, appears to have been extirpated from the lowland forests, most likely as a result of human disturbance. The Authors emphasize the need to prevent loss of preferred low-altitude habitats in order to conserve these species.

The protection of rare primate species living at high altitudes is of high priority, but conservation plans to accomplish this must be biologically feasible. Twinomugisha et al. argue that long-term monitoring of populations is critical to effective conservation. They present their survey of the endangered golden monkey (*Cercopithecus kandti*) in Mgahinga Gorilla National Park, Uganda, and compare it to prior survey data to determine the population trends. They found that the number of infants per female is lower than comparable populations of *Cercopithecus mitis* spp., indicating a decline in numbers, although density figures were not substantially lower than previous surveys. The Authors interpret this as evidence of a general contraction of the monkeys' home range as they cease the use of marginal habitats. They also suggest that protection of rare fruiting trees within the habitat is critical, as the loss of these trees may have a greater negative impact on resident monkeys than bamboo harvesting.

Two species of great apes are known to have occupied higher elevations. Rothman et al. examine the effects of high-altitude habitat on the feeding ecology of mountain gorillas (*Gorilla beringei beringei*) at Bwindi Impenetrable National Park, Uganda. As with other primates that colonize higher altitudes, gorillas show dietary flexibility. The Authors found that this population had a more diverse diet than mountain gorillas at Virunga, but less so than that of lowland gorillas. The bulk of their macronutrient intake comes from just a few species of herbaceous leaves, whereas other commonly eaten foods may provide important micronutrients. Rothman et al. conclude that primates may alter the composition of their diet considerably without much variation in its nutritional profile.

Wich et al. explore the characteristics of Sumatran orangutans (*Pongo abelii*) at the only currently known high-altitude site for this species, Batang Toru. This population is relatively isolated from other Sumatran orangutans, a fact which is reflected in its distinct genetic profile. Orangutans at Batang Toru occur at low density and must cope with reduced availability of fruit. In spite of this, the Authors found that fruit comprised the highest proportion of the diet by far. They also observed the consumption of species of fruit that are not known to be eaten at any other site. The population at Batang Toru, while not immediately threatened by habitat loss, is vulnerable to hunting and should be considered a conservation priority.

Weinstein considers the biological adaptations humans have acquired as a consequence of invading high-altitude habitats thousands of years ago. In order to examine the development of these traits in an Andean population over time, she has collected data on skeletal characters that have been preserved in the archaeological record. Three aspects of high-altitude lifestyle which can affect skeletal morphology are colder temperatures, poor nutrition, and hypoxia. She finds a complex pattern of variation between ancient coastal and montane samples, suggesting that populations adapt differently in response to different selection pressures, and that gene flow plays a critical role in this process. This result is concordant with trends observed in high-altitude humans from all over the world showing that these populations respond independently to their marginal environments and converge in only some respects.

Finally, Sayers places the study of primates inhabiting high-altitude and other marginal environments in the context of general concepts in ecology. He argues that our understanding of human evolution and the lifestyles of our hominid ancestors is limited by a narrow, and historically recent, focus on a few living species, namely African apes. However, no primate serves as an adequate referential model for putative hominid behavior. A superior approach is to study all the primates (as well as relevant non-primates) to identify the ecological "rules," the common strategies animals use to cope with similar selection pressures, that would have influenced hominid evolution. The intraspecific variation within primates that have large geographic ranges which encompass marginal (including high-altitude) habitats, such as Rhesus macaques (*Macaca mulatta*) and gray langurs (*Semnopithecus entullus*), is particularly salient. Observations from all corners of the order Primates are necessary if we are to make sense of our shared past.

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Part I
High Altitude Prosimian Primates

Effects of Altitude on the Conservation Biogeography of Lemurs in SouthEast Madagascar

Shawn M. Lehman

Introduction

A fundamental issue in biogeography is determining how plants and animals respond to altitudinal gradients (Darlington 1957). This issue is of considerable scientific interest because animal diversity tends to be inversely related to elevation, but many of the world's biodiversity hotspots—those containing at least 1,500 endemic plant species and retaining at least 70 % of their original habitat—are found in mountainous regions, such as the tropical Andes, Afromontane region of eastern Africa, and western Ghats in India (Myers et al. 2000). For example, the tropical Andes comprises 385,661 km^2 of vegetation (equal in area to modern Egypt), yet contains at least 15,000 species of plants, which represents approximately 5 % of all vascular plants on Earth (Kessler 2001). Concomitantly, biogeographers are also interested in understanding ecological correlates to species diversity and endemicity along altitudinal gradients because of reduced habitable area as elevation increases, which is contrary to the general pattern of a positive relationship between species diversity and area (Rosenzweig 1995). Körner (2007) estimated that only 8.2 % of the global land area is above 1,500 m.a.s.l (meters above sea level). Although much is known about macroecological patterns of species endemicity and diversity along altitudinal gradients in temperate regions, there are relatively fewer biogeographic data on the effects of altitude on plant and animal distributions in the tropics (Colwell et al. 2008).

There are two differing biogeographic patterns of plant and animal diversity and distribution along altitudinal gradients in the tropics (Grytnes and Vetaas 2002).

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The more common pattern is a clinal distribution of taxa that is typically expressed statistically as a correlation between altitude and some biotic characteristic of the organisms (e.g., species diversity, abundance, dendrometrics). For example, increasing altitude results in a greater aboveground biomass of trees species in the plant family Fagaceae in tropical montane rain forests in Sulawesi (Culmsee et al. 2010). Many animal species exhibit a reverse pattern of reduced abundance and species diversity with increasing altitude (Shmida and Wilson 1985). Thus, plant diversity tends to increase, whereas animal diversity tends to decrease with increasing altitude. A less common specialization pattern occurs when taxa are adapted to the low air pressure and variable climate of high-altitude habitats. Altitudinal specialization is most common in plants, with fewer animals adapted for life at high altitudes. The wild yak (*Bos mutus*) is one of the few mammals specialized for high-altitude sites, existing only at elevations of 3,000–5,000 m.a.s.l in the Himalayan mountains (Leslie and Schaller 2009). Determining which of these two biogeographic patterns (clinal distribution or specialization) pertain to plants and animals is critical for conservation assessments and planning because taxa that are restricted to high altitudes may be at an increased risk for extirpation or extinction (Doumenge et al. 1995). It is important to note that clinal distribution and altitudinal specialization tend to be mutually exclusive biogeographic patterns for animal species, which means that high-altitude specialists are essentially living on ‘island habitats’ with little recourse to alter their distribution patterns to exploit habitats at lower elevations (Early and Sax 2011). Conversely, researchers have documented that animals exhibiting clinal distribution patterns can extend their altitudinal ranges into higher elevations (Pounds et al. 1999; Raxworthy et al. 2008).

The conservation biogeography of rare taxa that exploit high-altitude habitats has become particularly important given strong evidence for the deleterious effects of global warming on extinction vulnerability for plants and animals (Thomas et al. 2004). Although predictive models of future temperature patterns are necessarily complicated and thus contentious, surface temperatures have been increasing over the last 200 years, with the highest rate of increase being in the northern hemisphere (Smith et al. 2007). Tropical regions are also experiencing increased ambient temperatures with resulting changes in other abiotic and biotic parameters (Hughes 2000). These stochastic abiotic and biotic changes can then cause a cascading effect on resident mammals in high-altitude sites (Williams et al. 2003). For example, global warming has caused increasingly stochastic rainfall patterns, which are correlated with temporal patterns of reduced reproductive success in some primate species (Dunham et al. 2011). Moreover, mammals living at high altitudes lack access to riparian forests found at lower altitudes, which can serve as a critical source of keystone resources during droughts (Tews et al. 2004).

Another biogeographic effect of global warming is the increased potential for upslope distribution displacement (UDD). UDD occurs when abiotic and biotic changes, such as increasing ambient air temperatures and alterations in forest habitats, results in an upward movement in the distribution of plants and animals from lower elevations to higher elevations (Chen et al. 2011). In extreme cases, UDD can result in the extirpation of high-altitude specialists, who are out-competed and then displaced by other taxa moving upslope. Although initially documented in some temperate zones, recent studies indicate UDD patterns in tropical forests (Pounds et al. 1999; Raxworthy et al. 2008). For example, Pounds et al. (1999) documented the disappearance of 40 % ($N = 20$) of frog and toad species in highland forests at Monteverde, Costa Rica. These extirpations were linked to a complex, cascading pattern of atmospheric warming (loss of the cloud bank), which resulted in changes in plant and animal communities, and the eventual displacement of taxa from the highlands forests

Of the 420 extant primates species listed in the IUCN Red List, 42.3 % ($N = 178$) range into high-altitude or montane habitats, which can be generally described as forests growing at elevations of greater than 1,000 m.a.s.l (Lomolino et al. 1989). Most of the 178 primate species that range into high-altitude or montane forests do so in only parts of their geographic range (Lehman and Fleagle 2006), indicating a clinal distribution pattern in response to altitudinal gradients. For example, white-fronted capuchins (*Cebus capucinus*) range from lowland forests at 350 m.a.s.l up to montane cloud forests (2,000 m.a.s.l) in Central and South America (Fragaszy et al. 2004), with lower densities in high-altitude sites. Conversely, few primates are endemic to high-altitude forests (Table 1), and those that do so are rarely subjects of longitudinal studies. Only two primate species, namely gelada baboons (*Theropithecus gelada*) and mountain gorillas (*Gorilla beringei beringei*), have been the focus of studies lasting more than 5 years in high-altitude habitats (Dunbar 2002; Eckhart and Lanjouw 2008). Moreover, *T. gelada* was the subject of the first study investigating primate responses to global

Table 1 List of extant primate taxa found in high-altitude habitats and their conservation status

Taxa	Region	Elevation range (m)[a]	Habitat(s)[b]	Conservation status[c]
Gorilla beringei beringei	Africa	1,500–3,400	TMF	CR
Macaca sylvanus	North Africa	Sea level-3500	MDF, MS	EN
Macaca thibetana	Asia	1,000–1,250	TMF	NT
Oreonax flavicauda	South America	1,400–2,700	TMF, CF	CR
Rhinopithecus bieti	Asia	3,000–4,700	MEF	EN
Rhinopithecus brelichi	Asia	570–2,300	MEF	EN
Rhinopithecus roxellana	Asia	1,400–2,800	MEF, MDF	EN
Rhinopithecus strykeri	Asia	2,745+	MEF	CR
Tarsius pumilus	SE Asia	1,800+	CF	DD
Theropithecus gelada	Africa	1,800–4,400	MG	LC
Trachypithecus hatinhensis	SE Asia	500–1,080	KF	EN
Trachypithecus laotum	SE Asia	500–1,080	TMF, KF	VU

[a] Elevation range data from IUCN Red List (http://www.iucnredlist.org/)

[b] *TMF* tropical montane forest; *MDF* mixed deciduous forest; *MS* scrub; *CF* cloud forest; *MG* montane grassland; *MEF* montane evergreen forest; *KF* karst forest

[c] *DD* data deficient; *LC* least concern; *NT* near threatened; *VU* vulnerable; *EN* endangered; *CR* critically endangered from IUCN Red List (http://www.iucnredlist.org/)

warming (Dunbar 1998). Dunbar (1998) employed a systems model to predict that the lower elevation limit of *T. gelada* would rise by approximately 500 m for every +2 °C increase in world mean temperature. Concomitantly, only a +7 °C rise in global temperature is predicted to result in a population crash from 250,000 to about 5,000 individuals as animals are pushed upward into smaller areas.

Conservation assessments indicate that two-thirds of primates that are high-altitude specialists are either endangered or critically endangered (Table 1). However, from a conservation biogeography perspective, it is difficult to determine whether primates endemic to high altitudes prefer these habitats or are relegated to high-altitude habitats by anthropogenic disturbance in lower altitude sites. For example, Barbary macaques (*Macaca sylvanus*) used to range from lowland to highland forests in parts of western Europe and north Africa, but are now found predominantly in fragments of forest and scrub at or above 1,000 m.a.s.l in Algeria and Morocco (van Lavieren and Wich 2010).

Although the lemurs of Madagascar are recognized as a global conservation priority (Kremen et al. 2008), there have been few assessments of their conservation biogeography as it pertains to species assemblage patterns across altitudinal gradients. The island of Madagascar is characterized by high levels of biodiversity and endemism (Vieites et al. 2009), with at least 70 % of the 12,000 plant species and all of the primate species being endemic to the island (Goodman and Benstead 2005). These biogeographic patterns are remarkable given that on-going climate change and anthropogenic disturbances, such as agriculture and fires, have resulted in the conversion of 40 % of the original forest cover into grasslands and agricultural fields (Bloesch 1999; Gade 1996; Harper et al. 2007). The remaining forest is highly fragmented and prone to extreme edge effects, and the lemurs to varying but largely unexplored intensities of hunting (Golden 2009; Irwin 2008; Lehman et al. 2006a). This ecological incongruence between high lemur diversity, on one hand, and massive forest conversion, on the other, provides for an ideal natural laboratory for research on lemur biogeography (Ganzhorn et al. 2006).

Biogeographic changes in species assemblages along altitudinal gradients can indicate nested distribution patterns. These patterns occur when a species is present in all sites of equal or greater size than the smallest one in which it occurs (Atmar and Patterson 1993). Nested models hold that site-specific extirpations operate in an ordered pattern, such that the absence of species should not occur randomly (Patterson 1991). Nested patterns can also represent interspecific variations in colonization abilities (Cook and Quin 1995; Lehman 2006). For example, Ganzhorn (1998) documented that species-poor lemur communities represent nested subsets of species-rich communities in both eastern humid and western dry forests in Madagascar. However, there was a distance effect on species only for lemur communities in western Madagascar. Ganzhorn (1998) suggested that this pattern of differential colonization reflects selective species extinctions from a common species pool in eastern Madagascar. In western dry forests, lemurs dispersed north and south from the SW part of the island. Subsequent genetic and biogeographic analyses of mouse lemurs support a north–south pattern of speciation and dispersal in western dry forests (Yoder et al. 2000). Although some researchers have successfully used nestedness to investigate how elevation influences plant biogeography (Alexander et al. 2011; Presley et al. 2012), no studies have investigated nestedness as a model for lemur assemblages along altitudinal gradients.

There tend to be some species that are either present at sites not predicted by nestedness models or absent at sites where they are predicted to exist (Cook and Quin 1998; Puyravaud et al. 2003; Wright et al. 1998). Four ecological mechanisms are responsible for these species-specific departures from the model predictions (Atmar and Patterson 1993). First, post-isolation immigration of new species into the site may generate idiosyncratic distributions. Second, these distributions may also be the result of competitive exclusion. For example, generalist primates may be excluded from larger sites dominated by competitively superior specialists (Ganzhorn 1997; Thiollay 1994). These generalist species may then be relegated to small peripheral sites. Third, the distributions may result from the presence of a fundamental disjunction in the historical evolution of community structure. Last, the presence of unique ecogeographic features, such as mountains and rivers, in the region of some sites may influence species closely associated with such features.

In this chapter, I review and analyze the biogeography of extant lemurs that range into montane and cloud forests in Madagascar. Specifically, I address the following two questions: (1) how do species assemblage patterns vary along altitudinal gradients and (2) do lemurs exhibit nestedness patterns in high-altitude sites in southeast Madagascar?

Lemur Biogeography and Altitudinal Variations

Madagascar is approximately 592,800 km^2 in area, and it is located in the Indian Ocean separated by the Mozambique Channel from the southeast coast of Africa (Fig. 1). The island is bisected by a central plateau, where altitude varies from 750 to 1,500 m.a.s.l, however, there are few forests or mammals remaining in these areas (Goodman and Rakotondravony 2006). The western half of the island is composed primarily of dry grasslands and remnant forests that slope down from the central plateau to the western shore (Ganzhorn et al. 1999), where there are highly fragmented dry forest landscapes. The eastern half of the island is dominated by a steep escarpment which maintains most of the remaining tropical forest (Du Puy and Moat 1996), although there are unique tropical forests at Montagne d’Ambre in the north and in the Sambirano region in the northwest part of the island (Mittermeier et al. 2006). Furthermore, the three highest mountain peaks all arise in the eastern escarpment: Maromokotro at 2,876 m.a.s.l in northern Madagascar, Boby Peak at 2,658 m.a.s.l, and Tsiafajavona at 2,643 m.a.s.l in central Madagascar (Goodman and Ganzhorn 2003). It is these relatively high altitude eastern forests that will be the focus of the remainder of this chapter.

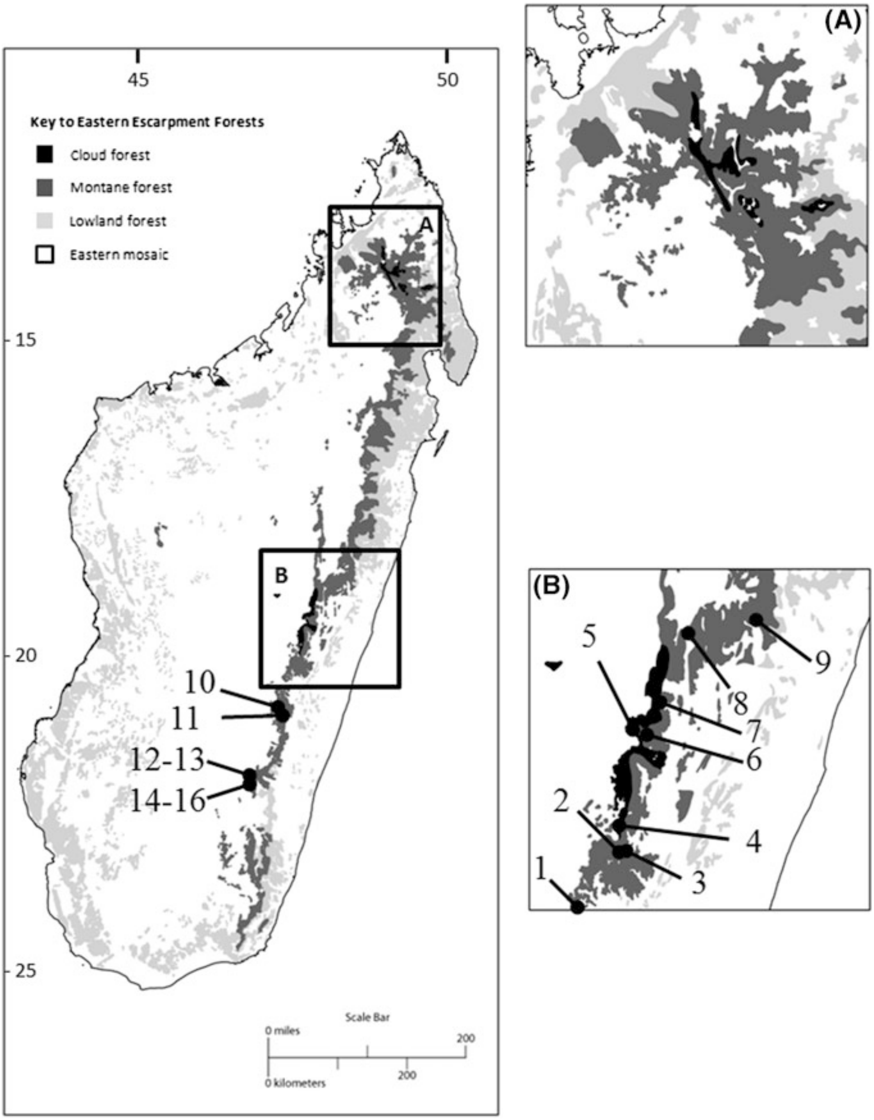

Fig. 1 Elevation map of Madagascar. Inset map A shows high altitude sites in NE Madagascar. Inset map B shows location of 16 lemur survey sites in high altitude areas in SE Madagascar. Numbers refer to site names listed in Table 2

Forests along the eastern escarpment can be classified based on abiotic and biotic characteristics into the following four categories: eastern mosaic, lowland forest, montane forest, and cloud forest (Brown and Gurevitch 2004; Consiglio et al. 2006; Dumetz 1999). Eastern mosaic represents anthropogenically disturbed secondary and fragmented forests occurring from sea level up to 800 m.a.s.l that run up and down the entire eastern side of the escarpment. The matrix is composed of intensive slash-and-burn agriculture, dominated by rice, sugar cane (*Saccharum officinarum* Poaceae), and tobacco (*Nicotiana tabacum* Solanaceae). Colonizing tree species, such as *Harungana madagascariensis* (Clusiaceae), and woody plants form a secondary thicket in abandoned cultivated areas, resulting in an abrupt edge between the matrix and forest habitats. Lowland forest occurs from sea level to 800 m.a.s.l and is a biologically rich ecosystem characterized by high humidity, high levels of rainfall (ca. 200 cm/year), and a well-developed, continuous canopy. Most of the remaining lowland forest is found in remote areas in northeast Madagascar (e.g., Masoala, Makira, and Mananara-Nord). Montane forest (800–1,300 m.a.s.l) differs from lowland forest by having cooler ambient temperatures, a lower, less continuous forest canopy, and a greater abundance of epiphytes. Cloud forest (above 1,300 m.a.s.l) maintains short trees with a low canopy of 10–15 m and the ground layer contains a thick layer of moss, ferns, and other terrestrial herbaceous vegetation. In cloud forests, ambient temperatures are lower than in montane forests and heavy clouds tend to cover the landscape. Cloud forests are limited to mountainous regions, such as Marojejy (within inset map B in Fig. 2) in the north and Andringitra in the south.

Of the 93 extant lemurs species described by the IUCN, 30 % ($N = 28$ species) range into montane or cloud forests along the eastern escarpment (Fig. 2). Three species (*Lemur catta*, *Eulemur rubriventer*, and *Hapalemur griseus*) have been sighted in forests above 2,000 m.a.s.l, and *E. rubriventer* has been seen traveling through the extremely rare montane shrubland (Lehman, pers. obs.), which is only found near mountain peaks above 2,000 m.a.s.l. A further 22 species have maximum elevation limits above 1,300 m.a.s.l.

The altitudinal profile, floristic habitats, and lemurs within Marojejy National park are illustrative of general lemur biogeographic patterns across altitudinal gradients. The sharp elevation gradients throughout this protected area produce abrupt changes in abiotic and biotic factors, resulting in a variety of forest types within a remarkably small area (55,000 ha). In addition to high levels of endemism for plants and animals within the park, 12 lemur species have been sighted in Marojejy (Duckworth et al. 1995; Goodman and Raselimanana 2002; Sterling and McFadden 2000). Most of these lemurs range from the lowland forest up through the montane forest and to the cloud forest at elevations above 1,400 m.a.s.l. For example, even the small-bodied *Microcebus rufus* (40–50 g) can be found in forests above 1,600 m.a.s.l. The steep topography has limited detailed studies of many lemur species. Nonetheless, concerted efforts have been made to collect data on the critically endangered *Propithecus candidus* (Patel 2011). Although early reports indicated that *P. candidus* rarely ranged below 700 m.a.s.l (Mittermeier et al. 2006), new surveys have found animals in forest at 289 m.a.s.l (Patel and Andrianandrasana 2008). Thus, this rare lemur has an elevation range of 1,586 m (289–1,875 m). Despite the critical status of this lemur species, there are few data on the effects of elevation and habitat on its ecology, behavior, and ranging patterns.

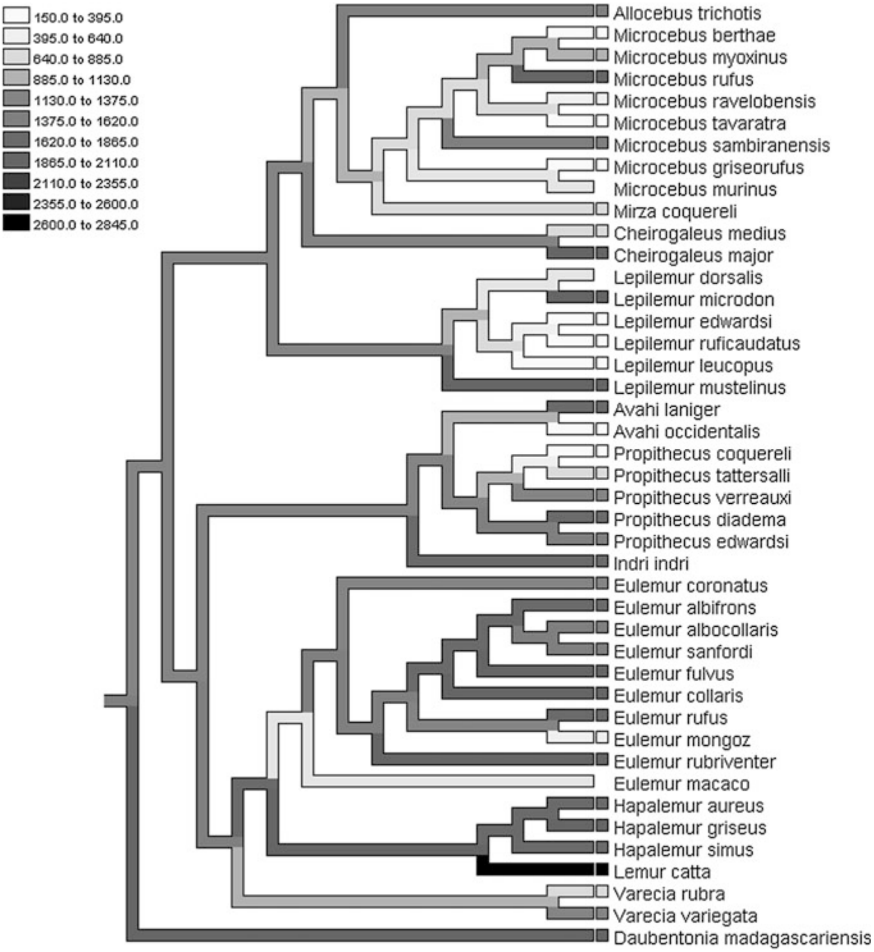

Fig. 2 Maximum elevation in an evolutionary context using the phylogeny presented in Arnold et al. (2010). Elevation data from: Lehman (unpub. data), Goodman and Ganzhorn (2004), Goodman and Rasolonandrasana (2001), Freed (1996), Jolly (2003), Vargas et al. (2002), Vasey (2003)

This consistent biogeographic pattern of broad altitudinal ranges in lemurs of the eastern escarpment is not the result of partitioning of vertical ranges by altitudinal specialists; rather, each clade within the phylogeny shows a remarkable level of species diversity in maximum elevation. For example, the speciose *Eulemur* clade contains taxa that range from a maximal altitude of 1,500 m.a.s.l for *E. albicollaris* to a high of 2,050 m.a.s.l for *E. rubriventer* along the eastern escarpment. Thus, most lemur clades and genera contain species that exhibit a remarkable range of altitudinal tolerances, although the biological and ecological reasons for such diverse tolerances are poorly understood for high elevation sites in eastern Madagascar. However, Goodman and Ganzhorn (2003, 2004) undertook the most comprehensive study to date of altitude midpoint variation and lemur biogeography, noting a unique pattern of elevation zone use compared to primates in South America, Africa, and Asia. Specifically, the 24 lemur taxa included in Goodman and Ganzhorn's (2003, 2004) studies showed a broader range of elevation midpoints compared to monkeys and apes. Lemur species diversity was relatively highest in elevation zones at 800-1,200 m.a.s.l compared to monkeys and apes, which were more speciose at elevation zones below 400 m.a.s.l. Goodman and Ganzhorn (2003, 2004) concluded that the most likely explanation for these differing biogeographic patterns is that Madagascar in general, and the eastern escarpment in particular, does not maintain ecologically stable lowland forest relative to the larger, more ecologically stochastic montane forest. This compelling argument also holds that these geographic patterns have existed for millions of years, such that ecological flexibility must have been selected for in terms of the evolutionary history of extant lemur taxa. Recent studies of lemur biogeography and evolution have focused on the relationship between ecological flexibility and phylogeny (Dehgan 2003; Kamilar et al. 2012; Kamilar and Ossi 2006; Wright 1999), although no consensus has been reached on an operational definition of or quantifiable response variable(s) for ecological flexibility. Moreover, variations in species assemblages of lemurs along elevation gradients have not been explored in any detail, nor has the effects of maximum elevation on community assemblage. Understanding how maximal altitudinal limits influence species assemblages, such as nestedness patterns, represents a key element to a comprehensive understanding of the biogeography of many plant and animal taxa (Alexander et al. 2011).

Nestedness and Lemur Biogeography

Methods

I determined the nestedness of species assemblages from survey data I collected as well as from published sources across 16 sites in eastern and southeastern Madagascar (Goodman and Shütz 1999; Goodman and Rasolonandrasana 2001; Lehman 2000; Lehman et al. 2005; Lehman et al. 2006d; Schmid et al. 1999; Sterling and Ramaroson 1996). Site elevations ranged from a low of 810 m.a.s.l (Andringitra 2) upto 2,050 m.a.s.l (Andringitra 7). All sites were located in either montane or cloud forests (Fig. 2). Lemur taxonomy is in a considerable state of flux, as penetration into remote areas combined with advanced genetics work has resulted in new species descriptions occurring at a remarkable pace, and many subspecies being elevated to full species (e.g., Louis et al. 2006a, b; Olivieri et al. 2007). Despite the importance of these species designations for conservation biology, little is known about their range limits and distribution, which complicates biogeographic analysis (Tattersall and Species 2007). Consequently, I used a conservative phylogeny of 43 species from the '10 k trees' project (http://10ktrees.fas.harvard.edu/) (Arnold et al. 2010).

I used ordinary least squares (OLS) regression models to determine how altitude influenced lemur species diversity and how species-specific site diversity (i.e., how many sites each species was present at) covaried with LN body mass across the 16 sites. Body mass data was taken from Kamilar et al. (2012). A one sample Kolmogorov–Smirnov test indicated that the dependent variable (species diversity) was normally distributed (K–S $= 0.889$, df $= 16$, $P = 0.054$). The homoscedasticity of the data further precluded data transformation. I used a Loess curve with a Gaussian kernel set to 50 % for the species diversity and altitude data to undertake more refined data explorations without the need for complex curvilinear regression models (Quinn and Keough 2002). A Spearman's rank correlation was used to determine if total site presence by each species correlated with species-specific IUCN endangerment levels using a ranked system of Least Concern (1), Near Threatened (2), Vulnerable (3), Endangered (4), and Critically Endangered (5).

I estimated nestedness in the lemur binary data matrix using distinct metrics in ANINHADO (Guimaraes and Guimaraes 2006). This software computes two metrics: (1) the classic system temperature T formulated by Atmar and Paterson (1993) and (2) the recently proposed NODF (nestedness metric based on overlap and decreasing fill) metric, which has been shown to be more theoretically consistent with nestedness concepts, is statistically conservative, and is robust to idiosyncratic patterns in "real" datasets (Almeida-Neto et al. 2008). The system temperature T ranges from 0 (complete order) to 100 (complete disorder). Thus, a perfectly ordered dataset of $T = 0$ will contain a subset of the species at all of the sites above it. As T approaches 100, complete disorder exists in terms of the biogeography of the sites or species in question. I also used two predetermined null models (Er and Ce) in the ANINHADO software to compare the lemur data matrix with theoretical predictions underpinning nestedness [see Almeida-Neto et al. (2008) for detailed descriptions of these null models]. ANINHADO was then used to calculate idiosyncratic T values by site and by species, which accounts for the presence or absence of unexpected species within the packed matrix.

Results

Lemur diversity ranged from a low of 3 species at Garonina (elevation of 1,670 m.a.s.l) to a high of 12 species at Ranomafana and Andringitra 2 (1,019 and 810 m.a.s.l, respectively) across the 16 sites in SE Madagascar (Table 2). In terms of species diversity across the 16 sites, *E. rubriventer* was found at 14 sites whereas *Propithecus diadema* and *Indri indri* were each found at only 2 sites. There was a statistically significant negative correlation between the presence of species and their IUCN Red List category ($r_s = -0.590$, $N = 13$, $P = 0.034$) across the 16 sites. Thus, rare taxa were less common than widely distributed

Table 2 Site name, altitude, lemur species presence (1)/absence (0), and nestedness idiosyncratic metrics by site and species for 16 survey sites in southeast Madagascar. IUCN categories follow those used in Table 1

		Altitude	Microcebus	Cheirogaleus	Avahi	Euelmur	Eidemur	Eulemtir	Lepilemur	Hapalemur	Hapalemur	Prolemw	Varecia	Propithecus	Propithecus	Indri	Daubentonia	Idiosyncratic
Site	Site#	(m.a.s.l)	rufus	major	laniger	rubriventer	rufus	fulvus	sp.	griseus	aureus	simus	variegata	edwardsi	diadema	indri	madagascariensis	T
Vohibola III	1	1,180	1	1	1	1	1	0	1	1	0	0	1	1	0	1	0	54.90
Mananjara	2	1,353	1	1	1	1	0	0	0	1	0	0	1	0	0	0	0	10.30
Ranomena	3	1,345	1	1	1	1	0	0	0	1	0	0	0	0	0	0	0	61.98
Korikory	4	1,555	0	1	1	1	0	0	0	1	0	0	0	0	0	0	1	24.82
Garonina	5	1,670	1	0	0	0	0	0	1	0	0	0	0	0	0	0	1	11.89
Adrafisaka	6	1,685	1	0	0	1	0	0	1	1	0	0	0	0	0	0	1	0.60
Bezavona	7	1,223	1	1	0	1	0	1			0	0	0	0	0	0	1	6.76
Tsinjoarivo	8	1,590	1	1	1	1	0	1	1	1	0	0	0	0	1	0		12.21
Mantadia	9	920	1	1	1	1	0	1	1	1	0	0	1	0	1	1	1	0.77
Ranomafana 1	10	977	1	1	1	1	1	0	1	1	1	1	0	1	0	0	1	13.79
Ranomafana 2	11	1,019	1	1	1	1	1	0	1	1	1	1	1	1	0	0	1	2.59
Andringitra 2	12	810	1	1	1	1	1	0	1	1	1	1	1	1	0	0	1	60.15
Andringitra 3	13	1,210	1	1	1	1	0	1	1	1	1	1	0	0	0	0	1	21.88
Andringitra 4	14	1,625	1	1	1	1	0	1	1	1	1	1	0	0	0	0	1	9.85
Andrmgitra 5-6	15	1,990	1	1	0	1	0	0	1	1	0	1	0	0	0	0	1	26.33
Andringitra 7	16	2,050	0	1	0	1	0	0	1	1	0	0	0	0	0	0	1	0.82
IUCN category			LC	LC	LC	VU	DD	NT	NA	VU	EN	CE	CE	EN	EN	EN	NT	
Idiosyncratic T			42.56	0.70	5.80	21.49	6.35	3.13	7.52	0.53	34.44	68.52	29.90	9.43	15.07	68.52	54.23	

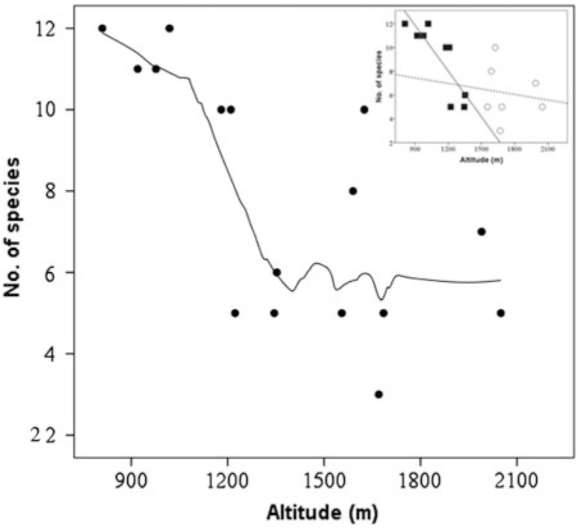

Fig. 3 Elevation variability in lemur species diversity across 16 survey sites in SE Madagascar. Main scatterplot shows Loess curve with a Gaussian kernel set to 50%. Inset scatterplot shows best-fit OLS lines for lemur species diversity below (filled squares) and above (open circles) the 1,500 m elevation threshold

lemur species. Moreover, LN body mass was negatively correlated with species diversity across the 16 sites ($R = -0.681$, $F_{1,13} = 11.22$, $P = 0.005$). Thus, larger bodied folivores and frugivores, such as *P. diadema, V. variegata*, and *I. indri*, were found only at sites below 1,200 m.a.s.l. Although altitude explained 42.7 % of the variation in species diversity across the landscape ($R = -0.682$, $F_{1,14} = 12.15$, $P = 0.004$), the Loess fit line for site altitude and diversity revealed a horizontal slope at an elevation threshold of approximately 1,500 m.a.s.l (Fig. 3). Splitting the data into sites below and above the threshold revealed that species diversity was significantly and negatively correlated with altitude at sites below 1,500 m.a.s.l ($R = -0.839$, $F_{1,7} = 16.67$, $P = 0.005$) but not for sites above 1,500 m.a.s.l ($R = -0.132$, $F_{1,5} = 0.09$, $P = 0.778$).

Lemur diversity across the 16 sites had a nestedness T value of 19.98 ($P < 0.001$), and differed significantly from the two null models: T (Er) = 58.51 ($P < 0.001$) and T (Ce) = 41.73 ($P < 0.001$). Similarly, the NODF null models revealed nestedness in lemur diversity, with statistically significant null metrics for both NODF (Er) = 51.99 ($P < 0.001$) and NODF (Ce) = 60.18 ($P < 0.001$), respectively. However, six species (*M. rufus*, *H. aureus*, *I. indri*, *Prolemur simus*, *Varecia variegata*, and *Daubentonia madagascariensis*) and three sites (Vohibola III, Ranomena, and Andringitra 2) returned idiosyncratic temperatures that departed appreciably from the total matrix T.

Discussion

My first question was to determine how species assemblage patterns vary along altitudinal gradients. Lemur species diversity was highest at sites within the elevation range of 810–1,019 m.a.s.l, which falls within the range of maximum lemur species diversity noted by Goodman and Ganzhorn (2004). However, not all taxa were represented equally in the sites above 1,500 m.a.s.l, where increased altitude no longer correlated with species diversity. At these high-altitude sites, the most common species assemblage included two vulnerable species (*E. rubriventer* and *H.* griseus) and two least concern species (*M. rufus* and *C. major*). Conversely, lemur taxa assessed as endangered or critically endangered were absent from the high-altitude sites, such as Andringitra 7 (2,050 m.a.s.l), Andringitra 5–6 (1,990 m.a.s.l), and Garonina (1,670 m.a.s.l). For example, critically endangered *V. variegata* and endangered *P. edwardsi* were absent from sites with elevations above 1,353 and 1,180 m.a.s.l, respectively. However, this pattern did not hold for two species of ecologically specialized, endangered bamboo lemurs (*H. aureus* and *P. simus*), which were found at many of the sites with the highest elevations. Their dietary specialization on bamboo combined with their patchy distribution has so far precluded biogeographic explanations for their ranging patterns (Tan 2000; Wright et al. 2008). Their enigmatic biogeography is all the more complex given that *H. griseus*, which exhibits a similar ecology, is widely distributed throughout eastern Madagascar (Grassi 2002).

My second question was to determine if lemurs exhibit nestedness patterns in high-altitude sites in southeast Madagascar. I found that lemur assemblage patterns exhibit nestedness across the 16 montane and cloud forest sites. Thus, lemur species that range into the relatively higher altitude sites are a subset of those that range in relatively lower altitude sites. These nestedness patterns likely relate to the combined effects of altitudinal variations in temperature and food resource availability. Strepsirhines are noted for their low basal metabolic rate (BMR) and unique behavioral ecology, such as sunbathing behavior and hibernation, to deal with stochastic abiotic and biotic conditions in Madagascar (Harcourt 2008; Wright 1999). Although low BMR is hypothesized to allow some species to deal with varying environmental conditions, there is a biological limit to tolerances for lower temperatures, such that reduced ambient temperatures at higher altitude sites may preclude species persistence in these marginal habitats. For example, energy expenditure and body composition in ring-tailed lemurs (*L. catta*), whose altitudinal range exceeds 2,000 m.a.s.l, is lower than those in sympatric brown lemurs (*Eulemur* sp.), which rarely range above 1,500 m.a.s.l. Thus, cooler temperatures at higher altitudes may preclude some lemur taxa from ranging into these habitats.

Lemur nestedness is also due to altitudinal variations in resource abundance. I found that the relatively large-bodied folivores and frugivores were present only at low altitude sites, compared to the presence of smaller bodied, dietary generalists at higher elevations. Although there are few data on the effects of altitude on resource abundance in montane and cloud forests in this region, trees are of smaller diameter and lower height in these habitats (Lehman, unpublished data), which likely results in lower fruit and flower abundance in these habitats. These effects of altitude on resource abundance and nestedness patterns have been documented in other mammals and regions (e.g., Cottenie and De Meester 2004; Grow et al. 2013; Presley et al. 2012). Grow et al. (2013) noted that pygmy tarsiers (*Tarsius pumilus*) deal with low food abundance at high altitudes by preferentially foraging in anthropogenic forest edges, which represent habitats with high insect abundance despite being at high altitudes in central Sulawesi, Indonesia. Comparable results were found in a study of nestedness in bat metacommunities along altitudinal gradients in the Peruvian Andes (Presley et al. 2012). Specifically, the researchers suggested that reduced resource abundance in forests above 1,500 m.a.s.l led to nestedness favoring small-bodied frugivorous bats. It is interesting to note that this altitudinal threshold matches the one I documented in lemurs across the 16 sites in SE Madagascar. Therefore, the combined effects of altitude on temperature and resource abundance are the two factors influencing the lemur nestedness patterns.

Despite statistically significant evidence for nestedness patterns in the lemurs, the models also returned appreciable idiosyncratic temperatures for six species (*M. rufus*, *H. aureus*, *I. indri*, *P. simus*, *V. variegata*, and *D. madagascariensis*) and three sites (Vohibola III, Ranomena, and Andringitra 2). The unexpected absence of *M. rufus* from Korikory and Andringitra 7 is likely due to the fact that both sites are at or near to the maximum elevation within their respective regions. Despite Korikory being at an elevation below that of other sites that maintain *M. rufus*, this site, like Andringitra 7, is located on a mountaintop with considerable exposure to winds and rain along the eastern escarpment. The exposure and resulting low-ambient air temperatures may preclude adequate conditions for effective torpor in *M. rufus* (Atsalis 1999).

Idiosyncratic temperatures for the bamboo lemurs (*H. aureus* and *P. simus*) and *I. indri* highlight a critical issue with any biogeographic dataset, proving species absence is more complex than proving species presence, particularly for rare taxa. For example, a male *I. indri* was serendipitously sighted by a member of my field team returning to camp from a nearby village but not throughout the course of 1,318 km of diurnal and nocturnal lemur surveys in Vohibola III (Lehman, unpublished data). In observing this species, we extended its clearly patchy distribution southward by almost 100 km, which also explains the idiosyncratic temperature for Vohibola III.

Idiosyncratic temperatures for *V. variegata* and *D. madagascariensis* as well as two survey sites (Ranomena and Andringitra 2) relate to altitudinal and distribution limits. Critically endangered *V. variegata* did not fit model predictions on site presence at high-altitude sites, which is likely due to a fundamental disjunction in its distribution due to a maximum elevation threshold of 1,353 m.a.s.l (Lehman et al. 2006c). The enigmatic *D. madagascariensis* is more widespread and abundant than previously thought (Mittermeier et al. 2006), but is still one of the most difficult lemurs to locate during standard surveys. In fact, site presence for this species is often based on tree markings due to foraging by the lemur rather than actual sightings of this species. Thus, its absence from Ranomena, which was in a highly fragmented landscape dominated by local slash and burn agriculture, largely drove the idiosyncratic temperature for this site. Finally, the idiosyncratic metric for Andringitra 2 was due to the absence of three lemur species that the model predicted should be at the site: *E. fulvus*, *P. diadema*, and *I. indri*. However, the geographic range of all three species is well north of Andringitra, irrespective of its elevation suitability for each lemur species.

The conservation biogeography of lemurs indicates serious issues with population viability across the 16 high-altitude sites. Forest loss and conversion is progressing from low-to-high altitudes in this region (Lehman and Ratsimbazafy 2000; Lehman and Wright 2000). If lemurs seek to disperse to avoid this anthropogenic disturbance but are incapable of moving upslope, then there is a strong likelihood for the extirpation of the most threatened taxa. If lemurs do move upslope, then they face potential competition with conspecifics for scarce resources in small, mountainous habitats, particularly in habitats with low resource abundance above 1,500 m.a.s.l. Moreover, upslope dispersal increases the risk for intraspecific and interspecific UDD. Herpetologists have already linked upslope range increases of 8–53 m in eight species of reptiles and amphibians to patterns of global warming in high-altitude forests in northern Madagascar (Raxworthy et al. 2008). Displacement models predict that only minimal increases in ambient air temperature should result in the extirpation of at least three frog and lizard species. Raxworthy et al. (2008) concluded that these patterns should hold for other high-altitude areas of Madagascar. In fact, a recent study on increasingly stochastic rainfall patterns and reproduction in female *P. edwardsi* in Ranomafana National Park, which is represented by two survey sites in my nestedness analysis, indicated that female birth rates and lactation are being negatively impacted by global warming (Dunham et al. 2011). Moreover, accelerating rates of forest loss and fragmentation will result in an increased proportion of edge habitat across the forest landscape. These changes are of conservation concern because some lemurs species, such as *C. major* and *E. rufus*, avoid edge habitats (Lehman 2007; Lehman et al. 2006b). Therefore, lemurs face an uncertain future across the elevation gradients within this landscape, irrespective of their tolerance for high-altitude habitats.

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Hibernation Patterns of Dwarf Lemurs in the High Altitude Forest of Eastern Madagascar

Marina B. Blanco and Laurie R. Godfrey

Introduction

The unusual ecophysiology of dwarf lemurs (*Cheirogaleus* spp.), the only obligatory hibernators among primates, was first documented both in captivity and in the wild between 1962 and 1980 (Petter 1962; Petter et al. 1977; Hladik et al. 1980; Petter-Rousseaux 1980). Petter (1962) described dwarf lemur hibernacula as well as aspects of their hibernation behavior and ecology. Yet, the ecophysiology of these tropical hibernators remained poorly known until after the turn of the century, when researchers supplemented ecological and behavioral data with records of body temperature and metabolic measurements of hibernating and nonhibernating individuals in the wild (Dausmann et al. 2004, 2005, 2009; Dausmann 2005). A population of the western dwarf lemur, *C. medius*, at Kirindy (a low altitude western dry deciduous forest near the coastal city of Toliara) was the object of almost all of this research; thus, for an extended period of time, virtually all that was known about the ecophysiology of hibernation in dwarf lemurs was derived from studies conducted at a single locality. A combination of high seasonality, low annual rainfall, and high fluctuation in daily ambient temperature makes Kirindy forest unique, and it is likely that the hibernation patterns found there are uncharacteristic of hibernation patterns manifested in other dwarf lemur species, most of which live in moister, less seasonal habitats, and some of which live in cold, high-altitude forests.

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Today, the high-altitude rainforests of Madagascar stretch along the peaks of the escarpment that forms the eastern border of the central high plateau. Although they were originally part of a forested "corridor" extending north–south from Mantadia to Ranomafana, and likely east–west across part of the Vakinakaratra region of the Antananarivo district, deforestation and habitat disturbance have broken the corridor's continuity and high-altitude plant and animal communities have become increasingly isolated. One of the few remaining high-altitude forests is Tsinjoarivo, located about 80 km to the southeast of the capital Antananarivo. Tsinjoarivo forest is comprised of a domain of primary forest toward the eastern half and of forest fragments with different levels of anthropogenic disturbance on its western side, just to the east of the central high plateau. The latter extends far to the west of this north–south corridor, decreasing gently in elevation from east to west so that, at its westernmost boundary, it rises only a few hundred meters above sea level. The west-to-east profile of the escarpment at Tsinjoarivo also represents an altitudinal gradient, ranging between 1,700 to 1,300 m. Effectively, Tsinjoarivo sits atop the escarpment that separates the central highlands from the eastern lowland forests (Irwin 2008) (Fig. 1).

We argue that it was in habitats like this, in the cold and relatively high-altitude forests of Madagascar, that obligatory hibernation evolved. Because all species of the genus *Cheirogaleus* (but no other cheirogaleids) are obligatory hibernators, we assume that obligatory hibernation was a derived feature of their common ancestor. Recent molecular genetic research (Groeneveld et al. 2010) has affirmed that *C. sibreei*, the only dwarf lemur species apparently restricted to high-altitude habitats today, holds a basal position in the *Cheirogaleus* clade. It may retain the

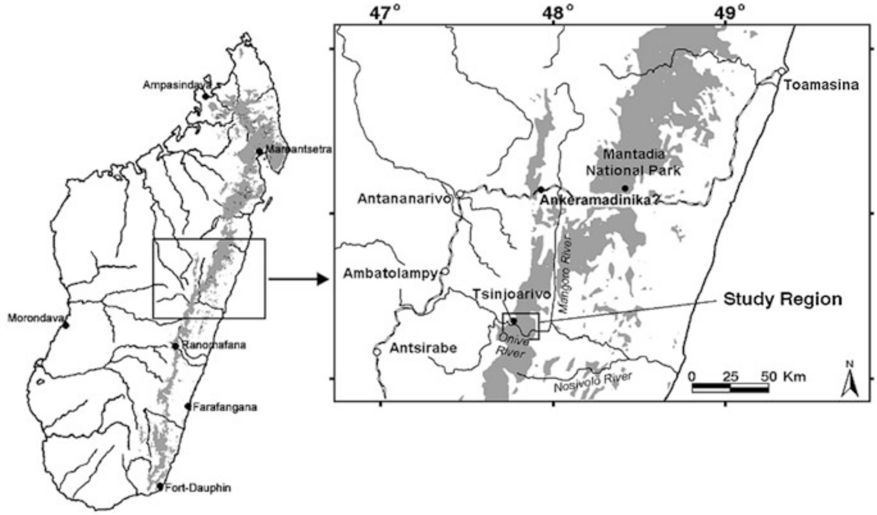

Fig. 1 Map of our main study area (*Tsinjoarivo*) and reference to other sites mentioned in this chapter. Map courtesy of Mitchell T. Irwin

ancestral dwarf-lemur condition for a number of traits. In some ways, the *low* altitude, smallest-bodied, western dwarf lemurs (*C. medius*) are the most specialized. Whereas individuals belonging to all species of *Cheirogaleus* accumulate fat in their tails to sustain them through prolonged hibernation, no eastern species does this to the extreme manifested in the western dwarf lemurs (who therefore have been dubbed the “fat-tailed” dwarf lemurs).

Here we review what is known about the ecology, behavior, and ecophysiology of hibernation of eastern dwarf lemurs, with an emphasis on the two species living in the high-altitude forests of Tsinjoarivo—*C. sibreei* and *C. crossleyi*—and with comparisons to western dwarf lemurs. We explore that variation within the context of the environments in which they live, and ask whether and how altitude affects the biology and behavior of dwarf lemurs. Does body size vary with altitude, as might be expected under Bergmann’s rule, or is some other factor such as primary productivity the main driver of body size variation in eastern dwarf lemurs? Do sleeping sites and hibernacula preferences vary with altitude? Does the duration of hibernation vary with altitude? Finally, on the basis of these data, as well as the broader context of paleoecological data, we offer some thoughts on the evolution of hibernation in the genus *Cheirogaleus* and the hypothetical relevance that altitude may have had in their evolutionary history.

Dwarf Lemur Distributions

There are four recognized living species of dwarf lemurs, two of which live in sympatry at Tsinjoarivo forest, central-eastern Madagascar: *Cheirogaleus sibreei* and *C. crossleyi*. Tsinjoarivo harbors the only living population of *C. sibreei* studied to date. This species is found today exclusively on the western side, at elevations between 1,400 and 1,700 m. It may occur as well at Ranomafana (southeastern rainforest) where an individual similar to *C. sibreei* was captured at a high-altitude location (at 1,474 m, on the top of Mt. Maharira, the highest mountain in Ranomafana National Park); this report warrants further confirmation (Wright et al. 2012). Additional evidence in support of this argument can be garnered from the accounts of Forsyth Major (1896), who collected the type specimen of *C. sibreei* at Ankeramadinika, a locality situated in the central high plateau. Although Forsyth Major failed to report the exact location (he gave a vague reference, “one day’s journey east of Antananarivo”), the altitude of this town was documented by his contemporaries at over 1,400 m (see Groeneveld et al. 2010).

Unlike Sibree’s dwarf lemurs, *C. crossleyi* is also found at low, middle, and high altitude forests, from northern to southern Madagascar, including sites along the eastern edge of the central plateau (Blanco et al. 2009; Groeneveld et al. 2009, 2011; Groves 2000; Hapke et al. 2005). Whereas it does not occur in the dry forests of the west or south, it does tolerate a wide range of habitats, differing in both temperature and mean annual rainfall. Tsinjoarivo may be the high elevation limit for *C. crossleyi*.

The third species of "eastern" dwarf lemur is *C. major*, which also has been found in eastern littoral to high-altitude, escarpment forests. It had a broad geographic range from the eastern lowland forest to the middle of the central plateau, well to the west of the eastern escarpment. The skull of a very large individual, likely *C. major*, was found at a subfossil site Ampasambazimba (Standing 1908) located at 1,036 m near Lake Itasy. This site lies in the middle of the Itasy District of the Antananarivo Province of the central highlands (18°56'S, 46°39′43″E), approximately halfway between Antananarivo (to its east) and Tsiroanomandidy (to its west). The dwarf lemur specimen has not been dated but radiocarbon dates for other specimens from subfossil sites in the central highlands range from around 1,400 Cal B.P. to 9,000 Cal B.P. (Crowley 2010).

Petter et al. (1977) described *C. major* as still living today in the central highlands—indeed further west, in an "eastern-like," isolated forest called Bongolava (now Ambohijanahary Special Reserve). This forest, between 800 and 1,600 m in elevation, is located near the western border of the Central Plateau just east of the Bemaraha tsingy massif and northwest of Tsiroanomandidy (Bongolava District of the Antananarivo Province) (see also Ausilio and Raveloanrinoro 1998; Thalmann 2000; Thalmann and Rakotoarison 1994). Thalmann (2000) published a photograph of an adult. Whereas this individual was considerably smaller than the adult *Cheirogaleus* photographed beside it, and not nearly as large as that described by Standing (1908) from the subfossil site, Ampasambazimba, mentioned above, the individual was nevertheless significantly larger than adult western dwarf lemurs. Groeneveld et al. (2011) tentatively identify the dwarf lemur from Bongolava as *Cheirogaleus crossleyi*. If this is correct, then the range of *C. crossleyi* extends broadly across the central highlands.

The fourth species, *C. medius*, is found primarily along the western dry deciduous forests, from Ankarana in the north to Tabiky in the south, but its range extends to the northeastern rainforest of Sambava and the southeastern littoral forest of Mandena and St. Luce. The highest altitudinal record for a *C. medius* site is 590 m, from an unnamed locality 170 km east of Toliara (Groeneveld et al. 2009). No *Cheirogaleus* is found in the southernmost spiny forests, between the western dry deciduous forests and the southeastern littoral forests.

Tsinjoarivo Dwarf Lemurs

Study Sites

One of us (MBB) has conducted research at Tsinjoarivo since 2006, at locations previously selected by Mitchell Irwin and collaborators for the study of diademed sifakas, *Propithecus diadema* (Irwin 2006, 2008; Irwin et al. 2010). Blanco and her collaborators conducted surveys and trapped cheirogaleids (mouse and dwarf

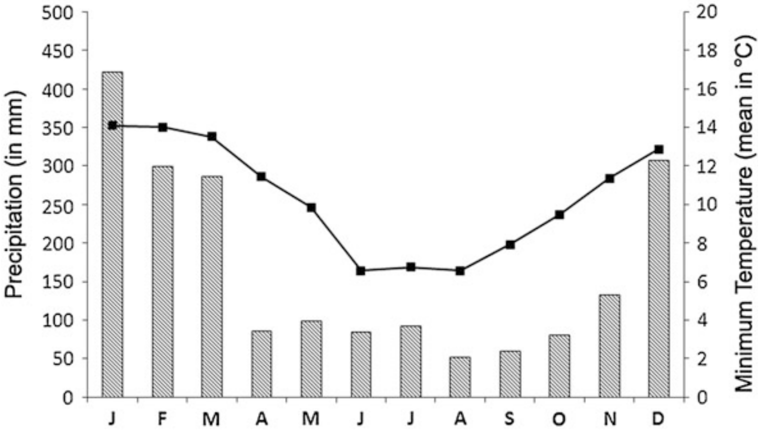

Fig. 2 Precipitation and mean minimum temperature data from the forest fragment at Tsinjoarivo forest. Data are compiled from >5 years between 2002 and 2008

lemurs) at three study sites: in one of the western forest fragments, Andasivodihazo (~225 ha, 1,600–1,700 m); an intermediate location (Ankadivory 1,400 m); and a site within continuous forest about 10 km to the southeast of Andasivodihazo (Vatateza 1,300 m). Climate is seasonal at Tsinjoarivo. A "rainy" season extends from December to March, but rain falls during the "dry" season as well, albeit to a lesser degree. Annual rainfall is generally higher in the continuous forest toward the east (~2,500 mm) than in the western fragments (~2,000 mm). Temperatures are highest in December and January (Irwin 2008). The monthly mean temperature minimum at Tsinjoarivo ranges between 6 and 14°C in the forest fragment of Andasivodihazo (Fig. 2) which is much lower than values recorded for low altitude forests such as the western dry deciduous forest at Kirindy (11.7–23.6°C) or the littoral southeastern forest at Mandena (16.3–23.8°C) (Lahann and Dausmann 2011). Unlike Kirindy, where maximum temperatures in the coldest months (June and July) exceed 30°C during the day (Dausmann et al. 2009), maximum temperatures at Tsinjoarivo during the same 2 months do not reach 30°C and average 19°C (Irwin 2006). Tsinjoarivo is indubitably one of the more extreme environments in Madagascar. As one of the coldest forests in Madagascar, it offers ideal conditions for the study of the metabolic strategies of hibernating species.

Measurements

At Tsinjoarivo, dwarf lemurs were live-trapped using Tomahawk traps set between 3–10 m along trails and baited with small pieces of banana. Traps were set around 17:00 and checked at 4:00 the following morning. All captured dwarf lemurs were brought to the campsite, marked with microchips (AVID Identification Systems, Inc., CA, USA), weighed, and measured. All individuals were released at the site of capture at dusk on the same day. Measurements used in this study include: head and body length (cm), measured dorsally, from the tip of the rhinarium to the cranial margin of the first caudal vertebra; tail length (cm), ventrally, from the base of the anus to the distal end of the last caudal vertebra; head length (mm), maximum length of the head from the most projecting margin of the rhinarium to the back of the braincase; head width (mm), maximum bizygomatic breadth; ear (or pinna) length (mm), maximum length between the base of the tragus and the tip of the pinna.

For studies of hibernation, a subset of captured individuals was fitted with external transmitters with temperature sensors that recorded skin temperature every 15 min (Advanced Telemetry Systems, Isanti, MN, ~10 g). Data loggers were used (Thermoworks, Lindon, UT) to collect hibernacula and ambient temperature. Hibernation periods were defined as skin temperature below 25 °C for a minimum of 2 days.

Does Altitude Correlate with Variation in the Morphometrics of Dwarf Lemurs?

Under Bergmann's rule, body mass is predicted to increase in colder environments (e.g., at higher latitude or altitude). Simply put, larger animals reduce heat loss to the environment by decreasing their surface-to-volume ratio. Although this principle was initially proposed to explain intraspecific size variation in endotherms (Blackburn et al. 1999; Mayr 1956; Roberts 1953), it has been applied to a variety of organisms and across species since its inception (Huston and Wolverton 2011; Lahann et al. 2006; Lin et al. 2008; Taylor et al. 1985).

A second possibility is that body size varies in accord with resource productivity; low productivity limits available energy and favors selection for small body size. Accordingly, body size should be positively correlated with rainfall, assuming that the latter acts as a good proxy for resource productivity. Resource productivity, seasonality, and quality may interact with body size in important (albeit not necessarily obvious) ways. Thus, for example, small-bodied species living in resource-poor habitats may experience a shortfall in food availability that becomes increasingly taxing (due to thermoregulatory stress) in habitats that are also cold. Reducing body size may be one way to cope with energy deficits; reducing body temperature and metabolic rate may be another. If the supply of food is limiting, rainfall may better predict body size than temperature or altitude. Large body size might be favored in resource-rich but cold environments, while small body size might be favored in resource-poor but equally cold or even colder environments (Ellison et al. 1993).

A recent treatment of size variation among lemurs has demonstrated that neither Bergmann's rule nor the productivity hypothesis explains size differences (Kamilar et al. 2012). However, Kamilar et al. (2012) did not test intraspecific variation. We tested these hypotheses specifically for Crossley's dwarf lemurs, using means for four variables (head length, head width, head and body length, and tail length) at six sites that vary in altitude and mean annual rainfall (Table 1). There is no correlation between altitude and rainfall across these six sites; thus, we are able to test competing hypotheses regarding size variation. Our data came from several sources, including our own collected at two Tsinjoarivo forests (a higher-altitude, disturbed fragment, and a somewhat lower-altitude primary forest) and at Ranomafana National Park. Hapke et al. (2005) reported measurements of a small set of individuals captured at various locations (mostly lowland) in southeastern Madagascar, including humid and littoral forests. Thalmann (2000) reported measurements taken on a single wild-caught adult female at Bongolava and another at Andasibe. Because we lack body mass data for individuals from southeastern Madagascar, and because body mass fluctuates tremendously in single individuals, we did not use body mass to test Bergmann's rule or the productivity hypothesis.

Our data do not support Bergmann's rule. Across the six sites, none of our size metrics is significantly correlated with altitude (CORRELATION: Pearson's r ranges from -0.20 to 0.16; P ranges from 0.71 to 0.81); even the signs of the correlation coefficients vary. Crossley's dwarf lemurs at Tsinjoarivo are smaller than conspecifics at Ranomafana (captured at 1,000 m altitude) (Blanco et al. 2009); however, they are larger than *C. crossleyi* from lower altitude littoral and humid eastern forests (Hapke et al. 2005). The productivity hypothesis fares somewhat better as a predictor of body size. Each of our body size metrics correlates weakly positively with rainfall in Crossley's dwarf lemurs (CORRELATION: Pearson's r ranges from 0.36 to 0.91). The compound probability of finding this consistent a result is $P < 0.001$. Ranomafana has the highest rainfall (>4,000 mm per year) and generally the largest individuals; Tsinjoarivo (with ~2,000 mm annual rainfall) is next, and individuals from the humid and littoral forests in the south (~1,325 mm rain at the range midpoint) as well as forests in the central highlands such as Bongolava (~1,500 mm rain) are small.

We also compared ear (or pinna) length at each of our six sites (Table 1). The classic explanation for variation in pinna length is Allen's rule, which holds that the relative size of exposed body parts should decrease as temperature decreases in order to conserve heat. Allen's rule thus predicts negative correlations of pinna length with altitude and latitude. However, thermoregulation should not be expected to influence ear length in primates, as primates lack a carotid rete and therefore do not exploit counter-current heat exchange mechanisms for brain cooling. In rabbits, carnivores, elephants, and bovids (animals that do in fact exploit counter-current heat exchange mechanisms; Parmeggiani et al. 1998), pinna size varies with both external temperature and activity levels. But even here, species that occupy a wide altitude range can violate the expectations of Allen's rule (e.g., Liao et al. 2007, on the lagomorph *Ochotona daurica* in northern China, which ranges over altitudes of 400–4,000 m above sea level). Generally, among primates, there is no correlation between ear size and ambient temperature (see, for example, Herskovitz 1977, on marmosets and tamarins).

Table 1 Body mass and morphometrics of *C. crossleyi* inhabiting high to low altitude forests

Location	Tsinjoarivo-FRAG	Tsinjoarivo-PRIM	Ranomafana	Fort Dauphin region	Bongolava	Andasibe
Altitude (m)	1,600	1,300	1,000	500	1,200	1,075
Mean annual rainfall (mm)	2,000	2,500	>4,000	1,425	1,500	1,700
Body mass (g)						
Mean	394.84	335.69	368.36	–	302	383
SD	54.31	55.03	44.44			
Range	321–461	282–456	312–472			
n	9	13	14	–	1	1
Head and Body length (mm)						
Mean	260.16	256.85	261.82	264.00	250	240
SD	15.22	9.73	12.83	6.00		
Range	235.9–287.5	243.7–274.7	245.5–286.7	255–270		
n	9	13	14	6	1	1
Tail length (mm)						
Mean	258.97	252.15	277.07	246.70	240	240
SD	13.88	10.06	13.04	14.30		
Range	240–276	235–267	255–300	229–270		
n	9	13	14	6	1	1
Head length (mm)						
Mean	57.90	56.58	58.73	53.20	44	48
SD	1.74	1.08	1.50	0.50		
Range	54.8–60.9	54.1–58.1	56.6–61.3	52.5–53.7		
n	9	13	14	6	1	1
Head width (mm)						
Mean	35.99	33.53	35.90	33.30	29	32
SD	0.88	1.12	1.51	0.30		
Range	34.6–37.2	32–35.6	33.8–39	32.7–33.6		
n	9	13	14	6	1	1
Ear length (mm)						
Mean	22.53	22.13	19.06	23.68	22	23
SD	1.72	1.47	4.26	1.94		
Range	18.5–24.2	18.9–24.1	11.9–26.5	20.9–26.4		
n	9	13	14	6	1	1

Range midpoints provided for altitude and rainfall when not available for specific capture sites

Other variables that might influence external ear morphology in primates include habitat structure (because of its influence on acoustics) and sexual selection. Predation risk can vary with habitat structure, which in turn may relate to rainfall, temperature, and disturbance. If predation pressure increases in more open habitats, and if large ears enhance the ability to detect predators, then large ears may be advantageous in open habitats. With regard to acoustics, however, the selective advantage of large or small ears depends on the range of sound frequencies that are of value to the species. A larger external ear can effectively amplify (and act as a directional receiver for) a broader range of sound frequencies. In particular, increasing pinna size should lower the frequency threshold of concentrated sounds because then the pinna can only effectively block or concentrate sounds with a larger wavelength. It is not clear that ear size matters to species relying on ultrasonic wavelengths.

Our data on pinna length variation in *C. crossleyi* demonstrate a pattern distinctly different from that seen in other morphometric traits. There is no correlation with altitude (CORRELATION: Pearson's $r = -0.16$, $P = 0.77$); thus, unsurprisingly, Allen's rule is not supported. However, in contrast with all other morphometric variables measured, pinna length is significantly *inversely* (not positively) correlated with rainfall (CORRELATION: Pearson's $r = -0.92$, $P < 0.01$). Crossley's dwarf lemurs living in more open habitats have the longer ears (both relatively and absolutely), and those living in dense forests have the shortest. Ear length is smallest at mid-altitude Ranomafana (where rainfall is highest), and greatest at low-altitude Fort Dauphin (where rainfall is the lowest) as well as high-altitude forests with relatively low rainfall. The same contrast is manifested at Tsinjoarivo, where ear length is greater in the higher-altitude fragment (with lower rainfall and higher daily temperature fluctuation) than in the somewhat lower-altitude primary forest.

Hibernation in Dwarf Lemurs

New Results on C. sibreei and C. crossleyi

At the forest fragment of Tsinjoarivo, we recorded daytime sleeping site information for 15 dwarf lemurs and hibernacula preferences for 6 individuals wearing radio collars. *C. sibreei* was observed using tree holes exclusively as sleeping site locations during the active season (three individuals in March, four individuals in October–November 2011, one individual in March 2012). During hibernation (between April and September), individuals occupy underground hibernacula. One of four individuals chose the inside of a dead tree stump as hibernaculum but switched to an underground location later in the same year. The remaining three individuals all used underground hibernacula during the entire hibernation period (Blanco, unpubl.). Unlike Sibree's dwarf lemurs, *C. crossleyi* alternated between tree holes and nest-like structures as sleeping sites during the active season, although some individuals only slept in nest-like structures during our study period (two individuals in April 2009, one individual in March 2011, four individuals in October–November 2011 and two in March 2012). Nest-like structures ranged from simple rearrangements of dried leaves (mostly bamboo) resembling open bird nests to more complex structures—"ball-like"— built with leaves of different tree species, a small opening on the side and inconspicuously located inside the tree crown (Blanco, unpubl.).

Fig. 3 Adult female *C. sibreei* wearing radio collar with a sensor to record skin temperature

Behavioral (focal) observations and skin temperature recordings from radio-collared individuals confirm that dwarf lemurs occupying tree holes and nest-like structures are able to maintain euthermy and remain active at night. Nest use by *C. crossleyi* is not restricted to the reproductive season; nests are also used by adult females preparing for hibernation (presumably after their infants have been weaned) and by adult males who were observed foraging and sleeping alone, which suggests that nest construction is not simply linked to parental care activities. Like Sibree's dwarf lemurs, Crossley's individuals ($n = 3$) hibernated underground.

During the hibernation period, skin temperature was recorded for a total of 6 individuals (3 *C. crossleyi* and 3 *C. sibreei*) between March and September in 2009 and 2011 (Fig. 3). Hibernation periods varied between species and individuals and ranged from 2 to 13 days. Figure 4 shows skin, ambient, and hibernacula temperature during hibernation in a *C. sibreei* adult male recorded between June 27 and July 16, 2011. Skin temperature remained below 20°C for almost 13 days

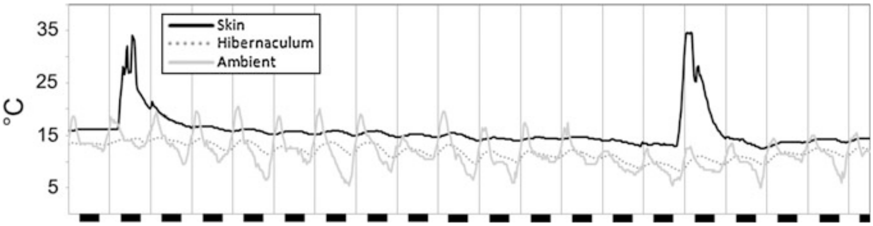

Fig. 4 Records of skin (*solid black*), ambient (*solid gray*), and hibernacula (*dotted*) temperature during hibernation in a *C. sibreei* adult male recorded between June 27 and July 16, 2011

between periods of arousal. The temperature within the hibernaculum was generally 2°–3° lower than the individual's skin temperature, although this may be the result of the data logger being more superficially situated than the individual's hibernaculum. Underground hibernation provides good insulation against daily ambient temperature fluctuation. Similar hibernation profiles were observed in *C. crossleyi* individuals.

Do Sleeping Sites and Hibernacula Preferences Vary with Altitude?

Altitude does not correlate in a simple fashion with variation in preferences for different types of hibernacula or sleeping sites. Descriptions of sleeping sites and hibernacula preferences for *C. crossleyi* in middle and low altitude forests are very sparse. Petter (1962) and Petter et al. (1977) referred anecdotally to the use of tree holes as well as nests by "*C. major*" in forests like Ranomafana during the active season and underground locations "enterré au pied des abres" as hibernacula. Note that *C. crossleyi* was considered a subspecies of *C. major* in the 1960s and 1970s. More recent reports at Ranomafana document nest construction by female dwarf lemurs during the birth season (Wright and Martin 1995); the authors also indicate that individuals may hibernate underground at this location. It is worth noting that Wright and Martin (1995) believed they were describing *C. major*, but later genetic analysis of *Cheirogaleus* at this study site identified it as *C. crossleyi* (Groeneveld et al. 2010). *C. major* at Mandena prefer tree holes as sleeping sites and no references to nest construction have been made (Lahann 2007).

Interestingly, no underground hibernation has been described for *C. medius*, which shows strict preference for sleeping and hibernating in tree holes or hollow tree trunks. Petter (1962) reports that fat-tailed dwarf lemurs were never observed in nests and always chose tree holes as sleeping sites and hibernacula. Furthermore, Petter et al. (1977) mentioned the use of live trees (instead of dead tree stumps) and presence of debris (e.g., humus) inside tree hollows to maintain a humid environment, which may be of critical importance in the hot and dry deciduous forests of western Madagascar. This further supports the notion that the common ancestor of all species belonging to the genus *Cheirogaleus* evolved in a humid environment.

Does the Duration of Hibernation Vary with Altitude?

Lahann and Dausmann (2011) argue that seasonality (and not temperature) correlates with the duration of hibernation in dwarf lemurs; seasonality is hypothesized to be important because of its effect on food and water availability. These authors compared *C. medius* inhabiting low altitude forests in western and southeastern Madagascar. Fat-tailed dwarf lemurs at the highly seasonal Kirindy forest in the west hibernated 6–7 months a year whereas their southeastern counterparts in the more humid and less seasonal Mandena forest hibernated for only 4–5 months. Time of emergence at Mandena was ~2 months earlier (at the beginning of September) than in the west (early November).

Our preliminary data on eastern dwarf lemurs offer some support for an association between duration of hibernation and seasonality, and little for altitude *per se*. All eastern dwarf lemurs live in habitats that are less seasonal than Kirindy (this is particularly the case for eastern lowland sites), and none exhibits hibernation periods as long as that seen in Kirindy *Cheirogaleus*. Eastern dwarf lemurs do not show the degree of variability manifested in western dwarf lemurs. *C. sibreei* have hibernation periods (~5 months) that are roughly similar to those of eastern dwarf lemurs living in lower altitude rainforests. Indirect evidence of hibernation (lack of sightings during censuses) in *C. crossleyi* at mid-altitude Ranomafana suggests that these dwarf lemurs hibernate for a maximum of 5 months (Wright and Martin 1995); this needs confirmation. A comparable hibernation period was reported for the similarly sized *C. major* at the low-altitude forest of Mandena (Lahann 2007). Better records for sympatric *C. crossleyi* and *C. sibreei* at Tsinjoarivo suggest shorter hibernation time for the former (3–3½ months) than the latter (4–5 months) (Blanco and Rahalinarivo 2010, Blanco, unpubl.) (Table 2). In fact, hibernation in *C. sibreei* may be longer than 5 months at Tsinjoarivo. Furthermore, there may be a difference between sexes, with adult females beginning hibernation earlier than males. No adult females of this species were trapped in March 2009, 2011, or 2012 and a single adult female was observed already hibernating in mid-March 2008 (pers. obs.). More samples per year and across years will be necessary to determine whether these interspecific and intraspecific differences hold.

If indeed *C. sibreei* hibernates longer than any of the other eastern dwarf lemurs, and if indeed *C. sibreei* is limited to high altitude forests, then a case might be made that increasing the duration of hibernation is adaptive in extreme environments, be they very cold and somewhat seasonal (as at Tsinjoarivo) or very dry and highly seasonal (as at Kirindy). If it is also true that female *C. sibreei* hibernate longer than males, it behooves us to explore how the duration of hibernation may or may not relate to female dominance and access to preferred food resources. In this regard, it is of interest to note that females of *C. sibreei* and *C. medius* both have masculinized genitals (Blanco et al. 2009), whereas *C. crossleyi* and *C. major* do not (Fig. 5). Certain other lemur species exhibit the same phenomenon (see Drea and Weil 2008, on *Lemur catta*), as do some other mammals in Madagascar and beyond (Hawkins et al. 2002). The functional significance of masculinized genitals in females is poorly understood, but this phenomenon has been related to female dominance (Ostner et al. 2003), specifically to the notion that masculinization confers higher fitness to females. If it helps females attain greater access to preferred food, there is a reason to expect greater expression in the harshest environments where such foods may be limited. In the cold forests of Tsinjoarivo,

Table 2 Duration of hibernation in radio-collared dwarf lemurs from a forest fragment at Tsinjoarivo

Individual	Species	Sex	Age category	Hibernation started	Hibernation ended	Duration (days)	Years
ID "Me"	*C. sibreei*	Female	Adult	~15-Mar			2009
ID "A"	*C. crossleyi*	Female	Adult	9-Jun	10-Sep	93	2009
ID "C"	*C. crossleyi*	Male	Juvenile	2-Jun	11-Sep	101	2009
ID "H"	*C. crossleyi*	Male	Adult	26-Apr	14-Aug	110	2011
ID "R"	*C. sibreei*	Male	Adult	23-Apr	20-Aug	119	2011
ID "M"[a]	*C. sibreei*	Male	Subadult	10-Apr	5-Sep	148	2011
ID "J"[a]	*C. sibreei*	Male	Subadult	10-Apr	28-Aug	140	2011

[a] Likely brothers, shared same tree hole during active season, hibernated individually

Fig. 5 Female genitalia of *C. crossleyi*, *C. sibreei* and *C. medius*, from left to right, respectively. Note "masculinized" clitoris in the last two species. Pictures courtesy of Noel Rowe/alltheworldsprimates.org (*C. sibreei*) and David Haring (*C. medius*)

preferred access to high quality food sources by females will likely affect the degree and rate at which prehibernation fattening can be achieved.

The Evolutionary Context of Hibernation in Lemurs

The status of hibernation as ancestral versus derived condition in lemurs has been contested for decades and is still debated by primatologists. Although hibernation has been considered a "primitive" condition retained in the cheirogaleid group (Dausmann et al. 2012), it can be argued that hibernation may have evolved in basal cheirogaleids when Madagascar was transitioning to the modern climatic pattern of environmental unpredictability. In this context, the evolution of energy-saving metabolic strategies, particularly in small-bodied primates, could be seen largely as a result of selective environmental forces during major climatic changes in the history of Madagascar. In favor of the traditional position, Nowack et al. (2010)

point out that hibernation is expressed in members of all major mammalian lineages, and that some expression of heterothermy (albeit not true hibernation) has been reported in the sister taxa of lemurs, the galagos and lorises. Heterothermy, according to this view, is a plesiomorphic trait present in the ancestral strepsirrhine (Dausmann et al. 2012).

In support of the alternative hypothesis, that hibernation is a derived condition in the Cheirogaleidae, are multiple lines of evidence (e.g., Masters et al. 2007). Generally, molecular phylogenetic studies of hibernating mammals suggest that all mammals have the developmental capacity for hibernation; making it obligatory may not be difficult especially if selective pressures favor the heterothermic phenotype. Molecular analyses (e.g., see Chap. 4, Groeneveld 2008; Perelman et al. 2011) show that the divergence and diversification of the genus *Cheirogaleus* is deeply embedded in the phylogeny of lemurs (around 22–25 mya) and there is no evidence of heterothermy in any of the “older” noncheirogaleid lineages. Basically, the radiation of all lemur families (extinct and extant, excluding the Daubentoniidae which diverged much earlier) began less than 40 mya, with the divergence of three clades in rapid succession (the Lemuridae-Megaladapidae clade, the Indriidae-Palaeopropithecidae-Archaeolemuridae clade, and the Lepilemuridae-Cheirogaleidae clade). The Cheirogaleidae had its origin around 35 mya (Perelman et al. 2011). Its basal member, *Phaner*, does not hibernate (Schülke 2004), and whereas there is evidence of some fattening and facultative torpor in the cheirogaleid clade more closely related to *Cheirogaleus* (i.e., *Allocebus*, *Mirza*, and *Microcebus*; Meier and Albignac 1991; Pastorini et al. 2001; Schülke and Ostner 2007), none of these is an obligate hibernator. Paleoclimate data point to severe climatic events occurring around the time of dwarf lemur diversification, most importantly the establishment of the monsoon climate of southern Asia and surrounding oceans around 23 million years ago (Samonds et al. 2012). Later climatic events may have also played a role in the diversification and distribution of dwarf lemur species. There was a second major cooling at around the time the Tibetan Plateau reached its current elevation (between 14 and 15 mya), associated with an expansion of the East Antarctic ice sheet. The monsoon climate continued to intensify until around 8 mya. Climate fluctuations have been also recorded in the not-too-distant past. Thus, for example, Gasse and Van Campo (1998) documented three exceptionally cold episodes at 40,000–39,000 BP, 37,000–32,400 BP, and 22,700–16,900 BP (the latter being the last glacial maximum). During colder episodes, the species that are today restricted to high altitudes would have had broader geographic distributions. Hence, whereas the central plateau is largely devoid of lemurs today, a subfossil site well to the west of Antananarivo has yielded the skeletal remains of ca. 20 species of lemurs and many other vertebrates at an elevation exceeding 1,000 m (Godfrey et al. 1999).

The Evolution of Obligatory Hibernation: A Hypothesis

We have argued that temperature does not correlate in a simple fashion with body size, choice of sleeping site or hibernacula, or the duration of hibernation. Yet, we have also argued that the basal *Cheirogaleus* may be restricted to high altitude forests, suggesting that obligatory hibernation may well have evolved in high altitudes. Other data (e.g., the maintenance of humid hibernacula conditions in dwarf lemurs living in dry habitats) suggest that hibernation likely evolved in moist habitats. The question arises, why might life in the moist, high altitude forests of Madagascar favor the establishment of obligatory hibernation? Clearly, species of the genus *Cheirogaleus* have spread to virtually all habitats in Madagascar, and hibernation "works" in all of these environments.

We suggest that seasonal montane environments provide the exact conditions under which selection may favor obligatory hibernation. Low ambient temperatures during the season of scarce resources (indirectly resulting in low temperatures in available sleeping sites) should affect energy expenditure during periods of inactivity. In effect, low ambient temperature should favor heterothermy, which would promote survival at reduced metabolic rates. Indirect estimates of metabolic rates in high-altitude dwarf lemurs, ascertained by calculating oxygen consumption before and during hibernation, should confirm or refute this proposition.

One hypothesis that purports to explain body mass or size variation among populations of single species under different environmental conditions is Bergmann's rule (Lahann et al. 2006). Bergmann argued that larger animals "conserve" more energy by reducing their surface-to-volume ratio, which in turn decreases heat dissipation to the surrounding environment. Evidence in favor as well as against Bergmann's rule has been published for a variety of organisms although the rule was originally meant to pertain exclusively to mammalian homeotherms (e.g., Lin et al. 2008; Taylor et al. 1985). The failure of dwarf lemurs to follow Bergmann's rule contrasts with the pattern reported for *Microcebus murinus*, another cheirogaleid species with a broad geographic distribution; body size variation in *M. murinus* does conform to Bergmann's rule (Lahann et al. 2006). This difference is not entirely surprising as *Cheirogaleus* spp. are obligatory hibernators (whereas mouse lemurs experience only facultative seasonal torpor), and they remain inactive for most of the season of scarce resources. Heterothermic species such as dwarf lemurs show physiological adaptations that are lacking in homeotherms. Because the latter need to maintain a fairly constant body temperature year round, they may be subject to higher thermic stress.

When animals undergo hibernation, they forego euthermy and adjust their body temperature to approximate the temperature of the hibernacula. By reducing body temperature, their metabolic rates decrease as well, resulting in net energetic savings that do not exist in individuals that must maintain homeothermy in cold climates. Thus, although low ambient temperature is not necessarily a trigger for hibernation, it contributes to its energetic benefits. At Tsinjoarivo, ambient temperatures during the season of scarce resources fluctuate between 5 to 19°C, and can drop below 0°C. Due to such extreme conditions, dwarf lemurs at Tsinjoarivo, unlike their "low-altitude" counterparts, cannot passively raise body temperature over 30°C by tracking the temperature of hibernacula, and consequently they must experience regular arousals. At the same time, they can consistently maintain body temperatures around 15°C when hibernating underground. These values are lower than those reported for *C. medius*, which hibernate in highly insulated hibernacula and experience regular arousals at Kirindy (Dausmann et al. 2004, 2009).

Our hypothesis, simply put, is as follows: The common ancestor of the *Microcebus*-*Mirza*-*Allocebus* clade and *Cheirogaleus* would have shared a tendency to accumulate some fat in anticipation of the season of scarce resources; however, that ancestor would have maintained the flexibility observed in species of mouse lemurs, and would not have accumulated fat to the degree observed in species of *Cheirogaleus*. In environments where ambient temperatures are *always* lower than body temperature (during the day and night), a loss of euthermy during the day—when nocturnal animals are inactive—would result in net energy savings (compared to individuals maintaining euthermy). This, in turn, creates a selective premium for extreme fattening, which is a precondition for prolonged hibernation. On the other hand, low altitude environments, such as Kirindy forest, display great daily temperature fluctuation, with temperatures surpassing 30°C during the day even during the austral winter (the season of scarce resources, and lowest temperature maxima). Under these conditions, a loss of daytime euthermy in some individuals would not have provided much of a metabolic advantage over individuals maintaining homeothermy. In these environments, presumably, selective pressures favoring extreme fattening in anticipation of the austral winter would be relatively low.

This is a grossly simplified scenario; further development of these ideas will require more research on the sister taxa of *Cheirogaleus*. For example, it is known that a portion of the gray mouse lemur population (*M. murinus*) at Kirindy does fatten prior to the season of scarce resources and can save up to 40% of daily energy expenditure by using torpor. Interestingly, mouse lemurs terminate torpor actively when temperature rises over 28°C so that mouse lemurs occupying highly insulated tree holes are able to stay in torpor a little longer than others, thus saving up to 5% additional energy (Schmid 1998). Hence, although torpor saves energy in the highly fluctuating habitat of Kirindy, even subtle changes in the temperature of the sleeping site can affect net daily energy savings.

In the final analysis, the role of altitude in the evolution of obligatory hibernation will remain obscure until direct measurements of oxygen consumption of dwarf lemurs in different habitats are made. Such measurements will shed light on the importance of hibernation to their energetic budgets and whether high altitude dwarf lemurs win the bid for the highest daily energy savings.

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Altitudinal Distribution and Ranging Patterns of Pygmy Tarsiers (*Tarsius pumilus*)

Nanda B. Grow

Introduction

The distribution of a primate species is related to current ecological conditions and historical dispersal patterns (Lehman and Fleagle 2006). The biogeography of island primates is particularly important to understanding primate distribution patterns. As Darwin (1845) observed, islands are a good means to explore adaptation, speciation, and radiations because of their small land area, distinctive boundaries, relative geographic isolation, and unique dispersal and diversification potential for colonizing fauna (Losos and Ricklefs 2009). Given that tarsiers probably originated in Asia in the Middle Eocene (Beard 1998; Fleagle and Gilbert 2006) and are currently distributed across Southeast Asian islands, tarsier diversity holds particular importance for understanding primate distribution patterns. This chapter examines how the ranging patterns and elevational distribution of high altitude pygmy tarsiers compare to those of lowland tarsier species.

Tarsiers [Genus *Tarsius*; see Groves and Shekelle (2010) for an alternate classification system] exhibit geographic distributions that closely relate to their taxonomic distinctions; all tarsier taxa exhibit complete allopatric separation or parapatric (adjacent) species ranges, while no species are sympatric (Shekelle 2008). Eastern tarsiers (Genus *Tarsius*), found in Sulawesi and surrounding smaller islands, are the most species of all tarsiers, with five species occurring on mainland Sulawesi: *Tarsius tarsier* (junior synonym *Tarsius spectrum*); the spectral tarsier (Brandon-Jones et al. 2004; Pallas 1778); *Tarsius dentatus* (junior synonym *Tarsius dianae*); Dian's tarsier (Brandon-Jones et al. 2004; Niemitz et al. 1991); *Tarsius lariang*, the Lariang tarsier (Merker and Groves 2006); *T. wallacei*, Wallace's tarsier (Merker et al. 2010); and *T. pumilus*, the pygmy tarsier (Miller and Hollister 1921; Musser and Dagosto 1987). Elevation factors into the

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allopatric separation of the species, and pygmy tarsiers are the only highland form to occur in Sulawesi (Musser and Dagosto 1987; Grow et al. 2013).

The taxonomic diversity of tarsiers is greater in Sulawesi than any other island on which they occur (Merker et al. 2009) (although this may reflect a lack of tarsier research outside of Sulawesi), and their diversity corresponds to geographic variation. Sulawesi is a four-armed Indonesian island located east of Borneo and northwest of Australia. It is located within a biogeographic region called Wallacea, an area of biotic transition between Asia and Australia (Shekelle 2003). Small fragments of land from Asia and Australia aggregated to form Sulawesi during the Pleistocene (Shekelle 2003). The resultant landmass is relatively large, ranking as the 11th largest island in the world (Shekelle 2003), with a high degree of endemism. The island is home to fewer than expected species of non-mammalian fauna, and more than expected species of mammals (Whitten et al. 2002), indicating repeated colonizations and radiations by mammals (Shekelle 2003). Among these mammals are two primate genera, *Macaca* (macaques) and *Tarsius* (Eastern tarsiers).

One factor that affects the current geographic distribution of Sulawesian tarsier species is the movement of Ice Age landmasses. Tarsiers exhibit species distribution patterns that correspond to past plate tectonic and glacial activity (Merker et al. 2009). DNA evidence and vocalization patterns indicate that two parapatric tarsier species in central Sulawesi, Dian’s tarsier and the Lariang tarsier, split 1.4 mya, with their distribution reflecting a split between the species along a faultline (Merker et al. 2009). Although the timing and migration path of the first tarsiers to colonize Sulawesi is unknown, their migration is thought to have occurred before Sulawesi converged into a single landmass (Shekelle 2008), during the Miocene (Merker et al. 2009). Thus, the currently parapatrically separated tarsier populations may have began as allopatric populations, isolated across smaller islands, but may have been pushed together on Sulawesi by plate tectonics (Shekelle 2008).

These prior colonization events are likely related to the current altitudinal geographic distribution of Sulawesian tarsier species. Sulawesi is mountainous, and the montane zone from 1,000 to 2,400 m covers approximately 20 % of land on the island (Culmsee 2011). *T. pumilus* is the only species of tarsier to live above 1,500 m, and have only been found at altitudes above 1,800 m a.s.l. (Grow et al. 2013; Musser and Dagosto 1987). In comparison, Dian’s tarsier occurs in the same central Sulawesi region and has been studied at approximately 700 m (Merker et al. 2005) up to 1,100 m (Merker 2003).

The number of species that occur in an area further affects the altitudinal range of a species. Lower elevation forests include a more diverse range of taxa that occupy narrow altitudinal ranges, while mountains show a decline in species richness with an increase in the altitudinal range of each species (Stevens 1992). This idea, known as Rapoport’s Rule, was originally developed to suggest that species ranges increase with latitude, as distance from the equator increases (Rapoport 1982), but has also been found to apply to increases in elevation (Stevens 1992). As a consequence of the Rapoport effect, the elevational distribution of primates may positively correlate with altitude. For example, groups of chacma baboons (*Papio ursinus*) at high altitudes occupy altitudes from 2,000 to 3,000 m, while those at lower altitudes occupy a narrower range from 1,600 to 2,000 m (Whiten et al. 1987).

A large altitudinal niche may be explained local ecological conditions, higher ecological tolerance levels, and by spatial constraints. With linear increases in elevation, measurable ecological changes occur, including decreases in temperature, reduced species diversity, and changes in forest structure (Körner 2007). All of these variables may influence primate elevational distribution patterns. First, primate's altitudinal ranges are known to correspond to altitudinal changes in food resources. For example, black-and-white snub-nosed monkeys (*Rhinopithecus bieti*) of the highly seasonal Tibetan plateau have been found to use higher elevations during the winter, where sunlight availability is higher (Quan et al. 2011) and there is greater access to lichens, an important fallback food (Grueter et al. 2012). Another explanation for increased ranges is that higher altitude species may be more broadly adapted to a range of climatic conditions, such as decreases in temperature, while lower altitude species have more narrow climatic tolerances (Stevens 1992). Finally, the availability of land area can explain the altitudinal range of species. For example, it has been proposed that the lemurs of Madagascar exhibit broad elevational ranges, and high species diversity at mid-range altitudes, because of the relative lack of lowland habitat (Goodman 2004). Thus, altitudinal variation in ecological conditions may affect the altitudinal ranges of tarsier species.

Altitude may also positively correlate with the home range sizes of individuals within a species. Home range is related to the diversity and abundance of resources in a given area, and biomass declines at higher altitudes (Körner 2007). Intraspecific altitudinal variation in home range size is seen among primates, with larger home ranges at higher altitudes. For example, rhesus monkeys (*Macaca mulatta*) occupy a wide range of environments, and have larger mean home ranges in mountainous regions of China (16 km^2; Wenyuan et al. 1993) and Pakistan (8 km^2; Richard 1985) than in lowland China (0.37 km^2; Southwick et al. 1996). Similarly, larger group home ranges have been observed among chacma baboons (*P. ursinus*) at high altitudes, in comparison to those at lower altitudes (Whiten et al. 1987). Tarsiers specifically are known to alter their home range sizes in response to spatial and temporal variation food availability. Spectral tarsiers increase home ranges during the dry season when prey abundance is low (Gursky 2000), while Dian's tarsiers occupy a greater percentage of their home range on a nightly basis in disturbed, less productive habitats (Merker 2006).

Compared to lowland tarsiers, little is known about pygmy tarsier ranging behavior and habitat usage. This paper reports results from surveys and observations conducted from May to October 2008, June to September 2010, and January to March 2012. This study seeks to (1) assess the altitudinal range of pygmy tarsiers, and determine if there is overlap with lowland tarsier species; (2) describe the ranging patterns of pygmy tarsiers; and (3) compare home range sizes of pygmy tarsiers to lowland Sulawesi an tarsiers. Given that species ranges should increase as elevation increases (Stevens 1992) and tarsier food resources decline at higher altitudes (Grow et al. 2013), I hypothesized that pygmy tarsiers would have a larger altitudinal range than lowland tarsiers. Further, given that an altitudinal reduction in resources has been observed in pygmy tarsier habitat (Grow et al. 2013), I hypothesized that pygmy tarsiers would have relatively large home ranges.

Methods

Study Species

Tarsiers are nocturnally active primates that are found only on Southeast Asian islands. As many as 11 tarsier species are recognized (Groves and Shekelle, 2010), and further species and subspecies may exist (Shekelle and Salim 2009). The five species of tarsier in mainland Sulawesi exhibit allopatric and parapatric separations (Fig. 1), with spectral tarsiers in northern Sulawesi (Niemitz 1984), Lariang tarsiers in Central Sulawesi, southwest of the Palu-Koro faultline (Merker et al. 2009), Dian's tarsiers located east of the Lariang river in Central Sulawesi, *T. wallacei* in a discontinuous distribution both northwest of the Palu-Koro faultline and near the city of Palu (Merker et al. 2010), and *T. pumilus* in the montane cloud forest of Central Sulawesi.

Pygmy tarsiers are the smallest tarsier species, with an average body mass of 55 g (Grow 2012). They exhibit distinctive traits among tarsiers, including their anatomy (see Musser and Dagosto 1987) as well as cryptic behavior and communication (Grow and Gursky 2010). Until the first live observations of this species in 2008 (Grow and Gursky 2010), pygmy tarsiers were known only from three museum specimens, two of which were collected over 70 years ago: USNM 219454, found at 1,800 m at Rano Rano, AMNH 196477, found at 2,200 m at Latimojong, and MZB 22593, found at 2,200 m on Mt. Rore Katimbu (Maryanto and Yani 2004; Musser and Dagosto 1987). The most recently found specimen, MZB 22593, was collected in the year 2000 and led to subsequent field observations of the species on the same mountain.

Study Site

Field observations were conducted in the mid and upper montane rain forest of Mt. Rore Katimbu, alternatively spelled Rorekautimbu or Rorekatimbu (base camp established at S 01° 18 33.8', E 120° 18 33.0', WGS 84) (Fig. 2). The mountain spans 1,800–2,400 m in elevation and is located within Lore Lindu National Park, Central Sulawesi, Indonesia. A trail bisects the study area, creating a channel of anthropogenic edges along either side.

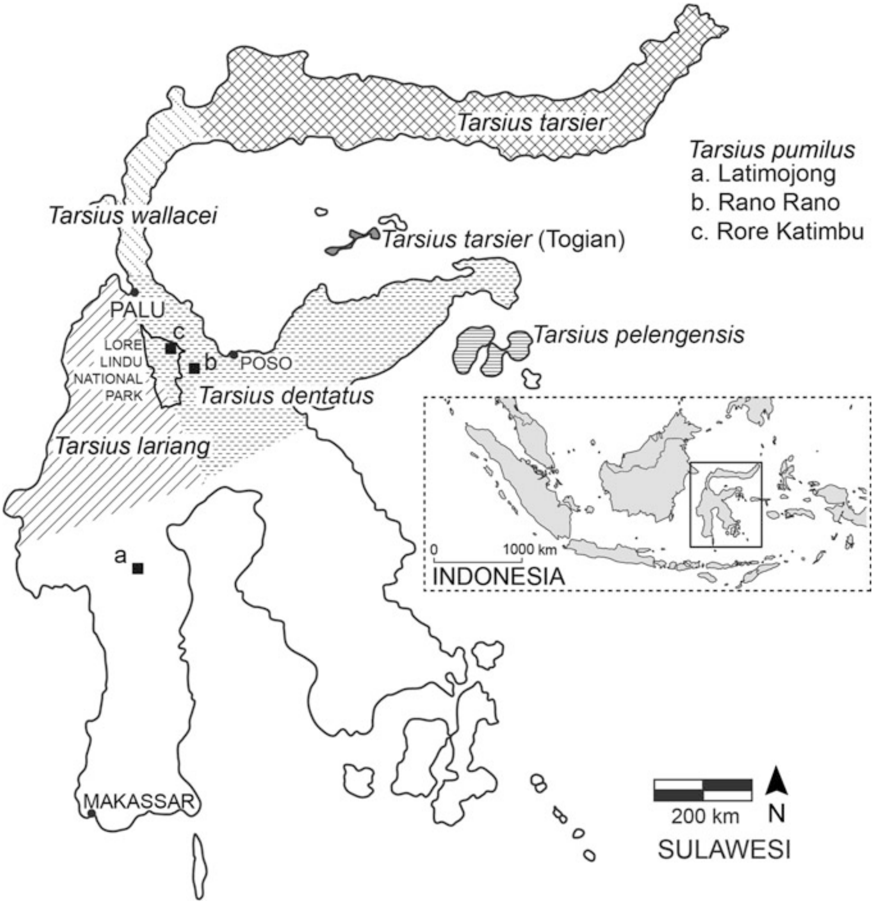

Fig. 1 Map of tarsier species distributions in Sulawesi, Indonesia, with locations of pygmy tarsier specimens. Shaded species distributions based on Merker et al. (2010), and locations of *Tarsius pumilus* based on Musser and Dagosto (1987).

Lore Lindu National Park, established in 1993, encompasses approximately 217,000 ha of protected forest (Pangau-Adam 2003). The park contains steep topography, and elevations higher than 1,500 m comprise 20 % of park (approximately 45,300 ha) (Latifah 2005). Mt Rore Katimbu consists of primary forest that contains both old-growth and disturbed forest.

Sampling

Tarsier surveys were conducted from May to October 2008, June to September 2010, and January to March 2012, over a period of 120 nights. Tarsiers were

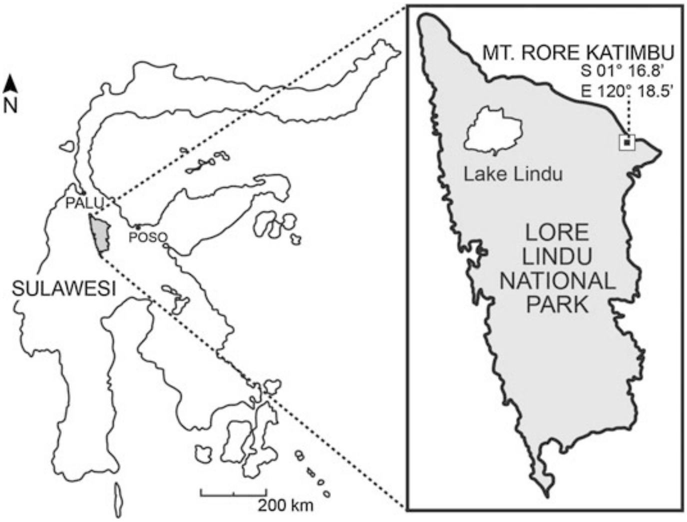

Fig. 2 Map of the study area on Mt Rore Katimbu in Lore Lindu National Park, Sulawesi (Indonesia)

sampled through capture and identification, as well as visual observation of non-captured individuals. A 1.2 km^2 area on Mt. Rore Katimbu was sampled across altitudes 1,800–2,300 m using a non-random high-probability sampling strategy. Elevation was measured with a GPS receiver (Garmin eTrex H) and verified with a digital altimeter (Suunto). At six 100 m altitudinal intervals (1,800, 1,900, 2,000, 2,100, 2,200, and 2,300 m), 12–20 mistnets (Avinet, 4-shelf nylon, 6–12 m) were established in premeasured quadrats and monitored nightly in 12 h shifts. The use of mistnets is a commonly used method to capture Sulawesi tarsiers (Fogden 1974; MacKinnon and MacKinnon 1980; Gursky 1995; Merker 2006). Each 100 m altitudinal interval was sampled for approximately 3 weeks.

The sex of all captured individuals was determined by palpation, which also assessed reproductive condition (pregnant, not pregnant, or lactating). Tarsiers were placed into broad age categories (infant, subadult, adult) based on body weight, wear on dentition, and reproductive anatomy (e.g., descended testes). Captured adults were fitted with a radio transmitter (Wildlife Materials Inc. or Lotek Wireless) that weighed 2 g by gluing the transmitter to the lower back fur; these transmitters adhered for less than 1 month, and all were recovered. The age and sex for observed but non-captured individuals remain unknown, although observed but non-captured infants were identifiable based on their small body size and inability to leap between trees.

Radio-Tracking

Adult individuals fitted with radio transmitters were located during daytime using a radio receiver (Wildlife Materials Inc.) and a three-element Yagi antenna (Lotek). Once the sleeping site was located, observation of group members who shared the sleeping site was possible. Group composition was determined by counting the number of males and females to share a sleeping site (e.g., observed in or leaving/entering the sleeping site).

Nightly focal follows (Altmann 1974) were conducted for radio-tagged individuals, in 12 h shifts that began at dusk and ended at dawn at the sleeping site. Tarsiers were followed by following the radio signal to pinpoint individual trees that the tarsiers were occupying. Locations were sampled every 15 min, by marking the tree with flagging tape indicating the date, time, and focal individual. Recording was limited by battery drain and the travel speed of focal individuals. During the daytime, coordinates of flagged trees were recorded with a GPS receiver. The angle and distance between the forest edge, as well as the sleeping site, to all observation points were recorded with GPS and verified with manual measurement.

Data collected on ranging patterns include home range size (ha), the altitudinal range of each group, and proximity between group members and between groups. Data on travel patterns include nightly travel distance, travel height, substrate usage, and leaping distances. Data on sleeping sites include tree diameter, height, and species, its occupancy duration, height of occupancy, and times when the site is entered and exited. All occurrences data was recorded continuously for the height at which the focal tarsier was traveling, substrate usage (tree trunk, branch, undergrowth, ground), and leaping distances.

Data Analysis

Home Range Home range, the area used by tarsiers, was calculated for all radiotracked individuals. Garmin BaseCamp 4.0.1.0 was used to download spatial movements recorded with GPS, as well as to visualize and measure nightly distances. For each focal individual, minimum home range size based on all known focal sightings (Bearder and Martin 1979) was estimated using the minimum convex polygon (MCP) method (White and Garrott 1987).

The software package BIOTAS 2.0a (Ecological Software Solutions LLC) was used to calculate MCP. Because the 100 % MCP estimator is sensitive to sample size, data area curves were calculated to explore sample size effects. Home ranges are only reported for individuals with a sufficient number of location points to accurately calculate home range. This number was established by creating individual sample size area curves using BIOTAS 2.0a, to ensure an asymptote had been reached prior to estimating home range (Haines et al. 2006). The degree of spatial overlap between individual home ranges was assessed by the Schluter multivariate test for significant associations between points (Schluter 1984), where the null hypothesis is that there is no association. This analysis is performed on a grid of square quadrats and compares the densities of points for each individual in each quadrat.

Nightly Path Length

The distance traveled on a nightly basis, nightly path length (NPL), was calculated for radiotagged individuals. NPL is determined by adding together the consecutive distances (measured with an electronic rangefinder and tape measures) between locations obtained from radiotracking during 12 h shifts. NPL was estimated as both a rate per hour, and as a total length. Locations were sampled every 15 min, and coordinates were recorded using a GPS receiver. In the event that the focal tarsier's location could not be discerned at a 15 min interval, the distance between the next available point and the last known location was used in the calculation of total NPL. The NPL of all individuals started and ended at the sleeping site.

Results

Altitudinal Distribution

Over the course of this research, six groups comprising a total of 22 individuals were observed on Mt. Rore Katimbu. The altitudinal distribution of observed groups (Table 1) ranged from 2,000–2,300 m. Although altitudes 1,800–2,300 m were sampled, no pygmy tarsiers were found below 2,000 m. Groups tended to be large; three groups of four individuals were found at 2,000, 2,250, and 2,300 m, while a group of five individuals was found at 2,100 m.

Ranging Patterns

To test for the effects of sample size, sample size area curves were compared (Fig. 3). Based on the curves that reached a plateau, only four out of 13 adult individuals were sufficiently radiotracked allowing for home range estimation. From this sample, the average home range size for pygmy tarsiers is 2.0 ha, with an average of 1.77 ha for the three females, compared to 2.75 ha for the one male (Table 2). The home ranges of the male (ID 250) and female (ID 115) from Group 6 exhibit a high degree of overlap (Fig. 4) (Table 3). The intersecting area of

Table 1 Altitudinal distribution of groups for *Tarsius pumilus* on Mt. Rore Katimbu; question marks indicate unknown age or sex

N	Altitude	Sex	Age
4	2,300	Female	Adult
		Female	Adult
		Male	Subadult
		?	Juvenile
4	2,250	Male	Subadult
		Male	Subadult
		Female	Adult
		?	?
2	2,150	Female	Adult
		Male	Adult
3	2,100	Male	(Older) adult
		Female	Adult
		?	Infant
5	2,100	Male	Subadult
		Male	Subadult
		Male	Adult
		Male	Adult
		Female	Adult
4	2,000	Female	Adult
		Male	Adult
		?	Adult
			Infant

overlap is 1.993 ha, with a perimeter of 537.36 m. The Schluter test for multivariate association rejected the null hypothesis of no association ($n = 432$ sampling units, variance ratio = 1.155, $W = 498.99$, p value = 0.001), indicating the locations of the male and female were associated.

The average NPL for adult pygmy tarsiers is 365.36 m (Table 4). The average NPL for females is 392.29 m (7 nights; 3 females), while the average for the one male is 318.25 m (4 nights).

Discussion

Results indicate that lowland and highland tarsier species experience an altitudinal separation. Pygmy tarsiers are allopatrically separated from lowland tarsier species in Sulawesi, including *T. dianae* that occurs in low and mid altitudes in central Sulawesi (Table 4). This finding is in alignment with the observation that all other tarsier taxa that are allopatric or parapatric, but not sympatric (Shekelle 2008).

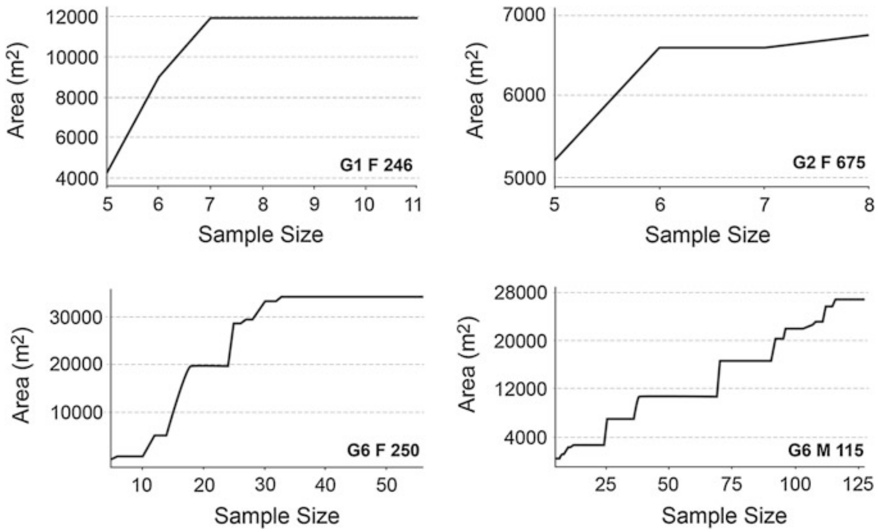

Fig. 3 Sample size area *curves* for four radiotracked individuals, as indicated by group, sex, and radio ID

Table 2 Home range sizes for each of the radiotracked pygmy tarsiers at the study site

Radio ID	Age and sex	Altitude	Data points	Home range (ha)
115	Adult male	2,000	129	2.75
250	Adult female	2,000	57	3.43
675	Adult female	2,300	9	0.68
246	Adult female	2,250	12	1.19

The specialized diet of tarsiers may relate to this observation, given that tarsiers are entirely faunivorous and feed primarily on airborne insect prey.

This study did not encounter pygmy tarsiers below 2,000 m on Mt. Rore Katimbu, despite numerous surveys at lower altitudes, although a pygmy tarsier specimen was previously recorded at 1,800 m (Musser and Dagosto 1987); it is possible that this measurement is inaccurate, as it was taken over 70 years ago. Lowland Sulawesi tarsier species occur up to approximately 1,000 m (Merker 2003) and have been reported as high as 1,400 m (MacKinnon and Mackinnon 1980). The only other tarsiers that have been found above 1,000 m were observed in Borneo, where Gorog and Sinaga (2008) report tarsiers captured above 1,200 m; however, this is not common. Even with these lowland species extending as high as 1,400 m, there is still a clear 400 m separation between lowland and pygmy tarsiers.

Pygmy tarsiers were found at 2,000–2,300 m and do not occupy a wider elevational range than lowland tarsiers, as was predicted by Rapoport's rule. However, the Rapoport effect is not a universal phenomenon. For example, a

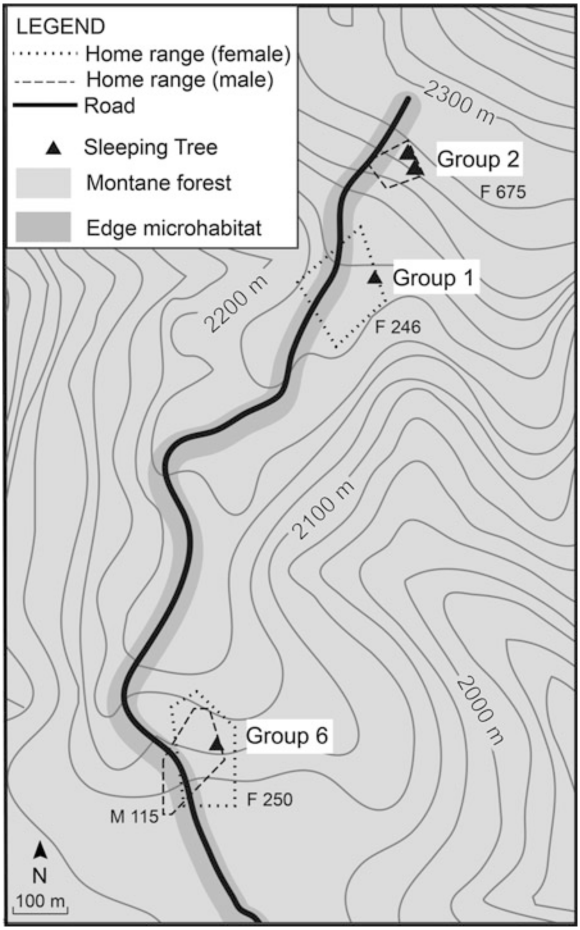

Fig. 4 Home ranges for individuals in Groups 1, 2, and 6. Numbers indicate group

cross-species analysis of the latitudinal and altitudinal ranges of Andean passerine birds found that neither latitude nor altitude could explain spatial variation in size ranges (Ruggiero and Lawton 2008). The ecological variation between the lowlands and highlands of Sulawesi may be a significant factor in determining the altitudinal niches of Sulawesi tarsier species. Forest at high altitudes in Sulawesi exhibits a marked reduction in food resources for tarsiers, with insect size and abundance decreasing at progressively higher altitudes (Grow et al. 2013). With a wide altitudinal gap between pygmy tarsiers and lowland tarsiers, pygmy tarsiers may be specifically adapted to occupy a narrow high-altitude range. Pygmy tarsiers also exhibit adaptations to this altitudinal decrease in resource, and bias their spatial positions near forest edges, where insects are found in greater abundance (Grow et al. 2013). Meanwhile, lowland tarsiers may represent species with broad niches, or tolerance to a range of conditions, that occupy wider ranges.

Table 3 Travel distances and altitudinal ranges for radiotracked adult pygmy tarsiers during 12 h night shifts. Listed here are nightly travel distance NPL, the minimum and maximum altitude at which locational points were recorded, and the number of data points

Date	Group	ID	Sex	NPL (m)	Min altitude	Max altitude	Data points
8/23/08	1	246	Female	547	2,250	2,266	8
8/26/08	1	246	Female	204	2,250	2,266	6
7/16/10	2	675	Female	436	2,221	2,242	9
2/9/12	6	250	Female	330	2,018	2,038	9
2/10/12	6	250	Female	479	2,003	2,032	12
2/12/12	6	250	Female	520	1,996	2,027	23
2/13/12	6	250	Female	230	2,014	2,022	12
2/24/12	6	115	Male	318	1,986	2,018	23
2/25/12	6	115	Male	236	2,018	2,024	45
2/26/12	6	115	Male	235	2,018	2,028	22
2/28/12	6	115	Male	484	1,998	2,028	39

Table 4 Comparison of altitudinal range, nightly path length, and home range size for tarsier species. Values are averages for females (F) and males (M)

Species	Altitudinal range (m a.s.l.)	Nightly path length (m)	Home range (ha)
Tarsius pumilus	2,000–2,300	F 392	F 1.77
		M 318	M 2.75
T. dentatus (*T. dianae*)	0[a]	F 945	F 1.58
	650–990[b]	M 905[b, d]	M 1.77[d, f]
	0–1400[c]	(25–48 % of range$_{e}$)	
T. lariang	500[g]	n/a	n/a
T. tarsier (T. spectrum)	0–500[h]	F 447.68	F 2.3
	0–1400[i]	M 760.62[i]	M 3.1[j]
T. wallacei	500[k]	n/a	n/a
T. bancanus	0 $_{k}$–1,200[l]	F 1448.1 (66–100 %)	F 7
		M 2081.6 (50–75 %)[m]	M 10[m]
T. syrichta	69–200[n,o]	F 1119 (6–57 %)	M 6.45
		M 1636 (3–74 %)	F 2.45[o]

a. Shekelle et al. 1997, b. Merker 2003, c. MacKinnon and MacKinnon 1980, d. Merker 2010, e. Merker et al. 2005, f. Merker 2006, g. Merker and Groves 2006, h. Nietsch 1999, i. Gursky 1995, j. Gursky 1998, k. Merker et al. 2010, l. Crompton and Andau 1987, m. Gorog and Sinaga 2008, n. Řeháková Petrů et al. 2012, o. Neri-Arboleda et al. 2002

Differentiation between lowland and highland forms of taxa, with high-altitude dwarfing, is seen in other Sulawesi taxa. The smaller mountain anoa (*Bubalus quarlesi*) occurs at higher elevations while the larger lowland anoa (*Bubalus depressicornis)* inhabits lower elevations, although it has been suggested that the two forms may reflect clinal altitudinal variation in body size within one species of anoa (Burton et al. 2005; Whitten et al. 2002). One isolating mechanism between low-altitude and high-altitude populations might be differences in plant diversity at low, middle, and high altitudes.

In some cases, species diversity along altitudinal gradients peaks in the middle, an occurrence known as the mid-domain effect. The mid-domain effect is thought to occur because of spatial constraints of species' ranges, where more overlap occurs at mid-range elevations on a mountain (McCain 2007). This phenomenon does not universally describe all gradients of phylogenetic diversity (Zapata et al. 2003). Previous studies in the mountains of Sulawesi have found an opposite effect, where plant species diversity increases with increasing altitude; it is highest in upper montane forest at 2,400 m a.s.l., while it is lowest at low and mid-montane elevations (Culmsee et al. 2010). Although anthropogenic influences may affect this observation, lower plant diversity at lower altitudes may also relate to the wider altitudinal range of lowland tarsiers.

Pygmy tarsier home ranges are comparable to, or relatively larger than, those of lowland tarsiers (Table 4), although interpretation of these results is limited by a small sample size. One female (#250) of Group 6 had a relatively large home range size, with an area curve that reached an asymptote based on a large number of data points. The full home ranges of two additional females (#246 and #685) may not have been fully tracked, if their area curves have only reached local plateaus and not yet their respective asymptotes. Thus, the home ranges of females #246 and #685 may be larger than estimated. If this is the case, pygmy tarsier home ranges could very well be larger than lowland tarsier ranges. Compared to the home ranges of tarsiers in the Philippines and Borneo, all Sulawesi tarsier home ranges are much smaller, which may relate to differences in habitat or anthropogenic disturbance. Larger home ranges are beneficial in habitats where food is scattered or limited (Altmann 1974).

While pygmy tarsier home ranges and area are larger, their nightly path length is shorter, indicating that pygmy tarsiers do not utilize a large proportion of their home range on a nightly basis. On different nights, pygmy tarsiers use different parts of their home range. The relatively small nightly path length of pygmy tarsiers is unexpected, given that nightly travel distances are known to increase in habitats with lower productivity. For example, spectral tarsiers (*T. spectrum*) increase home range sizes and travel distances during the dry season when prey abundance is low (Gursky 2000). Similarly, Dian's tarsiers (*T. dianae*) have been observed to increase their nightly travel distances in more disturbed forest (Merker 2006). One explanation for the short nightly travel distances of pygmy tarsiers is their biased distribution near anthropogenic forest edges (Grow et al. 2013), where insects are more abundant, lessening the need to increase for aging area.

A possible confounding variable is seasonal changes in resources. However, there is no clear seasonality in Central Sulawesi in terms of rainfall (Schweithelm et al. 1992), and tropical montane forest exhibits less seasonality than temperate forest. This study sampled during both the monsoon period between November and April (Pangau-Adam 2003), and during the dryer months of the summer, thereby reducing the potential effect of seasonality.

An important variable that affects the ranging patterns of all Sulawesi tarsiers is habitat disturbance. Forest that is unaltered by human activity is quickly disappearing from Central Sulawesi. As Merker et al. (2004) observed, in 2001 there was no pristine forest below 950 m, although only 3 years earlier he observed pristine forest at 700–750 m. Because of the rapid rate of habitat loss in the region, care must be taken to determine how human habitat disturbance affects tarsier populations. As human activity encroaches on high-altitude forest in the region, highland tarsiers may have further challenges to face in the future.

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Part II
High Altitude Monkeys

Biogeography and Conservation of Andean Primates in Peru

Sam Shanee, Noga Shanee, Nicola Campbell and Nestor Allgas

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 (55 taxa in 35 species), third in diversity of genera (13 genera) and joint first in diversity of primate families (5 families, together with Brazil, Colombia and Madagascar) (IUCN/PSG 2012). The country's biogeography is dominated by the Amazonian lowlands in the east, the coastal deserts in the west and the Andean cordillera, which transects the entire country north to south for over 1,500 km (Fig. 1) (Brack Egg 1986; Olson and Dinerstein 1998; Young and Leon 1999; Rodríguez and Young 2000; Olson et al. 2001). The highlands of Peru are an important ecogeographic zone to consider despite their limited area; although covering only 5 % (35,000 km^2) of Peru's tropical humid forests, the country's eastern Andean cloud forests contain comparable species diversity to that of the much larger (700,000 km^2) Amazonian lowlands (Mittermeier 1988; Bubb et al. 2004; Pacheco et al. 2009).

The biogeography of primates is the result of the complex relationship between geographical, historical and ecological factors (Bush 1994; Tuomisto and Ruokolainen 1997; Lehman and Fleagle 2006). The major geographical and historical factors affecting the biogeography of Andean primates are the uplift of the Andes Mountain range, the presence of refugia and barriers such as major rivers

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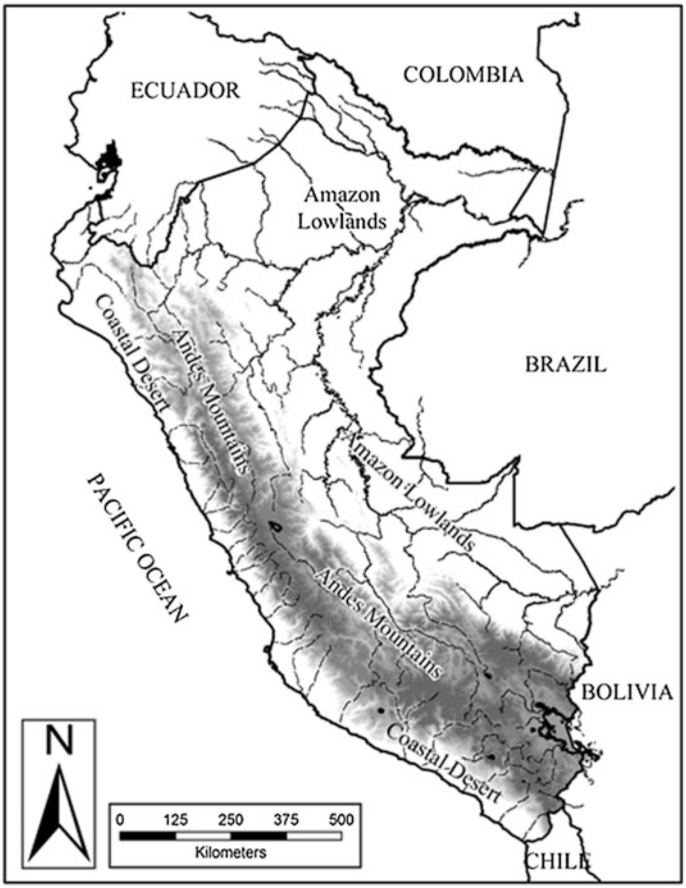

Fig. 1 Eco-geographical areas of Peru, showing major river systems and Neighbouring countries

(Kinzey and Gentry 1979; Ayres and Clutton-Brock 1992; Collins and Dubach 2000; Lehman and Fleagle 2006). Ecological factors such as habitat heterogeneity across the environment may also be determining factors in primate biogeography (Tuomisto and Ruokolainen 1997; Lehman and Fleagle 2006; Stevens and O'Conner 2006). In the Andes, habitat heterogeneity is a result of changes in temperature, humidity, rainfall and soil types across altitudinal and latitudinal gradients (Tognelli and Kelt 2004; Kreft and Jetz 2007).

The Andes is a relatively young mountain range, particularly the central and northern cordilleras, with the northern Andes only reaching their current height since the late Pliocene and Pleistocene (Gregory-Wodzicki 2000). This recent uplift has played a major role in determining the biogeography of Peru, particularly in Andean biota (Herzog 2011). Other determining factors in the biogeography of Peru have been climatic cycles and the presence of rainforest refugia during the geological past (Bush 1994; Bush and Oliveira 2006; Josse et al. 2011). This interplay between historical, geologic and climatic changes led to the development of many major river systems furthering adaptive radiations and the development of Peru's current primate biogeography (Ayres and Clutton-Brock 1992; Lehman and Fleagle 2006; Meijaard and Groves 2006). The first colonisation of primates in the neotropics is thought to have been ca. 30–50 million years ago (mya) (Poux et al. 2006; Oliveira et al. 2009), although several subsequent radiations may have taken place, with the last common ancestor of extant platyrrhine families existing ca. 20 mya (Hodgson et al. 2009). The earliest fossil evidence of primates in what is now the Andean region comes from the upper Magdalena valley in Colombia (13.5–11.8 mya) and Salla in Bolivia (26 mya) (Rosenberger et al. 2009). Other fossil primates have been found in Acre, Brazil (9–6.8 mya) (Rosenberger et al. 2009); although it is not an Andean site, it is significant given its proximity to modern day Peru.

Andean habitats vary considerably because of elevation, latitude and aspect (ONREN 1976; Brack Egg 1986) with different canopy heights, floral diversity, density of epiphytes and bryophytes as well the presence of elfin forest on ridges and exposed areas within the cloud forest belt (Patterson et al. 1998). Depending on latitude montane forests in Peru are predominantly found on the eastern slopes of the Andes, from approximately 1,000 m above sea level (m.a.s.l.) to the transition zone between montane and elfin forests between 3,200 and 3,600 m.a.s.l. (Schulenberg et al. 2010). The main montane forest type, Peruvian *Yungas,* reaches from the Bolivian border in the south to the *Maranon* river valley in the Departments of Cajamarca and Amazonas in the north, on both the eastern and western cordilleras (Olson et al. 2001). North of the *Maranon* to the Ecuadorian border the major montane habitat type is Cordillera Real moist forest, along the inter-Andean *Maranon* valley dry forests extend to 1,500 m.a.s.l. (Olson et al. 2001). Other forests types extending into the montane belt in Peru include Bolivian *Yungas*, Napo moist forest, Ucayali moist forest and southwest Amazon moist forests (Olson et al. 2001).

Peru has one of the highest diversities of primate fauna of any country with current estimates between 32 and 40 species (Aquino and Encarnacion 1994; Pacheco et al. 1995; Pacheco 2002; IUCN/PSG 2012; Rowe and Myers 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 Encarnacion 1994). The Amazonian species are generally thought to be restricted to areas of seasonally flooded and *terra firme* lowland forest bellows approximately 500 m.a.s.l. Even so, early reports were made of the occurrence of some lowland species at higher altitudes (Durham 1975; Hershkovitz 1977). It is now known that many of these 'lowland' species also have sizeable distributions at higher altitudes. The less favourable ecological conditions at higher altitudes has consequences for 'lowland' species often reducing population densities, lowering abundance and reducing species diversity (Durham 1975; Caldecott 1980; Aquino and Encarnación 1988; Geise et al. 2004; Marshall et al. 2005; Peck 2008; Shanee 2009).

Due to their inaccessibility and steep terrain, the Andean forests of Peru remained relatively undisturbed until recent decades (Leo Luna 1987; Buckingham and Shanee 2009; Schjellerup et al. 2009). However, the proliferation of development projects, particularly road construction, mining and hydroelectric dams, has opened these forests to mass immigration of people and consequently high rates of deforestation (Dourojeanni et al. 2009). The low productivity of montane soils and the slow adaptation of migrants to new agricultural conditions result in unsustainable farming methods causing further deforestation (Bebbington 1990; Loker 1996; MINAG 2010).

Climate change is a global problem that is affecting many of the world's habitats. Because of a predicted upward shift in optimum climatic conditions (Foster 2001) tropical montane cloud forests are considered the most vulnerable ecosystem to climate change of all tropical forests systems (Markham 1998; Still et al. 1999; Bubb et al. 2004). This is especially important for cloud forests occupying peaks where it will not be possible to spread upslope (Bubb et al. 2004). This climate change in Andean Peru is already manifesting itself through droughts, floods and uncontrolled wild fires. This is increasing pressure on forest species through shifting phenologies and also adding pressure to local farmers, leading to further deforestation (Shanee 2012a).

This chapter examines the distribution of primates in the Peruvian Andes, primates endemic to the Andes and the conservation needs of these species, using both published and newly reported data.

Field Methods

Surveys of primates were carried out at 65 sites in northern Peru between March 2007 and October 2012. We surveyed forested areas between 300 and 3,000 m above sea level (m.a.s.l.). Habitat types we surveyed included montane and premontane cloud forests, lowland *terra-firme* forests; Shade coffee plantations, forest plantations, forest fragments and dry forests. Daytime temperatures for these areas vary between 8 and 36 °C. Average monthly rainfall is approximately between 15 and 1,500 mm.

Using methods developed for rapid biological inventories (Vriesendrop et al. 2004; Shanee 2011a) surveys took place in forests of varying size, from isolated forests of ~400 ha to areas of contiguous forest. Data were gathered using a combination of field surveys and key-informant interviews. Field surveys took between 3 and 7 days at each site with multiple visits to most sites. The location of all sites was recorded with a handheld GPS, as were points of visual, audio or incidental. Secondary data on species occurrence was gathered from local informants. Photographs and drawings of primate species were used to aid identification. All identifications were cross referenced between several informants.

Peruvian Primates at High Altitudes

The majority of Peruvian primates are found in the eastern Amazonian lowlands (Aquino and Encarnacion 1994), but many of these ‘lowland’ species have distributions that include mid and high altitude sites. Two species, the white fronted capuchin (*Cebus albifrons*) and common squirrel monkey (*Saimiri sciureus*), have trans-Andean distributions, both in the far north of the country where the Andean cordillera is at its lowest (Aquino and Encarnacion 1994; Encarnacion and Cook 1998; Amazon et al. 2003), with two more Amazonian species, the red howler monkey (*Alouatta seniculus*) and Spix’s night monkey (*Aotus vociferans*), found in the northern inter-Andean valleys of the *Santuario Nacional Tabaconas-Namballe* (Fig. 2) to elevations over 2,000 m.a.s.l. (Amazon et al. 2003). Only the mantled howler monkey (*Alouatta palliate*) is restricted to the western slopes of the Andes. In the *Parque Nacional Cerros de Amotape* (Fig. 2) *A. palliata* occurs at elevations up to 800 m.a.s.l., although in our own observations and those of other researchers in neighbouring Ecuador and Costa Rica have recorded this species in excess of 2,000 m.a.s.l. (Encarnacion and Cook 1998; Fedigan et al. 1998; Gavilanez-Estrada 2006; Hughes 2006).

The only member of the Callitrichidae found at high altitude sites in Peru is the saddle-back tamarin (*Saguinus fuscicollis*), and it is also the only small-bodied primate (Table 1) found outside the Amazon lowlands in Peru (Vriesendrop et al. 2004). With a wide lowland distribution, *S. fuscicollis* has also been reported at higher altitudes in the *Parque Nacional Megantoni* (Fig. 2) (Vriesendrop et al. 2004) and is probably present throughout the Yungas up to approximately 1,800 m.a.s.l. (Hershkovitz 1977; Aquino and Encarnacion 1994) although our surveys have not recorded this species above 1,000 m.a.s.l. Both of Peru’s squirrel monkey species, *S. sciureus* and *S. boliviensis,* and capuchin species, *C. albifrons* and *C. apella*, are found at high altitude sites throughout their distributions (Grimwood 1968; Aquino and Encarnacion 1994; INRENA 2002a, b; Amazon et al. 2003; INRENA 2003; Vriesendrop et al. 2004; Shanee 2011a). We also found that both *Cebus* spp. are commonly found well above 2,000 m.a.s.l. throughout Amazonas and San Martin departments. Three owl monkey species are found at high elevation sites: *A. vociferans*, in the northern Andes and the black-headed night monkey (*A. nigriceps*) in the southern Andes (INRENA 2002a). Nancy Ma’s night monkey (*A. nancymae*) (cited as *A. trivigatus*) possibly occurs at high elevation sites, although the locality, in *Parque Nacional Otishi* (Fig. 2) (INRENA 2002b) is more likely to be *A. nigriceps. Aotus miconax*, one of Peru’s endemic primates, is restricted to high altitude forests in the countries northeast at altitudes between 1,000 and 3,100 m.a.s.l. (Aquino and Encarnacion 1994; Butchart et al. 1995; Cornejo et al. 2008; Campbell 2011; Shanee 2011a; Shanee and Shanee 2011). The Andean titi monkey (*Callicebus oenanthe*) is another attitudinally restricted species; endemic to the region of San Martin, it is found at intermediate altitudes up to approximately 1,200 m.a.s.l. (Bóveda-Penalba et al. 2009; Shanee et al. 2011). Our surveys found this species to be common up to approximately 1,100 m.a.s.l. in two locations (Table 1).

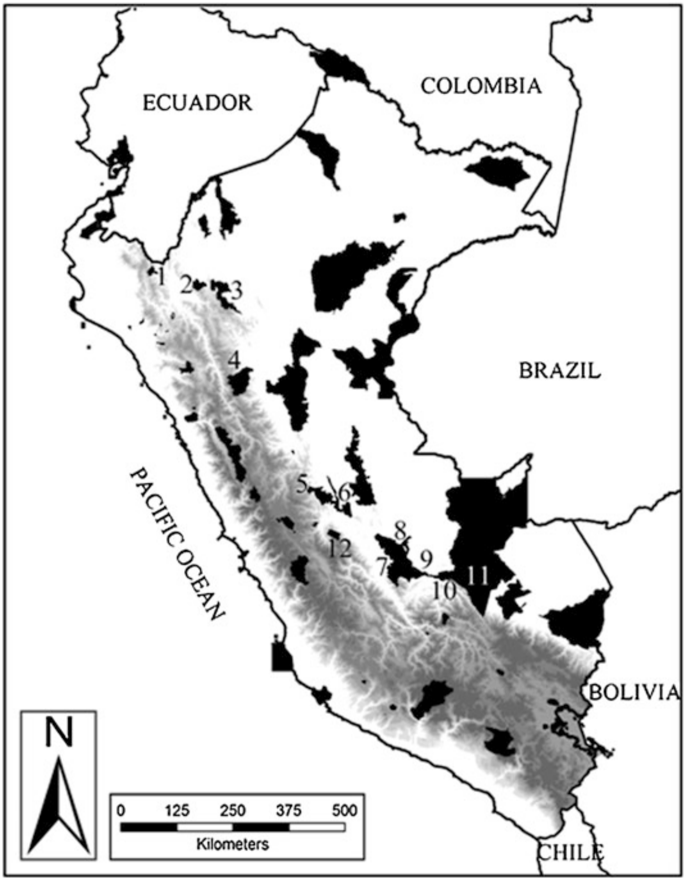

Fig. 2 National State Protected Area System (SINANPE), showing major protected areas within the distribution of Andean primates: *1* Santuarion Nacional Tabaconas-Namballe; *2* Santuario Nacional Cordillera Colan; *3* Bosque proteccion Alto Mayo; *4* Parque Nacional Rio Abiseo; *5* Reserva Comunal Yanesh; *6* Bosque de Proteccion de San Matias San Carlos; *7* Parque Nacional Otishi; *8* Reserva Comunal Machiguenga; *9* Reserva Comunal Ashaninka; *10* Santuario Nacional Megantoni; *11* Parque Nacional del Manu; *12* Bosque de Proteccion Pui Pui

The most common family of primates found at high altitudes in Peru is the Atelidae. Both Peruvian spider monkey species, *Ateles belzebuth* (INRENA 2003; Shanee 2011a) and *A. chamek* are commonly found at elevations of 2,000 m.a.s.l. (INRENA 2002a, b). During field surveys we observed of *A. belzebuth* at many locations reaching 1,800 m.a.s.l. *A. seniculus* is widely distributed throughout the cloud forests of the eastern cordillera at altitudes up to approximately 3,000 m.a.s.l. (Grimwood 1968; Aquino and Encarnacion 1994; INRENA 2002b; Amazon et al. 2003; INRENA 2003; Vriesendrop et al. 2004), and has been found at 3,200 m.a.s.l. in the Colombian Andes (Hernandez-Camacho and Cooper 1976; Defler 2004). In the north of Peru we observed *A. seniculus* up to 1,700 m.a.s.l. in

Table 1 Ecological characteristics of primates found at high altitudes in Peru

Species	IUCN redlist status	Highest altitude (meters above sea level)	Average body weight (g)[a]	Primary dietary components[b]
Alouatta palliata	LC	<800	6,200	Leaves
Alouatta seniculus	LC	>2,000	5,750	Leaves
Aotus miconax	VU	>3,000	Not available	Fruit, insects
Aotus nigriceps	LC	>1,500	900	Fruit, leaves
Aotus vociferans	LC	>2,000	650	Fruit, leaves
Ateles belzebuth	EN	>2,000	8,150	Frugivore
Ateles chamek	EN	>2,100	8,150	Frugivore
Callicebus oenanthe	CR	~1,100	Not available (similar to other *Callicebus* spp., ~1,000)	Not available (similar to other *Callicebus* spp., fruit, leaves)
Cebus albifrons	LC	>2,000	2,100	Fruit, insects
Cebus apella	LC	>2,000	2,600	Fruit, insects
Lagothrix cana	EN	~2,600	8,500	Fruit, leaves
Lagothrix poeppigii	VU	<3,000	5,800	Fruit, leaves
Oreonax flavicauda	CR	~2,800	10,000	Fruit, leaves
Saguinus fuscicollis	LC	~1,500	350	Fruit, exudates
Saimiri boliviensis	LC	>2,000	800	Fruit, insects
Saimiri sciureus	LC	~1,400	650	Fruit, insects

[a] Authors calculation of average body weights given in Campbell (2011), Rowe and Myers (2012)

[b] Dietary data taken from Campbell (2011)

a number of locations. This species has also been found at higher elevations in Colombia (Hernandez-Camacho and Cooper 1976; Crockett 1998). Three of Peru's four woolly monkey species, *Lagothrix poeppigii*, *L. cana* and *Oreonax flavicauda*, have high altitude distributions. Both the distributions of *L. cana* and *O. flavicauda* reach nearly 3,000 m.a.s.l., with *L. poeppigii* reaching just over 1,000 m.a.s.l. (Grimwood 1968; Aquino and Encarnacion 1994; Vriesendrop et al. 2004; Shanee 2011a). Woolly monkey diets are highly variable between species (DiFiore and Campbell 2010). In previous studies, fruit accounted for 70–80 % of the diets of *L. lagotricha* and *L. poeppigii* (Defler and Defler 1996; DiFiore 1997; Dew 2001; DiFiore 2004), whereas *O. flavicauda* and *L. cana* were found to rely much less on fruits, including greater amounts of leaves, buds and insects in their diets (Peres 1994; Shanee S. In press). This suggests that the general reduction in resource quality and quantity available to frugivorous consumers at higher elevations (Durham 1975; Caldecott 1980; Marshall et al. 2005) could be the limiting factor in the altitudinal distributions of *L. lagotricha* and *L. poeppigii*.

With the notable exception of Peru's three endemic primates all other primate species in Peru are primarily found at lowland sites (Aquino and Encarnacion 1994). For the lowland distributions of these species it is probably the historical presence of barriers such as major rivers and changes is habitat structure that are the determining factors in their current distributions (Ayres and Clutton-Brock 1992; Peres et al. 1996; Silva and Oren 1996). However, the effect of riverine barriers is greatly reduced at the head waters of the major river systems (Ayres and Clutton-Brock 1992; Peres et al. 1996), such as those of the Peruvian Andes (Fig. 1). However, the cutting action of larger rivers in the Andes leaves were very steep valleys, often of bare rock with little vegetation, which can act as effective barriers to dispersal.

The presence of these predominantly lowland species at sites with lower temperatures, higher solar radiation, reduced resource availability and other ecological impacts of increased altitude (Durham 1975; Caldecott 1980; Lawes 1992; Marshall et al. 2005; Shanee and Peck 2008; Beck et al. 2010) seems to be a case of outlying populations expanding their distributions, either naturally or under anthropogenic pressures, to areas with sub-optimal conditions. Indeed, several studies have reported lower densities and abundance of frugivorous primates with increasing altitudes in South America (Durham 1975; Aquino and Encarnación 1988; Geise et al. 2004; Shanee 2009), Africa (Marshall et al. 2005) and Asia (Caldecott 1980). The effect on folivorous primates is less clear (Marshall et al. 2005) as the effects of high altitudes on leaf abundance is less pronounced (Marshall et al. 2005).

Andean Endemic Primates

Peru has three endemic primate species: the yellow-tailed woolly monkey (*O. flavicauda*), the Peruvian night monkey (*A. miconax*) and the Andean titi monkey (*C. oenanthe*). All three species are endemic to the country's north-eastern

Andean forests. This centre of primate endemism lies at the heart of the Tropical Andes Biodiversity Hotspot, a global centre of biodiversity and endemism for all types of flora and fauna (Myers et al. 2000; Myers 2003).

O. flavicauda is listed as Endangered on Appendix I CITES (2012) and as Critically Endangered (A4c) by the IUCN (2011). It has also featured on the list of the World's 25 Most Endangered Primates continuously since 2006 (Mittermeier et al. 2009). The authors estimate a species population loss of 60–80 % in the last 30 years, with at least 56 % habitat loss (Buckingham and Shanee 2009). *O. flavicauda* has a very limited geographical range within the Departments of Amazonas and San Martín. There are also populations in bordering areas of the Departments of Huánuco, La Libertad and possibly Loreto (Graves and O'Neill 1980; Parker and Barkley 1981; Shanee 2011a) from approximately 5°25′S south to 9°00′S, and 6°22′W west to 77°40′W (Shanee 2011a) in an area approximately 6,854 km^2 (Shanee and Shanee In press). The species is found only in pre-montane and montane cloud forests between 1,500 and 2,700 m.a.s.l. (Leo Luna 1980; Aquino and Encarnacion 1994; Buckingham and Shanee 2009; Shanee 2011a). We recently observed a small population of this species at approximately 1,000 m.a.s.l. in the south of San Martin department, the first record of this species at such a low altitude.

A. miconax is listed on Appendix II of CITES (2012) and as Vulnerable (A2c) by the IUCN (2012). No reliable estimates exist on this species population size or actual conservation status, although its population is almost certainly declining due to habitat loss (personal observation). It is largely sympatric with *O. flavicauda* throughout its range (Shanee 2011a). This species is also restricted to pre-montane and montane cloud forest habitat in the Departments of Amazonas, Huánuco, La Libertad, Loreto and San Martin (Aquino and Encarnacion 1994; Cornejo et al. 2008; Shanee 2011a). It is thought that the distribution of *A. miconax* is larger than that of *O. flavicauda*, with observations between 1,500 and 3,100 m.a.s.l. (Thomas 1927; Campbell 2011) from approximately 5°25′S south to 10°00′S, although no studies have been made of the species actual distribution. Based on our continuing surveys and estimates of remaining habitat this species current distribution, given available habitat, is unlikely to exceed 13,000 km^2.

O. flavicauda and *A. miconax* have distributions limited by the lowlands of the Huallaga river valley and the highlands between the Huallaga and Maranon river valleys (Fig. 3) (Shanee 2011a). This area is also a sub-centre of species endemism within the Tropical Andes of Peru with many other endemic species (Cracraft 1985; Smith and Yacher 2008). Within the Huallaga-Maranon landscape these species are limited by changes in habitat type, with increasing and decreasing altitudes related to changes in climate and soil type. Both species distributions are highly habitat dependent and are largely restricted to *Ficus spp.* dominated forests (Clark 2009; Shanee 2011a). During field surveys we found both species to be scarce in areas of white sand forest and absent from certain areas dominated by *Podocarpus spp.* where *Ficus spp.* is absent, this is true even in areas of predicted habitat within their altitudinal, climatic and latitudinal limits.

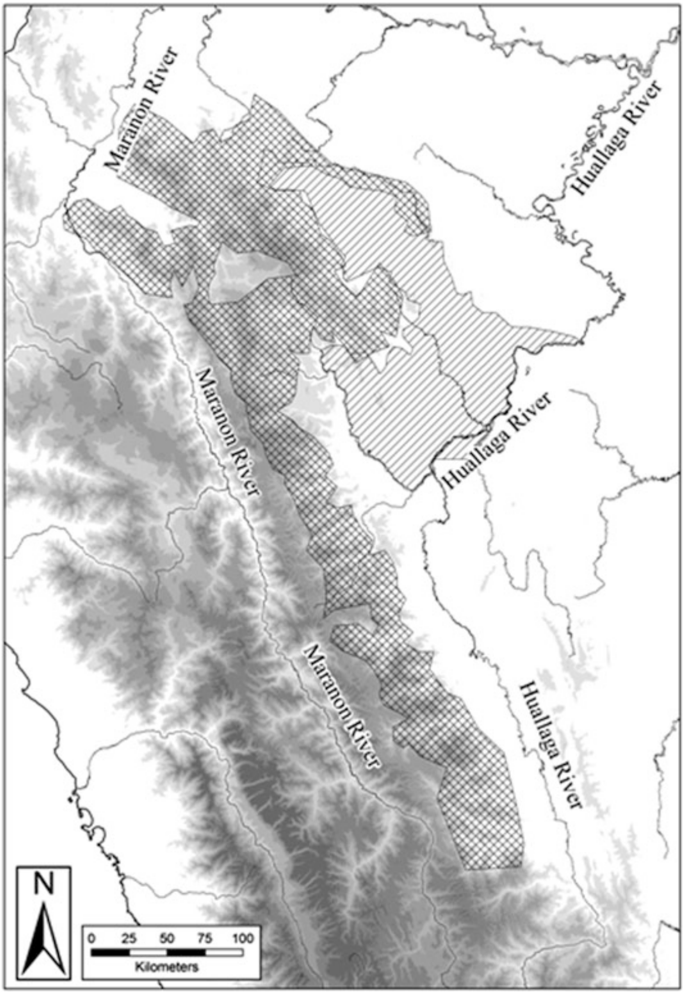

Fig. 3 Maranon-Huallaga landscape showing the distribution of Peru's endemic primate species: Yellow-tailed woolly monkey (*Oreonax flavicauda*) and Peruvian night monkey (*Aotus miconax*) shown as 10 % cross-hatch, Andean titi monkey (*Callicebus oenanthe*) shown as 10 % simple hatch

The Andean titi monkey (*C. oenanthe*) has an attitudinally restricted range in the Rio Mayo valley and the western side of the central Rio Huallaga valley in San Martin between 500 and 1,200 m.a.s.l. (Bóveda-Penalba et al. 2009; Shanee et al. 2011), within an area approximately 6,515 km^2 (Shanee et al. 2011). Although not strictly a high altitude primate, *C. oenanthe* is endemic to the same biogeographical area as *O. flavicauda* and *A. miconax,* and its evolution was probably subject to the same environmental pressures. Possibly the biological and ecological constraints of *Callicebus spp.* prevent its extension into higher altitude forests although as yet no studies have tried to determine the reason for this. Similarly, no other *Callicebus spp.* have been reported at high altitude sites in Peru.

Recent phylogenetic analyses put the estimated time of speciation of *O. flavicauda* from its last common ancestor with other woolly monkeys at 2.6 mya (Chaves et al. 2012). At this time it is possible that the Maranon-Huallaga landscape was the location of forest refugia during climatic shifts (Bush 1994; Josse et al. 2011) which also coincide with the final uplift of the northern Andes (Gregory-Wodzicki 2000). Combined, these two factors could have played a major role in isolating the Maranon-Huallaga landscape, leading to the speciation and current biogeography of Peru's high altitude and endemic primates.

Conservation in the Andes

An estimated 4.5 million people live in the Peruvian *Yungas* (CDC-UNALM and TNC 2006), many of the recent migrants from neighbouring highland and lowland regions (INEI 2007). The subsistence and developmental needs of these people place growing pressures on forests. According to Peruvian government publications, by the year 2000, Peru had lost 7,172,953 ha (10.3 %) of its original forest cover. The Departments 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 are the main habitat for Peru's three endemic primate species (Leo Luna 1980, 1987; Cornejo et al. 2008; Bóveda-Penalba et al. 2009; Shanee 2011a; Shanee et al. 2011, 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 methods (Soto et al. 1995; Juo and Manu 1996; McDonald et al. 2002; Rumpel et al. 2006). Although many different crops are farmed in the Peruvian Andes, cattle ranching is the main cause of deforestation and biodiversity loss (Kaimowitz 1996; Steinfeld et al. 2006; Shanee 2012a).

Cloud forests are naturally fragmented on steep slopes and peaks, creating a mosaic of isolated ecological niches (Young and Leon 1999). Deforestation patterns further fragment the land, often leaving only islands of natural vegetation on mountain tops and ridges (Bubb et al. 2004). This further restricts wildlife but also exposes them to increased hunting pressure by local people and studies have shown an increase in zoonosis and capture during terrestrial movement (DiFiore 2002; Perea-Rodriguez et al. 2010; Shanee and Shanee 2011). Preliminary results from our studies of parasite load in *A. miconax* and *O. flavicauda* show a significant increase in gastrointestinal parasites in groups living in forest fragments and forest edges compared to those in larger forest interiors. Forest patches can also exceed carrying capacity for a species, resulting in a population crash or selective pressures reducing population numbers (Cowlishaw and Dunbar 2000). Moreover, many primate populations survive in totally isolated forest fragments (Shanee et al. 2007, 2011; Shanee 2011b; Shanee and Shanee 2011), increasing the risk of genetic drift through inbreeding (Frankham 1995; Marsh 2003). Isolated forest patches also increase accessibility for hunters, putting extra pressure on large-bodied primates that are often hunted for subsistence or trade (Robinson and Bodmer 1999; Peres 2001; Tabarelli and Peres 2002; Shanee 2012b).

Mining in Peru occurs mainly in the mineral rich Andes (Dourojeanni et al. 2009). In many cases this has a direct effect on Andean primate habitat via deforestation, river diversion, contamination and major landslides. Another impact of mining at higher elevations is land conflict which drives mass migration from the highlands towards the Peruvian *Yungas* (Schjellerup 2000; Bury 2007; Bebbington and Bury 2009). Mining operations, occupying the most fertile lands of the high Andes, in combination with large-scale industrialised agriculture in much of the lowlands further pushes farmers into Andean forests (Bury 2007; Bebbington 2009; Shanee 2012a). There are about 45,000 mining concessions in Peru, covering approximately 192,000 km^2, (about 15 % of the national territory), with the majority of these in the highlands and *Yungas*. However, few of these mines are operational, and therefore the full extent of their impact is difficult to assess. Legal loopholes, lack of supervision and imperfect environmental controls are common in Peru, generating social and environmental damage, even in the exploration stage (Dietsche et al. 2007; Arellano-Yanguas 2008; Shanee 2012a). The contribution of these operations to land degradation goes beyond direct deforestation and pollution. Indirect influences through road building and the attraction of a migrant work force lead to increased deforestation, habitat fragmentation and hunting (McMahon and Remy 2001).

Roads are a common cause of deforestation and forest degradation (Dourojeanni 1981; Young 1994; Dourojeanni et al. 2009; CIAT 2012), through intensified migratory agriculture and logging (Fearnside 1986), increased forest fires (Nepstad et al. 2001) and wildlife traffic (Peres and Terborgh 1995; Wilkie et al. 2000). Humid montane forests are especially vulnerable to the ravages of road construction, putting specialised species at greater risk (Young 1994). Studies in the Peruvian Andes show a high probability of deforestation up to 10 km either side of roads, an effect that only diminishes when valleys are particularly steep (CDC-UNALM 2004; CIAT 2012). In lowland Amazonia some degree of deforestation can reach up to 100 km from paved highways (Laurance et al. 2001, 2002). Hunting is also aided by road construction with hunting occurring anywhere within 9 km of any access point (Jerozolimski and Peres 2003). Leo Luna (1987) estimated that approximately 600 yellow-tailed woolly monkeys were hunted between the mid-1970s to the mid-1980s, causing the local extinction of several populations. Our surveys, carried out between 2007 and 2011, recorded 23 *O. flavicauda* infants extracted from the wild in San Martin and Amazonas (Shanee 2012b). For every infant removed from the wild at least one individual, the mother, has been killed, greatly increasing the impact of hunting for the pet trade (Shanee 2012b). This is a minimum estimate, for great Apes it is estimated that 10 individuals are killed for every individual that enters the pet trade (BCTF 2013). Also, our data does not include hunting in indigenous communities which are reported to heavily hunt this species for bushmeat (DeLuycker 2007; Shanee et al. 2007). *C. oenanthe* and *A. miconax* are smaller species; therefore, they are less hunted for bushmeat but are hunted for the pet trade (Shanee 2012b).

Researchers predict a chain reaction of climate change effects will further endanger Andean primates and their habitat. These include a significant upslope shift of lower altitude ecosystems and species; reduced cloud immersion by vegetation; recurring droughts and extreme rains; intensification of catastrophic wildfires and alterations in plant phenologies (Bawa and Dayanandan 1998; Corlett and Lafrankie 1998; Chapman and Peres 2001; McCarty 2001; Bubb et al. 2004; Lenoir et al. 2008; Fisher 2011). The imbalance produced by these processes could lead to a dramatic decline in food supply and limit primate reproductive success (Bawa and Dayanandan 1998; Wright 2007). Consequently montane forest endemic species, because of their restricted altitudinal ranges, would be more prone to extinction (Foster 2001; van der Hammen 2005; Malhi et al. 2008). The increasing effects of climate change and land degradation also increase pressure on farmers who need to increase efforts to maintain the same levels of production, thus leading to more clearing, uncontrolled burning and illegal resource use and thus the pressure spirals back on the environment (Laurance and Williamson 2001; Young and Lipton 2006; Shanee 2012a).

Conclusions

The biogeography of Andean primates in Peru is the result of the complex relationship between geographical, historical and ecological factors. Many species have population distributions in both the lowlands and higher altitude areas. The presence of lowland species at higher sites seems to be a case of outlying populations expanding their distributions, either naturally or due to anthropogenic pressures, to areas with sub-optimal conditions.

The montane clouds forests of the Tropical Andes are under threat from a series of anthropogenic factors including road construction, mining, cattle ranching and agriculture. These factors have a direct impact on this fragile habitat as it is driven by mass immigration of people to the area exploiting the natural resources, causing widespread deforestation and fragmentation. The subsequent effect on wildlife is reduced dispersal and genetic flow and increased pressure from hunting for sustenance and trade. Holistic, political solutions tackling unsustainable exploitive practices in the highlands and industrial monocultures in the lowlands need to be implemented to tackle the root causes of mass migration.

Climate change is also predicted to impact attitudinally restricted species and habitats globally (Pounds et al. 1999; Foster 2001; Vuille et al. 2003; Bertin 2008; Fisher 2011). The migration of lowland species to higher altitudes may not only force ‘higher’ species from their habitat but also offer only a short-term solution to the survival of ‘lowland’ species (Fisher 2011). High altitude areas offer sub-optimal conditions for many species including reduced space, ecological quality and resource availability. As changes in climate show increasing trends, it is possible that they will become one of the main threats to primates dwelling at higher altitudes.

To ensure the survival of Peru's Andean primate fauna and in particular its three endemic species, attention to future research and conservation actions should highlight the effects of climate change on habitats. If habitats do migrate upslope as predicted then protection should be afforded to the largest contiguous areas of suitable habitat for Andean species with emphasis on reducing isolation of populations on small mountain top islands.

More studies on the current and historical biogeography of primates in the Peruvian Andes are required and in particular what factors influenced the distribution patterns of the country's three endemic primate species and how this information can be used to help with future conservation strategies.

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Population Density and Ecological Traits of Highland Woolly Monkeys at Cueva de los Guacharos National Park, Colombia

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Introduction

There is a large variation in population density of New World monkeys (Emmons 1983). Hunting and fruit production of key resources are an important limiting factor for large species ranging in undisturbed environments (Stevenson 2001; Peres and Palacios 2007). However, conservation plans for endangered species are difficult to carry out for populations from which we lack basic ecological information (e.g., sites with enough resources to sustain a viable population). The most endangered Neotropical primates belong to the family Atelidae, which includes several large and critically endangered taxa (e.g., *Lagothrix lagothricha lugens, Ateles hybridus, Brachyteles hypoxanthus*, and *Oreonax flavicauda*; IUCN 2008). These species tend to be susceptible to forest destruction and hunting (Defler 2004; Peres and Palacios 2007). For instance, woolly monkeys have long maturation times and long inter-birth intervals, with an average of 36.7 months (Nishimura 2003), which makes them susceptible for population declines. In order to conserve these endangered primates and their habitats, we need more information on their distribution, population densities, and ecology. Woolly monkeys, as other primates, are important seed dispersers in Neotropical forests (Stevenson 2000, 2007; Russo and Augspurger 2004; Dew 2005; Link and Di Fiore 2006). Therefore, the role of Atelines seems to be relevant in maintaining plant diversity due to their roles in forest regeneration (Stevenson 2011). This function might come to an end with the decline or local extinctions of their populations.

Neotropical primates live in seasonal environments where food abundance varies throughout the year. Thus, their social structure exhibits some flexibility and this is reflected on behavioral responses to different ecological conditions (Jones 2005). Additionally, atelines belong to a subfamily with a wide variation in the use

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of space, diet, and foraging strategies (Di Fiore et al. 2011). Although these species prefer fruits when available, diet composition has been observed to vary. For instance, Muriquies (*Brachyteles*) may consume mostly leaves during times of fruit scarcity (Di Fiore et al. 2011). Spider monkeys also complement their diet with young leaves in times of low fruit availability (Di Fiore et al. 2011). Woolly monkeys rely heavily on fruits, which make up at least 60 % of their total feeding time, and they increase leaf consumption in scarcity periods (Defler 2004; Stevenson 2006). In some populations, they include a significant amount (up to 23 %) of arthropods in their diet (Stevenson 1992), which is not a common dietary item within Atelids. Furthermore, they include unripe fruits, flowers, and small vertebrates, but the relative importance of these items varies with temporal and spatial scales (Stevenson et al. 1994).

L. l. lugens inhabits lowland forests in the upper Amazon basin and Andean forest in Colombia (Defler 2004; Botero et al. 2010), reaching altitudes up to 3.000 m above sea level (Hernandez-Camacho and Cooper 1976). Most studies on woolly monkeys have been carried out in lowlands due to the fact that most of research stations are in lowlands and information on the behavior, diet and population status of mountain populations is needed. For instance, densities are necessary to estimate demographic changes that lead to extinction for a particular population. Furthermore, resource quality, quantity, and seasonal food availability are important factors limiting natural primate populations (Stevenson 2001; Brugiere et al. 2002; Hanya et al. 2011). Available reproductive and vegetative plant parts are resources that vary in time, thus creating abundance and scarcity periods for consumers (van Schaik et al. 1993). This resource variation is usually associated with changes in the behavior of frugivorous primates. For example, woolly monkeys' daily path length tends to be higher during periods of fruit abundance (Stevenson 2006), because they usually follow an energy maximizing strategy in abundance periods, and change to energy minimizing strategies in scarcity periods (Di Fiore and Rodman 2001; Stevenson 2006). However, in a woolly monkey population in the Caparú Biological Station (Colombia), the pattern is different, since groups have to move large daily paths even in scarcity periods (González and Stevenson 2011). This pattern can be explained by a low general productivity and differences in crop size.

It has also been suggested that forest productivity influences primate diversity and density (Kay et al. 1997; Stevenson 2001). Then, population density estimates are needed to evaluate their long-term viability and to determine management and conservation priorities (Defler and Pintor 1985; Chiarello and de Melo 2001). It is important to study the density and behavior of Colombian woolly monkeys in highlands, since the Andean Mountains include a large part of their geographical distribution (Defler 2004), and there are no studies in this type of habitat.

Therefore, the main aim of this study was to estimate population densities of *L. l. lugens* at Cueva de los Guacharos National Park, and to gather preliminary data on habitat use, diet, and activity patterns of one group of woolly monkeys.

We hypothesized that forests productivity falls with height over sea level (Kitayama 2002), and hence, we predict that fruit production as population densities of woolly monkeys will be lower in the study site than in lowlands. We also predicted that primate densities and the abundance of other frugivores will be higher in Sub-Andean than in oak forest, because the latter are dominated by black oaks (Prada 2011), which do not produce fleshy fruits.

In addition, woolly monkeys have been described as fruit generalist that avoid some fruits with secondary chemical compounds (Stevenson 2004), therefore we predict that they would eat of the most common fleshy fruits in the environment and probably from different species than in lowlands, since the floristic composition changes with altitude (Gentry 1988). Due to floristic composition change, we predict a less diverse fruit diet than in lowlands.

Methodology

Study Site

The study was carried out in Cueva de los Guacharos National Park, located in the south of the Huila department in Colombia (N 1° 36′ 57.1314″, W 76° 6′ 7.38″), in the Municipality of Acevedo at approximately 2,000 m.a.s.l., from July 2009 to July 2010. The predominant habit is primary and secondary Sub-Andean forest; mostly composed by open canopy forest that rarely exceeds 30 m; this includes two different type of oak forest (Vásquez and Serrano 2009). We measured rainfall and temperature at the study site between July 2009 and June 2010. We found an estimate of 2,284 mm annual precipitation and a mean temperature of 18.8 °C (Fig. 1). The rainy season comprised most part of the year (February to October), and the dry season was between November and January.

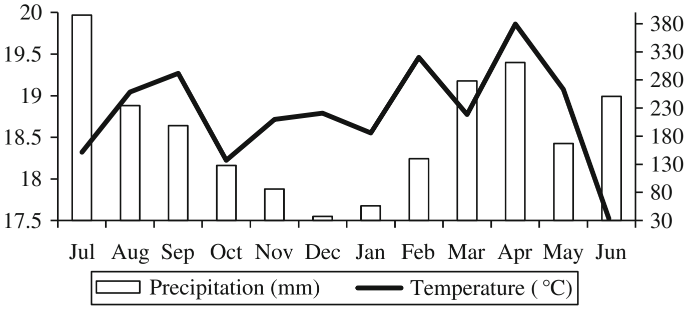

Fig. 1 Monthly variation in precipitation (*bars*) and mean temperature (*line*) at Cueva de los Guacharos National Park, Colombia, from July of 2009 to June of 2010

Data Collection

Primate Density

We carried out linear transects to estimate the population density of woolly monkeys and other frugivores at the main forest types (black oak forests and Sub-Andean forests). We recorded date, transect, as well as the starting and ending time of each census (Peres 1999), most of the census were done between 7:30 and 9:00 am, except for special occasions (for instance, rainy days). Upon detection of an animal, we recorded the distance between the first animal observed and the researcher's location and we estimated perpendicular distances between the animal and the transect. Furthermore, we noted subgroup size and sighting location along the transect. We used 10 transects (total of 11.6 km) (Fig. 2) that were visited once a month during the study period, to obtain a total of 139.2 km walked distance from a total of 120 samples. The mean density of groups was estimated for each transect using the king's method and we report the average for all transects (distinguishing between oak forests and other Sub-Andean forests). Then, we estimated population densities per individual, by multiplying group density by the average number of individual seen per subgroup (i.e., sightings from the transect).

Phenology

Fruit abundance was estimated using 12 phenological transects (450 m each one) of 5.4 km in total length (Stevenson 2002), which were monitored each month. For each tree dropping fruits over the transect, we recorded the perpendicular distance between the trunk and the transect, diameter at breast height (DBH) and species. Visually, we estimated the fruit crop size for each tree, this estimation was corrected using the slope of the relation between visual and real estimats (Stevenson 2002). To calculate productivity we weighed 10 dried fruits of each species and calculated the average for each one. We also estimated the effective sampling area, this was calculated such as the effective width for every species by long transect (Stevenson 2004). Unidentified plant species were collected and vouchers deposited in various museums and herbaria (e.g., Universidad de Los Andes and Herbario Nacional Colombiano).

Behavior

To record behavioral events, we used instantaneous samples every 10 min on a focal monkey. Focal follows from dawn to dusk were conducted for at least 5 days each month, and focal sessions were of variable duration (when a focal individual

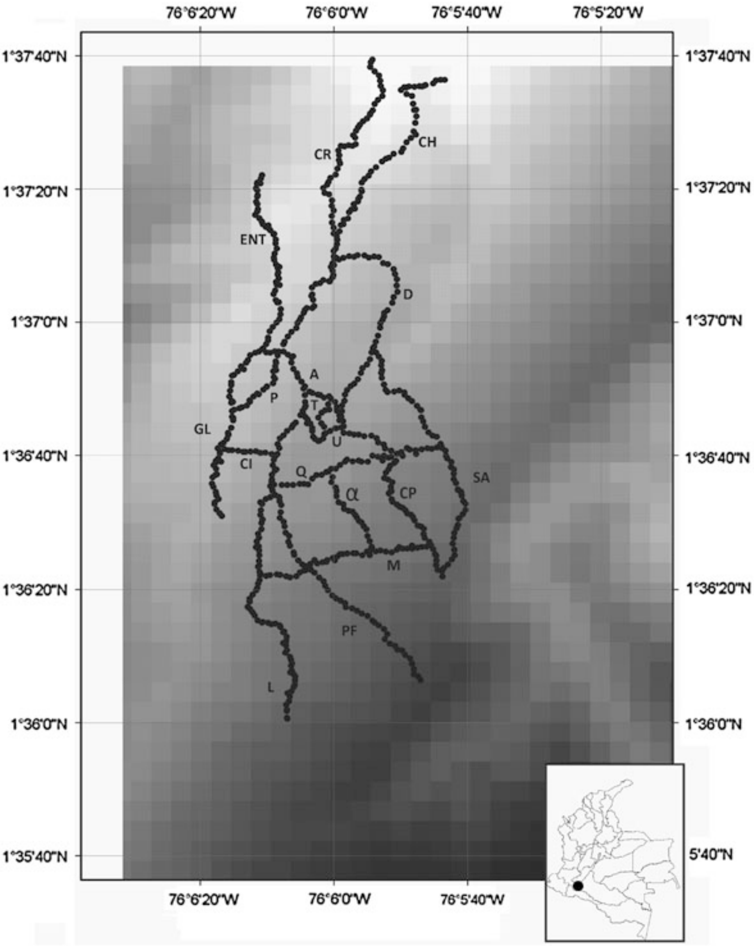

Fig. 2 Map of the trails of the Guacharos National Park used in this study. The black dot indicates the location of the Park, at the south Andean region of Colombia

was lost an individual of the same age/sex was used as replacement within 10 min). Individuals were distinguished based on markings (facial traits, broken fingers, scars, and natural spots in the genitals), age, and sex categories. Activities were categorized as: moving, resting, feeding, and social interactions (Stevenson et al. 1994; González and Stevenson 2011). Feeding was classified in the following categories: Ripe fruit, unripe fruit, young leaves, mature leaves, flowers, arthropods, and others. We recorded the spatial location of the focal animal for each 30 min, using a GPS in order to estimate home ranges and daily travel routes.

Diet

We recorded continuously all plant items consumed by the monkeys during the focal events. For each feeding event we registered the feeding time, plant species and part consumed. The proportion of arthropods in the diet was estimated based only on instantaneous records every 10 min.

Results

Population Densities

We estimated a density of woolly monkeys in Guacharos National Park as 18.4 individuals/km^2. However, different forest types showed contrasting density of woolly monkeys. In particular, black oak forests showed depopulated levels of frugivore densities (Table 1), and no observations of woolly monkeys were made in this kind of forest. Similarly, during focal follows, woolly monkeys never entered this type of habitat. Considering other Sub-Andean forests where they were observed, the population density of woolly monkeys was 20.5 individuals/km^2. Other diurnal mammals and large birds relatively abundant in transects were *Sciurus cf. pucheranii*, *Aburria aburii*, and *Rupicola peruviana*. Other diurnal primates were present at low densities (*Alouatta seniculus*: 3.93 individuals/km^2 and *Cebus apella* 1.41 individuals/km^2). A small population of squirrel monkeys was also registered outside census sampling.

Productivity

Fruit abundance varied considerably during different months of the year. The lowest production was observed between September and December, and in April. The scarcity periods were characterized by production of individuals with small crops (although numerous plants in some cases). We found three peaks of productivity, one in July and August, coinciding with the production of as *Cissus trianae* (Vitaceae) and *Tapirira sp*. (Anacardiaceae), a second between January and March that matches with production of *Tapirira sp*. and *Nectandra cf. purpurea*, the third in June which coincides with production of *Miconia sp*. (Fig. 3). Overall, 88 plant species grouped in 68 Genera from 36 families were registered producing mature fruits in transects, representing 327 kg.ha^{-1} year^{-1}. An important fact to consider is that four species represent half of total productivity, and these are equivalent to 4.6 % of all recorded species.

Table 1 Population density estimates for the diurnal mammals and large frugivorous birds recorded in the transects at Cueva de Los Guacharos National Park

	Species		*Alouatta seniculus*	*Cebus apella*	*Lagothrix lugens*	*Dasyprocta punctata*	*Sciurus cf. pucheranii*	*Aburria aburri*	*Rupicola peruviana*
Forest type	Transect	Width (m) Length (m)	6.83	14.33	21.00	1.00	2.18	6.59	4.8
Mature	CP	1,000	0.00	0.00	7.14	0.00	11.5	7.59	0.0
Old growth	CR	1,500	0.00	0.00	3.34	0.00	24.1	2.66	59.0
Old growth	Ent	2,200	3.99	1.27	0.43	9.09	12.5	2.76	32.5
Old growth	G-Gl	925	0.00	0.00	3.22	0.00	93.0	20.51	14.2
Old growth	GL	300	0.00	0.00	0.00	0.00	382.3	0.00	87.6
Old growth	Gu	625	13.02	0.00	0.00	0.00	40.8	40.48	18.7
Mature	L	1,200	0.00	0.00	19.84	0.00	0.0	63.24	0.0
Mature	PF	1,000	0.00	0.00	4.33	0.00	20.9	6.90	0.0
Mature	SA	1,900	0.00	0.00	3.13	0.00	0.0	29.96	0.0
Mature	Q	900	0.00	0.00	0.00	0.00	51.0	33.73	23.4
		Mean	1.70	0.13	4.14	0.91	63.60	20.78	23.53
		Weighted	1.43	0.24	4.23	1.69	27.2	17.02	17.8
	Group density/km^2		2.75	6.00	4.85	1.00	1.00	1.44	1.32
Individual	*density/km^2*		*3.93*	*1.41*	*20.54*	*1.69*	*27.19*	*24.58*	*23.57*
	Standard deviation		11.00	2.00	29.00	3.00	39.00	115.00	39.00
Oak Forest	R	2,000	0.00	0.00	0.00	0.00	0.0	0.00	0.0

Transects were monitored between July 2009 and July 2010. The main forest types correspond to black oak forests and Sub-Andean forests, which include mature and old growth forests. *Note* None of these species were observed on forests dominated by oaks (in 2.0 km of transects)

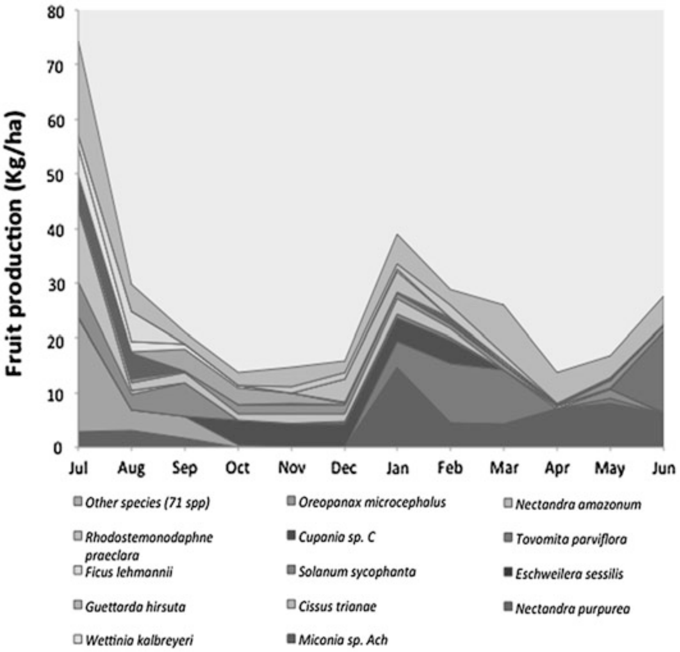

Fig. 3 Monthly variations in fruit production at Cueva de los Guacharos National Park, Colombia. Each pattern represents the production of the most productive species and the upper part combines information of less productive species, such that the upper line represents the overall production in Sub-Andean forests

Activity Patterns

We observed that woolly monkeys resting in 29.5 % of the monthly records, moving in 42.3 %, feeding in 25.5 % and engaged in social behavior is 2.7 %. The activity budgets varied across the year (Fig. 4). In the second semester (August to December) of 2009 the monkeys spent more time resting, and in the first semester (January to June) of 2010 they spent more time moving. Woolly monkeys used the first hours in the morning for resting and the afternoon for moving. In particular, we observed peaks of resting between 6 to 7 a.m. and 5 to 6 p.m. We registered more social interactions between 12 and 1 p.m., and a peak of movement between 3 and 5 p.m. (Fig. 5). Juveniles spent more time in social interactions (typically playing) than other age/sex classes.

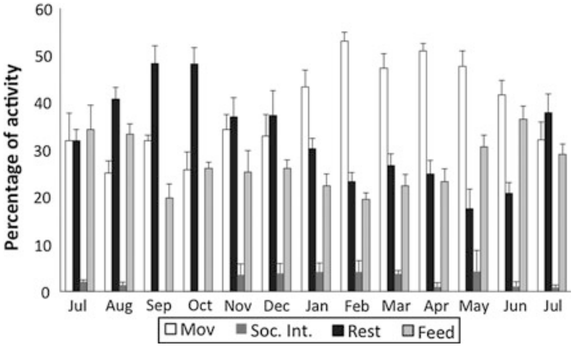

Fig. 4 Monthly variation in percentage of each activity carried out by woolly monkeys across 1 year (July 2009–July 2010) in Cueva de Los Guacharos National Park, based on the instantaneous each 10 min (N = 360 for each month). The *bars* represent the standard error

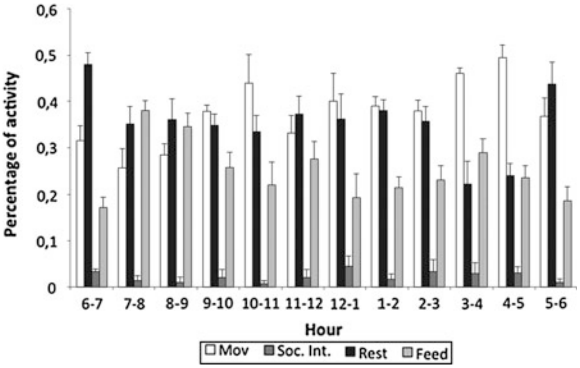

Fig. 5 Variation in the percentage of each activity performed by woolly monkeys across the day (N = 360 for each hour) in Cueva de Los Guacharos National Park, Colombia

Diet

Woolly monkeys fed on fruits more frequently (42.6 % of feeding samples) than leaves (11.3 %). However, the production of feeding scores in arthropods was similar to the proportion devoted to fruits (39.5 %). The proportions of records they spent feeding on flowers was relatively low (6.7 %). These percentages vary throughout the year. Additionally, they ate roots, wood, mushrooms, and reptiles (e.g., *Leptophis aetula*). They consumed more fruits in the second semester of 2009, while this tendency changed in the first semester of 2010, when arthropods were the most consumed food category. They also complement their diet with flowers and leaves (Fig. 6). They fed on a range of approximately 37 families of plants that include 47 genus and 88 species. The most consumed fruits were *Tapirira sp*. (Anacardiaceae) and *Cissus trianae* (Vitaceae) (Table 2).

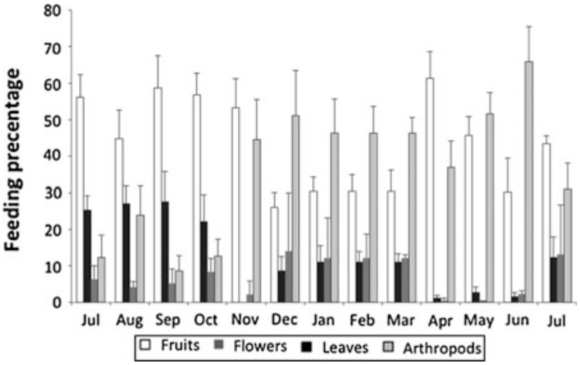

Fig. 6 Monthly variations in the feeding of different items in the woolly monkey's diet at Guacharos National Park, Colombia

Daily Path Length and Home Range

Average daily distance travelled by the woolly monkeys was 1,580 m (n = 46), with a minimum daily path length of 522 m, and a maximum of 2,993 m (Fig. 7). The monkeys moved more in the first semester of 2010 compared to the second semester of 2009. Using instantaneous samples, the study group used 276 ha. Using the minimum convex polygon method (Mohr 1947), we obtained an estimate of 300 ha (Fig. 8).

Discussion

We found a relatively dense population of woolly monkeys in the area. However, it is important to mention that population density varies within the park, since woolly monkeys were not observed in black oak forests and they seem to avoid the Andean forests which are found at more than 2,400 m.a.s.l. Lower population densities have been reported in lowlands with low fruit productivity or high hunting pressure (Table 3; González and Stevenson 2011). The high density of this population may be associated with the absence of hunting and a medium level of fruit production. It is also important to mention that woolly monkeys are the most abundant primate species in the area, and thus have few competitors.

In general, mountains are considered to show lower productivity than lowland forests, but our results suggest that during our study period fruit production was similar to some Amazonian lowlands forests (e.g., González and Stevenson 2011). This level of fruit production seems to be an important factor to explain the density of woolly monkeys in Sub-Andean forests.

Although lowland forests have greater tree diversity than highland forests (Gentry 1988), epiphytes are more diverse in mountains forest than lowlands, and they are more than 30 % of vascular flora of the Andean forest (Gentry and Dodson 1987; Wolf and Flamenco 2003). Epiphytes provide shelter and breeding

Table 2 Main dietary species consumed by woolly monkeys at Cueva de Los Guacharos National Park, based on time that focal animals were observed ingesting fruits, leaves, and flowers

Species	%	Time (min)	Fruits	%	Time (min)	Leaves	%	Time (min)	Flowers	%	Time (min)
Tapirira sp. nov	17.3	1,113	*Tapirira sp. nov*	17.3	1,113	*Philodendron sp.*	2.9	190	*Solandra cf. odorifera.*	0.9	61
Cissus trianae	16.8	1,081	*Cissus trianae*	15.4	991	*Nectandra cf. purpurea*	1.4	92	*Magnolia colombiana*	0.7	42
Guettarda hirsuta.	8.1	522	*Guettarda hirsuta.*	8.1	522	*Cissus trianae*	1.4	90	*Hedyosmum cuatrecazanum*	0.6	39
Morus insignis	7.5	486	*Morus insignis*	7.5	486	*Magnolia colombiana*	1.3	82	*Rhodostemonodaphne praeclara*	0.5	30
Miconia sp.	7.4	474	*Miconia sp.*	7.4	474	*Helicostylis tovarensis*	0.9	55	*Wettinia kalbreyeri*	0.4	23
Sauraiua brachybotrys	3.9	252	*Sauraiua brachybotrys*	3.9	252	*Euporbiaceae*	0.2	14	–		
Philodendron sp.	2.9	190	*Sapium stylare*	2.0	127	Struthanthus cf. orbicularis	0.1	7	–		
Nectandra cf. purpurea	2.9	184	*Clusia sp.*	1.8	118	*Gonolobus cf macrotis*	0.1	7	–		
Sapium stylare	2.0	127	*Hedyosmum cuatrecozanum*	1.8	113	*Mikania sp.*	0.0	3	–		
Magnolia colombiana	1.9	124	*Nectandra cf. purpurea*	1.4	92	–			–		
Clusia sp.	1.8	118	*Rollinia dolichopetala*	0.4	25	–			–		
Hedyosmum cuatrecazanum	1.8	113	*Vismia mandurr*	0.3	18	–			–		
Wettinia kalbreyeri	1.5	99	*Stepnanopodium cf. angulatum*	0.0	3	–			–		
Drymonia crassa	0.7	42	–			–			–		

(continued)

Table 2 (continued)

Species	%	Time (min)	Fruits	%	Time (min)	Leaves	%	Time (min)	Flowers	%	Time (min)
Rhodostemonodaphne praeclara	0.4	27	–			–			–		
Rollinia dolichopetala	0.4	25	–			–			–		
Stepnanopodium cf. angulatum	0.3	18	–			–			–		
Vismia mandurr	0.3	18	–			–			–		
Psammisia sp.	0.2	10	–			–			–		
Gonolobus cf macrotis	0.1	7	–			–			–		
Guatteria sp.	0.0	2	–			–			–		

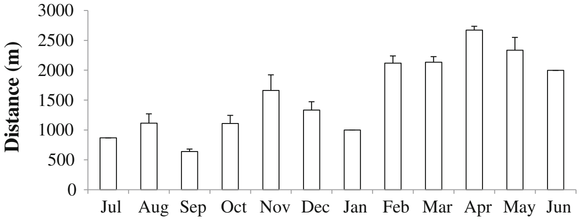

Fig. 7 Monthly variation in the average daily distance travelled by the woolly monkeys at Cueva de Los Guacharos National Park

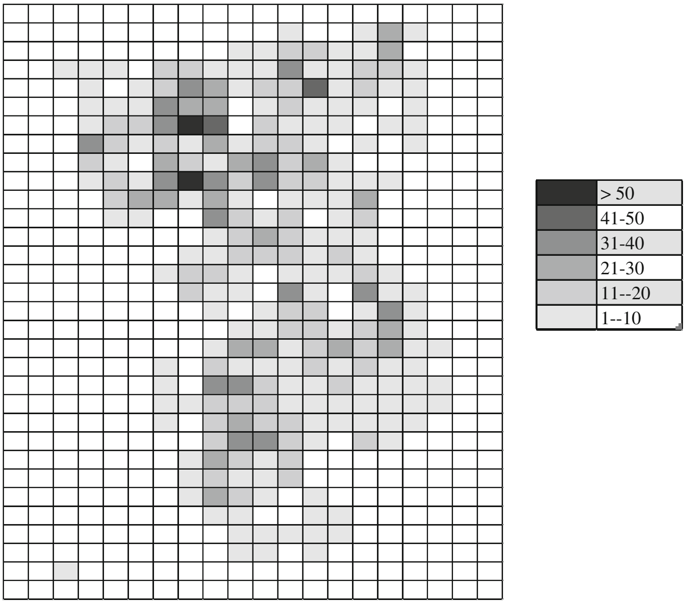

Fig. 8 Use frequencies of the study group home range based on instantaneous of each 30 min during the study

sites for many arthropods (Wester et al. 2011). A recent study that compare the epiphyte diversity between Cueva de los Guacharos National Park (Sub-Andean forest) and Nature Reserve Palmarí (Amazonia) shows that Guacharos National Park have 26 % more of epiphytes than Palmarí. This could explain why highland woolly monkeys complement their diet with more arthropods than monkeys from other sites (Table 3). For instance, comparing the relation between fruit and arthropods consumption, highland woolly monkeys were observed consuming fruits and arthropods in similar frequency, while woolly monkeys consume more frequently fruits than arthropods (up to sixfold difference. Table 3). The most contrasting comparison corresponds to a fragment where the risk of extinction of

Table 3 Comparison between different studies about woolly monkeys made in different kind of forest and using two different sampling methods

Study	Density/ Km^2	Home Range	Daily Path	Activity patterns				Diet				Sampling
				Feeding	Resting	Movement	Social Int.	Fruits	Leaves	Arthropods	Other	
Peres 1994[1]	–	–	–	–	–	–	–	81	16	–	6	Scan
Di Fiore 1997[2], 2004[3]	–	–	2,500 m[2]	–	–	–	–	77[3]	7[3]	9[3]	7[3]	Scan
Di Fiore and Rodman 2001[4]	–	–	–	36	23	34	5	76	7	–	13	Scan
Dew 2005[5]	31	120 ha	1,200 m	–	–	–	–	73	10	12	5	Focal
Defler 1995[8], 2004[6], Defler and Defler 1996[7]	13[6]	760 ha[7]	2,880 m[7]	26[8]	30[8]	38[8]	6[8]	84[7]	11[7]	4[7]	1[7]	Scan
Stevenson 2000[9], 2006[10]	30–50[9]	200 ha[10]	2,001 m[10]	36[10]	35[10]	26[10]	3[10]	59[10]	13[10]	25[10]	1[10]	Focal
Zarate and Stevenson 2009[11]	50	126 ha	2,330 m	31	35	33	2	67	21	11	1	Focal
González and Stevenson 2011[12]	–	596 ha	2,332 m	18	50	29.5	2.5	69	16	13	2	Focal
Current study[13]	20	300 ha	1,580 m	25	30	42	3	43	11	39	7	Focal

[1] Peres 1994 (Urucú, Amazonas Brasil): Productive forest, [2] Di Fiore 1997, [3] Di Fiore 2004, [4] Di Fiore and Rodman 2001, [5] Dew 2005: (Eastern Ecuador) Productive forest (Yasuní, National Park), [6] Defler and Defler 1996, [7] Defler 2004, [8] Defler 1995: Nonproductive forest (Caparú, Amazonas Colombia), [9] Stevenson 2006, [10] Stevenson 2002: Productive forest (Tinigua, National Park), [11] Zarate and Stevenson 2009: Fragmented forest (Guaviare, Colombia), [12] González and Stevenson 2011: Nonproductive forest (Caparú, Amazonas Colombia), [13] Current study Sub-Andean Forest (Huila, Colombia)

local populations of epiphytes is high (Hietz-Seirfert et al. 1996) and may decrease the habitat for arthropods. This result is remarkable and possibly explains why this population moves more than lowland populations, yet they do not travel longer daily distances. We found a home range area within the reported for the species (Table 3), in accordance with a relatively productive habitat.

In terms of behavior, aside the above-mentioned increase in moving records and arthropod feeding, woolly monkeys in Cueva de Los Guacharos National Park are remarkable for the incidence of resting early in the morning (6–7 a.m.) and late in the afternoon (5–6 p.m.). We suggest that this difference in relation to the behavior in lowlands represents a mechanism to save energy by being inactive at daily hours when temperatures are low.

Only two plant species made up a large proportion (ca. 44 %) of the plant diet of woolly monkeys at Cueva de Los Guacharos (a large tree *Tapirira* sp.—likely an undescribed species- and an abundant vine: *Cissus trianae*, Table 2), suggesting that their populations may be highly susceptible to changes in their main plant sources. Interestingly, both species are frequently dispersed by the monkeys (Ramírez et al., this volume). It is possible that the dominance of only two species in the diet is due to lower plant species richness in mountain than in lowland forest (Gentry 1988). Aside from plant species, it seems clear that arthropods are an important dietary source and for conservation purposes, it would be necessary to assure that woolly monkeys in mountains have mature forests, where they can find enough fruit sources and trees covered by mosses and other epiphytes (the main substrate where they look for arthropods). Therefore, the conservation of woolly monkeys seems also important for plant populations, since they are playing roles as seed dispersers for the majority of species consumed for their ripe fruits, similar to what has been described at lowland forests (Stevenson 2007).

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Seed Dispersal by Woolly Monkeys in Cueva de los Guacharos National Park (Colombia): An Amazonian Primate Dispersing Montane Plants

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Introduction

In tropical forests, plant regeneration processes depend to a great extent on the effectiveness of animals as seed dispersers (Cordeiro et al. 2009). Seed dispersal is the movement or transport of seeds away from the parent plant, and in this particular case we focus on endozoochory dispersal, which is one of the essential factors determining the distribution of individuals within a population. Additionally, it promotes successful establishment by the colonization of new habitats, and has positive effects on diversity (Connell et al. 1984; Janzen 1971; Nathan and Muller-Landau 2000). To evaluate the effect of seed dispersal in the reproductive success of plants, two parameters must be considered: a quantitative and a qualitative one (Schupp 1993). The quantitative value is described as the number of seeds removed from the parental tree in relation to the number of visits and consumption time. The qualitative component includes the type of treatment that a seed receives when it is manipulated and passes through the mouth and intestinal tract of the animal, and also to the conditions where the seed is deposited (e.g., with or without dung, seed density, seed mixing, forest type, and distance from parental trees).

Large ateline primates have been recognized as efficient seed dispersers in terms of quality and quantity (Dew 2005; Link and Fiore 2006; Stevenson 2000). Furthermore, Stevenson (2011) found a positive relationship between the presence of ateline primates and the diversity of seedlings in Neotropical forests. This relationship possibly exists due to the benefits that plants receive from dispersal processes, since their reproductive success increases when seeds are deposited far from the parental plant, thus avoiding negative distance-dependent processes

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(Swamy and Terborgh 2010), and/or when seeds are deposited in adequate places for their development (Schupp 1992; Julliot 1996; Stevenson 2007a). The woolly monkeys have been recognized as an efficient dispersers for most species of plant they consume, due to three main elements (1) the estimates of seed numbers dispersed, (2) the relationship between the number of seeds dispersed and manipulated, and (3) the large proportion of seed mass that they disperse in the study area (Stevenson 2007b).

This study examines seed dispersal by Colombian woolly monkeys (*Lagothrix lagotricha lugens*) in a montane forest. Although the genus *Lagothrix* have been deeply studied compared to some other primates in the New World, where no studies had been performed on the ecology of these primates in high lands habitats, due to the lack habituated populations in these areas. Additionally, this population has the greatest heights recorded for this genus (2,400 m.a.s.l.). The floristic composition of montane forests is quite different from that of lowland Neotropical forests (Gentry 1988), where it is presumed that this group of primates evolved because of its current distribution, sister taxa, and relatively recent origin (Schrago 2007). Thus, to examine whether in highland habitats, woolly monkeys play a similar role to the one they play in lowland forests. This relationship is not evident, because the history of some ecological interaction should be relatively recent, due to some of the plant elements came to the Andes in recent times (e.g., *Hedyosmum* sp. which is included on their diet, and arrived from the north nearly 10 million years ago) (Hammen 2000). For this purpose, we analyze plant consumption and dispersal patterns at the individual and population level. As proposed by González and Stevenson (2009), dispersal estimates can vary as a function of local primates density; therefore, we can expected that in this highland population where densities are low, the seed dispersal patterns present a different dynamic from the one expected for lowland forests with higher woolly monkey densities.

Additionally, limitations or morphological differences related to age and size the different group members have been documented affect the seed dispersal contribution (Stevenson et al. 2005). Therefore, we expect that juveniles disperse smaller seeds than adults because of gut size restrictions.

Methods

Study Area

The Cueva de los Guácharos National Natural Park is a continuous forest located on the Andean Eastern Mountain Range, in the departments of Huila and Caquetá, in Southern Colombia. The altitude range goes from 1,610 to 2,840 m.a.s.l., with an annual precipitation of 2,284 mm. The predominant rainy season goes from February to October, and the dry season occurs from November to January (Vargas, this volume). The PNNCG is part of the wet tropical mountain systems, which include sub-Andean and Andean forests and also *páramo* vegetation of the Eastern Cordillera of the Andes (Minambiente 2005).

Field Protocol

We obtained data in the field over a period of a year and information on seed dispersal was gathered for 11 continuous months between September 2009 and July 2010. For data collection, we used focal animal sampling (Altmann 1974). Each age-sex class (adult male, female, female with infant, and juvenile), which were identified by body size and genitals, was sampled for at least 12 h per month (distributed from 6:00 to 18:00 h). One of the classes was repeated with the purpose of having records of 5 days each month, which is considered as a minimum sampling effort to study feeding behavior (Stevenson 2003).

Diet

We quantified consumption times as the interval from which the focal animal arrived to a feeding tree, until it left, or until it stopped its activity (Stevenson et al. 1994). The type of food item was registered (ripe and unripe fruits, young and mature leaves, and flowers) (Stevenson 2003). When individuals fed on fruits, we annotated the quantity of fruits ingested during a period of 30 s to estimate consumption rates for each plant species. Additionally, we made observations on fruit and seed manipulation, and the maturation state.

We collected a voucher sample, fertile if possible, from each one of the consumed species, and then we identified the botanical sample in the Ecologia de Bosques Tropicales y Primatología laboratory at the Universidad de Los Andes. Samples were identified to species or genera in most cases.

Feces Samples

In order to identify and quantify the seeds, we collected the highest possible quantity of fecal samples from focal individuals during the follows. When the focal individual was in proximity of other group members and we were not sure which monkey defecated, we also collected the fecal sample. To estimate deposition rates, we registered the time of deposition, even for samples that were not collected due to the location where they were deposited (e.g., over branches, epiphytes, bodies of water, or when they could not be found). To quantify the number of seeds in each fecal sample, we deposited and washed the feces using latex gloves and a metallic sieve of small pore size (1 mm). Next, we differentiated seeds by species or morphotypes and counted them. Seeds with sizes less than 0.5 mm in width were not included in the quantitative analyses, due to the difficulty in the identification process and since most of them were not retained by the sieve. For small seeded species ($\geq$1 mm) (e.g., *Saurauia* spp.) we did not count them individually. Instead, before washing the fecal sample the number of seeds present in a determined piece (e.g., ¼ of the whole fecal sample) was estimated and the total number of seeds in the whole sample was extrapolated by this value.

Statistical Analyses

To evaluate possible differences between juvenile and adult individuals in dispersed seed size, we performed an initial test to check whether the data were parametric, and a Wilcoxon test was performed. To evaluate whether the availability of food resources had an effect on the number and biomass of seeds, regression tests were performed. These analyses were performed using the program R (version 2.13).

Results

We collected a total of 178 fecal samples with an average of three samples per day. However, in a single day we registered up to 12 depositions from focal individuals. The collected samples contained an average of 2.72 different plant species (of a range from 0 to 9). In the depositions, we registered a total of 3,062 seeds of more than 2 mm in width, and 62,828 seeds of inferior sizes, for a total of 65,890 seeds (Table 1), belonging to 36 different plant species. Additionally, almost 73 % of the total fruit species included in their diet were dispersed and only 10 species were not dispersed (Table 2), which means that these primates are dispersing most of the consumed species.

Taking into account, the density of woolly monkeys reported in the sub-Andean forest (21 individuals km^2; Vargas et al., this book), we estimated the quantitative role of the whole population of woolly monkeys as dispersing at least 11.000 seeds km^{-2} day^{-1}. When applying the correction factors suggested by Stevenson (2007b), which consists of an estimate of the number of fecal samples that cannot be collected during the follows and during the night period, the contribution of the population could be of 234.952 seeds km^{-2} day^{-1}, of which 19,519 would be relatively large seeds (>3 mm).

The relative importance of each dispersed species varied along months and depending on the quantification way (the number of seeds and/or their biomass). For instance, *Guettarda hirsuta* and *Cissus trianae* were frequently dispersed and these plant species were ingested registered in 7 of the 11 sampling months (showing extended fruiting periods). Species with seeds of less than 2 mm in width

Table 1 List of plants species dispersed by *(L. lagotricha lugens*) in Cueva de los Guacharos National Park, Huila, Colombia

Plant species	No. seeds	Biomass g	No. of months used
Saurauia brachybotrys	18,992*	22.79	4
Tapirira sp.	464**	**640.47**	4
Guatteria sp.	5	2.16	2
Rollinia sp.	133**	33.92	5
Hedyosmum cuatrecazanum	334	40.08	4
Tontelea sp.	1	5.21	1
Hyeronima huilense	8	0.40	2
Sapium stylare	39	5.85	3
Drymonia sp.	550	0.16	1
Vismia mandurr.	5,308	26.54	4
Indet. 1	1	“	1
Indet. 2	2	“	1
Indet. 3	8	“	1
Indet. 4	11	“	1
Indet. 5	22	“	2
Indet. 6	32	5.51	2
Indet. 7	1	“	1
Indet. 8	5	“	1
Miconia sp.	365	“	4
Guarea sp.	11	23.10	1
Anomospermum cf. *reticulatum*	1	4.93	1
Ficus cf. *lehmannii*	2,304	2.30	1
Ficus cf. *mutisii*	96	0.10	1
Ficus sp.	3,235	3.24	4
Morus insignis	4,610	13.83	1
Faramea sp.	58	1.74	3
Guetarda hirsuta	536	1.61	**7**
Caseana cf. *macrocarpa*	116**	**162.40**	5
Juanulloa sp.	10	0.04	2
Solanum sp.1	492	78.14	2
Solanum sp.2	34	2.11	1
Solanum sp.3	298	0.89	6
Cecropia angustifolia	13,158*	5.26	4
Cecropia mutisi	80	0.02	1
Cecropia telenitida	14,055*	12.65	3
Cissus trianae	515	51.50	**7**
Total	**65,890**	**1,141.74**	

The table shows number of seeds recovered from each species, their fresh weight and the number of months when they were recorded

*maximum values for seeds <3 mm

**maximum values for seeds >3 mm. And also the highest values for seed biomass dispersed

Table 2 List of plants included in the diet of *L. l. lugens* with few or no samples registered in this study

Family	Species	Dispersed but no record	Handled not dispersed	Handled but infrequently dispersed	Predated
Melastomataceae	*Miconia* sp.	X			
Rosaceae	*Prunus* cf. *muris*				X
Lauraceae	*Nectandra* sp.	X	X		
Clusiaceae	*Tovomita* cf. *parviflora*	X			
Arecaceae	*Wettinia kalbreyeri*		X		
Lauraceae	*Ocotea* cf. *insularis*		X		
Lauraceae	*Rhodostemonodaphne praeclara*		X		
Lauraceae	*Nectandra* cf. *obtusata*		X		
Meliaceae	*Guarea* sp.			X	
Clusiaceae	*Clusia* sp.	X			
Melastomataceae	*Blakea turbinata*	X			
Lauraceae	Indet.1		X		
Menispermaceae	*Anomospermum* cf. *reticulatum*			X	
Dichapetalaceae	*Stephanopodium angulatum*				X
Margraviaceae	*Marcgravia brownei*	X			
Moraceae	*Helicostylis tovarensis*	X			
Lauraceae	*Endlicheria ruforomula*		X		
Melastomataceae	*Melastomataceae indet.*	X			
Lauraceae	*Rhodostemonodaphne* kunthiana		X		
Lauraceae	*Beilschmiedia* cf. *tovarensis*		X		
Lauraceae	*Nectandra purpurea*		X		
Lorantaceae	*Phoradendron* sp.	X			
Lauraceae	*Cinnamomum* sp.				X
Sapindaceae	*Alophyllus* cf. *punctatus*	X			
Fabaceae	*Mucuna* sp.				X
Myrtaceae	Indet. 2	X			
Celastraceae	*Tontelea* cf.			X	
Ericaceae	cf. *Thibaudia*	X			

The columns show the plant species whose seeds could be dispersed but not registered due to their size (<0.5 mm), also those were consumed but discarded, immature consumed fruits damaging their seeds and those that were consumed but scattered infrequently

such as *Cecropia telenitida, Cecropia angustifolia,* and *S. brachybotrys*, were the most representative in the fecal samples (70 %). However, seeds with sizes near or higher than 1 cm, such as *Tapirira* sp. (a species similar to *T. g. subandina*) (469), *Casearia macrocarpa* (116), and *Rollinia dolichopetala* (133) were also abundant. The most abundant families, in terms of the frequency of depositions where they were present, were Solanaceae, Urticaceae, Vitaceae, Anacardiaceae, Rubiaceae and Moraceae, with 67 % of total records (Fig. 1). In terms of dispersed fresh biomass, *Tapirira* sp., reached the highest value with 640.5 g, followed by *C. macrocarpa* with 162.4 g.

Differences in the Sizes of Seeds Dispersed by Adults and Juveniles

We found no statistical differences between adult and juvenile individuals in the sizes of seeds dispersed (Wilcoxson W = 6,800, $P = 0.41$, n = 369) (Fig. 2). However, fecal samples collected from juveniles included seeds with size ranges between 0.75 and 12.9 mm in width, and the species with the largest recorded size was *Tapiria* sp.; while for adult individuals, the two species with the largest sizes were *Guarea* sp. (11.6 mm), *Anomospermum* cf. *reticulatum* (14.3 mm) and *Tontalea* sp. (20.0 mm), suggesting that the adults can disperse larger seeds.

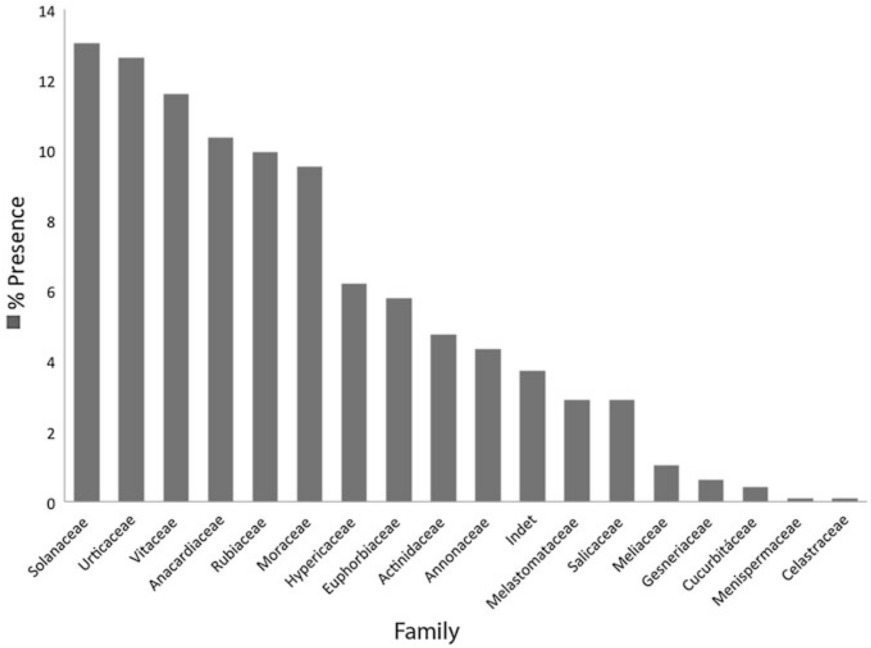

Fig. 1 Percentage of records of each family in the fecal samples collected from focal woolly monkeys in Cueva de Los Guacharos National Park (Colombia). It is noted that the first 6 out of the 17 identified families exceed the 67 % of total records

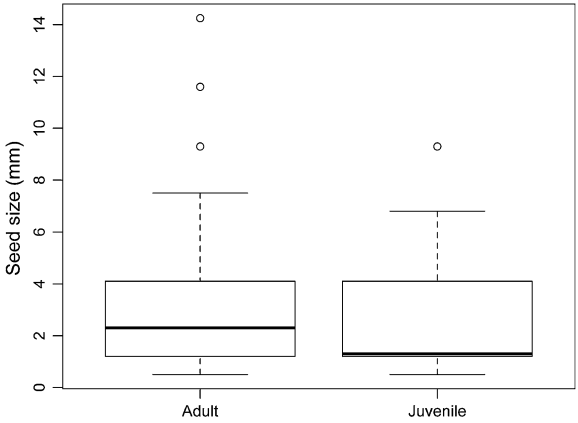

Fig. 2 Comparison of seed size (maximum width) between the seeds dispersed by *adults* and *juvenile* woolly monkeys (*L. l. lugens)* in Cueva de los Guacharos National Park, Colombia

However, the information from *Tontelea* seeds was not included in this analysis since there was uncertainty about the age of the disperser.

Discussion

Colombian Wooly Monkeys, How Efficient are they?

Colombian woolly monkeys (*L. lagotricha lugens*) play an important role as seed dispersers in montane ecosystems, almost equivalent in quantitative terms to the reported for lowland populations (Table 3). Even though the number of species dispersed by these monkeys is considerably lower than the one reported for *Lagothrix* populations in lowlands [e.g., (Stevenson 2000; 112, 2007b; 142)], it is noted that this is an important value considering the lower diversity of highland forests (Table 4), and that the interactions between species are more recent. Therefore, these monkeys could be considered to be excellent seed dispersers, as they meet the fundamental variables, which are: A large amount of seed dispersed, high rates of fruit species manipulated were dispersed (73 %), and they disperse a large proportion of seed mass in the study area. These results suggest that the role played by woolly monkeys as seed dispersers could be determined by intrinsic aspects of their behavior, and not by a close evolutionary history with plants from which the populations have fed-on the most (i.e., Amazonian plants). However, it is also possible that this behavior could also be affected by recent ecological process, in which the primate populations could be favoring the regeneration of the plant species that they consume the most. It is also highlighted that, in general, woolly monkeys are efficient seed dispersers, independent from the floristic composition of the forests they inhabit and in a similar way to other atelines (Russo et al. 2005; Fiore et al. 2008).

Table 3 Species dispersed by *Lagothrix spp.* and fruit productivity for each forest in lowland and highland populations

Study	Number of . sp dispersed	Number of . sp registered in phenological transects (5.6 km)	(%) Seed dispersed
Stevenson (2007b)[1]	147	169	87
Gonzalez and Stevenson (2009)[1]	>118	342*	35
This study[2]	36	90	40

[1] Lowland population
[2] Highland population
*10 km sampling effort

Table 4 Number of seed dispesed by woolly monkey population and their densities at lowland and highland areas

Study	Seed dispersed by population (Km^2/day)	Population density (Indi/Km^2)
Stevenson (2007b)[1]	1,064.289	41
This study[1]	234.965	21
Gonzalez and Stevenson (2009)[1]	70.100	15

[1] Lowland population
[2] Highland population

Although the majority of seeds had sizes of less than 2 mm in width, such as *S. brachybotrys C. telenitida, C. angustifolia,* this was expected, since it has been reported by other studies (Stevenson 2007b). However, the most representative contribution in terms of biomass and frequency of records was linked to species with larger seed sizes, such as *Tapirira* and *Guettarda* (Table 2). In fact, *Tapirira* was the most consumed species during the study period (Vargas et al. this book), and therefore it represents an important energetic contribution for this population.

Could be Differences Between Individuals?

Statistically, there were no differences between adult or juvenile individuals in the sizes of seeds dispersed, since these shared the majority of plant species. However, It is clear that two of the species with the largest seeds were only found in the feces of adults, similar to what has been found in lowland forests (Stevenson et al. 2005). It is possible that a larger sampling is required, in which the quantity of fecal samples among categories can be homogenized, to be able to determine whether species with larger seed sizes can really be dispersed only by adults. In addition, the similarity in diet and seed dispersal patterns may be explained by the fact that juveniles are almost always in the company of their mothers (Stevenson et al. 1998), and can learn similar behaviors which make the average seed size values to be alike. It is important to highlight that the maximum size of seeds reported in this study is higher than the values reported in previous studies (Dew 2005; Stevenson et al. 2005). This suggests that the body sizes of montane woolly monkeys could be larger than the ones of lowland woolly monkeys. Even though this could be expected due to an adaptation effect to the colder weather in higher lands (Bergman rule), there are no sufficient data on body weights to corroborate this idea yet.

Additionally, this study reiterates the efficiency of these primates as dispersers of relatively large seeds, which usually have a smaller set of dispersers than smaller seeds (Peres and Roosmalen 2002). Therefore, the conservation of these primates is particularly relevant in places where they are abundant and where there are no other large primates that can compensate their ecological roles, it has been established that woolly monkeys in general could be considered excellent seed dispersers in terms of the quantity and quality of seeds dispersed for the great majority of species they feed. At least four sources of information from woolly monkeys lead to the this conclusion: the estimates of seeds dispersed, the relationship between the number of seeds dispersed and manipulated, the large proportion of seed mass that they disperse, and the low rates of predated seeds.

The effect that hunting large frugivores has on plant regeneration has been demonstrated, mainly for species with medium- and large-sized seeds in lowland forests (Nuñez-Iturri and Howe 2007; Terborgh et al. 2008, Stevenson 2011), and could possibly occur in the same way in montane forests.

In conclusion, these results showed that woolly monkeys in subandean forests play an important and efficient role as seed dispersers in quantitative terms, showing values that approximate to the ones reported for *Lagothrix* individuals in lowlands. At the qualitative level, it could be said that woolly monkeys also play a successful role since the proportion of species predated is low. In addition, the reported daily path lengths (Vargas et al. this volume) and the prolonged retention rates in the gut (Stevenson 2000) suggest that woolly monkeys in this population leave most seeds away from parental plants. These results provide a clear idea of the importance of these primates in the destiny of the plant species that are part of their diet, and of the fundamental role that they would be playing in the dynamics of these montane forests.

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Distribution and Ecology of the Most Tropical of the High-Elevation Montane Colobines: The Ebony Langur on Java

Vincent Nijman

Introduction

Colobines are distributed over a wide range of habitats, and the Asian taxa occupy a distinctly larger range of habitats than their African counterparts (Kirkpatrick 2011; Fashing 2011). These habitats include various hill and mountain ranges. In Africa, it appears that only the Ethiopian highlands support permanent populations of a colobine, i.e. black-and-white colobus *Colobus guerza*, occurring up to 3,300 metres above sea level [m.a.s.l.] (Dunbar and Dunbar 1974). With respect to the occurrence of high-elevation colobines two large mountain areas stand out: (1) the mountains of south and central China where various species of snub-nosed monkey of the genus *Rhinopithecus* occur, and (2) the Himalayas, where in addition to snub-nosed monkeys several langurs occur. In the northeastern parts of the Himalayas, the Burmese snub-nosed monkey *R. strykeri* is confined to a small high-altitude region (Geissmann et al. 2010), in the southeastern parts several langurs of the genus *Trachypithecus* occur and throughout the Himalayas various species of hanuman langur of the genus *Semnopithecus* are found. Most of these species range from lowland into the montane areas, typically to about 2,500–3,000 m.a.s.l. (Table 1), with the hanuman langurs and the black snub-nosed monkey occurring, at least seasonally, above 4,000 m.a.s.l.

As can be seen in Table 1, a number of these high altitude colobines appear to be confined to montane regions with no extant populations occurring in the lowlands. This is especially true for the high-elevation montane hanuman langurs and the Chinese and Burmese snub-nosed monkeys. While the Himalayan hanuman langurs may indeed have evolved to persist in these montane regions (with several of their congeners being distributed allopatrically in the low-lying parts of the Indian Subcontinent), for the snub-nosed monkeys their exclusive montane

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Table 1 Colobines living in montane areas above 2,500 m.a.s.l., showing that all but one species occur in Asia with only four species (still) ranging from sealevel to the high mountains

Species	Altitudinal range	Montane range	Reference
Black snub-nosed monkey *Rhinopithecus bieti*	3,000–4,700	China	Kirkpatrick and Grueter (2010)
Grey snub-nosed monkey *R. brelechi*	1,400–2,300	China	Kirkpatrick and Grueter (2010)
Golden snub-nosed monkey *R. roxellana*	1,400–2,800	China	Kirkpatrick and Grueter (2010)
Myanmar snub-nosed monkey *R. strykeri*	1,700–3,200	Himalayas	Geissmann et al. (2010)
Gee's golden langur *Trachypithecus geei*	0–3,000	Himalayas	Choudhury (2008)
Capped langur *T. pileatus*	0–3,000	Himalayas	Choudhury (2008)
Kashmir hanuman langur *Semnopithecus ajax*	2,200–4,000	Himalayas	Minhas et al. (2010)
Nepal hanuman langur *S. schistaceus*	1,500–4,000	Himalayas	Sayers and Norconk (2008)
Ebony langur *T. auratus*	0–3,500	Java	Nijman (2000)
Black-and-white colobus *Colobus guereza*	0–3,300	Ethiopian highlands	Dunbar and Dunbar (1974)

distribution is almost certainly an artefact of the extinction of their populations at lower elevations. Li et al. (2002) report on the distribution of snub-nosed monkeys in China showing that in historic times these species indeed did occur at lower elevations down to 300 m.a.s.l. The langurs of the genus *Trachypithecus* and indeed the black-and-white colobus can still be found from sealevel up to the highest mountains in their respective ranges.

It is worthwhile noting that most of these high-elevation colobines live on the northernmost parts of their generic ranges, in areas that experience the largest amount of seasonal climatic changes. While few populations have been studied in great detail, for a fair number of these colobines it has been reported that they show a considerable amount of seasonal altitudinal migration. During the coldest parts of the years groups and populations migrate to lower elevations, only to take advantage of the milder conditions in summer allowing them to move higher up the mountains (Bishop 1979; Lui et al. 2004; Kirkpatrick and Grueter 2010; Geissmann et al. 2010; Niu et al. 2010). While these species occur at higher latitudes, typically north of the Tropic of Cancer thus outside the tropics, the ebony langur *Trachypithecus auratus* of the Indonesian islands of Java, Bali and Lombok, is the most tropical of all high-altitude colobines living very close to the equator.[1]

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[1] The other colobine endemic to Java, the grizzled langur *Presbytis comata*, has been recorded in Montane Zone such as on Mt Pangrango (up to 2,600 m.a.s.l.), Mt Slamet (up to 2,350 m.a.s.l.) and Mt Prahu (up to 2,565 m.a.s.l.). Overall, however, the species appears to be much more confined to the forest of the Lowland to Submontane Zones (Nijman 1997).

Here I provide an overview of the distribution and ecology of the ebony langur, focussing on the island of Java, emphasising their occurrence in high-altitude areas. Distinctly different from other regions where high-elevation colobines occur, I first provide a physical description of the island of Java and its montane environment. I document the distribution of ebony langurs in these mountains, emphasising their presence in the higher regions, note the occurrence of frost on these regions, and compare them to adjacent lowland areas. Finally, I present the results of surveys conducted on the island showing that there is a clear relationship between rainfall, elevation and group sizes and densities of ebony langurs.

Methods

Study Area

The island of Java, Indonesia's political and industrial centre, is one of the most densely populated areas in the world. The very fertile soils which lend themselves to terracing for irrigated rice, sustain about 121 million inhabitants, at an average population density of 914 people km^{-2} (data from 2000: BPS 2004). Java is largely deforested and most of the remaining forest fragments cover (parts of) the numerous volcanoes on the island. The remainder is essentially a mosaic of rice fields, cities and villages. Java has a long history of cultivation and deforestation that already started ca. 1,000 AD, but really took off in 1830 when the Dutch colonial Government imposed the so-called 'cultuurstelsel'. To support this agro-economic system, farmers were forced to grow export crops on communal grounds, which was often forest (Whitten et al. 1996). By the end of the nineteenth century the natural forest was severely fragmented, and at the beginning of the last century the remaining forest showed a fragmentation pattern very similar to that seen today (Fig. 1). At present, as little as 2 % of the original forest in the fertile lowlands remains; in the mountains, especially at higher elevations, about half of the original forest remains standing (Smiet 1992). Permanent human occupation in the mountains is less dense than in the lowland, and in most areas few if any villages are situated outside the submontane level above 1,600 m.a.s.l.; the highest villages in Java are situated between 2,000 and 2,100 m.a.s.l. on the Dieng plateau [number 19 in Fig. 1] and Mt Semeru [30].

It is true to say that the physical landscape of Java is dominated by its mountains (Stehn 1933), many of which are of volcanic origin. Most mountains are situated along the longitudinal axis of the island, with the mountains in the west forming a large cluster less interrupted by the low-lying plains than the more separated mountains in the east. In the province of West Java there are 12 peaks above 2,000 m.a.s.l. with the highest being Mts Gede-Pangrango (3,019 m.a.s.l. [number 6 in Fig. 1]) and Mt Ciremai (3,078 m.a.s.l. [12]). In Central Java there are 7 such peaks, the highest being Mt Slamet (3,432 m.a.s.l. [17]), and in East Java there are

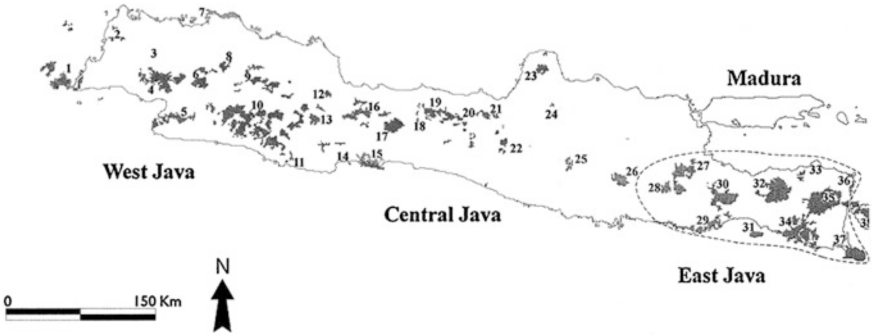

Fig. 1 Geographic distribution of ebony langur *Trachypithecus auratus* on Java, Indonesia, indicated in *grey* (after Nijman 2000). Montane populations are found in (**4**) Mts Halimun-Salak, (**6**) Mt Gede Pangrango, (**9**) Mt Tangkuban Perahu, (**10**) Mt Papandayan, (**12**) Mt Ceremai, (**17**) Mt Slamet, (**19**) Mts Dieng, (**22**) Mts Merbabu-Merapi, (**25**) Mt Lawu, (**26**) Mts Liman-Wilis, (**27**) Mt Arjuno, (**28**), Mts Kawi-Kelud, (**30**) Mts Bromo-Tengger-Semeru, (**32**) Yang plateau and (**35**) Mts Ijen-Raung

8 of which Mt Arjuno-Welirang (3,339 m.a.s.l. [27]) and Mt Semeru (3,676 m.a.s.l. [32]) are the highest. The zonation of the vegetation on the mountains of Java has been described in detail by van Steenis (1972) and, for the purpose of the present study, I adopt the following classification: Lowland Zone below 1,200 m.a.s.l., the Submontane Zone between 1,200 and 1,600 m.a.s.l., the Montane Zone between 1,600 and 2,400 m.a.s.l., and the Subalpine zone above 2,400 m.a.s.l. (and up to 3,676 m.a.s.l. on Mt Semeru).

The climate on Java differs greatly from the west to the east. The eastern part of Java and the north coast have a pronounced dry season, while in the western half it is weak and nowhere marked (RePPProT 1990). The amount of rainfall varies from <1,000 mm per year in the northeastern tip of the island at Baluran [36] to >8,000 mm on the southeastern slopes of Mt Rogojembangan in Mts Dieng [19]. The rainfall gradients on Java can be steep: moving just 25 km north from Mt Rogojembangan, the rainfall has dropped to <2,000 mm and likewise, moving 15 km southwest from Baluran, up Mt Ijen [35], the annual rainfall has increase to >3,000 mm (note that ebony langurs have been recorded in all the above-mentioned localities).

While the absolute amount of rainfall bears some significance for the distribution of plants and animals on Java, the length of the dry season seems to be of greater significance. In general, the wettest vegetation types (mixed lowland and hill rain forest and everest montane forest) only occur in areas with at least 30 rainy days during the driest four consecutive months (van Steenis 1965), and hence is mostly found in the west and central part of Java. Rainforest is also found throughout the otherwise seasonally dry east in the wet ‘islands’ which arise as a result of stowage on the southern and south-eastern slopes of the higher mountains (van Steenis 1972). In the drier areas rain-forest is replaced by moist forest and deciduous forest.

Data Aquisition

I collected data on ebony langurs by conducting surveys throughout the species' range on Java, Bali and Lombok, between 1994–2003 and 2012–2013, most of which are detailed in an earlier publication (Nijman 2001); here I restrict myself to Java only. All types of forest were surveyed and included the following mountains and plateaus (listed in a west to east sequence, Fig. 1): Mt Salak (1994, 1995, 1997, 1999, 2000), Mt Gede-Pangrango (1994, 1995, 1997–2001, 2003), Mt Tangkuban Perahu (1994), Mt Papandayan (1999, 2012, 2013), Mt Slamet (1994, 1995, 1999), Mts Dieng (1994, 1995, 1997–2002), Mt Sundoro (1994), Mt Merbabu (1994), Mt Merapi (1994, 1995), Mt Lawu (1994, 1995), Mts Liman-Wilis (1994, 1995), Mt Arjuno-Welirang (1997, 1998), Mt Kawi-Kelud (1997), Yang plateau (1997), Mt Ijen (2000, 2001). Surveys typically lasted several days, with multiple sites visited and most sites being re-visited over the years. While considerable time was spent in the Submontane Zone, surveys in the Montane Zone up to 2,400 m.a.s.l. were less frequent and the area above 2,400 m.a.s.l. was surveyed mainly by several single day trips, retreating to lower elevations for the night. The total survey effort in Submontane, Montane and Subalpine Zones, in areas where ebony langurs were indeed recorded, was 177 days.

Data were collected on the occurrence and altitudinal distribution of ebony langurs, and upon sighting of an individual or a group, an estimate was made of the group size and the altitude was measured with the aid of an altimeter (either on a wrist watch or on a handheld GPS receiver).

In 10 areas from across the island, densities and group sizes of ebony langurs were estimated along transects and forest trails following the methodology and assumptions described in Nijman and van Balen (1998). These areas comprised six sites in the Lowland Zone between sealevel and 800 m.a.s.l., three of which were in the wet climate zone (>20 rainy days during the four driest consecutive months) and three in the dry zone (<20 rainy days during the four driest consecutive months). Four Submontane and Montane sites between 1,300 and 2,800 m.a.s.l., were surveyed, with two in the wet and two in the dry climatic zone.

In addition to surveys I collected data on the distribution, elevation and group sizes of ebony langurs throughout Java as reported in the literature. While most of these were conducted in the lowlands they did allow me to evaluate differences between montane and lowland populations.

Analysis

I entered the locality data, at a precision of ~1 km^2, into a GIS model containing environmental layers comprising temperature, precipitation and altitude. The temperature and precipitation variables were extracted from the WorldClim database (Hijmans et al. 2005). These bioclimatic variables are derived from monthly temperature and rainfall values resulting in ecologically relevant layers on a grid resolution of ~1 km^2. These variables were used to explore the relationship between group size and environment, including altitude. I selected maximum group size per site as these showed the largest amount of variation across the island. I prepared a multiple linear regression model that was fitted on the (normalised) data to determine the best sub-set of environmental variables as predictors for the observed variation in maximum group sizes. The effects of collinearity were reduced by simply omitting predictor variables that correlated highly with the other predictor variables that remained in the model (Quinn and Keough 2002). The entered variable included altitude (in m.a.s.l.), annual precipitation (in mm), precipitation seasonality (reflecting the annual range in precipitation, expressed as a standard deviation) and temperature seasonality (reflecting the annual range in precipitation, expressed as a coefficient of variation). Statistical analyses were done in SPSS17 and a test was deemed significant when $P < 0.05$ in a two-tailed test (Siegel 1956).

Results and Discussion

Physical Condition of Mountains as Langur Habitats

Java is situated between 6° and 8° south of the equator, and experiences a true tropical climate. The uniformity of the temperature conditions in Java makes the differences between the climate of the higher regions and that of the low plains prominent. In addition to the decrease of temperature of about 0.6 °C for each rise of 100 m (Braak 1929), the climate also changes in other respects with increasing elevation (Whitten et al. 1996; van Steenis 1972). Heat is more quickly lost from high altitudes at night, and therefore the daily temperature fluctuations are greater in the mountains than in the lowland, viz ~15–20° C (up to 25° C, see below) compared to ~5–8° C. The climate of Java's Montane Zone shows some pronounced differences between the drier east and the wetter west, which is well illustrated by two examples: Mt Bromo-Tengger-Semeru [30 in Fig. 1] and the Dieng Plateau [19]. The climate of western slopes of Mt Bromo-Tengger-Semeru at ~1,750 m.a.s.l. is characterised by large amounts of rainfall (annually ~ 1,980 mm), with a marked dry season from June to October when average monthly precipitation falls below 100 mm. The average maximum monthly temperature remains constant at ~22 °C, while the minimum monthly temperature averages ~13 °C dropping to 11 °C during the dry season. At the height of the dry season, evaporation exceeds precipitation, indicating the area (and the langurs living there) experiences an arid period. Further to the west, on the Dieng Plateau at ~2,200 m.a.s.l., the rainfall is likewise high (annually ~2,180 mm), with a short dry season from July to September when average monthly precipitation falls below 100 mm. Like at Mt Bromo-Tengger-Semeru, the average maximum monthly

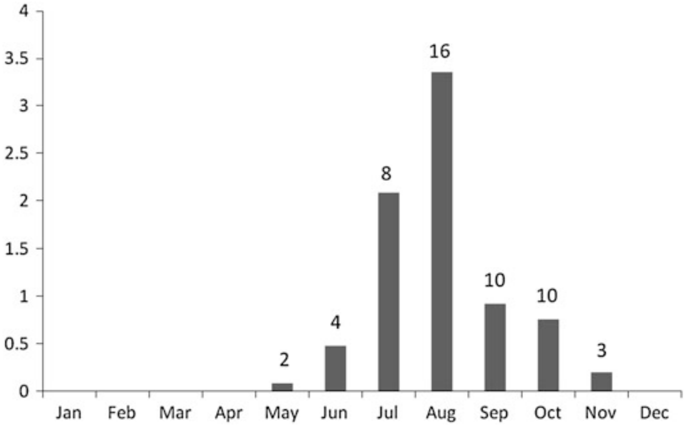

Fig. 2 Average number of frost days at Kertasarie Estate, West Java at 1,600–1,650 m.a.s.l. for the period 1909–1938. Numbers above the bars are the maximum number of days frost occurred within 1 month

temperature remains constant throughout the year but, at ~19 °C, slightly lower. The average minimum monthly temperature is in the single digits, averaging 7 °C but dropping to 3–4 °C in July–September.

Since cool air is heavier than warm air, when air cools down at night, it naturally will flow down slopes. If, however, there is no slope down which it can flow, for example in hollows, valleys or plateaus, the air will get progressively colder. The Dieng Plateau, surrounded as it is by mountains on all sides, illustrates this principle well, and the temperature drops more during the night than what might be expected purely based on altitude. During the dry season, ground frost often occurs daily.

Frost does occur, albeit irregularly, in the mountain areas of Java (Vrolijk 1934; van Steenis 1968, Domrös 1976). Frosts in these areas represent a typical *local* climatological phenomenon, favored by the volcanic small-scale topography. Frost may occur at low level ('ground frost') due to nocturnal radiation especially in 'frost holes' on high mountains, or on montane plateaus surrounded by higher mountains. Frosts occur at elevations above 1,500 m in depressions only, whereas slopes—even at much higher elevation, such as close to the peak of Mt Pangrango at 3,019 m.a.s.l.—can remain frost free year-round (Domrös 1976). Given the importance of the occurrence of frost for tea cultivation, ample data are available from tea plantations. Domrös (1976) summarised data from the Kertasarie Estate in West Java situated between 1,600 and 1,650 m.a.s.l. [near 10 in Fig. 1]. Here, between 1909 and 1938, frost was recorded in 4 out of every 5 years, with an average of ~10 nights a year, ranging from 0 to 38 nights. Frost occurred between May and November, but with a clear peak in July and August (Fig. 2). The largest number of frost nights recorded in 1 year was 38 (in 1925), and the largest number of frost nights in 1 month was 16 (in August 1914). The largest amount of temperature variation measured on a single day (20–21 August 1923) was 25 °C, from −2 °C to +23 °C. While in most nights the temperature fell just below the freezing point, on some nights temperatures dropped until −4.0 °C to −5.6 °C. No contemporary data are available from comparable sites at equal or higher elevations, but using the general rule of a decrease of temperature of about 0.6 °C for every rise of 100 m, one can, at least during clear nights in the dry season, expect the temperature to drop to minus double digits on the highest mountains. Indeed, van Steenis (1972) reported the temperature at ground level on Mt Papandayan [10] to have dropped to −10 °C.

As a general rule, in the mountains cloudiness increases as rainfall increases. On reaching higher altitudes, the intensity of the rains is reduced, but the total duration of showery weather increases. Instead of the heavy tropical cloudbursts, light showers becoming more frequent (Braak 1929). In terms of vegetation, the distinction between the Lowland Zone and the Submontane Zone is largely floristic, with several true lowland (megaterm) plant families being restricted to lower elevations, and other cold-loving (microterm) families occur only higher up. Moving from the Submontane Zone into the Montane Zone, the physiognomy of the forest changes into a closed high-stemmed forest, with decreasing stem diameter and increasing quantity of mass above 2000 m.a.s.l. In the Subalpine Zone, there is dense low forest with few emergents, often covered extensively in moss, and conifers become more common. Of course, these are the general aspects of botanical zonation and other factors may cause deviation (van Steenis 1972).

Altitudinal Distribution of Langurs on Mountains

There has been some confusion regarding the altitudinal distribution of ebony langurs on Java. Bennett and Davies (1994) stated that the species is restricted to coastal and riverine habitats. van der Zon (1978) reported them to be present in mangrove, swamp, and lowland rainforest up to 1,500 m.a.s.l., often near human settlements. Medway (1970) considered its habitat to be inland forest from the lowlands up to almost 2,000 m.a.s.l. For Mt Gede-Pangrango, Doctors van Leeuwen (1926, 1933) reported ebony langurs to occur in the higher parts of the mountains, >2,400 m.a.s.l., while Kohlbrugge (1896) reported that he regularly observed them at altitudes up to 2,300 m.a.s.l. on Mt Semeru. van Bemmel-Lenneman and van Bemmel (1940) reported on the occurrence of ebony langurs in Mts Bromo-Tengger-Semeru from altitudes of 2,100 m.a.s.l. to "near the summit of the Mt Semeru". Indeed, van der Veen (1940) recorded a number of ebony langurs that had died at Semeru's summit, i.e. close to 3,676 m.a.s.l.

During the surveys, ebony langurs were indeed found in mangrove, swamp and lowland forest, along the coast and along rivers, but also throughout the mountains, both in the wetter west and the drier east. Indeed, it appears that they are found in essentially all parts of Java where there is natural forest left. Ebony langurs were observed on 16 of the 18 mountain or mountain complexes on Java which have their highest peaks above 2,500 m.a.s.l. (I did not find them during a short survey on Mt Sundoro in central Java in 1994 and I have no data from Sundoro's twin volcano Mt Sumbing; I found little forest remaining on Mt Sundoro but good forest may still be found on Mt Sumbing).

Given that some of the best forest areas on Java are situated in montane areas, in terms of population numbers and sizes, these areas are the stronghold for the species. Ebony langurs were observed frequently in the Montane Zone between 1,600 and 2,400 m.a.s.l., but also at higher elevations. The tree line appeared to be the natural altitudinal boundary for the species, with groups observed at the tree line, and in gnarled forest and tall shrubs but not in the open subalpine fields adjacent to the forest. The tree line on Java is not situated at a fixed altitude. It is normally located below the highest point of the mountain on active volcanoes, such as Mt Gede [6] or Mt Arjuno [27], but can reach the summit on dormant volcanoes, such as Mt Pangrango [6] or Mt Prahu in Mts Dieng [19]. It is a well-documented phenomenon, known as the Massenerhebungeffect, that the tree line is situated at considerably higher elevations on taller mountains (van Steenis 1972). Indeed, on mountains such as Mt Slamet (3,432 m.a.s.l. [16]) and Mt Semeru (3,676 m.a.s.l. [32]) the forest, albeit somewhat dwarfed, extends to altitudes of well above 3,000 m.a.s.l. In the forests on these highest mountains, the highest altitude populations of the ebony langurs are found.

Groups were observed in high mountain areas during all months of the year, and at high elevation sites that were visited frequently, such as the higher parts of Mt Gede Pangrango [6] and especially Mts Dieng [19], ebony langurs were invariably present. Indeed, the permanent occurrence of ebony langurs at 2,100–2,200 m.a.s.l. in Mts Bromo-Tengger-Semeru has been noted (van Bemmel-Lenneman and van Bemmel 1940). As such, there is no indication that the ebony langurs migrate up and down along the elevation gradient, either daily or seasonally.

Group Sizes and Densities on Mountains

Densities and group sizes are related to both altitude and climatic conditions. Densities of ebony langurs appear to be higher in the drier forest types compared to the wet forest areas, with almost 5 groups km^{-2} in lowland deciduous forest and just over 3 groups km^{-2} in the lowland rainforest. With group sizes being considerably larger in lowland deciduous forest compared to lowland rainforests, this translates to a 2-fold difference in the number of individuals per unit area (Table 2). The differences between the four forest types are not statistically significant when comparing group densities ($\chi^2 = 0.87$, df = 1, P = 0.35) or group sizes ($\chi^2 = 1.90$, df = 1, P = 0.17) but it is when comparing individual densities ($\chi^2 = 29.08$, df = 1, $P < 0.001$). Individual densities in lowland deciduous forest are significantly higher than the other three habitat types combined ($\chi^2 = 26.7$, df = 1, $P < 0.001$), and conversely individual densities in montane rainforest are

Table 2 Densities and group sizes of ebony langurs *Trachypithecus auratus* in 10 forest areas in Java, showing differences between wet and dry forest types and lowland and montane areas

Elevation	Population parameter	Wet climatic zone	Dry climatic zone
Lowland <800 m.a.s.l.	Density	3.30 groups km^{-2} (3 sites)	4.80 groups km^{-2} (3 sites)
	Median group size	7 individuals (18 groups)	11 individuals (9 groups)
Montane >1,300 m.a.s.l.	Density	2.35 groups km^{-2} (2 sites)	3.60 groups km^{-2} (2 sites)
	Median group size	6 individuals (6 groups)	7 individuals (11 groups)

significantly lower than the other three habitat types combined ($\chi^2 = 10.0$, df = 1, P = 0.001).

We find a similar trend when comparing ebony langur populations in montane regions, albeit less pronounced. In the drier forest types, group densities are higher and groups have a tendency to comprise more individuals. When comparing lowland and montane populations within climatic zones, it becomes clear that densities are lower in montane areas and that group sizes are smaller as well. This is especially apparent in the dry forest areas, where groups in the lowlands typically comprise over 10 individuals where they tend to be around seven individuals in the mountains.

Group Composition on Mountains

While the typical ebony langurs group contains a single adult male and a number of immature males, females and young, groups with two adult males have been recorded (Brotoisworo 1983; Kool 1989, 1993; Kartikasari 1986; this study). While these have been recorded in areas where large groups of >20 individuals occur, the two adult male groups were not always the largest groups in the area [with for instance Kool (1989) reporting groups with two adult males containing of 13 and 17 individuals, respectively]. Two adult male groups were observed at sealevel (e.g. Pangandaran, Baluran) to ~1,400 m.a.s.l. (Ijen plateau), and judging by the distribution of groups larger than ~12 individuals (see Fig. 3), it is unlikely that they occur at higher elevations. As such, it appears that in the Lowland to Submontane Zone, below 1,600 m.a.s.l., the social organisation of the ebony langur comprises uni-male and multi-male groups but in the Montane and Subalpine Zone it is uni-male only. At present, it is not known what the relationships are between the males in these two-male groups. It is quite possible that they comprise of age-graded groups in which one of the males is a younger follower (as seen in for instance Thomas' langurs *Presbytis thomasi*: Steenbeek et al. 2000) or whether males mature and breed in their natal group (as seen in for instance Phayre's langurs *Trachypithecus phayrei*: Koenig and Borries 2012). An age-graded two-male group in a species that typically forms one-male units is

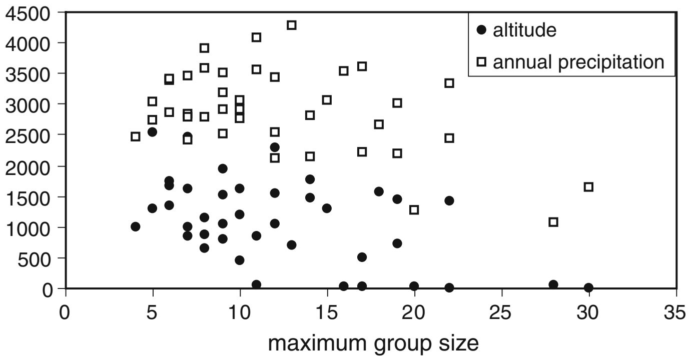

Fig. 3 Relationships between maximum group size of ebony langur *Trachypithecus auratus* and altitude (m.a.s.l.), and maximum group size and annual rainfall (in mm) for 40 sites in 27 forest areas on Java; group sizes are smaller at higher altitudes and in areas with higher rainfall

qualitatively different from for the multi-male, multi-female groups found in, for instance, hanuman langurs *Semnopithecus* spp (Newton 1988; Koenig 2000).

I obtained data on elevation and maximum group sizes from 40 sites in 27 forest areas (24 as part of my own surveys and 3 additional ones from the literature), covering an altitudinal range between sealevel to 2,500 m.a.s.l. (these are the average altitudes of survey sites: individual groups of ebony langurs were observed at higher elevations). With respect to localities where ebony langurs were recorded there were strong correlations between altitude, precipitation and temperature variables. As expected, altitude was strongly correlated with absolute precipitation and temperature variables (Pearson's product-moment correlation coefficient, all $r > 0.316$, $P < 0.04$) but not with the seasonal variability in these variables (all $r < 0.23$, $P > 0.16$). The variability in these climatic variables decreased with altitude. At the lowland sites where ebony langurs have been recorded included sites with little seasonality in rainfall and temperature as well as sites with marked seasonality, but the mountain sites tended to be constant in terms of climatic variability. Thus, with respect to precipitation seasonality, the standard deviation equals 43 % and 40 % of the average in lowland sites ($n = 9$) and hill sites ($n = 8$) below 1,200 m.a.s.l., but only 22 % and 17 % in Submontane sites between 1,200 and 1,600 m.a.s.l. ($n = 10$) and Montane sites above 1,600 m.a.s.l. ($n = 9$), respectively. Group sizes were significantly correlated with Altitude ($r = -0.420$, $P = 0.007$), Precipitation during the Warmest Quarter ($r = -0.409$, $P = 0.009$), Precipitation Seasonality ($r = 0.468$, $P = 0.002$), and Average Annual Temperature ($r = 0.424$, $P = 0.006$).

The best model to predict the observed variation in maximum group size included precipitation seasonality and altitude. Group size increased with seasonality in rainfall, with larger groups in more seasonal regions, and group size decreased with increasing altitude. In all this model explained some 50 % of the observed variation in maximum group size $\left(F_{1,37} = 19.24,\ P < 0.001,\ R^2_{adj} = 0.48\right)$.

Ebony Langur Mountain Ecology

A number of studies have been conducted on the ecology of ebony langurs, but the longer studies have been mostly at low elevations (Table 3). At least three studies have been conducted at the same site, Pangandaran. Pangandaran is a small protected area (5.2 km^2) located on a peninsula on the south coast of West Java. The highest peak on the peninsula is a mere 150 m.a.s.l., but the three research teams studied ebony langurs (Brotoisworo 1983; Kool 1989, 1993; Megantara 1994) all worked in the same coastal strip. Pangandaran is extensively used as a tourists resort, large parts of the area are covered with Teak *Tectona grandis* stands and the behaviour and ecology of ebony langurs inhabiting the part of the reserve where the studies have been conducted are likely to be influenced by the more than one million domestic and foreign tourists that visit the reserve each year. The ubiquitous presence of humans in the area may have resulted in reduced predation pressure and an increase in density of the ebony langurs. Brotoisworo (1983) started working in the area in 1976, habituating seven groups in an area of 0.8 km^2. In 1984, Kool (1989, 1993) spend a year studying two groups at Pangandaran, with home ranges between ~ 0.06 and ~ 0.09 km^2. Extrapolating from the data from Brotoisworo and Kool the population density reaches some 185–195 langurs km^{-2}. Comparing the densities in these areas with those found in the montane areas, as reported above, show that indeed densities are considerably lower in the mountains.

The feeding behaviour of ebony langurs has been studied in detail at six sites (Kartikasari, 1986, Supriatna et al., 1988, Brotoisworo & Dirgayusa, 1991, Kool, 1989, 1993, Djuwantoko et al. 1994; Beckwith 1995; Vogt 2003) often partially in teak plantations, and all but one (Beckwith 1995 from Mt Gede-Pangrango) at low elevations. Like all colobines, ebony langurs possess a fore-stomach digestive system, which allows them to break down cellulose. The fore-stomach microbes have a considerable potential to detoxify alkaloid defence chemicals in plant tissues. This enables the species able to cope with a substantial amount of foliage in their diet, but restricts the use of ripe fleshy fruits (Bennett 1983; Davies 1991; Kay and Davies 1994; Cork 2006; Nijman 2012). Ripe fruits, due to their high sugar content, are largely avoided and when fruit is eaten it is mostly unripe (Kool, 1989; Kartikasari 1986). Indeed, a large part of the diet of ebony langurs consists of leaves, although it varies based on habitat type and seasonality. The amount of foliage in the diet ranges from 46 to 58 % (Vogt 2003), 49 to 51 % (Kool, 1989), 56 % (Kartikasari 1986), 59 % Supriatna et al. (1988), 64 % (Beckwith 1995), 94 % (Djuwantoko et al., 1994).

The ability of this species to cope with considerable amounts of leaves in their diet allows the ebony langurs to live in a large variety of forest types, ranging from freshwater swamps and mangrove forests to the montane forests, and from the everwet rain forest to dry deciduous forests. Ebony langurs seem to be able to cope with some habitat disturbance and to survive in secondary forest types as well as some man-made forests as pine and teak plantations (e.g. Kool, 1993, Brotoisworo, 1983,

Table 3 Sites where the behavioural ecology of ebony langurs *Trachypithecus auratus* has been studied, showing that most work has been done at low elevations and mostly in areas with, for Javanese standards, low amounts of rainfall and marked dry seasons. Numbers between brackets refer to Fig. 1

Province site	Duration (months)	Habitat	Elevation (m.a.s.l.)	Rainfall (mm/year)	References
West Java					
Cikepuh [5]	?	Rainforest (coastal)	0–225	3,450	Ladjar and Simanjuntak (1994)
Muara Gembong [7]	8	Mangrove (coastal)	0–10	1,650	Supriatna et al. (1989)
Mt Gede-Pangrango [9]	11	Rainforest (inland)	1,450	3,400	Beckwith (1995)
Pangandaran [14]	12	Teak/rainforest (coastal)	0–50	3,350	Kool (1989, 1993)
Central Java					
Mts Dieng [19]	5	Rainforest (inland)	600–1,600	4,300	Nijman and van Balen (1998), Nijman and Nekaris (2012)
Cepu [24]	13	Teak forest (inland)	50–150	1,800	Djuwantoko (1991)
East Java					
Mt Semeru [30]	6	Rainforest (inland)	1,300–1,600	3,500	Subarkah et al. (2011)
Baluran [36]	6	Deciduous forest (coastal)	0–10	1,050	Kartikasari (1986)
Bali					
Bali Barat [opposite 36]	19	Deciduous forest (coastal)	10–100	1,500	Vogt (2003)

Djuwantoko et al., 1994; Nijman 2000) Often, however, these plantations are situated adjacent to other more natural forest areas, or are intersected by (river) valleys with a more diverse forest type; areas on which the species seems to depend as well. Fruit production in the montane forest, especially of fruits available for langurs, is lower than in the lowlands (Whitten et al. 1996; Van Steenis 1972). As indicated by the high proportion of leaves in the diet in Mt Gede-Pangrango, as studied by Beckwith (1995), and even more so as suggested by the study of Djuwantoko et al. (1994), it appears that the ebony langurs are indeed able to persist on leaves only. While no data are available on the diet of ebony langurs in the Montane or Subalpine Zone (i.e. above the 1,450 m.a.s.l. where Beckwith observed his study group), we can expect these populations to be amongst the most folivorous.

Conclusions

Ebony langurs do occur in high elevation forest with resident populations present between altitudes of 2,500 and 3,500 m.a.s.l., depending on the height of the mountains. This makes them the only truly tropical high mountain colobine.

Climatic conditions in the mountains of Java are distinctly different from the lowlands, with in regular occurrence of frost, larger variations in day-and-night temperature, and frequent rain. Temperatures at these altitudes average in single digits and are more reminiscent of temperate regions than the tropics.

Situated close to the equator Java experiences small climatic differences over the year, and groups of ebony langurs are present year round at these high altitudes. There are no indications that groups migrate up-and-down the mountain slopes in response to seasonal changes.

Maximum group sizes are related to altitude and seasonality in rainfall, with the largest groups in highly seasonal deciduous lowland forest and the smallest groups in high-altitude rainforest. The social organisation of ebony langurs in the mountains is restricted to single adult male groups only.

Despite important insights gained in the ecology of ebony langurs in the last 30 years since Brotoisworo's first detailed study of the species, there is a clear need for more detailed long-term studies in montane regions. This will allow a better comparison of the species' socio-ecology and population dynamics in areas under different climatic regimes.

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Snow Tolerance of Japanese Macaques Inhabiting High-Latitude Mountainous Forests of Japan

Hiroto Enari

Introduction

Approximately 430,000–630,000 years ago, founder ancestors of the Japanese macaque (*Macaca fuscata*) expanded their distribution from the Asian mainland into the Japanese archipelago (Aimi 2002). Morphological features inherent in ancestral macaques, typified by smaller crown-to-rump lengths, infer that macaques acquired cold tolerance before their expansion into Japan (Fooden 2000; Hamada and Yamamoto 2010). During their movement 120,000 years ago, up the mainland of Japan to the Shimokita Peninsula—the northernmost habitat of any nonhuman primate species—macaques are believed to have acclimatized further to survive in varied environments, including extreme cold and snow (Iwamoto and Hasegawa 1972). Their high phenotypic plasticity, in terms of behavioral, ecological, morphological, and physiological properties, led to the successful occupation of a range of habitat types, from lowland forests including artificially disturbed landscape (referred to as *Satoyama*) to subalpine forests with heavy snow (Biodiversity Center of Japan 2011; Iwano 1981). Such plasticity has been considered a common property specific to the genus macaque, except for species ranging only in broadleaved evergreen forests (e.g., Fooden 1982, 2000; Ménard 2002; Richard et al. 1989; Sinha 2005; Thierry 2007). However, it is likely that the geographical features endemic to the Japanese archipelago, which has an extremely high environmental gradient, serve as a major driving force for Japanese macaques to exhibit obvious intraspecific variations in physio-ecological characteristics, which are generated by plasticity (e.g., Hamada and Yamamoto 2010; Hanya 2010).

Northernmost macaque populations, located in the northern Tohoku region, were hunted excessively by local residents prior to the Second World War (Mito 1992).

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As a result, macaque populations in the region have remained seriously segmented and isolated (Biodiversity Center of Japan 2011). According to a landscape-scale study to identify potential macaque habitats in the region (Enari and Suzuki 2010), most of the optimal and suitable habitats remain untouched by the current macaque distribution (Fig. 1). In response to their vulnerable status, the Japanese Ministry of Environment has listed these regional macaque populations as endangered since 1991.

Ecological interests in the phenotypic traits of macaque species in cold areas, and conservation concerns for the vulnerable regional populations, provided the initial motivation for primatologists to study the northernmost macaque populations mainly in the Shimokita Peninsula (Izawa and Nishida 1963). This peninsula is not the optimal location for studying the phenotypic traits of macaques inhabiting cold areas, especially in terms of snow tolerance, because its climate, unlike

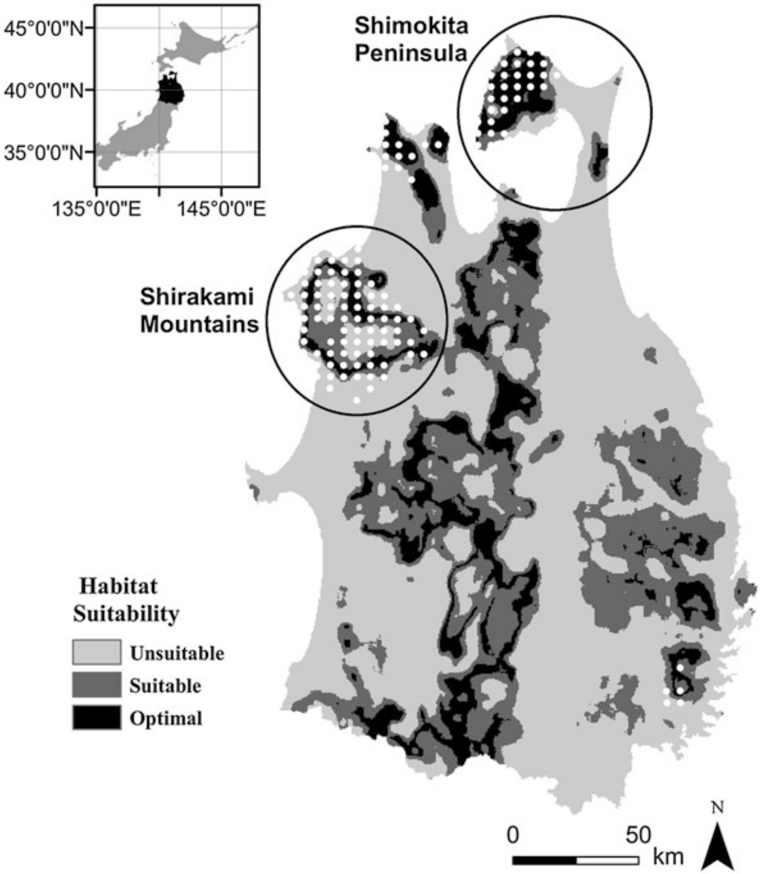

Fig. 1 Habitat suitability map for Japanese macaques inhabiting northern Tohoku, Japan, calculated by means of ecological niche factor analysis (modified from Enari and Suzuki 2010). The *white spots* inside the map indicate present distribution

that of the western region of Aomori Prefecture, is moderated by the Tsushima warm ocean current (Fig. 2). However, ecological studies of macaques inhabiting the western region of Aomori Prefecture are limited, because precipitous terrain and heavy snowfall make fieldwork difficult. Thus, questions remain about how northernmost macaque populations survive in extremely heavy snow and cold environments, without physiological tactics such as daily torpor or hibernation, to cope with cold. With the exception of *Cheirogaleus medius* (Dausmann et al. 2004), no primate possesses such a physiological acclimation.

In this context, a few researchers, including the present author, have conducted consecutive field works since 2000 to identify regional phenotypic traits of Japanese macaques specific to cold areas. These studies have focused on the Shirakami Mountains, which support the largest distribution of macaques among the remaining northernmost populations (Fig. 1). The Shirakami Mountains are one of the heaviest snowfall areas in the world, with snowfall usually lasting for almost half the year (Ministry of the Environment 2009) and reaching a maximum depth of 2 m in lowland areas and more than 4 m in mountainous areas. While coldness constrains macaque activity from a physiological aspect (see section Energy deficit in winter), heavy snowfall restricts their activities from a physical aspect—in particular, by making movement on the ground more difficult (Watanuki and Nakayama 1993; Izumiyama 1999), eliminating safe sites available for resting and

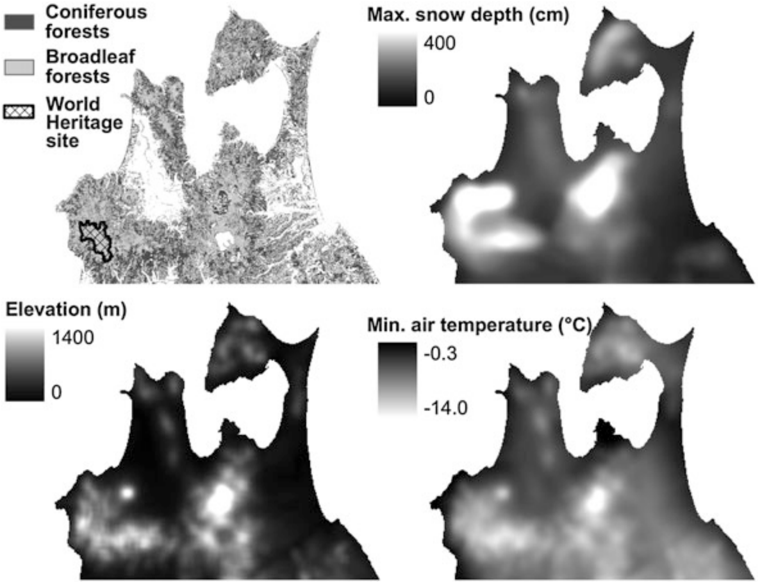

Fig. 2 Vegetation and climate conditions in Aomori prefecture, including Shimokita peninsula (*upper right*) and the Shirakami mountains (*lower left*). Vegetation maps were compiled using a public database derived from the Biodiversity Center of Japan. Climate data were composed of mesh climatic data with mean values from 1971 to 2000 (Japan Meteorological Business Support Center 2002). Maximum snow depth and minimum air temperature were mean values of each coldest month

sleeping (Wada and Tokida 1981; Wada et al. 2007), and leading to a significant decrease in available dietary resources (Suzuki 1965; Taroda 2002).

This chapter reviews recent studies on the overwintering tactics of Japanese macaques inhabiting the mountains. Together with the Japanese macaque, four other primate species inhabit higher latitudes than the Tropic of Cancer or the Tropic of Capricorn, namely, *M. sylvanus*, *Rhinopithecus roxellana*, *R. bieti*, and *Trachypithecus geei*. Recently, snub-nosed monkeys (*R. roxellana* and *R. bieti*), which inhabit the coldest environments among these high-latitude primates, have attracted increasing interest as research subjects for the wintering ecology and cold tolerance of primates: e.g., habitat uses (Cui et al. 2006; Li et al. 2008; Quan et al. 2011) and dietary strategies (Li et al. 2002; Li 2006; Grueter et al. 2009). However, the Shirakami Mountains constitute a rare primate habitat, with heavy snowfall, the accumulation of which greatly surpasses that of those monkey habitats. Hence, this chapter focuses on snow tolerance of macaques, by concentrating on regional phenotypic traits of the Shirakami population in terms of their dietary characteristics and habitat-use patterns. In the northern Tohoku region, including the Shirakami Mountains, higher altitudes remain unoccupied by regional populations because of past overhunting. Therefore, species- and regional-specific ecological characteristics of the macaque population are evaluated by substituting altitudinal gradient for latitudinal cline (or snowfall gradient). In this chapter, "light-snowfall area" and "heavy-snowfall area" are defined using a threshold value of 1 m for the deepest snowfall.

Study Area and Subject Primate

Geographical and Climatic Conditions

The Shirakami Mountains (40°N, 140°E) encompass a mountainous forest area of ~1,300 km^2, including the most extensive primary beech (*Fagus crenata*) forests in East Asia. The core area of the mountains (169.7 km^2) has been included on the UNESCO World Natural Heritage List since 1993.

The study area is in a cool-temperate climatic zone. According to the weather-monitoring station at the natural heritage site (615 m ASL) (Ministry of the Environment 2009), the mean temperatures of the coldest and warmest months (monitoring period 1999–2009) were −4.7 °C (January) and 20.5 °C (August), respectively (Fig. 2). The mean maximum snow depth was 3.87 m (March), with lower and upper limits of 2.90 and 4.71 m, respectively. Much of the mountains are covered by forests at elevations below 1,000 m with steep terrains.

In addition to macaques, 13 medium-to-large mammal species have historically inhabited the Shirakami Mountains. Gray wolves (*Canis lupus*) were eradicated from the whole of Japan, including the Shirakami Mountains, by the beginning of the twentieth century. Therefore, no large carnivores inhabit the study area, which means that the macaques have no predators.

Population Density

Macaques inhabiting the Shirakami Mountains constitute the largest remaining northernmost populations. In recent years, macaques have greatly expanded their geographic distribution coverage (Biodiversity Center of Japan 2011). Thus, they are expected to act as source populations for the ingress of individuals and troops into potential new habitats (Enari and Suzuki 2010). With the exception of areas with alpine meadows above the tree line, macaque troops are continuously distributed throughout the mountains (Biodiversity Center of Japan 2011). In the northeastern mountains, where the macaque population has been extensively monitored, the mean ecological population density (i.e., the population density within their utilization distributions) was 5.17 individuals/km^2 in 2008 (Enari and Sakamaki 2011). This value is comparable with those of other lower-latitude heavy-snowfall areas, such as the Shiga Heights [4.0–5.6 individuals/km^2 (Suzuki et al. 1975); 36°N, 1,000–2,000 m ASL] and the Hakusan Mountains [4.2–6.9 individuals/km^2 (Iwamoto 1978); 36°N, 500–1,500 m ASL], but lower than those of light-snowfall areas, typified by the Shimokita Peninsula [8.2 individuals/km^2 (Azuma and Ashizawa 1980); 41°N, 0–500 m ASL] and Kinkazan Island [19–29 individuals/km^2 (Izawa 2009); 38°N, 0–400 m ASL). These comparisons among cool-temperate forests demonstrate that regional variation in population density is not explainable in terms of latitudinal cline (Takasaki 1981; Hanya et al. 2006). The apparent differences in density between light- and heavy-snowfall areas may be explained by the availability of fallback foods (foods that are relied on when preferred items are unavailable), such as herbs growing on the forest floor, or bark and buds of deciduous trees (Hanya 2010; Hanya et al. 2006). The available dietary resources become reduced with increasing amounts of snow cover, thereby suppressing population increases in heavy-snowfall areas.

Morphological Traits

In accordance with Bergmann's rule, the body size of Japanese macaques generally correlates with the lowest monthly average temperatures (i.e., January) of their habitats (Hamada 2002; Hamada and Yamamoto 2010). Body-size growth contributes not only to a decrease in the ratio of body surface area to volume, but also to an increase in fat accumulation in the mesentery and the celom (Hayama et al. 1998). These features are commonly recognized means of cold acclimation in macaques.

Comparison of body size among macaques inhabiting the study area and other snowfall areas (Table 1) indicates that macaques inhabiting heavy-snowfall areas tend to have higher body weights and longer anterior trunk lengths than do macaques inhabiting light-snowfall areas.

Table 1 Regional variation in body size of adult Japanese macaques living in snowfall areas

Locality	Latitude (°N)	Snowfall	N		Body weight (kg)		Anterior trunk length (cm)		Source
			Male	Female	Male	Female	Male	Female	
Shimokita	41	Light	0	10	–	10.87 ± 1.05	–	36.79 ± 2.25	Hamada et al. (1996)
Shirakami	40	Heavy	8	17	13.23 ± 2.11	12.29 ± 1.65	40.63 ± 7.50	40.41 ± 4.96	Present study
Nikko	36	Light	15	20	12.09 ± 1.09	9.27 ± 0.85	39.91 ± 2.12	36.70 ± 1.50	Hamada (2002)
Hakusan	36	Heavy	0	14	–	12.77 ± 1.27	–	39.36 ± 1.48	Hamada (2002)
Shiga heights	36	Heavy	23	47	13.54 ± 2.07	11.68 ± 1.65	40.83 ± 2.06	38.87 ± 2.12	Hamada (2002)

Energy Deficit Compensation Under Heavy-Snowfall Conditions

Energy Deficit in Winter

Japanese macaques inhabiting heavy-snowfall areas are exposed to the dangers of hypothermia and famine during winter, resulting in an increased mortality rate. Extension of the snowfall period during abnormal weather has been associated with mass mortality of local populations (Koganezawa 1991; Taroda 2002; Izawa 2009). In 1984, abnormal weather (including extraordinarily heavy snowfall) on Kinkazan Island reportedly caused the death of 33.3 % of the total population (Izawa 2009). Even in cases where mass mortality does not occur, such harsh environments have a debilitating effect on the macaque body. Macaques inhabiting cool-temperate forests lose 10–17 % of their body weight during winter (Wada 1975; Nakayama 2002; Taroda 2002), whereas macaques inhabiting warm-temperate forests lose only 5 % of their body weight (Mori 1979).

A primary cause of the influences of snow and cold environments on mortality rate and body weight is deficient energy intake. Even in light-snowfall areas, such as the Shimokita Peninsula and Kinkazan Island, the energy intake of macaques during winter accounts for only 60 % of energy expenditure (Nakagawa 1989; Nakagawa et al. 1996; Nakayama et al. 1999). Energy deficit in macaques during winter is commonly considered to results from two limitations, physical and temporal (Nakagawa et al. 1996; Hanya 2010). The physical limitation is gut capacity. The maximum capacity of the macaque's gut is approximately 300 g dry weight (Iwamoto 1982). This means that whenever macaques fill their stomachs with only low-calorie diets, the total calorie intake is likely to fall below their basal metabolic rate. The temporal limitation is the time spent feeding per day. The activity budget assigned to feeding time is restricted by ambient temperature. In winter, the mean amount of time spent feeding generally accounts for approximately 40 % of the total activity budget in cool-temperate forests, and also in warm-temperate forests (Tsuji 2010). Thus, the time spent feeding does not necessarily increase in areas where dietary resources are deficient (i.e., snowy regions). This unexpected finding is explainable in terms of thermoregulatory cost. Macaques inhabiting colder areas require more time resting (such as sunbathing) to balance thermoregulatory cost in winter, which means that the time spent feeding is constrained (Watanuki and Nakayama 1993; Agetsuma and Nakagawa 1998; Izumiyama 1999). In heavy-snowfall areas, the time spent feeding accounts for 25 % of the total activity budget on snowy days, when the temperature falls below −5 °C, but may reach 50 % of the total activity budget on sunny days, when temperatures exceed −5 °C (Wada and Tokida 1981).

The activity budget of Japanese macaques differs greatly from that of *R. roxellana*, which is relatively insensitive to ambient temperature. For *R. roxellana*, the time spent feeding in the coldest season (mean ambient temperature −8 °C) exceeds 60 % of the total activity budget, which is longer than in any other season (Guo et al. 2007).

These interspecies differences in activity budgets during cold seasons indicate that the Japanese macaque tolerates cold less efficiently than does *R. roxellana*.

Alternative Dietary Resources in Deep Snow

The bark and buds of woody plants are considered dominant fallback foods for temperate-living primates (Grueter et al. 2009). The same holds true for Japanese macaques inhabiting deciduous forests (Hanya et al. 2006), including the study area (Enari et al. 2005). There is no major difference in calorie content per unit weight between bark and buds available in winter, and fruits available in fall (Nakagawa et al. 1996; Nakayama et al. 1999). Moreover, the digestive efficiency of bark and buds is similar to that of foliage (Nakagawa et al. 1996). However, bark has tough fiber tissue and buds have only a small edible part. Therefore, they are generally considered low-value dietary resources in terms of feeding rate (i.e., speed of nutrient intake) (Nakagawa et al. 1996; Nakayama et al. 1999).

Snow accumulation, depending on altitudinal gradient and latitudinal cline, is a determining factor in the variety and quantity of available food items for macaques. Suzuki (1965) summarized a general trend regarding the influences of snow accumulation on winter dietary habits in cool-temperate forests, and reported that the dominant foods of macaques are sedge (*Carex* spp.) and grass roots in snow-free areas, dwarf bamboo (*Sasa* spp.) in light-snowfall areas, and bark and buds in heavy-snowfall areas. Therefore, with increasing snow accumulation, macaques are obliged to forage on foods that have a lower feeding rate.

This trend does not absolutely support the dietary habits of macaques inhabiting the Shirakami Mountains. According to fecal analysis of macaque diets in the study area (Enari et al. 2005), graminaceous species were observed in feces during all seasons, including winter. In early winter (December and January), they were detected in 100 % of feces ($N = 62$), while in late winter (February and March), they were detected in 94.5 % ($N = 93$) of feces. The rationale for this finding may be the macaque's unique habitat-use pattern. An evaluation of winter habitat use in the study area, using an ecological niche modeling technique (Enari and Sakamaki 2012), revealed that macaques clearly selected steeply sloping land among the available landscape structures (Fig. 3). This potential selectivity of macaques for sloping land is comparable with that of the Japanese serow (*Capricornis crispus*), which is an ungulate typically found in precipitous mountains (Nowicki and Koganezawa 2001; Ishida et al. 2003). Avalanches are common on such steeply sloping land. When a large avalanche occurs, herbaceous perennials (such as sedge and dwarf bamboo) that are buried in snow temporarily become accessible as dietary resources (Fig. 4). Thus, macaques are likely attracted to avalanche-prone slopes, and successfully acquire alternative foods with a higher feeding rate than that of bark and buds. However, occupying such slopes has potentially deadly side effects, and may be a cause of death in macaques. Indeed, macaques buried in avalanches have occasionally been observed in the study area. To understand the trade-off between

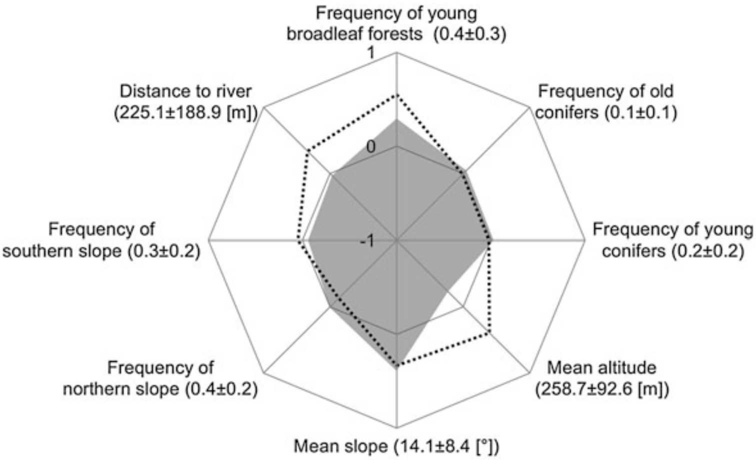

Fig. 3 Coefficients of the marginality factors of species niche for Japanese macaque troops (*gray area*) and Japanese serows (*dashed line*) inhabiting the Shirakami mountains, Japan (modified from Enari and Sakamaki 2012). The factors were calculated by means of ecological niche factor analysis, using the tracks of each mammal on the snow surface as evidence of species occurrence. Positive values represent positive selection, and negative values represent negative selection, relative to mean conditions within a reference area. Values in parentheses show the mean ±SD of the conditions within the reference area. "Frequency" is the average value for each variable within a circular moving window with a 250 m radius

risk and return in selection of avalanche-prone slopes, further empirical studies are needed to analyze the mortality statistics of macaques in winter.

Feeding Tactics During the Snowmelt Season

The conditions of dietary resources in late winter (i.e., the snowmelt season) are strategically important to increase the success rate of overwintering in heavy-snowfall areas. The mortality rate of macaques inhabiting the Hakusan Mountains—a typical heavy-snowfall area—increases significantly in late winter (especially March and April), and the success rate of overwintering declines with delayed snowmelt in early spring (Taroda 2002).

When the snowmelt begins, macaques inhabiting the study area alter their feeding tactics to access new dietary resources. One feeding tactic is the use of herbaceous perennials in streams. During the snowmelt season, ice and snow covering streams melt before snow on the ground. Macaques enter the streams and feed on the roots of reeds and leaves of sedge (Fig. 5). During late winter in the study area, the time spent feeding in streams accounts for 13.9 % of the total feeding time (Enari et al. 2005). Another feeding tactic is the use of autumnal berries. Most berries are consumed by frugivorous animals before the beginning of

Fig. 4 Avalanche-prone slopes (*upper right*) enable the use of alternative dietary resources with higher feeding rates, such as bamboo grass (*Sasa kurilensis*) and altherbosa (e.g., *Petasites japonicus*)

Fig. 5 Japanese macaques entering a frigid river to feed on the roots of reeds (mainly *Phragmites australis*) during the snowmelt season

winter in snow-free or light-snowfall areas. However, some remain buried under massive snow in heavy-snowfall areas where they are protected from bird and mammal feeding until the snowmelt season. As demonstrated by the previously described fecal analysis (Enari et al. 2005), macaques inhabiting the study area are known selectively to feed on cold-stored berries, especially those of spindle trees (such as *Eunoymus oxyphyllus* and *E. sieboldianus*), during early April.

Thus, macaques inhabiting heavy-snowfall areas are likely try to offset their energy deficit in winter, not only by feeding on bark and buds as fallback resources, but also by using concealed dietary resources buried in the snow. Further, nutritional and physiological studies are required definitively to assess the contribution made by consumption of concealed dietary resources to the success rate of overwintering.

Foraging on Bark and Buds of Broadleaf Trees as Fallback Resources

Bark and Bud Selection

In addition to the alternative dietary resources described above, bark and buds of broadleaf trees undoubtedly comprise a principle winter diet for macaques inhabiting heavy-snowfall areas, including the study area (Enari et al. 2005; Sakamaki et al. 2011). Feeding selectivity on bark and buds of specific tree species is generally observed, and varies according to location (e.g., Suzuki 1965; Wada and Ichiki 1980; Nakayama et al. 1999; Sakamaki et al. 2011). Sakamaki et al. (2011) demonstrated that selectivity shares a common feature, namely, a preference for shade-intolerant trees (i.e., heliophytes) rather than shade-tolerant trees, especially in shrubby and vine species (Table 2). Bark and buds of the Japanese mulberry (*Morus bombycis*)—a shade-intolerant shrubby tree—is in general the favorite winter diet for northernmost macaques (Watanuki et al. 1994; Nakayama et al. 1999; Enari and Sakamaki 2010; Sakamaki et al. 2011). This selectivity for mulberry trees may be because of their lower condensed tannin content as a digestion inhibitor, compared with other broadleaf trees (Ishii and Ohara 2004). However, the reasons for selective feeding on shade-intolerant trees other than mulberry trees remain to be elucidated. Inherent nutritional properties do not fully explain selective feeding, because caloric value does not differ substantially between shade-tolerant and shade-intolerant trees (Nakagawa et al. 1996; Nakayama et al. 1999).

Table 2 Frequency of feeding by Japanese macaques on bark or buds of woody plants in the Shirakami Mountains, northern Japan (modified from Sakamaki et al. 2011)

	Shade tolerance of trees					
	Intolerant		Tolerant		Middle	
	N (%)	S (%)	N (%)	S (%)	N (%)	S (%)
Shrubby species	565 (56.0)	4 (23.5)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)
Arboreal species	18 (1.8)	2 (11.8)	26 (2.6)	1 (5.9)	270 (26.8)	7 (41.2)
Vine species	130 (12.9)	3 (17.6)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)
Total	713 (70.7)	9 (52.9)	26 (2.6)	1 (5.9)	270 (26.8)	7 (41.2)

S means species richness

Fig. 6 Influences of selective foraging by Japanese macaques on the growth of Japanese mulberry trees. The plant above the snow-covered surface is heavily damaged by foraging (for reference, ground height at the tip of the striped pole = 2 m), resulting in the creation of a visible foraging line by macaques

Influences of Foraging on the Growth and Development of Dietary Plants

A question now arises. Does the selective feeding on bark and buds by macaques affect dietary plant growth negatively and, consequently, deplete their dietary resources? According to an empirical study conducted in warm-temperate forests (Iwamoto 1978), a natural troop of Japanese macaques consumes only 0.36–1.59 % of the primary production of the forests, which is considerably lower than the threshold (10–20 %) at which a potentially destructive effect on native vegetation becomes obvious. Furthermore, in cool-temperate forests, the influence of macaque feeding on dietary plants is limited (Izawa 1995a, b). Wada (1983) described a unique tactic of macaque troops to prevent depletion of their dietary resources in the Shiga Heights, a typical heavy-snowfall area. The troops rotate their temporal utilization distribution within their home range, before consuming all staple dietary plants in particular food patches. By contrast, in the Shimokita Peninsula—a light-snowfall area—the destructive influences of foraging macaques on the bark and buds of mulberry trees as their dominant dietary plant have been reported (Watanuki et al. 1994).

Enari and Sakamaki (2010) evaluated the influence of macaques on the growth and development of mulberry trees, under various environmental conditions, in and around the study area. They revealed that selective foraging caused potentially fatal damage to 5–10 % of the mulberry trees annually, and resulted in dwarfing of the tree morphology. The mean tree height in areas constantly occupied by macaque troops was 1.7 ± SD 0.5 m ($N = 152$), whereas in macaque-free areas it was 3.1 ± SD 2.1 m ($N = 79$) (Fig. 6). However, the mean stem density in the constantly occupied area was double that of the macaque-free area. This phenomenon may be explained in terms of a positive function of macaques as seed dispersers. In addition, foraging commonly resulted in compensatory plant growth by increasing shoot number. These findings indicate that sufficient snow cover is a key environmental factor, which establishes a nonantagonistic interaction between macaques and mulberries, by suppressing the negative influence of macaques as a destructive herbivore and improving their positive influence as a skillful pruner. This rationale may also explain the obvious feeding damage to mulberry trees often occurs in light-snowfall areas.

Strategic Use of Artificial Conifer Plantations as Alternative Habitats

Monotonous conifer plantations are frequently considered low-quality habitats for mammal species (Hunter 1990). According to empirical studies of mid-latitude warm-temperate forests, this is often true for Japanese macaques, but only in terms of availability of dietary resources (Agetsuma 2007; Hanya 2010). Detailed analysis of previous studies indicates that conifer plantations may provide useful resources for macaques inhabiting snowy areas. Studies conducted in the heavy-snowfall area of the Shiga Heights demonstrated that macaques select conifer plantations—comprising only evergreen arboreal trees in the cool-temperate forests of Japan—as sleeping and resting sites for protection against extremely cold wind and snow (Wada and Tokida 1981; Wada et al. 2007). Wada (1994) confirmed that the air temperature beneath conifer trees is a few degrees warmer than that beneath native broadleaf trees. Although research in the light-snowfall areas of the Shimokita Peninsula concluded that conifer plantations are useless as a food resource for macaques (Furuichi et al. 1982), recent investigations in the Shirakami Mountains revealed the opposite (Sakamaki et al. 2011; Sakamaki and Enari 2012).

The study by Sakamaki et al. (2011) was conducted during snowy seasons, which are considered the bottleneck seasons in terms of food availability. The findings revealed that species richness and biomass (as measured by stem density and total basal area [TBA]) of woody plants as possible dietary resources for macaques tended to decrease with increasing plantation age (or the progress of canopy closure), but recovered when dominant cedar trees were thinned at the proper time (40 years after planting) (Fig. 7). Furthermore, species richness and stem density in cedar plantations of any age compared favorably with those of the native natural vegetation (i.e., primary beech forests). Thus, available dietary resources in conifer plantations may not always be low for macaques, as long as appropriate tree thinning for timber production is implemented. This conclusion is reinforced by observations of winter habitat use in the study area, which indicate that macaques do not avoid landscape structures with conifer plantations (Fig. 8). Snow damage to plantations may serve as an adjusting function to prevent an excessive decrease in dietary resources in heavy-snowfall areas. In snowy areas, snow damage generally reduces the stem density of planted conifers, resulting in a more open plantation canopy than in warmer areas (Masaki et al. 2004).

Summary and Future Challenges

The Japanese macaque is often called a weed species (Richard et al. 1989) and has flourished as a unique generalist in the Japanese archipelago by acclimatizing to diverse environments along altitudinal and latitudinal clines. In snowbound forests, this ability enables macaques to seek out concealed dietary resources beneath snow and ice to compensate for their energy deficit. In addition to past excessive hunting pressure, existing strong artificial disturbances to native forests in severe environments with heavy snow have contributed to the eradication of various native mammalian species—gray wolf, ungulates (*Sus scrofa* and *Cervus nippon*), and black bear (*Ursus thibetanus*)—from part or all of the northern Tohoku region, including the Shirakami Mountains. For example, since the 1960s, more than 50 % of the native broadleaf forests around the Shirakami World Natural Heritage site have been replaced by conifer plantations—mainly Japanese cedar (*Cryptomeria japonica*)—on the basis of the national forest policy. Nevertheless, the northernmost macaques have strategically used artificially modified forests as alternative habitats, and are steadily recovering their distributions. It appears that the

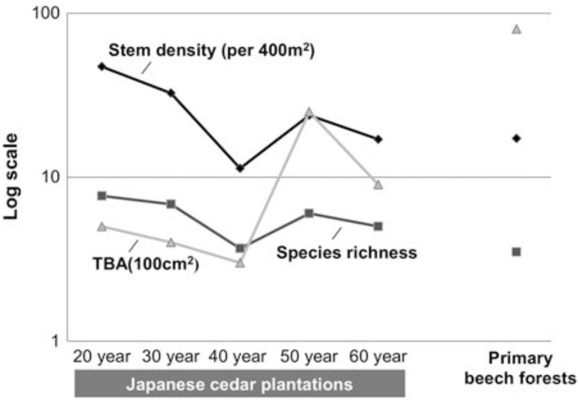

Fig. 7 Stem density, species richness, and total basal area (TBA) of winter food trees for Japanese macaques in conifer plantations of different ages, and also primary beech forests located in the Shirakami mountains, northern Japan (modified from Sakamaki et al. 2011)

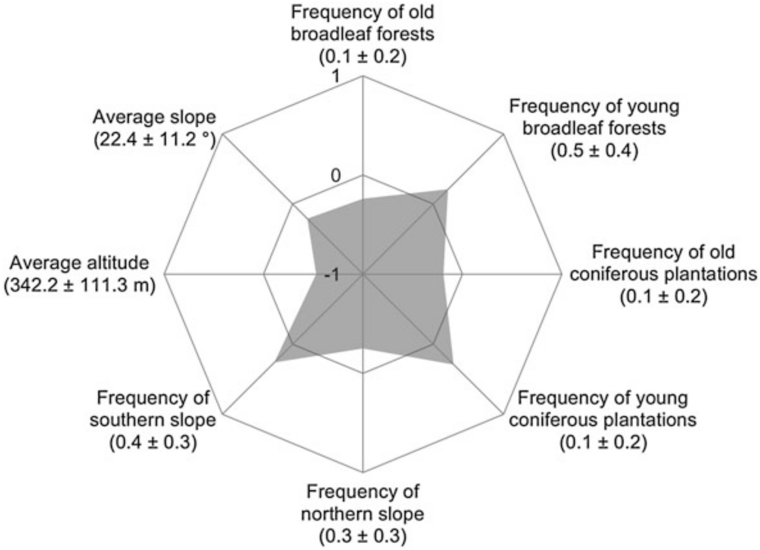

Fig. 8 Coefficients of the marginality factor of species niche for feeding sites of Japanese macaque troops inhabiting the Shirakami mountains, Japan (modified from Sakamaki and Enari 2012). The factor was calculated by means of ecological niche factor analysis, using the records of direct observations for each individual of wild macaque troops during winter. "Frequency" is the average value for each variable within a circular moving window with a 90-m radius. See Fig. 3 caption for details

astonishing plasticity of this species sustains their survival and recovery under heavy snow conditions.

Environments surrounding macaques change continually. Snow accumulation is on a declining trend, influenced by recent winter warming. This environmental change may have negative effects on sustainable biological interactions between macaques and dietary plants in heavy-snowfall areas. According to scenario analyses on climate change, beech forests—typical of snowy areas in Japan (including the Shirakami Mountains)—may be close to extinction in the next 100 years (Tanaka et al. 2006; Matsui et al. 2009). This prediction means the loss of regional biodiversity and landscape structures inherent in current snowy areas, potentially resulting in the gradual loss of acquired regional-specific characteristics of macaques. Conservation of northernmost macaque populations will require continuous monitoring of the influences of climate change on the regional macaque society.

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Seasonal and Altitudinal Migration of Japanese Macaques in the Northern Japan Alps

Shigeyuki Izumiyama

Introduction

The population density and home range area of wild animals often depend on the distribution of food sources (e.g., Iwamoto 1978; Freeland 1979; Caldecott 1980; Liberg and Sandell 1988; Sandell 1989). Severe climate conditions such as low temperature and snow cover directly affect animal life, particularly in higher altitudinal habitats, because availability and distribution of food resources shows not only seasonality but a large variation among habitat types. This causes various animals, including terrestrial mammals, to migrate. Mammals inhabiting northern latitudes show seasonal migration between summer home ranges and wintering sites; e.g., red deer in Scotland (Darling 1937) and Norway (Mysterud et al. 2001), mountain sheep in North America (Geist 1971), sika deer in Japan (Uno and Kaji 2000; Igota et al. 2004; Izumiyama and Mochizuki 2008; Izumiyama et al. 2009), moose in Norway (Herfindel et al. 2006), pronghorn antelope in North America (Cherney and Clark 2008), asiatic black bear (Izumiyama and Shiraishi 2004) and Japanese macaques (Izumiyama 1994a, b; Imaki et al. 2000).

The per capita home range area of Japanese macaques (*Macaca fuscata*) is demonstrated to be smaller in evergreen broad-leaved forests, which grows in regions with warmer climate throughout the year and which shows higher biodiversity than deciduous broad-leaved forests (Takasaki 1981). It has also been reported that the per capita home range area of macaque troops that use anthropogenic cultivated land with abundant food source is significantly smaller than the area of the troops that do not (Izumiyama et al. 2003). These studies indicate that habitat quality defines both troop size and home range area in Japanese macaque. In this chapter, I focus on the ecology of macaque troops that use habitats consisting of natural vegetation (Izumiyama et al. 2003). These troops do not utilize anthropogenic cultivated land but distribute up into the alpine zone where habitat

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conditions gradually deteriorate with the altitude, to the point where macaques cannot inhabit.

The Northern Japan Alps is located in the central area of the Honshu Island, Japan. The type of vegetation clearly change according to the altitude. Japanese macaques inhabit the entire altitudinal range, i.e., from the human residence area of 600 m altitude to elevations above the forest line (Izumiyama 1994a, b). However, habitat use by troops is expected to differ between those that inhabit the lower montane zone and those that inhabit the upper forest line. Some troops occupy the alpine and upper subalpine zones during the season without snow cover, although no troops have been observed in these zones during the snowy term. Studies of macaque populations in the Northern Japan Alps thus provide information on adaptability of primates in extremely harsh environments.

I tracked 11 macaque troops inhabiting the Takasegawa River basin in the Northern Japan Alps from 1988 to 2002 (Fig. 1). I investigated the variations in

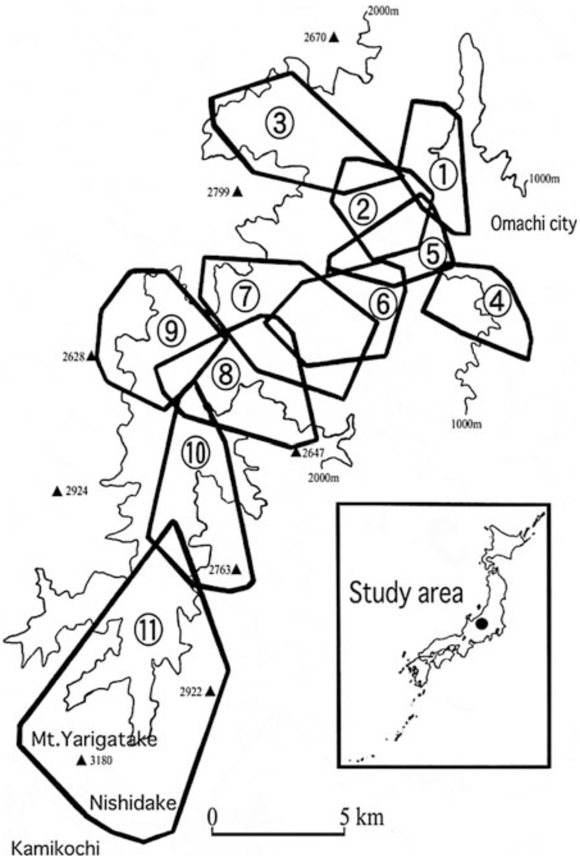


Fig. 1 Location of the study area. Enclosures shown in thick line indicate the home ranges of macaque troops (*circled numbers* are troop numbers)

habitat use among the troops and, through assessing the essential environmental conditions of the habitats, I aimed to clarify the seasonal migration characteristics of Japanese macaques in the study region.

Methods

Description of the Study Area

The study area is located on the eastern side of the mountains of the Northern Japan Alps. In this region, the Takasegawa River basin extends from Omachi City (Nagano Prefecture) to the southwest into the mountains (Fig. 1).

Wild populations of Japanese macaques inhabit this river basin. The habitat ranges from an elevation of 600 m to over 3,100 m. This range encompasses agricultural fields in the lower elevations to the highest mountain summit of Mt. Yarigatake (3,180 m.a.s.l.) (Izumiyama 1994a, Izumiyama et al. 2003). The distance between Mt. Yarigatake and the lowest inhabited forest is 25 km.

I observed temperatures by data loggers (Kona systems Co. Ltd.) at Kamikochi (1,530 m.a.s.l.) and Mt. Nishidake (2,680 m.a.s.l.). The thermistor sensor was valid within the range of −50 and 140 °C, and the accuracy was ±0.4 °C. Table 1 shows the climate characteristics of these three localities from 1992 to 1997, and temperatures at Omachi (720 m.a.s.l.) by Nagano Regional Meteological Office (2012).

Analysis of monthly temperatures of Nishidake, where macaques inhabit only in non-snowy term, and Kamikochi revealed that the average temperature in Kamikochi in 1996 was 3.8 °C, while that of Nishidake was −0.2 °C (Fig. 2). Plant growth occurs when the monthly average temperature exceeds 5 °C. Duration of months that exceeded 5 °C was 6 months in Kamikochi, and 4 months at Nishidake.

The type of vegetation generally changes in a predictable way with elevation (Yamanaka 1979). In the Northern Japan Alps, montane tree species occur at lower

Table 1 Climate characteristics compared among localities

	Omachi	Kamikochi	Nishidake
Altitude (m)	720	1,530	2,680
Inhabitance of macaques	All seasons	All seasons	Non-snowy
Mean annual temperature (°C)	9.6	4.3	−0.2
Maximum monthly temperature (°C)	22.2 (Aug)	16.6 (Aug)	13.3 (Aug)
Minimum monthly temperature (°C)	−2.9 (Jan)	−7.1 (Feb)	−13.3 (Feb)
Warmth index	77	40	24
Highest temperature (°C)	35.0 (2002)	25.6 (1996)	26.3 (1996)
Lowest temperature (°C)	−17.0 (2003)	−29.4 (1996)	−27.2 (1997)
Annual precipitation (mm)	1,395	2,716	
Maximum Snow depth (cm)	38–101	103–183	

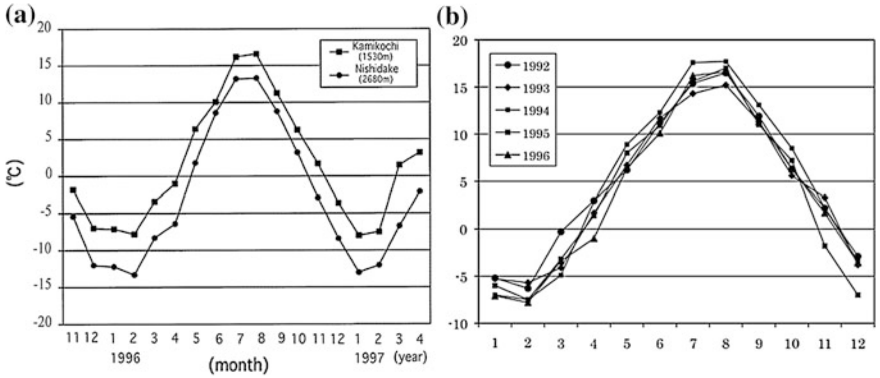


Fig. 2 **a** Monthly temperature fluctuation at Kamikochi (1,530 m) and Mt. Nishidake (2,680 m). **b** Monthly temperature fluctuation at Kamikochi (1992–1996)

elevations, and subalpine tree species occur above this montane zone usually at elevations above 1,600 m. Plantation forests are maintained throughout the region. For example, larch (*Larix kaempferi*) plantations are widely found from montane to subalpine zones, whereas cedar (*Cryptomeria japonica*) and cypress (*Chamaecyparis obtusa*) plantations are found in small patches at lower elevations (Fig. 3).

The habitats were categorized into 7 types: (1) birch (*Betula ermanii*) forest at ecotones between subalpine and alpine zones (referred to as alpine zone); (2) evergreen coniferous forest in the lower subalpine zones (referred to as evergreen coniferous forest); (3) deciduous broad-leaved forest; (4) larch plantation;

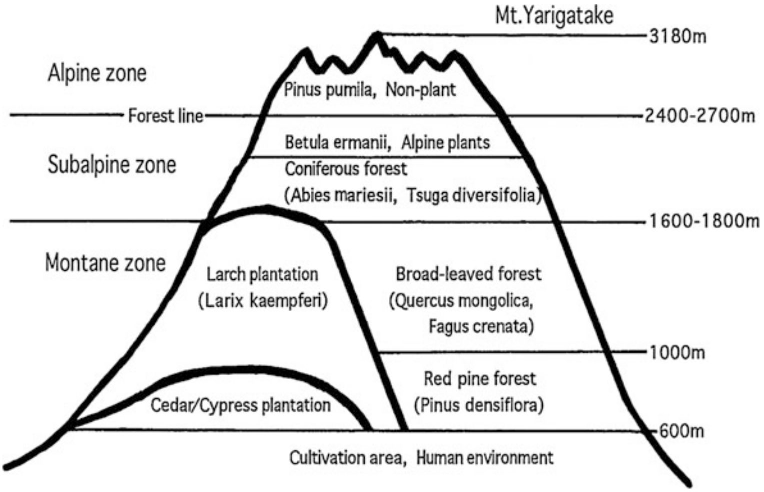


Fig. 3 Forest vegetation in the study area

(5) cedar and cypress plantation; (6) red pine forest (*Pinus densiflora*); and (7) cultivated land. The vegetation was visually determined in 250 × 250 m partitioned mesh referring to given vegetation (Environment Agency 1988), and areal percentage of utilized vegetation within each home range was calculated from MapInfo. Altitudes, main canopy species, and key species of each vegetation zones are shown in Table 2.

Tracking Methods

Eleven Japanese macaque troops were tracked from March 1988 to January 2002. One macaque from every troop inhabiting the Takasegawa river basin was captured by immobilizing it with a dart-gun by using a ketamine–xylazine mixture as a tranquilizer. Usually, only adult female macaque was captured from a troop and radio-collared (ATS Co. Ltd., Isanti, MN, USA), and the troop was tracked either visually or by radio-tracking (Izumiyama et al. 2003). The transmitter weighed 110 g, which was less than 1 % of the collared animal. I avoided collaring young small macaques. Animal capture and handling were according to the policies and guidelines provided by Saeki and Waseda (2006).

For one location data-point, radio waves were detected from at least 3 different directions (on an average from 4.1 directions; *SD* ± 5.11) within 1 h (White and Garrot 1990). When data for more than one location were obtained for one macaque within a day, only the last record of the day was selected as the position of that day. For troops that were visually tracked, the last visually recorded position of the day was used, together with the elevation and habitat status. All of the visually tracked data were used to delineate home ranges.

Troop size was determined by counting individuals as they crossed open spaces, such as creeks and cliffs. The locations of the troops were plotted on Geographical Survey Institute topographic maps and were digitalized using Map Info (Map Info Corp., NY. USA). Home range analysis was performed using the minimum convex polygon method (MCP: Mohr 1947). Differences in population density (per capita home range area; home range size/troop size) between troops occupying higher and lower elevations were tested using the Mann–Whitney's *U*-test.

The types of vegetation (habitat) in the macaque location points were determined by visual inspection of the location point. If visual observation of the site was not possible while radio-tracking the animal locations, I returned to the site later for observation and classification. I also identified the food items of macaques by direct visual observation or by checking foraging traces. The food items were categorized into four seasons based on plant phenology; winter (December–March), spring (April–June), summer (July and August), and autumn (September–November).

Tendency of habitat utilization was analyzed for snowy term and non-snowy term. The snowy term was defined as the 4 month period from December to March when macaque activity was limited by snow cover and snowfall, while the

Table 2 Altitudes, main canopy species, and key species of each vegetation zones

Habitat type	Alpine zones	Evergreen coniferous forest	Deciduous broad-leaved forest	Larch plantation	Cedar/cypress plantation	Red pine forest	Cultivated land
Altitude (m)	2,200–3,200	1,800–2,400	900–1,800	800–2,000	<1,100	600–1,100	<600
Main canopy species		*Abies mariesii*	*Quercus mongolica*	*Larix kaempferi*	*Cryptomeria japonica*	*Pinus densiflora*	
		Abies veitchii	*Fagus crenata*		*Chamaecyparis obtusa*		
		Tsuga diversifolia	*Ulmus japonica*				
		Picea jezoensis	*Acer mono*				
			Tilia japonica				
			Pinus parviflora				
			Abies homolepis				
Key species	*Betula ermanii*	*Sasa veitchii*	*Sasa veitchii*	*Sasa veitchii*		*Castanea crenata*	*Gramineae spp.*
	Pinus pumila		*Sasa kurilensis*			*Quercus serrata*	*Trifolium spp.*
	Umbelliferae spp.		*Fraxinus mandshurica*			*Sasa veitchii*	Field crops
	Gramineae spp.		*Sslix rorida*				
	Cyperaceae spp.						
	Umbelliferae						
	Compositae						
	Vaccinium spp.						
	Rubus spp.						

non-snowy term was defined as the 2 month period from July to August when activity was not limited by snow cover or snowfall. To detect the difference of utilized habitat type between snowy and non-snowy term, the rate of preferred vegetation area within the actually located area was tested against that within the whole habitat range for each troop using the χ^2-test (Chi square test for independence).

Results

Seasonal Changes in Home Range Area

I obtained 1,052 data locations (64.5 % from direct observation and 35.5 % from radio-tracking) for the 11 Japanese macaque troops in the Takasegawa river basin (Table 3). The mean troop size was 43.6 (*SD* ± 16.4, minimum, 25; maximum, 79), and the average home range area was 17.5 km^2 (*SD* ± 11.8, minimum, 8.4 km^2: maximum, 50.9 km^2).

The monthly distributions of the elevations of tracked locations are shown for each troop in Fig. 4. The mean elevation ranged from 878 to 2,266 m. The minimum elevation of troop locations varied between 712 and 1,339 m, while the maximum varied between 1,252 and 3,043 m.

During months with deep snow, all the macaque troops were located near the river at lower elevations. During months that had low or no snow, that is, from spring to autumn, some troops used habitats located at higher elevations. This shift was noticeable in troops inhabiting the upper river basin. The mean elevation of troop locations during the snowy term was significantly different from that during the non-snowy term for all troops, except two (Troops 1 and 4) that inhabited the most downstream area (Table 4).

Seasonal Changes in Habitat Use and Foods List

The types of vegetation that occur in the home ranges of each troop are shown in Table 5. Cultivated land occurred in the home ranges of 3 downstream troops (Troops 1, 4, and 5), and red pine forests occurred in the ranges of 4 downstream troops (Troops 1, 2, 4, and 5). The most frequently found vegetation type within the home range of the 6 downstream troops (Troops 1–6) was broad-leaved forest, while for the 4 upstream troops (Troops 7–10), it was coniferous forests, and for Troop 11, it was the alpine zone. Although habitat preference varied among troops, analysis of all the tracked locations indicated a general preference for deciduous forests, followed by red pine forest, larch plantations, cultivated land, cedar/cypress plantations, evergreen coniferous forest, and the alpine zone.

Table 3 Observation period, troopsize, and home range size of 11 Japanese macaque troops in the Takase river basin

Troop ID	Observation period	Number of locations	Troop size (head)	Observation date	Home range area				
					yearly		Snowy		Yearly/ snowy
					MCP100 % km^2	Per capita HRA	MCP100 % km^2	Per capita HRA	
1	1997. 2. 8–1998.12. 1	83	79	(1998. 3.23)	9.0	0.11	4.0	0.05	2.3
2	1998. 3.25–2001.10.27	85	31	(1999.11.30)	10.9	0.35	2.0	0.06	5.5
3	1997.12. 4–2001. 5. 1	80	44	(1999.11.25)	18.1	0.41	3.5	0.08	5.2
4	1997. 2. 8–1998.12. 1	81	61	(1997. 8.23)	8.4	0.14	3.4	0.06	2.5
5	1996.12.26–1998.12. 1	81	59	(1997. 9. 6)	9.5	0.16	3.1	0.05	3.1
6	1997. 5. 1–2002. 1.13	76	33	(1997. 9. 9)	14.8	0.45	2.1	0.06	7.0
7	1999. 1.23–2002.12.28	91	42	(1999.11.24)	19.5	0.46	3.0	0.07	6.4
8	1998.12.27–2002.12.28	106	34	(1999.11.29)	18.0	0.53	3.3	0.10	5.5
9	1998.12.19–2002.12.28	99	25	(2000. 5. 7)	15.6	0.62	1.8	0.07	8.7
10	1999. 5. 2–2002.12.10	96	31	(2000. 5.14)	17.6	0.57	2.3	0.07	7.7
11	1988. 3.22–2002.12.30	174	40	(1989. 8.31)	50.9	1.27	3.0	0.08	17.0

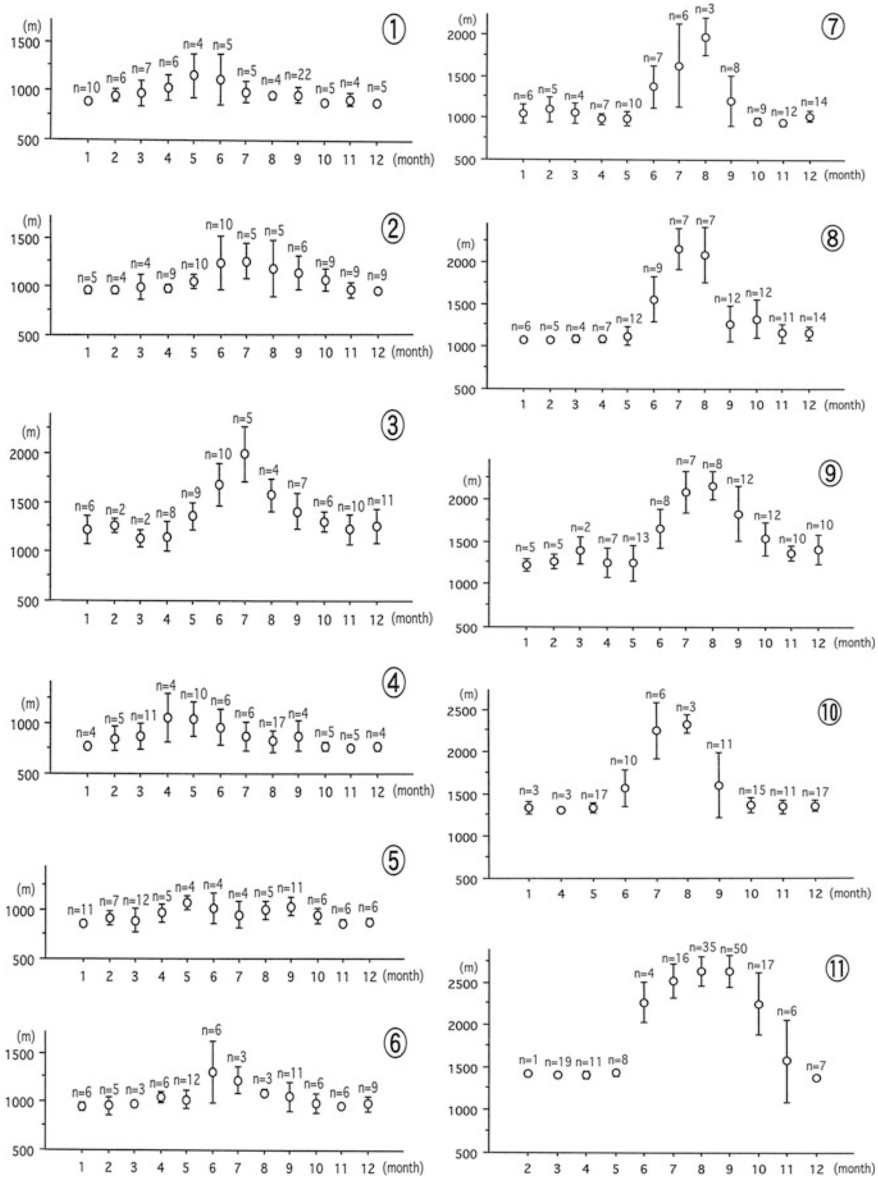


Fig. 4 Monthly elevation of the located macaque troops

The habitats used by troops in snowy term and non-snowy term are shown in Fig. 5. In snowy term, Troops 1, 4, and 5 used cultivated lands. The other troops most frequently used broad-leaved forests. Four troops inhabiting the downstream region (Troops 1, 2, 4, and 5) also used red pine forests, while 5 troops inhabiting

Table 4 U-value and significances of changes in elevations of each troop compared to previous periods

Troop ID	Snowy–Apr.	–May	–Jun.	–Jul.	–Aug.	–Sep.	–Oct.	–Nov.	–Snowy
1	33.0*	8.0	9.0	9.0	9.0	39.0	30.5	6.0	53.5
2	60.5	15.5*	25.0	21.0	8.0	13.0	20.0	16.0*	83.0
3	58.0	10.0*	9.0**	11.0	1.0*	5.0	12.5	20.0	104.0
4	14.0*	19.0	22.0	11.0	40.0	32.0	6.0	9.0	21.0*
5	34.0*	3.0	6.0	6.0	8.0	19.0	10.0*	6.0	102.5
6	16.0**	28.0	14.0*	8.0	1.0	7.0	21.5	18.0	44.0
7	42.0	32.0	5.0**	16.0	6.0	1.0*	9.0*	39.0	30.5*
8	45.0	39.5	3.0***	4.0**	23.0	1.0***	60.0	31.0*	70.5
9	43.0	38.0	9.0**	7.0*	22.0	18.0*	34.0*	27.5*	39.0*
10	18.0	12.0	22.0**	3.0**	9.0	4.0	36.5*	73.0	102.5
11	82.0	29.0	0.0**	11.0*	178.0*	825.5	156.5***	13.0**	50.0

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$

the upstream region (Troops 7–11) used coniferous forests. In non-snowy term, Troops 1, 4, and 5 used cultivated lands, as in snowy term. Only these 3 troops used red pine forests in non-snowy term. Seven down stream troops most frequently used broad-leaved forests (Troops 1–7), and 6 upstream troops used the alpine zone (Troops 3, 7–11). Troop 9 and 11 most frequently used the alpine zone. Except for the downstream Troops 1, 4, and 5, all other troops used coniferous forest.

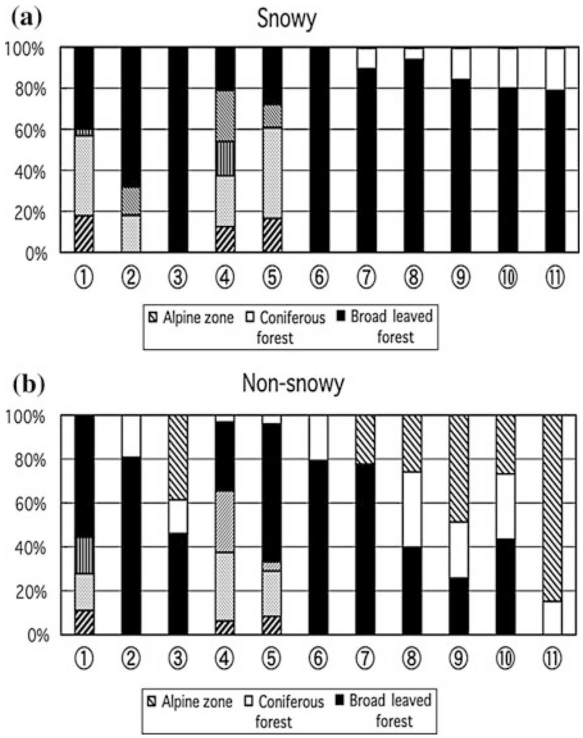
The troops were further categorized into 4 types on the basis of seasonal changes in habitat uses. Type A (Troops 1, 4, and 5) used cultivated land throughout the year, showed no marked seasonal migration, did not use the alpine zone during the non-snowy seasons, and inhabited the lower river basin throughout the year. Type B (Troops 2 and 6) showed a high dependency on broad-leaved

Table 5 Occurrence of habitat types (%) within the home ranges of Japanese macaque troops

Troop ID	Number of the mesh*	Alpine zone	Coniferous forest	Broad-leaved forest	Larch plantation	Cedar-cypress plantation	Red pine forest	Cultivated land
1	135	2.2	12.6	54.8	7.4	7.4	10.4	5.2
2	167	0.0	25.7	65.9	3.0	0.0	5.4	0.0
3	279	38.0	21.1	39.5	1.4	0.0	0.0	0.0
4	125	0.0	12.8	45.6	8.3	0.8	24.8	7.2
5	151	0.0	18.5	60.9	4.0	2.0	10.6	4.0
6	235	0.0	15.3	78.3	6.4	0.0	0.0	0.0
7	310	7.7	51.0	41.3	0.0	0.0	0.0	0.0
8	279	16.1	55.6	28.3	0.0	0.0	0.0	0.0
9	248	40.7	42.4	16.9	0.0	0.0	0.0	0.0
10	279	14.7	61.3	24.0	0.0	0.0	0.0	0.0
11	810	51.9	44.7	3.4	0.0	0.0	0.0	0.0

*indicates the number of 250 × 250 m mesh

Fig. 5 Habitats used by troops in snowy and non-snowy



forests and used coniferous forests in non-snowy term but did not use the alpine zone. Type C (Troops 3, 7–10) showed dependency on broad-leaved forests in snowy term but used coniferous forests and the alpine zones of higher elevations in summer. Type D (Troop 11) used different habitats in snowy term and non-snowy term and showed a high dependency on broad-leaved forests in winter but used coniferous forests and the alpine zone in summer. According to Izumiyama et al. (2003), Type A troops are categorized into rural group, and Type B, C, and D troops are categorized into natural group.

Statistical significance of habitat preference is shown in Table 6. In snowy term, 9 out of the 11 troops preferred deciduous broad-leaved forests, with this preference being more prominent in type C and D troops. The preference for evergreen coniferous forests was significantly high in the 5 troops categorized as type C. Two troops categorized as type A preferred red pine forests, but 1 type A troop did not. No significant preference was detected for other habitat types by any of the troops. In non-snowy term, Troop 10 and 11 showed a marked preference for the alpine zone and Troop 10 showed a marked preference for evergreen coniferous forests, but no significant preference was detected for other habitat types in any of the other troops.

Table 7 lists the food items of natural groups (Troops. 2, 3, 6-11) that do not utilize cultivation lands (Izumiyama et al. 2003). The number of identified food

Table 6 Chi square value and statistical significance of habitat preference of each troop in snowy and non-snowy terms

Troop ID	Alpine zone	Coniferous forest	Broad-leaved forest	Larch plantation	Cedar-cypress plantation	Red pine forest	Cultivated land
Snowy term							
1	–	–	2.5	–	0.5	14.9***	5.5*
2	–	–	0.0	5.4*	–	5.0*	–
3	–	–	29.1***	–	–	–	–
4	–	–	5.1*	5.2*	15.6***	5.2*	0.8
5	–	–	12.9***	2.9	–	23.5***	7.8**
6	–	–	6.2*	–	–	–	–
7	–	17.5***	25.0***	–	–	–	–
8	–	24.9***	48.9***	–	–	–	–
9	–	6.9**	55.7***	–	–	–	–
10	–	13.1***	29.2***	–	–	–	–
11	–	5.4*	261.9***	–	–	–	–
Non-snowy term							
1	–	–	0.0	–	1.1	2.9	1.7
2	–	0.5	2.3	–	–	–	–
3	0.0	0.5	0.4	–	–	–	–
4	–	2.6	2.5	8.1**	1.0	0.4	0.1
5	–	3.1	0.0	0.0	–	2.1	0.9
6	–	0.6	0.0	–	–	–	–
7	2.3	6.0*	2.6	–	–	–	–
8	2.0	5.7*	2.0	–	–	–	–
9	0.8	3.5	1.6	–	–	–	–
10	2.9	10.9***	5.3	–	–	–	–
11	40.8***	33.3***	–	–	–	–	–

$^*P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$

items was 116 in winter, 157 in spring, 62 in summer, 63 in autumn, and in total 261 species. Total 261 items included deciduous broad-leaved trees (47.9 %), herbaceous plants (33.3 %), insects (4.6 %), evergreen coniferous trees (3.1 %), evergreen broad-leaved trees (2.3 %), lichen (1.5 %), bamboo grass (1.1 %), and others.

Seasonal Altitudinal Movement

Spring migrations, from snowy term habitats to non-snowy term habitats, were noticeable in type C and D troops. The mean elevation of the 5 type C troop locations were as follows: 1,212 m in snowy term (from December–March), 1,414 m in April, 1,215 m in May, 1,574 m in June, and as high as 2,030 m in

July. The type D troop showed the greatest tendency of moving to higher elevations in non-snowy term: 1,402 m in snowy term, 1,414 m in April, 1,436 m in May, 2,272 m in June, and 2,529 m in July. The mean elevation of the 2 type B troops gradually increased from 964 m in snowy term, 1,014 m in April, 1,040 m in May, to 1,273 m in June, and then slightly decreased to 1,245 m in July. Those of the 3 type A troops gradually increased from 882 m in snowy term, 1,027 m in April, to 1,098 m in May, and then decreased to 1,040 m in June and 944 m in July (Fig. 4).

The routes of autumn migrations were the reverse of spring migrations, with shifts in elevation being again noticeable in type C and D troops. The mean elevations of the 5 type C troops markedly decreased from 2,031 m in August, 1,468 m in September, 1,303 m in October, to 1,212 m in November and snowy term (from December to March). A decrease in the mean elevation was even more prominent in the type D troop; 2,646 m in September, 2,261 m in October, 1,584 m in November, and 1,402 m in snowy term. The mean elevations of the 2 type B troops showed a gradual decline from 1,140 m in August, 1,100 m in September, 1,030 m in October, 964 m in November, to 964 m in snowy term. Those of 3 type A troops also decreased gradually from 964 m in September, 870 m in October, 852 m in November, to 882 m in snowy term (Fig. 4).

Population Density and the Mean Elevation of Troop Locations

The mean elevation of all 11 troops locations was 1,292 m (*SD* ± 407), and the mean population density of all the troops was 14.0 (*SD* ± 6.9, minimum, 3.9; maximum, 25.8).

A significant correlation was found between troop size and snowy home range area (100 % minimum convex method, $R^2 = 0.713$, $p < 0.001$, $n = 8$). The regression line was Y = 0.085X–0.348 (Fig. 6). However, no significant correlation was found between troop size and yearly home range area (100 % minimum convex method; $R^2 = 0.175$, $p = 0.303$, $n = 8$).

A significant correlation was found between mean troop elevation and per capita yearly home range area (100 % minimum convex method, $R^2 = 0.894$, $p < 0.001$, $n = 8$). The regression line was Y = 6.963X–0.403 (Fig. 7). No significant correlation was found between mean troop elevation and the per capita snowy home range area (100 % minimum convex method; $R^2 = 0.147$, $p = 0.348$, $n = 8$).

Discussion

Seasonal Migration of the Macaque Troops

Habitat use by Japanese macaques in the Northern Japan Alps is characterized by seasonal migration. The analysis of elevations obtained from troop locations in this study (Figs. 1, 4) revealed that, during the period following snowy term, the macaque troops used habitats in the lower montane zone. Then, as the months progressed, they moved to higher elevations.

In general, the troops inhabited the subalpine zone in June, and some migrated to the alpine zone in July. Izumiyama (1994b) used scat analysis to demonstrate that birch (*B. ermanii*) and forbs in the upper subalpine zone and creeping pine (*Pinus pumila*) in the alpine zone, are important food sources for the Japanese macaque. In the Northern Japan Alps, the foliation of birch starts at lower altitudes in spring and reaches the alpine ridges of 2,600 m in early June (Izumiyama 1994b). This is the period when herbaceous plants also start to grow in the alpine zone. Differences in the elevation and slope orientation, together with the prolonged melting of snow, result in diverse plant phenologies at this altitude (Izumiyama in press). Parsley (*Umbelliferae* spp.) and grasses (*Gramineae* spp., *Cyperaceae* spp., *Umbelliferae*, and *Compositae*) (Izumiyama 1994a) are found in this region until late summer. Furthermore, autumn fruiting occurs earlier at higher elevations. Hence, macaques can find berries, such as whortleberry (*Vaccinium vitis-idaea*), *Vaccinium ovalifolium*, *Vaccinium uliginosum*, and raspberry (*Rubus vernus*), after mid-August (Izumiyama 1994a). Macaques can also feed on the seeds of the creeping pine from late August to September (Izumiyama 1994a). Such food resources are abundant on slopes where occasional landslides occur or on slopes with retreating snow patches. Macaques were observed to forage on herbaceous plants growing near such sites. These sites are often found on steep slopes in or above the subalpine zones where evergreen coniferous forests grow. Although these coniferous forests occur frequently in the subalpine zone, food availability of the forests are low for macaques (Izumiyama 1994a, b), and macaque troops are likely to follow the development of available plant shoots passed through these coniferous forests, and consequently, their habitats shift to higher elevations as spring progresses into summer.

The meteorological observation revealed that monthly average temperature exceeded the temperature limit of plant growth (5 °C) for 6 months (May to October) in Kamikochi, but for 4 months (June to September) on the ridge of the mountains at Nishidake. Within these months, plants must finish their annual life cycle; develop leaves, flower, and fruit. The food items of macaques in spring significantly rely on plant flush such as leaves and flowers of deciduous broad-leaved trees (47.8 %) and leaves and stems of herbaceous plants (47.1 %).

In summer (July, August), the dependence on herbaceous plants (leaves and stems) increases to 75.8 % of the food items, but in autumn (September–November), fruits and seeds of deciduous broad-leaved trees increased to 58.7 %, and the leaves and stems of herbaceous plants decreased to 15.9 % (Table 7).

This suggests that macaques show seasonal use of their home range, which is characterized by the use of high-altitude habitats only in non-snowy terms. Sprouts, flush of immature leaves, and fruit production are early in these habitats, and they will not suffer from lack of food. They know the alpine environment and make good use of it. This behavior inevitably includes the alpine zone and results in a large home range area. In lower montane zones, flush of leaves is no more found in summer, and fruit production is early. During this seasonal interspace until autumn, rural macaque groups at lower elevation suffer from scarce food resources, and thus feed on agricultural crops (Izumiyama et al. 2003).

All macaque troops inhabited the montane zone of lower elevations in autumn. The ground surface is covered with snow in winter (from December to March), and buds and barks of deciduous broad-leaved trees (75.0 %) and barks of evergreen conifers (6.4 %) became the food sources. Some uses of beard mosses (*Usnea* sp.) and lichen (*Parmelia* sp.) were confirmed from direct visual observations, though these were not fallback foods as in the Yunnan snub-nosed monkey (*Rhinopithecus bieti*) (Grueter et al. 2009). Japanese macaques rely deeply on deciduous broad-leaved trees in snowy term (Izumiyama 1999, 2012).

In the snowy term, 5 troops used evergreen coniferous forests (Table 6). This probably is not only because Japanese macaques search food in coniferous forests but also because they always use coniferous trees as their sleeping site at night (Izumiyama 2012). Conifers seem to offer suitable shelter against wind, snow, and coldness (Izumiyama 1999, 2012).

Although the tracking period differed, all tracked troops between 1988 and 2002 exhibited similar behavioral patterns (Fig. 4). The analysis revealed that, during this period, Japanese macaque troops used montane deciduous broad-leaved forests dominated by oaks (Table 4). Masting (production of acorns) in montane oaks occurs after early September. This period coincides with the season when macaque troops moved to lower elevations. It has been repeatedly suggested that montane deciduous broad-leaved forests dominated by oaks are necessary for Japanese macaques to obtain sufficient fat reserves before the onset of severe winter conditions (Suzuki 1965; Shidei and Kawamura 1976). The seasonal habitat use of macaque troops shown in this study also supports these reports.

In the snowy term, food sources for macaques are highly limited (Nakagawa 1994). Troops that used environments at higher elevations in the non-snowy season moved to lower habitat elevations in snowy and inhabited deciduous broad-leaved forests (Figs. 3 and 4). This change indicates that broad-leaved forests at lower elevations are important for snowy survival of macaques. This may mean that the main habitat of Japanese macaques in this region is broad-leaved forests dominated by the Mongolian oak (*Quercus mongolica*). To maintain healthy macaque populations in the Northern Japan Alps, it is therefore essential to preserve vast expanses of natural environment, including broad-leaved forests situated at lower elevations.

Table 7 Food items of Japanese macaques in the Northern Japan Alps, and relative frequencies of seasonal use

No	Species	Winter (Dec.–Mar.)		Spring (Apr.–Jun.)		Summer (Jul., Aug.)		Autmun (Sep.–Nov.)	
1	*Allium victorialis*			+	Leaf, Stem				
2	*Disporum smilacinum*			+	Leaf				
3	*Erythronium*			+	Leaf, Stem				
4	*Hosta*			+	Leaf, Stem				
5	*Hostasp.*			+	Leaf, Stem				
6	*Lilium cordatum*			++	Leaf, Stem				
7	*Maianthemum dilatatum*			+	Leaf				
8	*Smilacina japonica*			+	Leaf, Stem				
9	*Smilacina sp.*			+	Leaf, Stem				
10	*Smilax china*			+	Leaf, Stem			+	Seed
11	*Streptopus streptopoides*			+	Leaf, Stem				
12	*Trillium smallii*			+	Leaf, Stem				
13	*Trillium tschonoskii*			+	Leaf, Stem				
14	*Alopecurus aequalis*			+	Leaf, Stem				
15	*Calamagrostis spp.*			++	Leaf	+++	Leaf	++	Leaf
16	*Deschampsia spp.*			+	Leaf	++	Leaf		
17	*Digitaria ciliaris*			+	Leaf	+	Leaf	+	Leaf, Seed
18	*Eleusine indica*			+	Leaf	+	Leaf	+	Leaf, Seed
19	*Eragrostis spp.*			+	Leaf	+	Leaf		
20	*Hierochloe sp.*			+	Leaf	+	Leaf		
21	*Miscanthus sinensis*			+	Leaf	++	Leaf		
22	*Paspalum spp.*			+	Leaf				
23	*Poa malacantha*			++	Leaf	+++	Leaf	++	Leaf
24	*Poa spp.*			++	Leaf	+++	Leaf	++	Leaf
25	*Sasa kurilensis*			+++	Shoot				
26	*Sasa veitchii*	+++	Leaf, Bud	+++	Shoot				

(continued)

Table 7 (continued)

No	Species	Winter (Dec.–Mar.)		Spring (Apr.–Jun.)		Summer (Jul., Aug.)		Autmun (Sep.–Nov.)	
27	*Sasamorpha borealis*	++	Leaf, Bud	+++	Shoot				
28	*Trisetum bifidum*			+	Leaf				
29	*Carex spp.*			++	Leaf	++	Leaf	++	Leaf
30	*Clethra barbinervis*	+	Bud, Bark	+	Leaf				
31	*Rhododendron obtusum*			+	Flower				
32	*Rhododendron degronianum*	+	Bud, Bark						
33	*Rhododendron brachycarpum*	+	Bud, Bark						
34	*Rhododendron albrechtii*			+	Flower				
35	*Vaccinium hirtum*							+++	Fruit
36	*Vaccinium oxycoccus*							++	Fruit
37	*Vaccinium uliginosum*							+++	Fruit
38	*Vaccinium hirtum*							+	Fruit
39	*Vaccinium vitis-idaea*							++	Fruit
40	*Fraxinus apertisqamifera*	++	Bud, Bark	++	Leaf, Flower				
41	*Fraxinus lanuginosa*	++	Bud, Bark	++	Leaf, Flower				
42	*Fraxinus mandshurica*	+++	Bud, Bark	++	Leaf, Flower				
43	*Fraxinus mandshurica*	++	Bud, Bark	++	Leaf, Flower				
44	*Ligustrum tschonoskii*	+++	Bud, Bark						
45	*Callicarpa japonica*	++	Bud, Bark	++	Leaf			+	Seed
46	*Leucosceptrum japonicum*			+	Leaf				
47	*Meehania urticifolia*			+	Leaf				
48	*Mosla punctulata*			+	Leaf				
49	*Viburnum dilatatum*	+	Bud, Bark					+	Seed
50	*Viburnum furcatum*	+	Bud, Bark					+	Seed
51	*Viburnum opulus*							+	Seed
52	*Viburnum phlebotrichum*	+	Bud, Bark						
53	*Arnica unalascensis*			+	Leaf, Stem	+	Leaf, Stem		

(continued)

Table 7 (continued)

No	Species	Winter (Dec.–Mar.)		Spring (Apr.–Jun.)		Summer (Jul., Aug.)		Autmun (Sep.–Nov.)	
54	*Artemisia sinanensis*					+	Leaf, Stem		
55	*Cacalia adenostyloides*			+	Leaf, Stem				
56	*Cacalia maximowitziana*			+	Leaf, Stem				
57	*Cacalia hastata*			+	Leaf, Stem				
58	*Cirsium japonicum*			+	Leaf, Stem	+	Leaf, Stem		
59	*Cirsium microspicatum*			+	Leaf, Stem	+	Leaf, Stem		
60	*Cirsium matsumurae*			+	Leaf, Stem	+	Leaf, Stem		
61	*Cirsium oligophyllum*			+	Leaf, Stem	+	Leaf, Stem		
62	*Cirsium spp.*			+	Leaf, Stem	+	Leaf, Stem	+	Leaf, Stem
63	*Erigeron canadensis*					+	Leaf, Stem		
64	*Eupatorium chinense*			+	Leaf, Stem				
65	*Ixeris dentata*			+	Leaf, Stem	+	Leaf, Stem		
66	*Petasites japonicus*			+	Leaf, Stem				
67	*Picris hieracioides*					+	Leaf, Stem		
68	*Senecio flammeus*					+	Leaf, Stem		
69	*Solidago virgaurea*					+	Leaf, Stem		
70	*Syneilesis palmata*			+	Leaf, Stem				
71	*Juglans ailanthifolia*			+	Leaf, Seed				
72	*Pterocarya rhoifolia*	+	Bud, Bark	+	Leaf				
73	*Chosenia arbutifolia*	+	Bud, Bark	+	Leaf				
74	*Populus maximowiczii*	++	Bud, Bark	+	Leaf				
75	*Populus sieboldii*	+	Bud, Bark						
76	*Salix bakko*	++	Bud, Bark	++	Leaf				
77	*Salix rorida*	+++	Bud, Bark	++	Leaf				
78	*Salix sachalinensis*	++	Bud, Bark	+	Leaf				
79	*Salix spp.*	++	Bud, Bark	+	Leaf				
80	*Alnus firma*	+	Bud, Bark	+	Leaf				

(continued)

Table 7 (continued)

No	Species	Winter (Dec.–Mar.)		Spring (Apr.–Jun.)		Summer (Jul., Aug.)		Autmun (Sep.–Nov.)	
81	*Alnus hirsuta*	+	Bud, Bark	+	Leaf				
82	*Alnus matsumurae*	+	Bud, Bark	+	Leaf				
83	*Betula ermanii*	+	Bud, Bark	+++	Leaf				
84	*Betula grossa*	++	Bud, Bark	+	Leaf				
85	*Betula platyphylla*	+	Bud, Bark	+	Leaf				
86	*Carpinus cordata*	+	Bud, Bark						
87	*Carpinus japonica*	+	Bud, Bark	+	Leaf				
88	*Corylus heterophylla*	+	Bud, Bark	+	Leaf			++	Seed
89	*Corylus sieboldiana*	+	Bud, Bark	+	Leaf			++	Seed
90	*Castanea crenata*	+	Bud, Bark	+	Leaf			+++	Seed
91	*Fagus crenata*			+++	Leaf, Flower			+++	Seed
92	*Quercus acutissima*			++	Leaf, Flower			+	Seed
93	*Quercus mongolica*	++	Bud, Bark	++	Leaf, Flower			+++	Seed
94	*Quercus serrata*	+	Bud, Bark	++	Leaf, Flower			+++	Seed
95	*Celtis jessoensis*	++	Bud, Bark	++	Leaf				
96	*Celtis sinensis*	+	Bud, Bark	+	Leaf				
97	*Ulmus japonica*	+++	Bud, Bark	+++	Leaf, Flower				
98	*Ulmus japonica f. suberosa Nakai*	++	Bud, Bark	++	Leaf				
99	*Ulmus laciniata*	+++	Bud, Bark	++	Leaf				
100	*Zelkova serrata*	+++	Bud, Bark	++	Leaf				
101	*Morus australis*	+++	Bud, Bark	++	Leaf, Fruit				
102	*Elatostema umbellatum*			+	Leaf, Stem	+	Leaf		
103	*Urtica platyphylla*			++	Leaf, Stem				
104	*Urtica thunbergiana*			+	Leaf, Stem				
105	*Aconogonum weyrichii*			+	Leaf, Stem				
106	*Persicaria spp.*					+	Leaf, Stem		
107	*Reynoutria japonica*			++	Leaf, Stem				

(continued)

Table 7 (continued)

No	Species	Winter (Dec.–Mar.)		Spring (Apr.–Jun.)		Summer (Jul., Aug.)		Autmun (Sep.–Nov.)	
108	*Reynoutria sp.*			++	Leaf, Stem				
109	*Rumex acetosa Linn.*			+	Leaf, Stem				
110	*Rumex spp.*			++	Leaf, Stem				
111	*Magnolia hypoleuca*	++	Bud, Bark					++	Seed
112	*Magnolia praecocissima*	++	Bud, Bark						
113	*Magnolia salicifolia*	++	Bud, Bark						
114	*Schisandra repanda*							+	Seed
115	*Lindera obtusiloba*	+	Bud, Bark						
116	*Lindera umbellata*	+	Bud, Bark						
117	*Anemone flaccida*			++	Leaf, Stem				
118	*Anemone narcissiflora*					+	Seed		
119	*Cimicifuga simplex*			+	Leaf, Stem	+	Leaf		
120	*Clematis stans*			+	Leaf, Stem				
121	*Ranunculus silerifolius*					+	Leaf		
122	*Ranunculus sp.*					+	Leaf		
123	*Ranunculus nipponicus*	+++	Leaf, Stem						
124	*Thalictrum aquilegifolium*			++	Leaf, Stem	+	Leaf		
125	*Thalictrum filamentosum*			++	Leaf, Stem	+	Leaf		
126	*Thalictrum sp.*			++	Leaf, Stem	+	Leaf		
127	*Diphylleia grayi*			+	Leaf, Stem				
128	*Akebia quinata*							+++	Fruit
129	*Akebia trifoliata*							+++	Fruit
130	*Actinidia arguta*							+++	Fruit
131	*Actinidia kolomikta*							++	Fruit
132	*Actinidia polygama*							++	Fruit
133	*Hamamelis japonica*							++	Seed
134	*Geum calthaefolium*					+	Leaf, Seed		

(continued)

Table 7 (continued)

No	Species	Winter (Dec.–Mar.)		Spring (Apr.–Jun.)		Summer (Jul., Aug.)		Autmun (Sep.–Nov.)	
135	*Kerria japonica*	+	Bud, Bark	+	Leaf				
136	*Malus baccata*							++	Fruit
137	*Malus toringo*	+	Bud, Bark	+	Leaf			++	Fruit
138	*Potentilla matsumurae*			+	Leaf, Stem				
139	*Pourthiaea villosa*			+	Leaf				
140	*Prunus apetala*			++	Leaf, Stem				
141	*Prunus grayana*	++	Bud, Bark	++	Leaf, Seed	+++	Seed		
142	*Prunus incisa*	+	Bud, Bark	++	Leaf, Seed				
143	*Prunus jamasakura*			++	Leaf, Seed				
144	*Prunus maximowiczii*			++	Leaf, Seed				
145	*Prunus nipponica*			++	Leaf, Seed	++	Seed		
146	*Prunus pendula*			++	Leaf, Seed				
147	*Prunus ssiori*	++	Bud, Bark	++	Leaf, Seed	+++	Seed		
148	*Prunus verecunda*			++	Leaf, Seed				
149	*Rubus crataegifolius*	++	Bud, Bark	+++	Fruit				
150	*Rubus microphyllus*			++	Fruit				
151	*Rubus palmatus*	++	Bud, Bark	+++	Fruit				
152	*Rubus parvifolius*			++	Fruit				
153	*Rubus phoenicolasius*			++	Fruit				
154	*Rubus vernus*					+++	Fruit		
155	*Sorbus alnifolia*	+	Bud, Bark						
156	*Sorbus commixta*	+	Bud, Bark						
157	*Sorbus matsumurana*							+	Seed
158	*Albizia julibrissin*			+	Leaf			+	Seed
159	*Amphicarpaea bracteeata*			++	Leaf, Stem	++	Leaf, Stem		
160	*Desmodium podocarpium*			++	Leaf, Stem				
161	*Lespedeza cuneata*			+	Leaf, Stem	++	Leaf, Stem	++	Seed

(continued)

Table 7 (continued)

No	Species	Winter (Dec.–Mar.)		Spring (Apr.–Jun.)		Summer (Jul., Aug.)		Autmun (Sep.–Nov.)	
162	*Pueraria lobata*			+++	Leaf, Stem	++	Leaf, Stem	++	Seed
163	*Robinia pseudoacacia*	+++	Bud, Bark	+++	Leaf, Flower				
164	*Trifolium pratense*			++	Leaf, Stem	++	Leaf, Stem	++	Leaf, Stem
165	*Trifolium repens*	++	Leaf, Stem	++	Leaf, Stem	++	Leaf, Stem	++	Leaf, Stem
166	*Vicia sepium*			++	Leaf, Stem	++	Leaf, Stem		
167	*Wisteria floribunda*			++	Leaf, Flower			++	Seed
168	*Mallotus japonicus*			++	Leaf, Flower				
169	*Phellodendron amurense*	++	Seed						
170	*Zanthoxylum piperitum*			+	Leaf, Flower				
171	*Rhus trichocarpa*	+++	Bud, Bark					+	Seed
172	*Acer argutum*	+	Bud, Bark	+	Leaf, Flower				
173	*Acer carpinifolium*	+	Bud, Bark						
174	*Acer crataegifolium*	+	Bud, Bark						
175	*Acer japonicum*	++	Bud, Bark						
176	*Acer sieboldiamum*	++	Bud, Bark						
177	*Acer mono*	++	Bud, Bark	+	Leaf, Flower				
178	*Acer nikoense*	++	Bud, Bark						
179	*Acer palmatum*	++	Bud, Bark						
180	*Acer rufinerve*	+	Bud, Bark						
181	*Acer tschonoskii*	++	Bud, Bark	+	Leaf, Flower				
182	*Acer ukurunduense*	++	Bud, Bark	+	Leaf, Flower				
183	*Aesculus turbinata*	++	Bud, Bark						
184	*Ilex macropoda*							+	Seed
185	*Ilex pedunculosa*	+	Seed					+	Seed
186	*Celastrus orbiculatus*	++	Bud, Bark					+	Seed
187	*Euonymus alatus*	+	Bud, Bark						
188	*Euonymus alatus (Thunb.) Sieb. f*	++	Bud, Bark						

(continued)

Table 7 (continued)

No	Species	Winter (Dec.–Mar.)		Spring (Apr.–Jun.)		Summer (Jul., Aug.)		Autmun (Sep.–Nov.)	
189	*Euonymus macropterus*	++	Bud, Bark						
190	*Euonymus oxyphyllus*	++	Bud, Bark					+	Seed
191	*Euonymus sieboldianus*	++	Bud, Bark	+	Leaf			+	Seed
192	*Staphylea bumalda*	+	Bud, Bark						
193	*Ampelopsis glandulosa*							+	Seed
194	*Vitis coignetiae*	+	Bud, Bark					++	Seed
195	*Tilia japonica*	++	Bud, Bark	+	Leaf, Flower				
196	*Schizopepon bryoniaefolius*					+	Leaf, Stem		
197	*Alangium platanifolium*							+	Seed
198	*Cornus controversa*	++	Bud, Bark	+	Leaf				
199	*Cornus macrophylla*	++	Bud, Bark	+	Leaf				
200	*Helwingia japonica*	++	Bud, Bark	+	Leaf				
201	*Acanthopanax sciadophylloides*	+++	Bud, Bark	+	Leaf				
202	*Aralia cordata*			++	Leaf, Stem				
203	*Aralia elata*	+	Bud, Bark	+	Leaf				
204	*Evodiopanax innovans*	+	Bud, Bark						
205	*Angelica polymorpha*			+	Leaf, Stem				
206	*Angelica pubescens*			++	Leaf, Stem	+++	Leaf, Stem	++	Stem
207	*Coelopleurum multisectum*			++	Leaf, Stem	++	Leaf, Stem		
208	*Conioselinum filicinum*			++	Leaf, Stem	++	Leaf, Stem		
209	*Heracleum dulce*			+	Leaf, Stem	+	Leaf, Stem		
210	*Ostericum sieboldii*			+	Leaf, Stem	+	Leaf, Stem		
211	*Peucedanum multivittatum*			+	Leaf, Stem				
212	*Pleurospermum camtschaticum*					+	Leaf, Stem		
213	*Spuriopimpinella nikoensis*					+	Leaf, Stem		
214	*Torilis japonica*					+	Leaf, Stem		
215	*Deutzia crenata*	+	Bud, Bark	+	Leaf, Stem				

(continued)

Table 7 (continued)

No	Species	Winter (Dec.–Mar.)		Spring (Apr.–Jun.)		Summer (Jul., Aug.)		Autmun (Sep.–Nov.)	
216	*Hydrangea paniculata*	+++	Bud, Bark	+	Leaf				
217	*Hydrangea petiolaris*	++	Bud, Bark						
218	*Philadelphus satsumi*	+	Bud, Bark	+	Leaf, Stem				
219	*Ribes japonicum*							+	Fruit
220	*Rodgersia podophylla*			+	Leaf, Stem				
221	*Schizophragma hydrangeoides*	++	Bud, Bark						
222	*Empetrum nigrum*					+	Seed	+	Seed
223	*Trillium smallii*			+	Leaf, Stem				
224	*Trillium tschonoskii*			+	Leaf, Stem				
225	*Matteuccia struthiopteris*			+	Leaf, Stem				
226	*Larix kaempferi*	+	Bark						
227	*Pinus densiflora*	+	Bark	+	Leaf			+	Seed
228	*Pinus koraiensis*	++	Bark					++	Seed
229	*Pinus parviflora*	+	Bark						
230	*Pinus parviflora*	++	Bark						
231	*Pinus pumila*	+	Bark			++	Seed	+++	Seed
232	*Tsuga diversifolia*	++	Bark						
233	*Thuja standishii*	+	Mistletoe						
234	*Taxus cuspidata*							++	Seed
235	*Usnea sp.*	+							
236	*Hypogymnia sp.*	+							
237	*Parmelia sp.*	+							
238	*Parmeliaceae spp.*	+							
239	*Fern spp.*			+				+	
240	*Fontinalis antipyretica*	++							
241	*Polyporaceae sp.*	+							
242	*Lentinula edodes*			+				+	

(continued)

Table 7 (continued)

No	Species	Winter (Dec.–Mar.)	Spring (Apr.–Jun.)	Summer (Jul., Aug.)	Autmun (Sep.–Nov.)
243	*Russila japonica*				+
244	*Russila virescens*				+
245	*Suillus granulatus*				+
246	*Fungi spp.*				+
247	*Baetidae.*	+			
248	*Cincticostella nigura*	+			
249	*Pothamanthus formosus*	+			
250	*Tadamus scriptus*	+			
251	*Plecoptera spp.*	+			
252	*Oxya sp.*			+	
253	*Acrididae spp.*			+	
254	*Carabidae spp.*			+	
255	*Staphylinidae sp.*			+	
256	*Pentatomidae spp.*			+	
257	*Lepidoptera spp.*		+	+	
258	*Lepidoptera spp.*			+	
259	*Acari spp.*		+		
260	*Viviparidae sp.*	+			
261	*Architaenioglossa sp.*			+	
262	*Rana tagoi*	+			
263	Soil, Concrete	+	+	+	

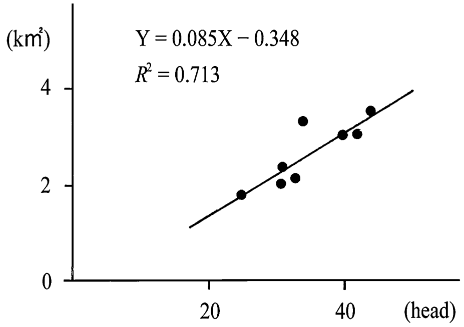


Fig. 6 Correlations between troop size and home range area (snowy)

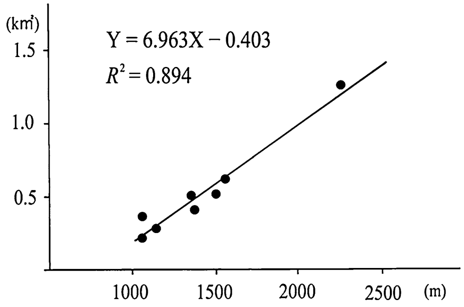


Fig. 7 Correlations between mean elevation and per capita home range area (yearly)

All but one troop inhabiting the upper river basin did not show particular habitat preferences during the non-snowy term. This may be because macaques that occupy higher elevations migrate through a wide area in search of food. However, during the snowy term, these troops moved to lower elevations, where they used broad-leaved forests. Troops inhabiting the lower river basin throughout the year depended on broad-leaved forests, in addition to red pine forests adjacent to cultivated lands. Because temperatures of the study area are higher at lower elevations (Table 1) and it is assumed that plants show higher production rates at these lower elevations, troops inhabiting lower elevations did not need to migrate through a wide area. This large difference in seasonal migration behavior appears to result in large differences in the home range area, and thus, population densities.

Macaque Population and Habitat Quality

The troop sizes of macaques inhabiting the Takasegawa River basin did not exceed 100 individuals. Troop size ranged from 23 to 79 individuals for the 11 troops (Table 3); this fell within the range of 8–166 individuals reported for troops elsewhere (Masui 1976). The home range area determined by the 100 % minimum convex polygon method indicated ranges of 8.4–50.9 km^2 (Table 3). It is reported that the home range area of macaque troops inhabiting the cool temperate zone ranges from several square kilometers to 10 km^2 (Akaza 1989; Koganezawa 1997). The home range area of some troops in this study fell within this range, but many exceeded this range.

A comparison of troop sizes between upstream and downstream troops revealed noticeable differences, with downstream troops having more individuals. Studies in the Kurobegawa River basin in the Toyama Prefecture (Akaza 1989) and those in the Ohigawa River basin in the Shizuoka Prefecture (Muramatsu et al. 1982) demonstrated the same tendency. However, the home range area of downstream troops was smaller. This meant that troops inhabiting the lower river basin had higher population densities than those inhabiting the upper basin. The reason for lower population density in the upper river basin may be that their home ranges involve more habitat types that could be used only in non-snowy term.

Macaque densities largely differ with habitat quality. For example, population densities of Japanese macaques in evergreen broad-leaved forests, which are distributed at lower latitudes and elevations than deciduous broad-leaved forests, are reported to be higher than those in deciduous broad-leaved forests. Evergreen broad-leaved forests are thus considered to be a more suitable environment for Japanese macaques (Takasaki 1981). In central Japan, however, Japanese macaques inhabit deciduous broad-leaved forests, and the altitudinal distribution limit of macaque is generally between 1,400 and 1,600 m riverbed elevations (Akaza 1989; Muramatsu et al. 1982; Izumiyama 1994a, b). In this study, it was revealed that Japanese macaques in the Northern Japan Alps also deeply depend on deciduous broad-leaved forests, and that the population densities showed a decline in the upper river basins where habitat quality gradually deteriorate to a point where no macaque can inhabit (Table 4).

Izumiyama et al. (2003) categorized macaque troops into rural and natural groups, according to the use of cultivated land, and pointed out that troop size was negatively correlated to habitat quality. Troops 1, 4, and 5 in the present study correspond to the rural group, with the other troops belonging to the natural group. A significant difference in population density was detected between the 2 groups. Moreover, a clear negative correlation was detected between population density and the mean elevation of troop locations. Population densities are negatively correlated to the proportion of coniferous plantations within home ranges (Hill et al. 1994), while home range areas are positively correlated to the proportion of coniferous plantations within the home ranges (Furuichi et al. 1982). In the subalpine zones of Japan Alps, although cedar forests are not plantations but naturally grown forests, the light penetration to the understory of exuberant forests is still low. This results in poor vegetation on the forest floor as in plantations, and the forest exhibits low habitat quality from the point of food resources for macaques. One reason for lower macaque densities in the Takasegawa River basin at higher elevation may therefore be the presence of extensive subalpine evergreen coniferous forests that yield scarce food for macaques. Overall, the results indicated that poor habitat quality resulted in larger home ranges and lower population densities in Japanese macaques.

In this study, 11 Japanese macaque troops inhabiting a 20 km region of the Takasegawa River basin showed diverse habitat use. This variation indicated that Japanese macaques exhibit broad ecological and behavioral adaptability to several extreme environmental factors, including low-temperature, heavy snow, and alpine and boreal environments above the forest line.

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Rhinopithecus bieti at Xiaochangdu, Tibet: Adaptations to a Marginal Environment

Zuofu Xiang

Introduction

An organism's physical environment is one of the strongest determinants of the selective forces to which it will be subject. This includes both abiotic factors, such as temperature, rainfall, and length of day, and biotic interactions, such as availability of food throughout the year, predation risk, and infection by diseases or parasites. Species frequently adapt to survive and reproduce within a particular habitat or 'niche'. Animals which are able to exploit marginal environments may enjoy a particular advantage from doing so if few potential competitors can successfully colonize the area. Therefore, understanding the ways in which primates have adapted to tolerate harsh environments such as high altitude temperate forests, which show extreme seasonal variation in temperature and food availability, may help us to understand the persistence of particular primate species when many others are in decline. Comparative studies which utilize data on the adaptive responses of primates living at different altitudes may provide insight into behavioral flexibility with regard to feeding ecology and social organization, since both are theorized to be influenced by environmental gradations.

There are 23 primate species which occur in China, of which five (*Macaca thibetana*, *Macaca cyclopis*, *Rhinopithecus roxellana*, *Rhinopithecus brelichi*, and *Rhinopithecus bieti*) are endemic (Smith and Xie 2009). Within the Chinese members of genus *Rhinopithecus*, the black-and-white snub-nosed monkey (*R. bieti*) displays the most extreme adaptations to high altitude living. It occupies a limited geographic range within the provinces of Yunnan and Tibet and occurs at altitudes of 3,000–4,300 m (Long et al. 1994). At present, only 15 groups totaling approximately 2,500 individuals remain in the wild (Long YC, *pers. Comm.*); the monkeys' habitat is threatened by selective logging for timber to build houses as

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well as the collection of firewood (Xiang et al. 2007a; Xiao et al. 2003; Zhao 1996).

The Xiaochangdu group of *R. bieti* occupies the northernmost tip of the species' distribution and endures many meteorological extremes in rainfall patterns and temperature (Xiang et al. 2007b). At Xiaochangdu, the total annual precipitation is 740 mm, but monthly averages show an uneven distribution of rainfall through the year. About 60 % of yearly precipitation occurs from June to August, often accompanied by dense fog. Snow accumulation begins in late November and may persist in the forest until mid-May. Regarding monthly mean temperature, the highest occurs in August (12.5 °C), and the lowest in January (−3.6 °C). The highest (26.9 °C) and lowest (−15.4 °C) single recorded temperatures also occurred in August and January, respectively. The mean temperature remained negative for 4 months out of the year. The resident monkey group is able to make use of only four habitat types (Xiang et al. 2011): (1) Primary conifer forest, composed primarily of *Picea likiangensis* and *Abies squamata* trees interspersed with bushes less than 2 m in height; (2) Secondary conifer forest, a habitat type artificially created by selective logging on the part of local people, where *Picea likiangensis* and *Abies squamata* trees along with dense bushes dominate the vegetation; (3) Larch forest, chiefly comprised of *Larix griffithiana* and *Rhododendron* spp. trees with a thick undergrowth of typically *Rhododendron* spp. bushes taller than 2 m; and (4) Evergreen broadleaf forest/montane scerophyllous oak forest, in which *Quercus aquifolioides* trees dominated the flora, interspersed with bushes which rarely grew over 2 m and remained at low density.

In light of the unusual characteristics of climate and habitat experienced by *R. bieti* at Xiaochangdu, Tibet, it is valuable to gain an understanding of their behavioral flexibility and adaptive responses. Historically, long-term observational study of *R. bieti* in its natural habitat has been limited by difficult field conditions, such as the unforgiving topography and strong seasonality of its habitat. This is particularly true for the Tibetan populations. In this chapter, I will first introduce the study site, subjects, and methods of a comprehensive research project at Xiaochangdu, Tibet which has lasted since 2003. I will review results pertaining to diet and range use, then turn to issues of reproduction. Finally, I consider problems pertaining to the conservation of *R. bieti*.

Study Area and Subjects

The study area, Xiaochangdu, is located at 29°15′N, 98°37′E within the Honglaxueshan National Nature Reserve, Mangkang County of Southeast Tibet (Fig. 1). The Reserve was founded in 1993 chiefly to protect *R. bieti*. It is located within the Hengduan Mountains, bounded by the Mekong River to the west and the Heiqu (Gatuo) River to the east. The majority of the mountains in this area rise above 3,500 m (Xiang et al. 2007a).

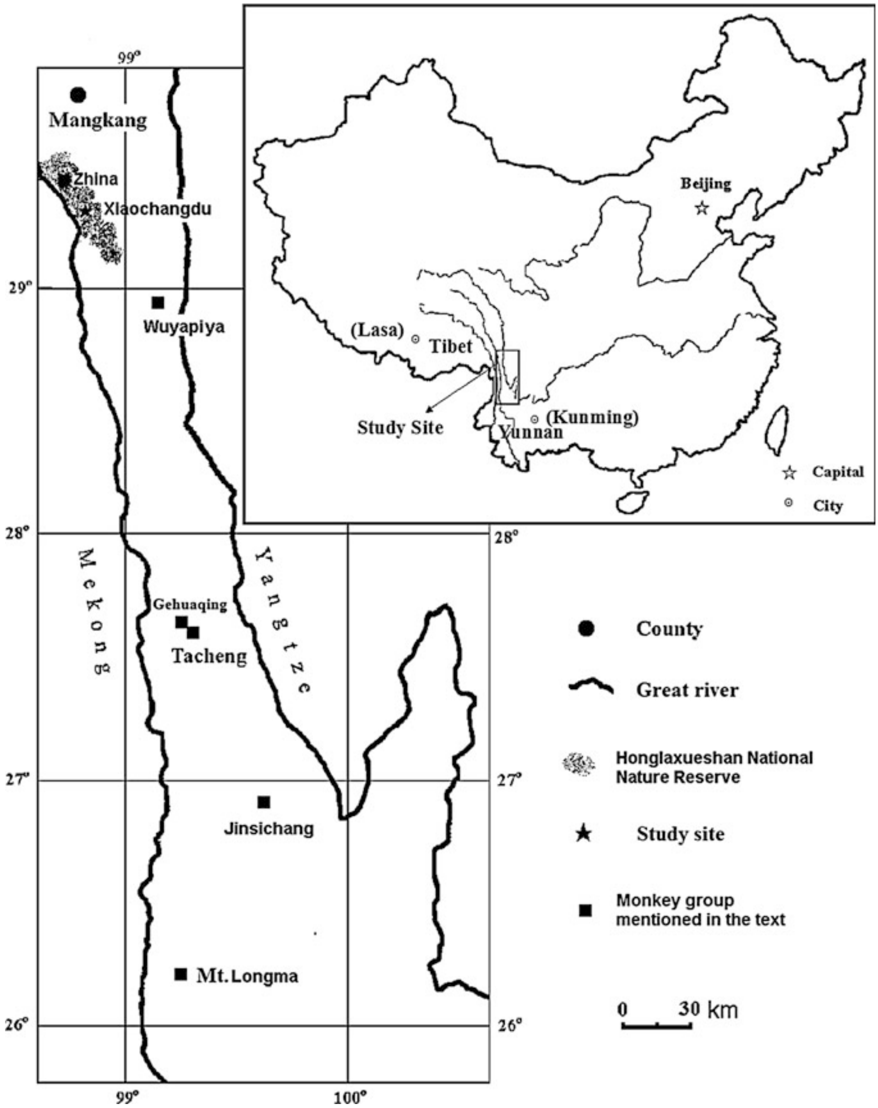

Fig. 1 Study site Xiaochangdu), Honglaxueshan national nature reserve 98°20′ ~ 98°59′E, 28°48′ ~ 29°40′N), and the localities of the monkey groups mentioned in the text

Seasonality at Xiaochangdu is pronounced. Due to the high altitude and the influence of monsoon winds, it may not be appropriate from a biological standpoint to define the seasons in the manner typical for the rest of the temperate northern hemisphere. I have suggested that winter be defined as those months in which the mean temperature remains below 0 °C, and summer be defined as those months in which the mean temperature is above 10 °C. According to this framework, spring at Xiaochangdu would occur from April to May, summer from June to August, autumn from September to October, and winter from November to the subsequent March.

The study group I observed contained 207 individuals and is comprised of 32 adult males, 71 adult females, 72 juveniles, and 32 infants. Accordingly, the adult sex ratio is 1:2.2. The ratio of adults to immatures (juveniles and infants included) is 1:1, and the ratio of infants to adult females is 1:2.3. These parameters indicate that the Xiaochangdu group is a stable population. This is the only population of *R. bieti* which has not declined in number since the last survey in 1988 (Xiang et al. 2007a). The basic social group of *R. bieti* is the multi-female, one-male unit (OMU) (Kirkpatrick et al. 1998). I have also observed a few multi-female, multi-male units, and at least one-male-unit (Xiang 2005). Infants were identified by behavioral characteristics and physical traits. Newborns have white coats except for isolated black hairs on the top of the head, back, and tail tip. They must be constantly carried before the age of 10 days; agile movement begins around day 25 (Zou et al. 1999). The small villages bordering the monkeys' range, totaling about 60 families, all occur below 3,800 m.

The study group's contact with humans remains limited. Monkeys have never been seen to take food from farmers or researchers, either directly or indirectly. Hunting is limited due to a religious taboo observed by the Tibetan Buddhist villagers (Xiang et al. 2007a). However, livestock range through the monkeys' habitat, and local inhabitants collect forest resources during the summer.

Methods

I conducted multiple continuous follows of the study group at Xiaochangdu between June 2003 and March 2005. I employed instantaneous scan sampling (Altmann 1974) at 15 min intervals to record data on diet composition and feeding behavior. Once I spotted an individual processing a food item, I tried to identify both the species and the category of the food. Monthly proportions were then averaged over a year to obtain an overall estimate of the relative contributions of different items to the diet of *R. bieti.* Food availability was estimated using the crown density method (Marsh 1981; *see also* Xiang et al. 2007b).

I obtained information on ranging behavior by following the monkeys either for their entire period of diurnal activity or from the time I first established visual contact or auditory contact (vocalization and sound of breaking branches) with the group, lasting until the monkeys ranged out of sight. I used a map of 1:100,000 scale, divided into a grid of 500 m × 500 m^2, to record the area used by groups and the position of the center of the group. A "used" grid cell was one in which greater than 50 % of the area was used by the group; habitat type for each cell was determined by whichever occupied the greatest area in the grid. Seasonal home range estimates are derived from plots of new grid cells entered over time, using the area at which the curve reached an asymptote during a certain study period

(Kirkpatrick et al. 1998). The tree in which the greatest number of individuals found together was defined as the center of the group. I recorded the location of the group's centroid every 2 hours using a GPS receiver, unless I was prevented from doing so by dense vegetation or a deep valley that limited signal reception. I marked the group's location on the map and used these records to estimate the group's daily travel length (DTL), defined as the distance between the sleeping sites of two consecutive days along the path demarcated by group centroids. On days in which the monkeys were not followed from the time they departed their sleeping site that morning, I estimated DTL from the foraging trails, following signs such as broken branches or freshly fallen feces, so long as the monkeys were tracked to their next sleeping site without losing contact.

After finishing the period of 15 min instantaneous scan sampling to collect diet and foraging records, I chose a clearly observable OMU as a focal group and noted any copulatory events. A copulatory event consists of solicitation, mount, intromission, pelvic thrusts, ejaculation, and dismount. External indications of ejaculation included cessation of thrusting with maximal insertion and a notable tensing of body musculature (Cui and Xiao 2004). As individual identification was generally not possible in primary or secondary conifer forest due to limited visibility, I censused adult females and new infants in the group either by scanning observation with a field scope (Nikon ED II, 25–56X) from 50 to 1,000 m away, or by close observation of the animals at distances of 15–50 m (with or without binoculars) (Xiang and Sayers 2009). Close observation, when possible, provides superior count data to that of long-range scans.

Dietary Adaptations to Extreme Seasonality

R. bieti at Xiaochangdu feeds upon at least 25 different species of trees, shrubs, and ground plants from 19 genera and 13 families (Xiang et al. 2007b). They also consume a minimum of three species of arboreal lichens, two species of grasses, three types of invertebrates retrieved from decayed wood or overturned rocks, and resin from two tree species. Although monkeys preferentially consumed leaves, fruits, and nuts when they were available, lichens were the most dependable and, hence, most frequently consumed resource, especially during periods of scarcity. Feeding records reveal a dietary composition as follows: 82.1 % lichens; 12.1 % buds and leaves; 1.1 % flowers, fruits, and nuts; 0.6 % invertebrates; 4.2 % other foods including resin, bark, and herbs.

The estimate of lichen consumption (82.1 %) from the feeding records of Xiaochangdu monkeys is slightly higher than the figure obtained from Kirkpatrick's (1996) observations of the Wuyapiya group. Compared to these two populations, the relative amount of lichen (ca. 60 %) consumed by monkeys at Tacheng, located centrally within the species' range, is low (Ding and Zhao 2004). The estimated percentage of lichens in the diet (ca. 5 %) at Jinsichang, to the south of those sites mentioned above, is lowest of all (Yang and Zhao 2001); however,

Table 1 Comparison of the diet of *Rhinopithecus bieti* at four field sites

Species/ study site	Location (N, E)	Range elevation (km)	Vegetation types[b]	Annual average temperature (°C)	Annual precipitation (mm)	Genus	Species	Parts eaten[a]							
								Bud	Leaves	Flower	Fruit/ seed	Lichen	Other	Total	Referencer
Xiaochangdu	29°15′, 98°37′	3.5–4.25	1 2	4.7	740	20	22	11	16	6	2	3	13	51	Xiang et al. 2007a
Tacheng	27°36′, 99°18′	2.7–3.7	1 2 3	7.5	–	42	59	15	29	/	29	>9	17	>90	Ding and Zhao 2004
Samage	27°34′, 99°17′	2.5–4.0	1 2 3	14.3	1,004	66	94	7	76	13	22	15	32	>165	Grueter et al. 2009
Longmashan	26°15′, 99°15′	2.7–3.4	1 2 3 4	8.8	1,501	52	97	93	38	51	41	1	25	249	Huo 2005

[a] not mentioned or not identify

[b] 1 = conifer forest; 2 = evergreen broadleaf forest oak forest); 3 = mixed conifer-broadleaf forest; 4 = deciduous broadleaf forest

this value was derived from analysis of fecal contents rather than direct observation. Thus, it may not be commensurate with figures reported from feeding behavior—though Ding and Zhao (2004) observed 60 % of food consumed to be lichen, fecal analysis revealed only 9 % lichen composition. The figure of 5 % lichen content from feces at Jinsichang may suggest a true dietary lichen content closer to 30 %. If this is the case, then the proportion of lichens consumed, from the northernmost group to the southernmost, decreases from 82.2 % (Xiaochangdu) to 75 % (Wuyapiya), 60 % (Tacheng), and lastly 30 % (Jinsichang). These observations suggest that lichens serve as a staple or fallback food rather than a preferred resource of choice for this species (Xiang et al. 2007b), since the proportion of lichen in the diet displays a direct relationship with altitude (and hence an inverse one with habitat richness).

The diet of colobine monkeys responds to environmental factors such as elevation and habitat composition (Bennett and Davies 1994). In general, habitats at lower elevations display more complex floral communities than those found at higher elevations. *R. bieti* displays considerable variability in habitat diversity and diet composition between groups living at higher or lower latitudes and altitudes. Xiaochangdu offers the poorest food resources of all studied sites in terms of number of different species consumed and plant parts eaten (Table 1). Traveling southward within *R. bieti's* range, monkeys tend to feed on more plant species and plant parts and to consume fewer lichens. In addition to being the least botanically diverse locality, Xiaochangdu has the most challenging weather conditions experienced by this species (Table 1).

Ranging Use Pattern and Response to Changing Environment

Home Range, DTL, and Population Density

Through a grid system, we estimated the home range of the Xiaochangdu group to be 16.75 km^2 in summer, 10.50 km^2 in winter, and 21.25 km^2 over a two-year observation period. Ranging data showed clear seasonal trends; during the summer, the monkeys expanded their range and decreased the intensity of use for particular areas (as measured by a lower reuse rate for each grid cell). The mean DTL of the study group was 765 m over the study period. Mean DTL was shortest between December and March, when lichen was the primary food consumed. Maximum DTL approached 1 km in May; this coincided with a period of abundant high-quality food and high human activity (mushroom and Chinese medicine collection) within the forest, making it difficult to distinguish which factor may have been chiefly responsible. Similar to observed ranging behavior, mean DTL also changed with the season. *R. bieti* had a significantly longer DTL in both summer and spring than in winter (Xiang 2005). Using an estimate for mean adult body mass of 9.1 kg (Kirkpatrick 1996), the population density and biomass of *R. bieti* at Xiaochangdu were calculated to be 9.7 individuals/km^2 and 88.6 kg/km^2, respectively.

Food availability is considered an important determinant of daily travel distance among primate species (Milton 1980; Champman 1988). When food items are widely dispersed, group-living primates should have to travel farther to satisfy nutritional requirements (Champman and Champman 1990; Oates 1987). Primates may also pursue a high-risk, high-reward strategy when the most preferred foods are abundant, responding to these conditions with increased daily travel as well (Norberg 1977). Lichens are low in protein, reducing their desirability as a resource (Kirkpatrick 1996). Compensatory feeding on fruits, nuts, and leaves may be a strategy to cope with this deficit, in addition to the capacity of colobine monkeys to get limited amounts of protein from intestinal bacteria during the process of proliferation accompanied with fermentation of celluloses (Kay and Davies 1994; Chivers 1994). Monkeys at Xiaochangdu show a strong preference for eating young leaves, flowers, fruits, and nuts (Xiang et al. 2007b). These items are only available in the forest understory from May to September (Xiang et al. 2007b). The results discussed above are consistent with the prediction that a proportional increase in fruits/leaves consumption will also increase both the travel requirement to find such fruits/leaves and the energy available to do so (Strier 2003).

Range size is typically influenced by a species' body size, average group size, and population density (Clutton-Brock and Harvey 1979; Olupot et al. 1994; Butynski 1990). Primates that occupy the largest home ranges tend to have large bodies, large social groups, or both (Altmann 1974; Chapman et al. 1995; Janson and Goldsmith 1995; Gillespie and Chapman, 2001). Black-and-white snub-nosed monkeys are relatively massive, especially by colobine standards, and often live in social groups exceeding 100 individuals. The home range of the Xiaochangdu group is approximately 21.25 km^2, consistent with other studies of *R. bieti* (Kirkpatrick et al. 1998; Liu et al. 2004; Huo 2005; Grueter et al. 2008; Ren et al. 2009) (Table 2).

Temperate primates are predicted to have larger home ranges than tropical primates due to increased environmental seasonality and the resulting patchiness of productive habitat (Bishop 1979; Takasaki 1981). This pattern has been observed in the odd-nosed colobines, a group which contains *R. bieti* (Kirkpatrick 1996). However, the species itself does not show any clear indications of latitudinal trends in range size. At Wuyapiya, about 100 km south of Xiaochangdu, the resident monkey group had a home range of 25 km^2 (Kirkpatrick et al. 1998). Another group of >410 individuals living to the south had a home range of 25 km^2 (Grueter et al. 2008), while a group of approximately 180 individuals occupied 23.3 km^2 (Ren et al. 2009).

Food availability and consequent population density for leaf-eating monkeys tend to increase with the species richness of their habitat's plant community. Within the range of black-and-white snub-nosed monkeys, plant diversity

Table 2 Comparative data on home range, population density, biomass, and daily travel distance of *Rhinopithecus bieti* at six field sites

Species/sites	Home range (km^2)	Daily travel length	Group size	Population density individuals/(km^2)	Biomass[a] (kg/km^2)	Vegetation types[b]	Reference
Xiaochangdu	21.25	765	207	9.7	88.6	1 2	This study
Wuyapiya	25.25	1,311	175	6.9	63.1	1 2	Kirkpatrick et al. 1998
Samage	25	1,514	410	12.8	106.6	1 2 3	Grueter et al. 2008
Jinsichang	23.3	–	180	7.7	70.3	1 2 3	Ren et al. 2009
Fuheshan	10.7	800	80	7.5	68.0	1 2 3 4	Liu et al. 2004
Longmashan	9.56	–	80	8.4	76.2	1 2 3 4	Huo 2005

[a] Calculated using average weights of 9.1 kg for *Rhinopithecus bieti*, 9.4 kg for *Rhinopithecus roxellana*, and 7.8 kg for *Rhinopithecus brelichi* Kirkpatrick 1996)

[b] 1 = conifer forest; 2 = evergreen broadleaf forest oak forest; 3 = mixed conifer-broadleaf forest; 4 = deciduous broadleaf forest

increases with decreasing latitude (Xiang et al. 2007b). Consequently, Xiaochangdu features the lowest botanical species richness of any recorded site, as well as the harshest weather conditions. However, results indicate that monkey groups occupying this site have greater population density and biomass than all southerly populations with the exception of Samage (Table 2). This could be attributed to more severe anthropogenic change in those areas, causing continual stress on monkey populations (Mt Longmashan: Huo 2005; Mt Fuhe: Liu et al. 2004). Xiaochangdu may support the only currently stable subpopulation of *R. bieti* (Xiang et al. 2007a), having reached local carrying capacity. On the other hand, other groups may experience a recovery over the near term, as conservation policies put into place during the 1990s have allowed for habitat recovery during the 2000s (Liu et al. 2004; Huo 2005).

Altitudinal Range

The monkeys range between elevations of 3,550 and 4,300 m, with a mean of 4,060 ± 105 m. Additionally, 92 % of all location records are distributed in a narrower altitude band, between 3,800 m and 4,200 m. The altitude of the monthly mean daily range did not vary significantly across the seasons (ANOVA, F = 2.22, $p > 0.05$). The results indicate that the monkeys do not generally prefer any particular altitudinal zone. However, we found that the monkeys can respond to snowstorms by vertical migration. From November 11 to December 8, 2004 the monkeys had remained between 4,100 and 4,300 m for about 2 weeks, with mean altitude 4,207, and then descended to about 3,800 m. The monkeys were observed searching for the fallen seeds of oak trees (*Quercus aquifolioides*) on the ground and feeding on lichens during this time. However, when a heavy snowstorm took place over 4 days in February 2005, the monkeys descended to 3,500 m, to lower altitude forests near the Lancang River, where they stayed for about 5 weeks.

In mountainous areas, ecological zones are observed to display altitudinal as well as climatic gradients (Wu 1991). As a result, primates living along these altitudinal gradients have been known to exhibit seasonal vertical migration, following the distribution of food (Bishop 1979; Hu et al. 1980; but *see* Kirkpatrick and Long 1994). Zhong et al. (2008) found, through analysis of *R. bieti* fecal samples collected along an elevational transect at Baimaxueshan North, that monkeys consistently roamed in higher altitudes but could travel to lower altitudes during spring to eat young sprouts and leaves and during winter to avoid bad snowstorms. Li et al (2008) observations at Baimaxueshan South are also consistent with this migration pattern. Yang (2003), Liu et al. (2004) found the use of lower elevations as a refuge from severe winter weather as well. However, except for severe snowstorms, we did not observe the same responsiveness to the environment in the monkeys' vertical ranging behavior that we did in their daily range size and travel distance. It is possible that there is a lower bound to the group's descent from the mountains because human occupation and disturbance become noticeable below 3,800 m, with 90 % of the home range at this altitude near a village. Measurement difficulty might also play a role—fine-grained distinctions in seasonal migration patterns could not be detected within a fairly narrow range of about 400 m generally pitched between 25 and 35° (Xiang ZF, unpublished data). We would expect the monkeys to range lower in the spring and summer in order to spend more time in the diverse secondary conifer forest habitat they seem to prefer (Xiang et al. 2011). However, human disturbance in the lower altitudes, particularly during good weather when animals roam free and villagers collect resources, may drive the monkeys back toward higher areas where people are less likely to go. Therefore, the monkeys' altitudinal ranging pattern at Xiaochangdu is a site-specific example of an adaptive response to a particular habitat.

Habitat Preference

Black-and-white snub-nosed monkeys are thought to depend on the accessibility of primary alpine fir forest (Zhao et al. 1988; Li et al. 1981) in the northern part of their distribution. In contrast, Li et al. (2008) found a preference for mixed deciduous broadleaf and conifer forest in the center of the monkeys' distribution. Further south, Huo (2005) has argued that the monkeys' preferred forest type is mixed deciduous broadleaf forest. However, the monkeys at Xiaochangdu spent more time in primary and secondary conifer forest than expected, avoiding other habitat types (Xiang et al. 2011). Monkeys appeared to ignore deciduous broadleaf forest and alpine shrubs. In fact, I never observed the monkeys entering shrub forest even in those instances when it was nearby.

Lichen constitutes the bulk of *R. bieti*'s diet during winter, when other options are scarce (Grueter et al. 2009). However, when young leaves and fruits are available, these foods are obtained preferentially (Xiang et al. 2007b). Primary conifer forest, with its typically higher lichen cover, may provide a comparatively rich resource patch during the winter months. However, secondary conifer forest still offers enough lichens to sustain monkeys through the lean season (Xiang et al. 2011). During other seasons, these lightly disturbed forest areas could actually contain the highest quality food resources, due to greater species richness. From the perspective of survival over the entire year, having a mix of habitat types in their range may provide *R. bieti* with the best opportunity for survival (Xiang et al. 2011).

Reproduction and Response to Changing Environment

Mating behavior was difficult to observe due to the dense tree and bush cover limiting visibility within the habitat. I was able to record the occurrence of only 10 mounts with intromission and pelvic thrusting between July and October, of which there were 8 ejaculatory mounts. In the seven instances in which the solicitor of copulation could be identified, it was a female in six instances compared to only one instance for a male. One mating event with ejaculation was observed in August at 1,625 h, and another without ejaculation in October at 1,100 h. Births were synchronized across the group, with newborns appearing only during February and March (Fig 2). The birth season of *R. bieti* at Xiaochangdu fits the pulse model, with a standard deviation (SD) of 6.5 days (Xiang and Sayers 2009). However, the timing of the birth season is earlier than that of two other wild populations, Wuyapiya (Kirkpatrick et al. 1998) and Mt. Longma (Huo 2005). Seasonal birthing may be an adaptation to harsh environmental conditions (day length, ambient temperature, food supply, nutritional state, or a combination thereof). Winter, which generally arrives earlier at higher than lower latitudes, is the leanest season for *R. bieti* (Xiang et al. 2007b). Low resource availability can affect the survival of infants directly and indirectly, via the nutritional state of the lactating mother. If infants have not reached a given threshold of development before the onset of winter, they may be unlikely to survive on the limited, nutrition-poor foods available during that time. Therefore, birth timing appears to be a strategy to maximize offspring survival, as reported previously for captive golden snub-nosed monkeys (*Rhinopithecus roxellana*) (Zhang et al. 2000) and Japanese macaques (*Macaca fuscata*) (Cozzolin et al. 1992).

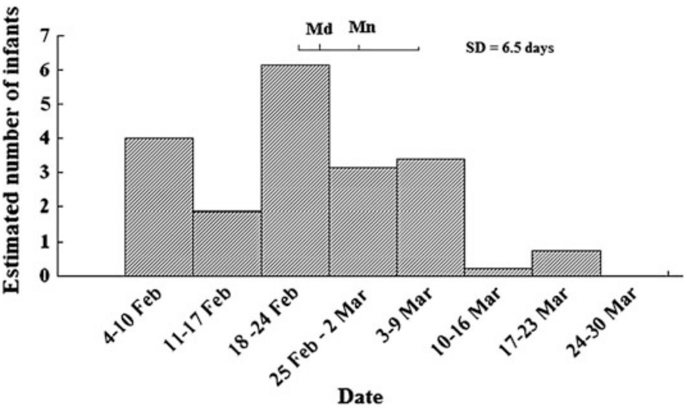

Fig. 2 Birth distribution of black-and-white snub-nosed monkeys (*Rhinopithecus bieti* at Xiaochangdu data are calculated from the observations from 25 January to 9 April, 2005). The mean birth date, median birth date, and SD are shown on the bar above the histogram. Each period code corresponds to 7 days after 4 February, 2005

Conservation Implications

The Xiaochangdu population of *R. bieti* has enjoyed greater protection from anthropogenic disturbance than snub-nosed monkeys at other sites for both cultural and practical reasons. Villagers in the areas surrounding monkey habitat within the reserve practice Tibetan Buddhism. If a Living Buddha (a senior Tibetan monk) declares a mountain to be sacred, the killing of animal life on the mountain becomes taboo. Honglaxueshan's status as one such sacred mountain contributes to its suitability as a refuge for monkeys and other wildlife living there. Another factor is that *qingke,* or slash-and-burn agriculture, is largely unproductive at altitudes above 3,800 m. This practice, which has degraded a multitude of primate habitats both within China (Zhao 1996; Xiang et al. 2004) and elsewhere (Vargas et al. 2002), does not occur within this reserve (Xiang et al. 2007a). Lastly, the composition of the floral community at Xiaochangdu appears to have a mediating effect on human disturbance. Despite a reduction in canopy cover by approximately 35 % as a result of logging, forest structure as measured by height and density of trees exceeding ≥33 cm circumference at breast height is relatively unchanged (Xiang et al. 2011). Selective logging by locals who take oak trees (*Quercus aquifoliodes*) for firewood and fir trees for construction has been going on for at least 50 years (Jiang Q, pers. comm.). At subsistence levels, selective logging may increase species diversity in localized patches by reducing the density of the most competitively dominant species. This may allow other species which the monkeys find desirable as food to grow more readily within the disturbed areas. Xiaochangdu may be a rare case in which certain anthropogenic disturbances actually benefit the monkey group.

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Nutritional Implications of the High-Elevation Lifestyle of *Rhinopithecus bieti*

Heidi Bissell

Introduction

The black-and-white snub-nosed monkey, *Rhinopithecus bieti*, is an endangered colobine monkey endemic to the Hengduan mountains of southeastern Tibet and northwest Yunnan Province, China (IUCN 2012). As one of the few "charismatic megafauna" in the region, *R. bieti* plays a crucial role in generating support for local conservation efforts. Concern for the monkey has spurred the establishment of the 2,820 km^2 Baimaxueshan Reserve to protect the numerous plants and animals in this designated UNESCO biodiversity hotspot (UNEP WCMC 2011; Weckerle et al. 2010). *R. bieti* lives at some of the highest elevations of any nonhuman primate (Long et al. 1996) and has a diet unique among mammals—the majority of their diet throughout much of their range is lichen (Kirkpatrick 1996; Xiang et al. 2007b). It is the only mammal that consumes lichen year-round. The aspects of *R. bieti's* behavior and physiology that enable them to use lichen are key adaptations for this species to exist in this harsh environment. However, warming temperatures and increasing human impact in the region are threatening this key resource and by extension, this species. Only 1–2,000 individuals are thought to exist in the wild (IUCN 2012; Xiang et al. 2007a).

The Hengduan Mountains are a narrow range of the eastern Transhimalayas bounded to the east and west by the Mekong (Lancang) and Yangtze (Jinsha) rivers as they flow south off of the Tibetan plateau. Within this narrow range, there are approximately 14 groups of *R. bieti* located between 26°14′ N (northwest Yunnan Province) and 29°20′ N (southern Tibet). The terrain is rugged and steeply sloped, and the climate is extremely harsh; snow covers the ground 4–6 months of the year, and the average monthly temperatures in winter are often below freezing.

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R. bieti occupies a narrow elevation band between 2,600 and 4,500 m that consists primarily of deciduous forests in the south, mixed broadleaf and conifers in the middle, and exclusively coniferous forests in the north, where the habitat is colder, drier, higher, and less biodiverse (Long and Kirkpatrick 1994; Xiang et al. 2007a, b; Xiao et al. 2003).

Lichen is a Key Fallback Food at High Elevations

In this harsh habitat, the foods that form the staple of other colobine monkey diets—leaves, fruits, and seeds—are often rare or completely unavailable (Grueter et al. 2009b). Lichen, however, is ubiquitous and generally abundant year-round (Grueter et al. 2009b; Kirkpatrick 1996). Lichen, a symbiotic organism composed of a fungal partner and a photosynthetic bacterium or algae (Nash 2008), forms the bulk of *R. bieti's* diet in winter when other diet items are unavailable, but also continues to constitute a large proportion of the diet in summer when other diet items are both available and abundant (Grueter et al. 2009b; Kirkpatrick 1996; Xiang et al. 2007b). In the northernmost extent of their range, *R. bieti* consumes primarily black lichen (heisongluo, Bryoria himalayana), while in the middle and southern part of their range, several species of lichen are available and consumed including black lichen, short lichen (duansongluo, Bryoria spp.), and long lichen (changsongluo, *Usnea longissima*) (Grueter et al. 2009b; Xiang et al. 2007b). It is unclear from behavioral observations whether monkeys prefer some lichen species to others when both occur in a group's range, although there is anecdotal evidence that they prefer black lichen when it is available (Long Yongcheng, personal communication).

In addition to lichen, *R. bieti* consumes the leaves of broadleaf trees and bamboo as well as more ephemeral flowers, buds, fruits, and seeds and they have occasionally been observed consuming bark, insects, and tubers (Grueter et al. 2009b; Xiang et al. 2007b). Unlike Rhesus macaques (Macaca mulatta), which share the lower elevations of *R. bieti's* range, *R. bieti* is not known to forage in agricultural crops (Grueter et al. 2010). In the southern and central part of the range, leaf consumption accounts for 20–60 % of the observed feeding time, even in winter (Ding and Zhao 2004; Yang and Zhao 2001).

However, in the central part of the monkey's range, seasonal, nonlichen foods are completely unavailable for 6–7 months of the year [November to March (Grueter et al. 2009b)], and in the northernmost part of the range, these foods can be unavailable for over 8 months each year [October to May (Xiang et al. 2007b)]. Lichen consumption can be seen in the vast majority (typically over 90 %) of behavioral observations during these times (Grueter et al. 2009b; Kirkpatrick 1996; Xiang et al. 2007b). Because *R. bieti* relies primarily on lichen during the winter months, lichen is considered as an essential fallback food for this species (Grueter et al. 2009b), particularly for the northern groups. In other words, if lichen was unavailable, or if the monkey was unable to consume it, they would not be able to inhabit most of their current range.

Colobine Digestive Physiology Uniquely Enables the Use of Lichen as a Feedstuff

Although little is known about *R. bieti's* unique relationship with lichen, our knowledge of how other foregut fermenting primates and other lichen-eating animals cope with similar challenges can shed light on the challenges faced by this monkey's unique diet.

The ability to make such extensive use of lichen is a unique and critical adaptation that allows *R. bieti* to inhabit these harsh regions where other foods are often unavailable, and likely gives them a competitive advantage over species without these adaptations. Despite its worldwide abundance (Nash 2008), lichen is an uncommon food source for mammals. Those that do consume lichen generally limit it to a small percentage of their diet or include lichen only seasonally in their diet. There are a number of reasons for this. Lichens have antifeedant properties that depress intake (Dubay et al. 2008; Robbins 1987). In addition, most lichens are extremely low in protein, and animals on high-lichen diets tend to be in negative nitrogen balance (Dubay et al. 2008; Robbins 1987). Lichens also contain many unique, biologically active compounds. Some of these compounds are potent toxins that can sicken or kill animals that lack adequate detoxification mechanisms (Dailey et al. 2008; Durazo et al. 2004; Guo et al. 2008).

R. bieti is clearly able to handle these otherwise negative nutritional aspects of lichen. These likely stems from their colobine lineage. Colobine monkeys utilize both pregastric and postgastric fermentation (Caton 1998; Chivers 1989). This digestive strategy confers the ability to obtain energy from many otherwise indigestible carbohydrates, detoxify several types of toxins, and improve nitrogen balance, all of which offer numerous advantages in the digestion of lichens.

Foregut Fermenters Get More Energy from Lichen

There are dozens of different types of carbohydrates and carbohydrate bonds, only some of which are digestible by mammalian enzymes. Microbial communities in the gut are able to digest many more of these bonds, and use the resulting catabolites for their own energy needs, while storing the excess as microbial glycogen—a carbohydrate that is highly digestible by mammals. In this way, microbial fermentation allows the energy from an otherwise undigestable carbohydrate such as cellulose to be made available to a mammal. Although lichen doesn't contain the types of fiber most commonly associated with plants (cellulose and hemicellulose), it does contains a diverse array of nonfiber polysaccharides, including lichenin and β-glucans, which are indigestible by mammalian enzymes but can be effectively fermented by gut microbes (Svihus and Holand 2000). Thus, colobine monkeys are able to make use of these carbohydrates better than monogastric animals would be.

Foregut Fermenters Require Less Dietary Nitrogen

In addition to being able to extract more energy from lichen than nonforegut fermenting animals, foregut fermentation also enables the use of lower protein feedstuffs such as lichen. Ruminant animals, which rely on pregastric fermentation, can subsist on diets with lower dietary protein quantity and quality than most monogastric animals because the ruminal microbes have the ability to use nonprotein nitrogen (NPN) sources to synthesize protein. In diets with sufficient nitrogen and energy, microbial protein can exceed 40 % of the post-ruminal protein supply (Polan 1988). Lichens contain substantial amounts of NPN (Claridge et al. 1999), and *R. bieti* can likely use this NPN to meet some of its dietary protein needs, which noncolobine monkeys would be less able to do.

In addition to dietary sources of NPN, gut microbes can utilize urea, an otherwise unusable product of mammalian protein catabolism, to synthesize proteins. In humans, approximately 40 % of the urea produced in the liver is returned to the gut, and in cattle and sheep, 60–70 % is returned (Lapierre and Lobley 2001). The microbes in the gut of foregut fermenters, however, can use the urea returned in this way to synthesize protein of value to the animal. Using these mechanisms, *R. bieti* can likely return a substantial proportion of the urea to the gut, which can then be used by the microbes for microbial protein synthesis, reducing nitrogen losses and decreasing the requirement for high quality dietary protein.

In the primate literature, the protein:fiber[1] ratio is often used as a proxy for diet quality, and has been linked to colobine abundance and distribution (Chapman et al. 2002; Milton 1979). The protein:fiber ratio of lichen (0.8–6.5; Svihus and Holand 2000, Bissell unpub. data) is similar to or even much greater than that of other colobine feeds (0.3–1.1; Chapman et al. 2002). However, the overall quantity of protein and fiber is much lower in lichens (2–8 % protein, 1–4 % fiber; Svihus and Holand 2000, Bissell unpub. data) than in vascular plants (10–25 % protein, 12–50 % fiber; Chapman et al. 2002). Because of the qualitative and quantitative differences in the protein and fiber fractions of lichens and plants, the protein:fiber ratio should not be used to compare lichenivorous versus nonlichenivorous habitats without careful consideration of the underlying values. However, the ratio may still be useful as a metric for comparisons among *R. bieti* habitats.

Nutritional Implications of a Lichen-Based Diet for *R. bieti*

Lichen is Low in Protein

Given that *R. bieti* subsists for lengthy periods on a diet that contains very little nitrogen or protein, it is interesting to speculate how their protein requirements are

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[1] Measured as crude protein (CP) and acid detergent fiber (ADF).

met during this time. On a hypothetical *Bryoria* or *Usnea*-only diet, the animals would only receive 0.5–1.0 % nitrogen or 3–6 % crude protein, well below the general primate recommendation for diets containing 6–18 % high quality protein (National Research Council 2002). The monkeys may supplement their diet with insects (Xiang et al. 2007b), although in winter these are presumably difficult to find. The previously mentioned protein-sparing mechanisms likely lessen the need for protein somewhat. Very few animals are known to store protein, and this mechanism has not been documented in primates. However, another lichenivorous species, reindeer (*Rangifer tarandus*), increases its lean body mass in the fall and catabolizes this protein during the winter when they feed on nitrogen-poor lichens (Barboza and Parker 2006).

Although body weight data from *R. bieti* are limited and body composition data are nonexistent, there are reports of some adult males weighing as much as 45 kg (Quan 2002; n = 9), including one male in winter (Ren et al. 2009; n = 1), but other reports, whose collection dates are unknown (but given the inaccessibility of the habitat in late winter, are likely from the spring and summer), give much lower maximum weights of only approximately 15 kg for adult males (Jablonski and Ruliang 1995; Long and Kirkpatrick 1994). With such limited data, it is mere speculation as to whether these weights simply reflect individual variations in size or are an indication that *R. bieti* exhibits seasonal changes in weight, as is common in many species inhabiting highly seasonal environments. Even if seasonal changes in weight occur, body composition and detailed isotopic studies would need to be conducted to determine whether the animals are changing in lean mass, or whether the changes in body weight are the more likely result of increased fat stores, a characteristic common to many seasonal animals.

Lichen is Toxic

In addition to their low nitrogen and protein content, lichens also commonly produced compounds that are toxic to mammals. There are dozens of lichen genera in the eastern Himalayas, although *R. bieti* consumes two genera of lichen most frequently, *Usnea* and *Bryoria* (Grueter et al. 2009a; Kirkpatrick 1996; Xiang et al. 2007b). Both of these genera typically contain usnic acid as well as other compounds toxic to mammals including vulpinic acid, evernic acid, barbatic acid (oxidative phosphorylation decouplers and potent toxins), fumaroprotocetraric acid (associated with allergic reactions), diffractic acid, and atranorin (cytotoxins) (Dailey et al. 2008; Marante et al. 2003; Perry et al. 1999). Microbial fermentation can detoxify at least some of these toxins, although only usnic acid has been studied in any detail. Although reindeer can consume large quantities of usnic acid in lichen without ill effect, approximately 400 elk near Yellowstone National Park died or had to be euthanized after consuming the lichen *Xanthoparmelia chlorochroa* (Cook et al. 2007), which contained high levels of usnic acid (Roach et al. 2006). The elk exhibited paralysis before death, and this was attributed to the usnic acid

(Cook et al. 2007). However, oral administration of usnic acid to sheep resulted in a different constellation of symptoms (lethargy, anorexia, muscle weakness, and abdominal discomfort), indicating that other compounds may have been involved, or that the elk microbial community metabolized the usnic acid into a different toxic compound, or that elk and sheep respond differently to usnic acid (Dailey et al. 2008). In monogastric animals including humans, usnic acid has been associated with liver damage and failure (Durazo et al. 2004; Pramyothin et al. 2004). It is thought to have antifeedant properties, perhaps as an antiherbivore defense (Dubay et al. 2008; Lawrey 1986). Many lichen compounds have been extensively studied for their use as antibiotics. For a foregut-fermenting animal, these compounds have the potential to interfere with the bacteria involved in the fermentation process. Indeed, samples of lichens consumed by *R. bieti* contained at least nine unique compounds that inhibit bovine fermentation (Bissell, unpub. data).

The development of microbial detoxification pathways is little understood. In some cases, it appears that only a single species of bacterium imparts the ability to detoxify a particular compound. Animals harboring the relevant microbial species can eat certain toxic plants, while those lacking this species sicken or die (Anjos et al. 2010; Glendinning 2007). In reindeer consuming usnic-acid containing diets, no trace of usnic acid was found in the rumen fluid or elsewhere in the digestive tract or feces, indicating that it was rapidly degraded within the rumen (Sundset et al. 2009). *Eubacterium rangiferina*, a bacterium resistant to a number of common lichen compounds (usnic, antranoric, fumarprotocetraric, and lobaric acid) has been identified from reindeer rumens and may be a key source of reindeers' ability to cope with lichens high in these toxins. Indeed, usnic acid may even increase diet digestibility rather than decrease it in reindeer (Palo 1993). Some lichen compounds have potentially beneficial medicinal properties because of their antibacterial, antitumor, antigrowth, and even antiprion properties (Bustinza 1952; Johnson et al. 2011; Lawrey 1986).

Clearly, *R. bieti* consumes large quantities of *Usnea* and *Bryoria* without experiencing lethal side effects despite the presence of a variety of lichen compounds that are potentially toxic to some mammals. However, detoxification can be costly to animals, and animals that eat highly toxic foods may pay the price through decreased fitness. While dietary specialists have typically evolved mechanisms to reduce these costs, they may still pay some price (DeGabriel et al. 2009; Iason 2005). In one study, a specialist beetle exhibited reduced fitness when consuming a more toxic variety of its host plant compared with a less toxic variety (Ballhorn et al. 2007). In this case, the host plant toxin was not lethal, but merely reduced weight gain, egg numbers, and time to hatching. Likewise, a lichenivorous diet may not be lethal, but it may reduce the fitness of individuals, particularly if the quantities consumed are large, such as during winter. Because the rugged habitat of *R. bieti* makes detailed observations difficult and few individuals can be identified, comparative data among groups that feed on different amounts of lichen are unavailable. Future studies are needed to examine whether differences in fitness exist among the groups and whether these are correlated with the groups' degree of lichenivory.

Many lichen compounds are strongly colored, and *R. bieti* likely can use this feature to distinguish among lichens. *R. bieti* have been observed carefully picking strands of the bright yellow and highly toxic *Sulcaria* virens out of clumps of *Usnea* (Bissell, pers. obs.). There can be differences in color even within a single species of lichen. *Usnea longissima*, for example, ranges in color from almost white to yellow, green, and dark gray. In one trial with semi-wild monkeys, they preferred green to white varieties of *Usnea longissima* (Bissell, unpub. data). In five samples of *Usnea longissima* collected from the habitat of four southern monkey groups, 14 separate compounds were identified using HPLC, only one of which was common to all five samples (Bissell, unpub. data). The relevance of these compounds to the health of *R. bieti* is still unknown.

Lichen is in Decline

Lichens in the area are in danger of declining for a number of reasons. Most immediately, lichen is in danger of being overharvested. Lichens are often harvested by local residents for food, medicine, and for sale to local and national markets (Wang et al. 2001, Bissell pers. obs.). With their slow regeneration times (1–9 cm per year for *Usnea longissima*; Jansson et al. 2009; Keon and Muir 2002), lichens can become locally depleted. In addition to human harvesting, the monkeys themselves can deplete lichen in some areas. Infrastructure development in the area, primarily road building, has led to fragmentation of *R. bieti* habitat, isolating the otherwise wide-ranging groups into smaller patches where they can also deplete the slow-growing lichens (Xiao et al. 2003). This has already happened to one group of monkeys in Baimaxueshan Nature Reserve, where staff now must collect lichens outside the area to feed an isolated group of monkeys each day (pers. obs.).

A larger threat to the lichen, however, is climate change. Climate warming in northwest Yunnan is progressing at one of the fastest rates on earth, increasing by 3.5–9.6 °C per 100 years whereas the average rate of global temperature increase has only been 1 °C per 100 years (Haynes and Kung, in prep; IPCC 2007). Lichens are extremely sensitive to environmental changes and are regularly used as bioindicators for changes in temperature and water and air quality (Aptroot 2009). Large changes in lichen communities have been observed after only mild changes in the climate (Aptroot 2009). Models of climate change in these mountains predict large declines in total forest area, as well as changes in forest composition (Wong et al. 2009). Similar changes in forest cover have resulted in declines of *Usnea longissima* in Scandinavia (Esseen et al. 1981) and California (Doell and Wright 2000). Similar declines in lichen in Yunnan could be catastrophic to the monkey because there are few other fallback foods throughout much of monkeys' range.

In addition to their sensitivity to changes in moisture and temperature, both *Usnea* and *Bryoria spp.* are sensitive to a variety of common environmental contaminants including nitrogen, sulfur dioxide, and fluoride (Geiser and Neitlich 2007; Geiser et al. 2010; Thormann 2006), both of which are commonly released during metal mining operations, a major industry in many parts of northwest Yunnan. In other parts of the world, increases in air pollution have lead to rapid declines in lichen populations (Batts et al. 2004; Geiser and Neitlich 2007). Lichens also strongly absorb metals from the atmosphere and have led to heavy-metal accumulation in reindeer that feed in polluted areas (Eriksson et al. 1990; Larter et al. 2010). Increased mining operations may therefore lead to the accumulation of heavy metals in lichens, and by extension, in *R. bieti*, where they are likely to have negative health effects.

Lichen's sensitivity to environmental change means that even if habitat destruction and fragmentation are halted, the most important food source of the monkey will almost certainly be changing. Monkeys' resilience to this change depends upon whether other species of lichens and plants will fill in the void in time, whether these new species contain compounds toxic to primates, and whether the monkeys (or their gut microbes) will be able to cope with these toxins. To better assess the risks to the monkey, further research is needed. Specifically, it is important to know how the Yunnan lichens (individual species as well as their chemical variants) are coping with the climate change in the area, whether they are absorbing toxins from local mining operations (and at what range from the mines), and whether plants are moving into the area at a pace to replace lichen as a winter food source. The current efforts to model the impacts of climate change on monkey habitat should be continued and expanded. If individual monkeys can be identified, examining the variation in biological fitness among groups more and less dependent on lichen would help determine the types of influence lichen has on the health and biology of these animals. Long-term monitoring of monkey groups, lichens, and other edible resources in the area is extremely difficult given the terrain and infrastructure available in the area. However, building the capacity to conduct large-scale monitoring should be a priority for conservation efforts, not only to protect the monkey, but also to help conserve the numerous unique plants and animals in this biodiversity hotspot.

Conclusions

The unique ability to use lichen as a fallback food has enabled *R. bieti* to occupy this extreme, high-elevation, seasonal niche. However, like all organisms dependent upon unique resources, this reliance on a single resource that is itself at risk also puts *R. bieti* at a high risk of extinction (Jernvall and Wright 1998; Wright 2007). In order for *R. bieti* to survive in its current range, it must continue to be able to obtain sufficient food resources during the long winters. While lichen plays this role today, the changing climate and the concomitant changes in forest elevation and composition may limit *R. bieti's* ability to rely on this sensitive resource in the future. Effective conservation of this species will require carefully monitoring food resource abundance throughout *R. bieti's* current range to determine if lichen is declining and whether incoming species are able to fill the dietary void. With proactive planning and careful resource management, *R. bieti* may be able to continue inhabiting its high-elevation habitat. Fortunately, although *R. bieti* is by necessity currently extremely reliant on lichen, it is not an obligate lichen feeder; it can and does subsist and reproduce on lichen-free diets in captivity and on low-lichen diets in the southern part of its range. Therefore, even if various forces do eventually lead to the extirpation of this species from its current range, the possibility exists that *R. bieti* could survive elsewhere if suitable conditions could be found.

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Variation in Primate Abundance Along an Elevational Gradient in the Udzungwa Mountains of Tanzania

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Introduction

Since Darwin (1839) and von Humboldt (1849) identified elevation gradients as geographical factors causing ecological variations, this topic has still received little attention (MacArthur 1972), especially when compared to the conspicuous literature associated with latitudinal gradients (Stevens 1989). In 2001, however, a volume of *Global Ecology and Biogeography* (Rahbek 1995) was dedicated to elevation gradients of species richness in mammals. Rahbek (1995) showed that most studies detected the highest species richness at lower and some at mid elevations. Several hypotheses on the cause of species richness and gradient relationship have been proposed since, but none of these has yet received clear empirical support (Brown 2001; Heaney 2001; Lomolino 2001). Species diversity may peak at intermediate elevation gradients because of overlapping ranges of species distributions that are bounded by the ends of the gradient (Colwell and Hurtt 1994; Rahbek 1995, 1997; Kessler 2001; Lomolino 2001; Rahbek 2005). This hypothesis fits with standard ecological theory on diversity and geographic ranges, in that temperature declines with elevation, leading to low productivity and consequent changes in habitat diversity and biotic interactions (Givnish 1999; Heaney 2001; Lomolino 2001). A second geographical component which is more poorly understood is the relationship between population density and elevation

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gradient. At present, it is not clear whether a density–elevation gradient relationship exists within a single species, since only one study is known to have investigated such an effect (Hanya et al. 2004).

The present study aims to assess the changes of population abundance with elevational gradient in four nonhuman primate species from the Udzungwa Mountains of Tanzania. The Udzungwa Mountains are part of the Eastern Arc Mountains chain, an area of global importance for biodiversity and endemism (Burgess et al. 2007). In particular, the Udzungwa represents one of the most important areas in Africa for primate diversity and endemisms, with two strictly endemic monkeys, the Udzungwa red colobus (*Procolobus gordonorum*) and the Sanje mangabey [*Cercocebus* (*galeritus*) *sanjei*], and the near endemic kipunji (*Rungwecebus kipunji*; Rovero et al. 2009). Of all the Eastern Arc Mountains blocks, the Udzungwa have the largest forested area, widest elevation gradient, and greatest habitat diversity, making the area an excellent model for studying changes of primate abundance with elevation. The study focuses on Mwanihana forest, one of the largest forest blocks and one of the only two forests (the other being the Udzungwa Scarp Forest Reserve) that have continuous forest cover from 300 to 2,300 m a.s.l.

A detailed study in woody vegetation along elevation gradients of the Mwanihana forest found that basal area, species' richness, and diversity increase with elevation (Lovett et al. 2006). In contrast, previous work on elevational variation in primate abundance is very limited. It either relates to studies conducted on a limited range of the overall forest elevational gradient, such as the long-term monitoring conducted in Mwanihana and Udzungwa Scarp Forest Reserve from lowland (300 m a.s.l.) to mid elevation (1,000 m a.s.l.; Rovero et al. 2006, 2012); or it relates to comparisons of abundance among forests with different elevation gradients (Marshall et al. 2005; Rovero and Marshall 2005). This latter approach would likely introduce biases from comparing forests which differ in overall area, floristic and/or structural tree community features, as well as for differences related to anthropological effects (e.g., hunting and habitat fragmentation). Nevertheless, these comparisons show that both diversity and relative abundance of primate populations were higher at lower elevation (e.g., Mwanihana Forest: 300–800 m) than at mid to high elevation (e.g., Ndundulu Forest: 1,400–2,100 m; Struhsaker et al. 2004; Rovero and Marshall 2005). The present study aims to (a) assess variation in primate abundance along the entire elevational gradient (300–2,300 m a.s.l.) within the same forest; and (b) correlate variations in primate abundance to elevation and vegetation parameters such as mean and total basal area, tree species' richness, and canopy cover.

Methods

Study Site

The Udzungwa Mountains are in south–central Tanzania and extends over 10,000 km^2. Overall elevations span from 290 (Kilombero valley on the eastern side) to 2,600 m a.s.l. (Mount Luhomero). The focal area for this study,

Fig. 1 Map of the Udzungwa Mountains of Tanzania, with forest blocks in *black* and the Udzungwa Mountains National Park highlighted in *gray*. The insert on the *right* shows Mwanihana forest, where the study was conducted, with primate census transects walked (*white lines*)

Mwanihana forest (centered on 7°46’S, 36°43’E; 177 km^2), covers a steep and east facing escarpment slope within the eastern side of the Udzungwa Mountains National Park (Fig. 1). This forest is a key site for conservation of the two endemic monkeys, the Udzungwa red colobus and Sanje mangabey (Dinesen et al. 2001; Rovero et al. 2009). For the latter, Mwanihana holds one of the two existing populations; the other one is in the southern Uzungwa Scarp Forest Reserve. Mwanihana forest is important for a range of plant and fauna species, including gray-faced sengi, or elephant-shrew (*Rhynchocyon udzungwensis*), Abbott’s duiker (*Cephalophus spadix*), and rufous-wing sunbird (*Nectarinia rufipennis*).

Forest cover at Mwanihana is continuous from 300 to almost 2,300 m a.s.l. and consists of different habitat types roughly corresponding to elevation zones (Lovett 1993; Lovett et al. 2006), from lowland deciduous ‘miombo’ forest, and semi-deciduous forest to submontane and montane evergreen forest, the latter including upper montane, bamboo-dominated forest (Lovett 1993; Lovett et al. 2006).

The forest is under the direct climatic influence of the east blowing Indian Ocean winds, and rainfall is therefore higher than in the surroundings, varying from 2,000 to 2,500 mm per year, usually distributed in two periods: November–December and March–May.

Primate Species

Four primate species out of the 13 primates (of which seven diurnal) found within the Udzungwa Mountains occur in Mwanihana forest and are considered in the current analysis (Fig. 2).Subfamily Colobinae:

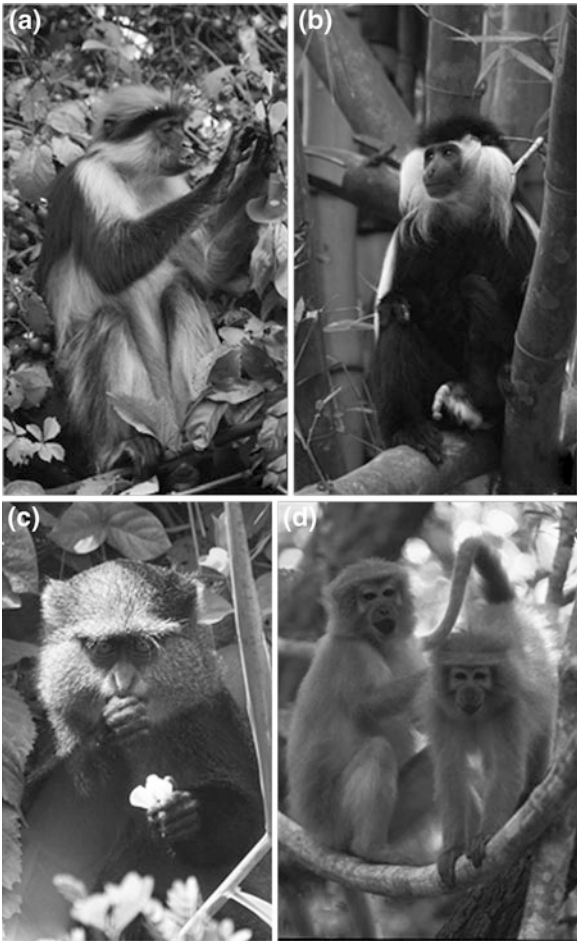


Fig. 2 The four forest-dwelling and diurnal primate species occuring throughout Mwanihana forest in the Udzungwa Mountains National Park: **a** Udzungwa red colobus (photo C. Gupfinger), **b** Angolan colobus **c** Sykes' monkey **d** Sanje mangabe

(1) Udzungwa red colobus (*P. gordonorum*)

This IUCN-Vulnerable monkey is one of the Udzungwa endemic primates. It occurs throughout the Udzungwa Mountains range but because of habitat destruction for farming and settlements, its presence in small forest fragments has decreased drastically in recent years. They live in multi-male/multi-female groups and range in size from 3 to 85 individuals (Struhsaker et al. 2004; Struhsaker 2010). Extensive work by Struhsaker and colleagues has shown that group size is affected by several habitat parameters, including tree density, degree of deciduousness, and forest size (Struhsaker et al. 2004). Thus, groups are bigger in size in the large blocks of mature, moist, mixed evergreen, and semideciduous forest (such as Mwanihana) but size does not appear correlated with elevation (Struhsaker et al. 2004; Marshall et al. 2005, 2010).

Like other colobine monkeys, the species is arboreal and is rarely seen on the ground. Colobus feed on leaves, especially young leaves (Rovero 2003; Pucci and Rovero 2004). Thus, the richness of food plant species in the forest is an important variable correlating with the abundance of red colobus (Rovero and Struhsaker 2007). Red colobus in the Udzungwas associate with all sympatric diurnal monkeys with the exception of yellow baboons, and are most frequently observed in association with Angolan colobus (Struhsaker 2010).

(2) Angolan colobus (*Colobus angolensis palliatus*)

This species occurs throughout the Udzungwa Mountains (Marshall et al. 2010) and, like red colobus monkeys, has decreased in recent years at heavily disturbed sites (Rovero et al. 2012). The distribution of Angolan colobus monkeys is very similar to that of red colobus monkeys, and it appears to be relatively more common at higher elevations, in the upper montane forest zone (Marshall et al. 2005). Like the red colobus, it is negatively affected by forest degradation, but to a lesser degree (Marshall et al. 2005; Rovero and Struhsaker 2007; Rovero et al. 2012).

This colobus species lives in one-male/multi-female groups (occasionally with 2 or 3 males) ranging in size from 2 to at least 14 individuals. Similarly to the pattern observed for the red colobus, group size decreases in degraded forests (Marshall et al. 2005). They are typically arboreal and spend large amounts of time resting, and feed predominantly on mature leaves.

Subfamily Cercopithecinae:

(3) Sanje mangabey [*Cercocebus* (*galeritus*) *sanjei*]

This endemic and IUCN-endangered monkey was discovered in 1979 (Homewood and Rodgers 1981) and it is present only in two forests, Mwanihana and Udzungwa Scarp Forest Reserve (Fig. 1). Habituation of two groups in the Mwanihana forest suggests that Sanje mangabeys live in multi-male/multi-female groups of approximately 40–60 individuals, with up to five adult males. Group home range size is approximately 4–6 km^2 and can encompass habitats including primary and secondary forest, which are all exploited over the year. Fruits form the greatest component of their diet, which also includes flowers, seeds, fungi, invertebrates, and small vertebrates. All strata of the forest are exploited; however, up to 70 % of time is spent for aging and traveling on the forest floor. Sanje mangabeys form polyspecific associations in Mwanihana with Sykes' monkeys and the two colobines (Jones and Laizzer unpublished data).

(4) Sykes' monkey (*Cercopithecus mitis* spp. *moloneyi/monoides*)

This species occurs throughout the Udzungwa Mountains range. In Mwanihana forest, it prefers secondary, regenerating, and semideciduous forest zones (Rovero et al. 2006); however, it is also common in higher elevation forests (e.g., Marshall et al. 2005) and it does not seem to be clearly negatively influenced by habitat degradation as the two colobines (Rovero et al. 2012).

This monkey lives in uni-male/multi-female groups ranging in size from 2 to at least 22 individuals (Rovero et al. 2006). It is an opportunistic species that uses all vertical forest strata and feeds predominantly on fruits. Sykes' monkeys are found in polyspecific association with Sanje mangabeys, Angolan colobus and Udzungwa red colobus.

Yellow baboons (*Papio cynocephalus*) also occur in Mwanihana but confined along the lower, miombo woodland, and thus not relevant for the study purpose. Vervet monkeys (*Chlorocebus pygerythrus*) are also sporadically present along forest edges.

Primate Census

Primate abundance data were collected in Mwanihana forest between July and November 2011 through line transects. A grid of 2 km-long transects, spaced 1 km apart (along both longitude and latitude) and oriented North–South was randomly overlapped with a satellite forest cover map (Fig. 1a). A set of 43 transects deemed feasible was chosen based on accessibility and actual forest cover (i.e., excluding areas with rock cliffs or large forest gaps). The transect areas were presurveyed to assess feasibility of conducting censuses, and the majority of transects did not involve any vegetation cutting, with exception of lower elevation transects that crossed secondary, regenerating vegetation that could not be properly walked without minimum precutting.

The line transect method is very well established and routinely deployed for forest monkeys (review in Marshall et al. 2008; see also Buckland et al. 2010). Transects were walked by a team of one observer and two assistants at an average speed of about 1 km per h, starting in the early morning (between 07:00 and 07:30) and completed in 2–3 h, depending on vegetation density (average: 2 h:53 m; range: 1 h:02 m–4 h:33 m). For each primate sighting, the following data were noted: Observer's position from the beginning of the transect (measured through a hip chain), species observed, position, and elevation were recorded by using a hand-held GPS unit (Garmin Map60 CSx). Solitary monkeys were also scored, but we included only social groups in the analysis. We did not analyze groups that were heard but not seen. An additional set of information was taken for other purposes than the present study, such as the number of individuals, if countable, the perpendicular distance from transect to the first animal seen, and the animal observer distance.

Vegetation Sampling Along Transects

To assess the relationship between primate abundance and arboreal vegetation structure and composition, after each census walk the field team conducted tree sampling on the way back to the starting point. Four, 25 by 25 m square plots centered on the line transect were established every 500 m along transects (at 250, 750, 1,250, and 1,750 m). All tree and woody climber species above 10 cm of diameter at breast height (DBH) within the plot were identified and measured by using a DBH measuring tape. In addition, we visually estimated the extent of canopy cover above each plot by using 5 classes: open canopy (0 %), semi-open (25 %), half-closed (50 %), semi-closed (75 %), and closed (100 %).

Data Analysis

We computed a primates' encounter rate (ER) as the number of groups seen per km of transect walked, and considered it an index of relative abundance, in accordance with several other primate studies (e.g., Chapman et al. 2000; Mitani et al. 2000; Rovero et al. 2006; Linder and Oates 2011; Lwanga et al. 2011). To assess variation of ER with elevation, we used the elevation of each sighting (or mean elevation when multiple sightings were scored per transect) to attribute the ER from each transect to three elevation classes. By dividing in approximately equal portions the overall elevation range (433–1,850 m a.s.l.) of primate sightings, we identified three classes of elevation: lowland (400–700 m a.s.l), submontane (700–1,200), and montane (1,200–1,800). Due to the steep terrain of the forest, transects inevitably crossed a range of elevation (minimum and max elevation gradient within each transect: 15–545 m). Thus, we considered it more accurate to classify the ER from each transect by the elevation of sightings rather than by the average transect elevation. However, when no sightings were scored per transect, we used the average transect elevation as the mean elevation of the four vegetation plots. By using the Kruskal–Wallis test, we then tested for differences in ER across elevation zones. We also used Pearson's correlation test to further assess the relationship between primates' ERs and elevation on a continuous scale. Correlation tests were also used to assess relationship between vegetation variables and elevation. Data from vegetation plots were used to compute the following variables: DBH values from each tree were converted into basal area, and used to compute both mean basal area (MBA) and total basal area (TBA); species' richness was computed as the total number of species per plot; and canopy cover was the index of canopy closure above the plot.

The influence of both elevation and vegetation variables on primates' relative abundance was assessed using generalized linear modeling (GLM), with Poisson error distribution that is appropriate when the response variables are counts (Maindonald and Braun 2003). Because of data overdispersion, we used a quasi-Poisson error distribution (Zuur et al. 2009). We implemented GLMs in R software version 2.10 (http://www.r-project.org). Vegetation variables (MBA, TBA, canopy cover, and species' richness) were used as the mean values per transect from the four vegetation plots. Variables were first checked for collinearity through a correlation matrix and using a threshold of Pearson's $r > 0.7$. As a result, canopy cover was not presented to GLMs because of positive, significant correlation with TBA ($r = 0.71$, $p < 0.001$). We preferred TBA instead of canopy cover because the latter is an estimate and, as such, it is subject to observer bias. TBA and MBA were also significantly auto-correlated ($r = 0.75$, $p < 0.001$). However, we retained both variables because they provide complementary information; TBA reflects the overall amount of tree cover, while MBA reflects the average size of trees. Species' richness and TBA were also auto-correlated ($r = 0.59$, $p < 0.001$) and both retained for regression analysis.

Results

Primate Density and Elevation Gradients

We walked a total of 80.05 km of transects from the 43 transects. Some transects could not be completed due to harsh terrain (range of transect length: 859–2,000 m). This sample size yielded 117 sightings of monkeys, which consisted of 43 Udzungwa red colobus monkeys, 38 Angolan colobus monkeys, 31 Sykes' monkeys, and 5 Sanje mangabeys. Accordingly, mean ER from all transects were highest for Udzungwa red colobus (0.54 groups per km walked), followed by Angolan colobus (0.49), Sykes' monkey (0.38), and Sanje mangabey (0.06; Fig. 3).

For all species, ER varied markedly across elevation zones (Fig. 4). Udzungwa red colobus' ER decreased steadily and significantly from lowland to montane (Kruskal–Wallis test: $\chi^2 = 12.67$, $p < 0.005$), while Angolan colobus' ER was similar in lowland and submontane zones but decreased in the montane zone, and the overall difference was significant ($\chi^2 = 6.61$, $p < 0.05$). Sykes' monkey's ER also decreased steadily and significantly ($\chi^2 = 19.47$, $p < 0.001$). Sanje mangabeys were not sighted in the lowland zone, and sightings were almost equally divided between the submontane and montane zones. However, sample size was

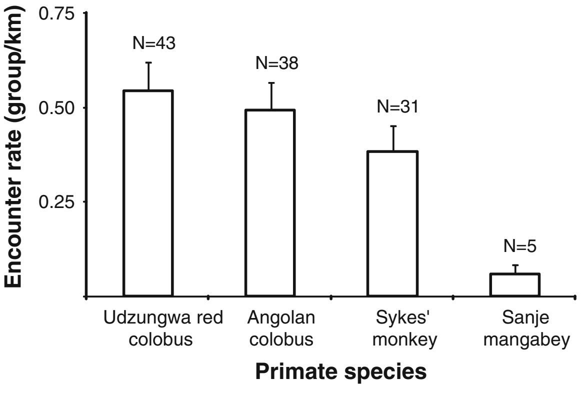


Fig. 3 Mean encounter rate (number of groups observed per km walked) and SE of four primate species from 43 transects conducted in Mwanihana forest during July–November 2011. *N* indicates the total number of groups sighted

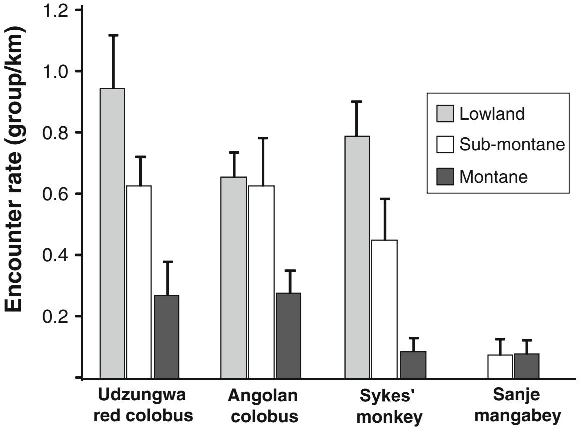


Fig. 4 Mean encounter rate (groups observed per km walked) and SE for each of the four primate species along elevation zones (lowland: 400–700; submontane: 700–1,200; montane: 1,200–1,800 m a.s.l.) in the Mwanihana forest, Udzungwa Mountains, Tanzania

too small for statistical analyses. As noted in other studies (e.g., Rovero et al. 2012), line transects are not an efficient method to census Sanje mangabeys, as they move predominantly on the ground and are very elusive.

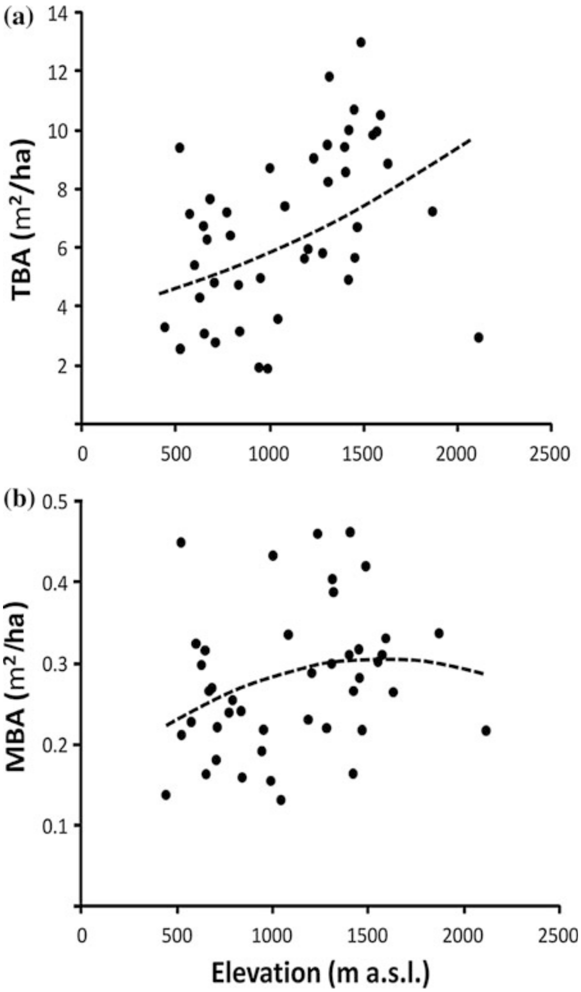
Correlative analysis of relative abundance values from each transect against elevation of sightings confirms the trends presented above: the correlation was negative and significant for the three species, with highest coefficient for the Sykes' monkey ($r = -0.63$, $p < 0.001$), followed by the Udzungwa red colobus, ($r = -0.50$ $p < 0.001$) and Angolan colobus ($r = -0.35$, $p < 0.05$).

Effect of vegetation parameters and elevation on primate abundance

Correlation tests between vegetation parameters (using mean values from the four plots per transect) and mean transect elevation show that positive and significant correlations emerged between: (1) elevation and TBA ($r = 0.43$, $p < 0.005$; Fig. 5a), (2) elevation and canopy cover ($r = 0.46, p < 0.005$), while the correlation was low and not significant between, (3) elevation and MBA ($r = 0.25$, $p = 0.10$; Fig. 5b), and (4) elevation and species richness ($r = 0.21, p = 0.17$). In particular, while TBA increases throughout the elevation gradient, MBA increases less steeply than TBA and appears to peak at elevation gradients of 1,000–1,500 m (Fig. 5).

Multivariate regression analysis on the effect of vegetation parameters and elevation on primate relative abundance resulted in elevation, TBA, and MBA being retained by the models for all three species tested (deviance explained by the model: Udzungwa red colobus 31.5 %, Angolan colobus 32.6 %, Sykes' monkey 36.9 %; Table 1). Canopy cover was not used a priori (see methods) and species' richness was manually excluded during model selection as it did not improve the fit in any model. As expected, elevation had a significant, negative effect on all three species. MBA had a positive effect on all species, which was relatively more marked for the colobines than the Sykes' monkey. TBA, on the contrary, had a negative effect on all species, but it was significant only for the colobines and it appeared of less importance than the effect of MBA.

Fig. 5 Plots showing the correlations between two vegetation parameters, total basal area (TBA, chart *above*), mean basal area (MBA, chart *below*), and elevation from tree plots established in the Mwanihana forest, Udzungwa Mountains, Tanzania. The *dotted line* indicates the shape of the correlation



Discussion

Results of the current study clearly show that relative abundance of diurnal primates in Mwanihana forest varies sharply with elevation. ER decreases with increasing elevation, according to different patterns in the four investigated species. These results confirm the trend inferred in previous studies (Marshall et al. 2005; Rovero et al. 2006) by addressing, for the first time, an elevation gradient spanning about 1,500 m (433–1,850 m a.s.l.) and occurring within the same forest. Even though all target species in Udzungwa Mountains range well up to above 2,000 m a.s.l. in the western, Ndundulu-Luhomero forest (review in Rovero et al. 2009), this study indicates that highest abundances are recorded within the

Table 1 Results of Generalized Linear Modeling (quasi-Poisson error distribution) for testing the effect on primates' relative abundance of vegetation parameters and elevation. Data are from 43 census transects

	Udzungwa red colobus		*Angolan colobus*		*Sykes' monkey*	
Variables	Z ± SE	p(z)	Z ± SE	p(z)	Z ± SE	p(z)
Elevation	−1.047 ± 0.381	0.0092	−1.061 ± 0.365	0.0061	−1.690 ± 0.465	0.0008
TBA	−1.062 ± 0.473	0.0309	−1.135 ± 0.464	0.0194	−0.767 ± 0.586	0.1981
MBA	1.596 ± 0.651	0.0190	1.611 ± 0.644	0.0169	1.031 ± 0.769	0.1881

TBA total basal area; *MBA* mean basal area; all explanatory variables were natural log transformed

lowland, or lowland to submontane forest, for the two colobus monkey species and Syke's monkey. The Sanje mangabey, in contrast, appears to prefer submontane and montane altitudinal zones, even though counts were too few to draw definitive conclusions.

In accordance to another study on density–elevation gradient relationship (Hanya et al. 2004), also Udzungwa primates show a preference for lowland altitude. Dietary preference of red colobus for young leaves (Waterman and Kool 1994; Usongo and Amubode 2001; Rovero 2003; Chapman et al. 2004; Struhsaker 2010) may explain its preference in lowland forest where trees are deciduous and semideciduous, and therefore availability of young leaves is greater (Chapman et al. 2002). Angolan colobus, on the contrary, is known to be able to better digest mature leaves (Bocian and Anderson 2013), which may explain their sustained abundance in the evergreen, submontane forest (e.g., Fimbel et al. 2001). Sykes' monkey, instead, is an omnivore and opportunistic species, not influenced by habitat degradation, thus capable of using all vertical forest strata (Butysnki 1990). As already suggested for primates residing in the Udzungwas (Marshall et al. 2005), as well as from other areas (Durham 1975; Caldecott 1980; Fimbel et al. 2001; Chapman et al. 2002), knowledge on species' diets, and information on food quality and quantity available at different elevations, are required to test potential hypotheses. Physiological effects of altitude may also directly impact species' abundance and/or group sizes, such as through the increased nutritional demands of thermoregulation and locomotion in colder habitat (Caldecott 1980; Bryant et al. 1983; Dudt and Shure 1994).

Red colobus are dependent upon the richness of food plant species (Rovero and Struhsaker 2007) which may be related to overall tree species' richness. However, species richness as such does not seem to be of importance, as richness slightly increases over the altitude range investigated, an opposite effect from the increasing red colobus' abundance trend. Tree species diversity is likely to be more relevant but further studies are required. An approximation of forest structure (i.e., defined by the community of trees having DBH above 10 cm) appears to have a clear influence on abundance changes with elevation. In agreement with findings from focal vegetation studies (Lovett et al. 2006), the negative effect of TBA on primate abundance is consistent with the almost linear increase of TBA with elevation (the relation has however a weak explanatory power: $R^2 = 0.15$). Interestingly, this is slightly in contrast with previous studies that found positive influence of TBA on both Angolan colobus (Rovero and Struhsaker 2007; Rovero et al. 2012) and red colobus abundance (Rovero et al. 2012). However, previous studies focused only on low to mid elevation (300–1,000 m a.s.l.) and concluded that within that range, which includes optimal habitat, TBA is a proxy for closed-canopy cover, selected by typical arboreal primates as the colobines. The positive and significant influence of MBA on the abundance of colobines also fits well with the relationship between MBA and altitude; the relationship is not significant but shows a slight increase of MBA up to submontane forest, which is the higher end of the preferred altitudinal range for both species. A positive influence of MBA on red colobus was found at lower to mid elevation in Rovero and Struhsaker (2007), and can be explained by the species' preference for old-growth, mature forest habitat. The different pattern found for the Sykes' monkey is not surprising, given this opportunistic frugivorous-omnivore species' preference for secondary, regenerating vegetation (Butynski 1990) that is characterized by a high presence of woody climbers (Lawes et al. 2013). This degraded type of habitat is almost exclusively present along the lower forest belt (Rovero et al. 2006, 2012). Therefore, the non-significant effect of TBA and MBA is easily explained.

Red colobus monkeys appear to prefer lowland forests, with species that range nearly exclusively at low elevation, including the western red colobus (*Procolobus badius*) (0–900 m a.s.l.; Butysnki et al. 2013a), Preuss's red colobus (*P. preussi*) (50–1,079 m; Butynski and Kingdon 2013), and Pennant's red colobus (*P. pennantii*) (0–800 m; Butynski et al. 2013b). The higher altitudinal range of the Udzungwa red colobus resembles that of Central African red colobus (*P. rufomitratus tephrosceles*) that ranges up to 2,420 m in SW Tanzania (Struhsaker and Grubb 2013). For the Angolan colobus, the highest altitudinal range of 2,200 m in Udzungwa (Rovero et al. 2009) is only slightly smaller than the species' upper limit of 2,415 reported from Nyungwe, Rwanda (Bocian and Anderson 2013). On the contrary, the range reported for the *C. mitis* group of monkeys is much wider than in the Udzungwa Mountains, extending up to 3,800 m on Rwenzori Mountains, Uganda (Lawes et al. 2013).

Conclusions and Conservation Implications

This study is a first assessment of primate groups' relative abundance across an altitudinal gradient throughout Mwanihana forest. The pattern observed is unambiguous. From an intensive demographic study previously conducted, no differences in group size, among the Udzungwa red colobus, was found with elevation in mixed semideciduous and evergreen forests (Struhsaker et al. 2004). Thus, the pattern for the Udzungwa red colobus should remain unchanged when group size (number of individuals per group) is included into the analysis. At high elevation, Marshall and colleagues (2005) found smaller group size in the western Ndundulu forest, but they interpreted the results as driven by human disturbance and vegetation degradation effects rather than elevation (Struhsaker et al. 2004). Detailed dietary and habitat quality assessments, in parallel with an assessment of energy and climate gradients, will be necessary to understand causation in the relationships found.

The findings have relevant implications in conservation management, especially given the threatened status of both endemic monkeys and the documented decline of primates reported for the least protected forests in the Udzungwas, including the southern Udzungwa Scarp Forest Reserve (Rovero et al. 2012). The importance of large forest blocks, with large portions of old-growth, mixed evergreen, and semideciduous forest has been highlighted before (Struhsaker et al. 2004). This study stresses that the presence of original forest cover from the lowland belt of the mountains is especially critical, particularly for the Udzungwa red colobus. The greatest forest loss in recent decades (1955–2000) in the Eastern Arc Mountains has occurred in the lowland zone (200–800 m, 55 %) and in the submontane zone (800–1,200 m, 41 %), relative to montane zone (1,200–1,800 m, 20 %: Hall et al. 2009). The Udzungwa Mountains hold some of the few forests (Mwanihana and Udzungwa Scarp Forest Reserve) in the Eastern Arc retaining forest cover from lowland to montane. Besides the greater size of these forests relative to most of the Eastern Arc forests, such persistence of lowland forest may be the single, most important reason for the exceptional importance of Udzungwa for primate diversity and conservation. The near absence of Sanje mangabeys at lower elevation may well be an effect of disturbance caused by human activities. The lowland forest has faced historically, and may currently be subject to the greatest human pressure through timber and pole cutting, as especially documented in the southern, less protected Udzungwa Scarp Forest Reserve (Rovero et al. 2012). Increased protection of these forests is of great importance.

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Deriving Conservation Status for a High Altitude Population: Golden Monkeys of Mgahinga Gorilla National Park, Uganda

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Introduction

Human modification of ecosystems is threatening biodiversity on a global scale. For example, it is estimated that, during the 1990s, 16 million ha of forest were lost globally each and every year, of which 15.2 million ha were tropical forest (FAO 2005, 2010). Furthermore, even when the physical structure of the forest remains intact, subsistence and commercial hunting has had profound impacts on animal populations. For example, Chapman and Peres (2001) estimate that 3.8 million primates are consumed annually in the Brazilian Amazon alone. Human modification of ecosystems have also contributed to the approximate 0.6 °C warming of the earth's climate over the past 100 years, and some estimates suggest that the climate could warm by up by 5.8 °C this century (IPPC 2001; Walther et al. 2002). Such changes have led to an increase in the number of species being considered endangered (http://www.iucnredlist.org/ January 2012 update).

In Uganda, the country where this study focuses, threats to biodiversity are similarly grave. Closed-canopy tropical forest once covered 20 % of the country, but deforestation has reduced this to just 3 %, with 18 % of forest lost between 1990 and 2000 (Howard et al. 2000). The most recent estimate suggests that the annual rate of loss for tropical high forest in Uganda is 7 %, while 5 % of woodland and 4 % of bushland is lost each year (Pomeroy and Tushabe 2004). The

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highland areas of Uganda are an area of particular importance because of their high level of endemism (Bibby et al. 1992; Plumptre et al. 2003). To protect these endemic species, Uganda has set aside approximately 2,500 km^2 of high altitude land in national parks, including Mgahinga Gorilla, Bwindi Impenetrable, Rwenzori, and Mt. Elgon National Parks. Nonetheless, high altitude wildlife populations in Uganda are still particularly vulnerable to climate change and associated loss of habitat as animals typically have no refuge as they are confined by the tops of mountains and lack of forests at lower elevations due to human landscape modification. As in many tropical regions, human population densities at high elevations are extremely high (e.g., 400 + people/km^2) in Uganda compared to nontropical regions due to the amiable climate and rich soils that facilitate agriculture (Struhsaker 2010).

Setting up a system of protected areas is the primary conservation strategy used to protect most threatened species. This is particularly the case for high altitude species, because there is the additional desire to protect watersheds. Yet, little is known about long-term ecosystem dynamics in most protected areas that are essentially biological islands. Thus, what will happen to species in parks over the long term is unclear. Conservation workers often assume that once a species is protected inside a national park, it is no longer at risk and populations will either be stable or increase in size (Chapman et al. 2010). As we demonstrate here, this is not necessarily the case and continuous monitoring of the conservation status of endangered species, even for populations protected inside national parks, is needed.

A variety of approaches can be taken to investigate the conservation status of a species within a national park. If long-term data are available on changes in both population size and habitat structure, one can evaluate if regeneration or degradation of the habitat corresponds with predictable changes in population size (Plumptre and Reynolds 1994; Struhsaker 1976, 1997). Another approach is to evaluate the nutritional requirements of a species and consider whether the habitat in question is providing those needs (Balcomb et al. 2000; Chapman et al. 2004; Ganzhorn 1995; Rode et al. 2006; Twinomugisha et al. 2006). A third valuable approach is to identify a behavioral index, where variation in a particular behavior or suite of behaviors demonstrates the animal’s resource needs, and subsequently evaluate how changes in the habitat relate to changes in this behavioral index. For example, animals are typically viewed to move around their home ranges in ways that maximize the intake of required nutrients, while minimizing their travel and search costs (Pyke 1984; Rode et al. 2006). If this is the case, by examining the ranging patterns of a species and evaluating the resource availability in different areas of the home range, one can identify the most critical resources of the species. Subsequently, the effects of anthropogenic habitat change on the availability of those resources can be evaluated and then used to predict how future habitat change may alter resource availability. Lastly, the reproductive rates of a population can be compared to other populations of the same or similar species, with the expectation that populations that are having many infants per female are likely living in the most suitable environment and thus most likely to survive into the future.

Here, we build and synthesize a series of our studies and use each of these approaches to examine the conservation status of the endangered golden monkey (*Cercopithecus mitis kandti*) in Mgahinga Gorilla National Park, Uganda. The golden monkey is a high altitude specialist that has a small distribution (less than 5,000 km^2) and is found only in the Virunga volcanoes and Nyungwe National Park from 2,500 to 3,550 m (Aveling 1984; Kingdon 1971). The golden monkeys in the Virungas are likely the only remaining viable populations, as the Nyungwe population is very small; however, even within protected areas in Virungas their populations have been documented to be in decline (Twinomugisha and Chapman 2007). The population in Mgahinga spends 60 % of its time eating bamboo (*Arundinaria alpina*), but tree fruits appear to be critical in their diet and habitat selection (Twinomugisha et al. 2006). These populations occur mostly in bamboo and bamboo forest mix (http://www.iucnredlist.org/apps/redlist/details/4236/0) (Sheil et al. 2012) where fruiting trees are extremely rare and are represented by only a few species (Kalina 1991; Schaller 1963). First, we report on changes in abundance of the golden monkey based on three surveys conducted between 1989 and 2003. Second, we evaluate the nutritional ecology of this population to determine which resources are particularly important and consider the availability of potentially limiting foods. Third, we quantify ranging behavior to determine how the use of their home range varied in relation to spatial and temporal variation in resource availability. Lastly, we compared the reproductive rate of this population to other published rates for this species.

Methods

Study Site

Mgahinga Gorilla National Park, Uganda (33 km^2) encompasses the slopes of three volcanoes (Mgahinga 3,474 m, Muhabura 4,127 m, and Sabinyo 3,634 m) and is part of the greater Virunga Conservation Area, which covers 434 km^2 (Fig. 1). Mgahinga was first gazetted in 1930 as the Gorilla Game Sanctuary and covered 33.7 km^2, but in 1939, 15.5 km^2 were reclassified to crown forest to allow bamboo (*Arundinaria (Synarundinalia) alpina*) extraction (Malpas and Infield 1981). Due to an increasing shortage of land for agriculture, the forest reserve was further reduced by 10.4 km^2 in 1951 (Uganda National Parks 1996). In 1964, the Gorilla Game Sanctuary was renamed the Gorilla Game Reserve and enlarged to 47.5 km^2; however, this boundary was never demarcated and people remained settled on 13.8 km^2 (Malpas and Infield 1981; Uganda National Parks 1996). Anthropogenic pressure on this conservation area was compounded by illegal poaching of wildlife and bamboo harvesting. By the latter half of the 1980s, the

Gorilla Game Reserve had attracted international attention, and as a result, a number of conservation projects were initiated. This attention culminated in upgrading the reserve to a national park in 1991, which offers the highest level of protection under the Ugandan constitution (Uganda National Parks 1996). During the same year, the Global Environmental Facility of the World Bank established a trust fund to contribute to conservation efforts in and around the park (Uganda National Parks 1996). In June 1992, the Uganda government reached an agreement with the local people settled in the park and they were re-located. The vegetation types of the park are diverse and are broadly classified into three belts: alpine, subalpine (ericaceous), and montane forest (Fig. 1), with the subalpine belt being composed of moorland, montane grassland, and ericaceous zones.

Survey

We conducted line transect censuses twice a month during two periods totaling 13 months (March to August 1998 and January 2003 to July 2003). We compared our findings to a census conducted in 1989 by Werikhe (1991). Our censuses were conducted by walking approximately 1 km/h along three 4 km and one 5.7 km transects (Fig. 1). The transects were set along compass bearings and did not follow existing trains or altitudinal zones. One of the 4 km transects traversed a previously encroached and degraded part of the park that has been recovering since 1992. Werikhe (1991) conducted censuses in a similar fashion along eight

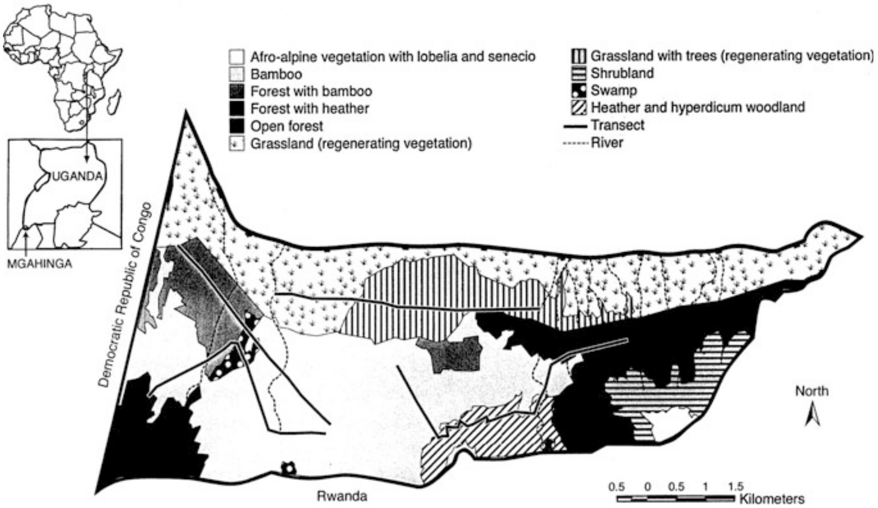

Fig. 1 A map of Mgahinga Gorilla National Park, Uganda, illustrating its major vegetation types and the transects used in golden monkey censuses

transects (ranging from 2.7 to 4.5 km) in the part of Mgahinga that was not settled. Werikhe's transects followed existing trails that mostly ran along an altitudinal gradient, and cut across vegetation types.

Upon sighting a social group we recorded the location, sighting angle, sighting distance from observer, height above ground, vegetation type, and number of individuals. Sighting distance was visually estimated. Most of the censuses began between 0640 and 0830 h and lasted to 1,040 and 1,140 h for all 4 km transects and until 1,400 h for the 5.7 km transect. Sighting distance frequencies were graphed and the Maximum Reliable Sighting Distance was estimated as that distance beyond which the sighting frequency declined by ≥50 % (National Research Council 1981). The Maximum Reliable Sighting Distance was 25 m. Sightings beyond 25 m were few and were dropped from the analyses.

In addition, as an index of relative abundance, we estimated the number of groups seen per km of census trail walked (Chapman et al. 2000; Mitani et al. 2000). This index does not take into account differences in visibility among periods or differences in the ability of the observers to detect animals; however, it is less likely to be biased by differences among observers in the ability to estimate sighting distance and difficulties in determining transect width (Teelen 2007). In our study, DT conducted all surveys, so it is unlikely that there were differences in the ability to detect golden monkeys between periods. We calculated the density and relative abundance twice: once, using all transects, and again by excluding the area in the regeneration zone that was not used by golden monkeys in 2003 and not sampled by Werikhe (1991). This will enable us to compare the density of golden monkeys in the entire national park with the density areas that are suitable habitat for golden monkeys.

Nutritional Ecology

Golden monkey diet was quantified during two periods. Starting in January 1998, two already partially habituated groups were further habituated for 2 months. In March 1998, instantaneous scan samples of feeding were conducted during day-long follows (dawn to dusk) for three consecutive days each month for 7 months (March to September 1998). Four 5 min scan samples separated by 10 min intervals were conducted each hour on as many individuals as possible. In a single scan, a feeding observation by any individual on a particular food item was scored only once unless the same individual fed on different parts of the same food plant. Group 1 was followed for 19 days during which 69 h of observations were made. Group 2 was followed for 17 days (85 h). At times, observations were difficult to make as the group could enter dense clumps of bamboo. Feeding observations were also recorded opportunistically. Furthermore, secondary indications (e.g., discarded fruit) and interviews of park rangers about the foods that they observed golden monkeys eating were used for determining diet. In the second period between January and August 2003, the same methods were used on a third group (Group 3), which was observed for a total of 57 days (485 h). On average, the group was observed for 7 days each month (range = 3–11 days). Given the greater duration of the second period, we focus on this period for all diet and nutritional analyses.

For nutritional analyses, food items were collected in a way that mimicked the golden monkey's feeding. For example, if the animals ate leaf petioles, the length of petiole typically consumed was collected. Samples were air-dried in a shaded area, sealed in plastic bags, and brought to University of Florida for nutritional analyses. For each sample, we quantified protein (nitrogen), fiber (Acid Detergent Fiber, ADF), sugars (organic acids and simple sugars [mono- and oligosaccharides]), and evaluated the presence or absence of three secondary compounds thought to deter monkey foraging (alkaloids, saponins, and cyanogenic glycosides). Details of the nutritional analysis can be found in Chapman and Chapman (2002) and Twinomugisha et al. (2006).

Ranging

We quantified patterns of habitat use between January 2003 and February 2004 based on all-day (0700–1,900 h) follows of one habituated golden monkey group over 105 days (Group 3). Observations were started after 12 months of habituating the group (January 2002 to December 2002). Habituation took time partly because, hunters and bamboo harvesters disrupted habituation efforts; individuals that were upset at the loss of opportunities to conduct illegal activities threw stones at the animals.

To systematically follow monkeys and place feeding observations and food availability data in a spatial context, a grid system with 0.25 ha cells (corners marked with flagging) was laid over an area perceived to be the group's entire home range. This grid size was selected because the group was typically spread across an area smaller than this. During each follow, the grid cell containing the center of the group was recorded every 15 min.

To quantify possible environmental drivers of habitat selection, we examined density of food trees, abundance of shrub and vine food plants and bamboo culm density, and phenology of food plants. This facilitated an evaluation of the pattern of grid cell use relative to food availability. In each grid cell, the following data were collected on each food trees ≥5 cm DBH (diameter at breast height): species identity, number, and size (DBH). The ≥5 cm lower limit was used since *Galiniera coffeoides* and *Hypericum revolutum* provided food items when trees reached this size. DBH of trees is a good indicator of fruit and leaf abundance (Catchpole and Wheeler 1992; Chapman et al. 1992; Harrington 1979). In total, 12,133 trees were measured. Phenological observations were made each month to quantify the temporal changes in food availability using a 0–8 phenophase scale (Kaplin et al. 1998; Lawes and Piper 1992; National Research Council 1981). Bamboo was very dense in some areas, thus to quantify its density, DBH, height, and broad age classes, measurements were made in six 0.5 m x 50 m strip subplots laid at regular intervals in each 0.25 ha grid cell and 103,548 bamboo stems were measured. Percentage vine and shrub coverage were also determined for 12 species that bear food items (estimated in 10 % intervals). We graphically contrasted range use to spatial and temporal variation in resources using Surfer Version 7.0.

Demography

We compiled group counts of any subspecies of *C. mitis* from any location in Africa from the literature and determined the number of infants that were present per adult female. We assumed that populations having many infants per female were a prospering population. We determined the number of infants per female for five subspecies of *C. mitis*.

Results

Survey

The density of golden monkey groups (degraded habitat included) declined from 5.11 groups/km^2 in 1998 to 3.31 groups/km^2 in 2003 (Table 1) (Twinomugisha et al. 2003). This decline was also evident if the regenerating habitat was excluded from the calculations (1998: 6.03 groups/km^2; 2003: 4.28 groups/km^2). In 1989, the density was 3.24 groups/km^2 (Werikhe 1991). Werikhe conducted censuses at a time when the regenerating zone was being used by people, thus his results excluded this zone. Unlike the 1998 census, no monkeys were encountered in the regenerating habitat in 2003. These results suggest an increase in golden monkey group density between 1989 and 1998, but a decline between 1998 and 2003 (the time of best park protection).

Table 1 Sighting rates and density estimates of golden monkeys in Mgahinga Gorilla National Park, Uganda, in 1989, 1998, and 2003

Park Area	Groups Seen	Censuses #	Census Length(km)	Census Area	Groups/ km	Sighting Rate/km
Set 1 2003	46	56	247.8	12.39	3.31	0.19
Set 2 2003	46	42	191.8	9.59	4.28	0.24
Set 1 1998[a]	–	–	–	–	5.11	0.44
Set 2 1998[a]	–	–	–	–	6.03	0.52
Set 2 1989+	–	–	–	–	3.24	0.91

Set 1 includes the area regenerating after human encroachment, while Set 2 does not

[a] From Twinomugisha et al. (2003), + from Werikhe (1991)

Evaluating changes in relative abundance indicated a progressive decline between 1989 and 2003 (Table 1). Encounter rates of monkey groups for each vegetation zone were lower in 2003 than in 1998 (Table 2). In three vegetation zones (i.e., *Hypericum* woodland, swamp-meadow, and regenerating), no social groups were sighted in 2003, but groups were previously seen in these habitats in 1998.

Nutritional Ecology

Golden monkey diet varied over time and between groups (Table 3). For example, the frequency with which young leaves (including bamboo [*Arundinaria alpine*]) were eaten varied between groups from 11.3 to 58.6 %, while the use of insects varied from 8.0 to 30.5 % (Table 3). Bamboo was particularly important in the diet of all golden monkey groups and they fed on bamboo leaves, culms, and shoots. The group observed in the 2003 ate bamboo for an average of 52.4 % of their foraging time and up to 61.7 % in any particular month (Fig. 2). Fruiting trees are rare in Mgahinga; however, fruit was still a major component of the diet of some golden monkey groups (average 26.3 %; Table 1).

The golden monkey diet was not very diverse; in 2003, they fed on between 3 and 12 species of plants per month, with only 16 plant species eaten in total and four of these were added from opportunistic observations. Over all time periods and across all groups the golden monkey fed on only 33 plant species. Their simple diet is further illustrated by the fact that in 2003 the group only fed on four food items from two species for more than 10 % of their feeding time: young bamboo leaves (33.4 %), *Maesa lanceolata* fruits (20.8 %), bamboo shoots (15.3 %), and bamboo branchlets (11.6 %).

In 2003, diet selection appeared to be strongly influenced by the availability of *M. lanceolata* fruit (Fig. 2). This species fruited primarily in the last month of the dry season (August) and during the first two months of the rainy season

Table 2 Sighting rates of golden monkeys in different habitats in Mgahinga Gorilla National Park, Uganda, in 1998 and 2003. Transect lengths are the same in both periods

		2003			1998		
Vegetation Type	Transect Length(km)	Groups Seen	Census km	Groups/km	Groups Seen	Census km	Groups/km
Bamboo mixed	1.9	7	26.6	0.26	33	35.6	0.93
Pure bamboo	6.3	36	87.5	0.41	60	105.5	0.57
Heath forest	1.9	2	26.6	0.08	7	33.4	0.21
Open forest	0.9	1	11.9	0.08	14	17.9	0.78
Swamp	0.4	0	5.6	0.00	1	7.0	0.14
Hypericum	2.4	0	33.6	0.00	10	43.2	0.23
Regenerating	4.0	0	56.0	0.00	2	56.0	0.13

Table 3 The percentage of foraging effort devoted to different plant parts by the golden monkey of Mgahinga National Park, Uganda

	1998 (Group 1)	1998 (Group 2)	2003 (Group 3)	Average
Fruit	31.1	36.7	11.0	26.3
Young leaves	47.4	11.3	58.6	39.1
Flowers	0.4	14.0	21.9	12.1
Stems	5.8	7.0	0.3	4.4
Insects	10.5	30.5	8.0	16.3
Other	4.8	0.5	0.2	1.8

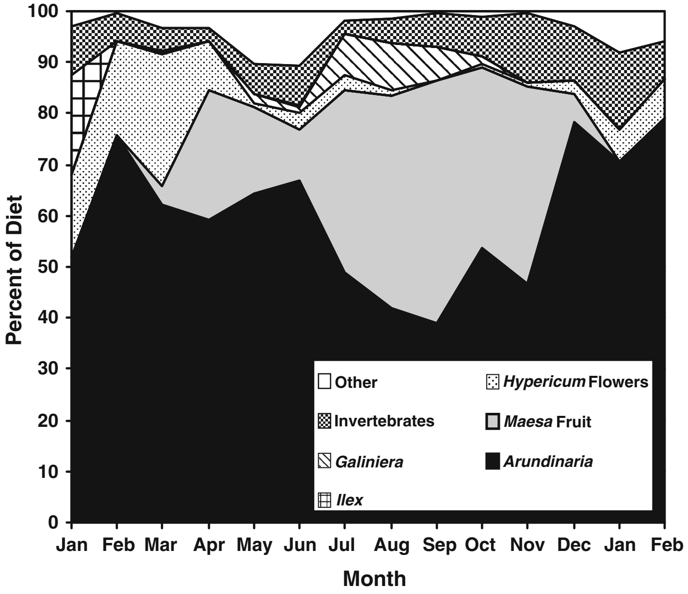

Fig. 2 The foraging effort that a group of golden monkeys (*Cercopithecus mitis kandti*) in Mgahinga Gorilla National Park, Uganda, invested each month on the major food items during 14 months covering 105 days between January 2003 and February 2004

(September and October). *M. lanceolata* fruit availability coincided closely with bamboo shooting. At this time, the monkeys switched between areas with *M. lanceolata* and areas of bamboo. Bamboo shooting occurs when the rainy seasons begin. Bamboo availability influenced range use and the monkeys foraged on bamboo shoots in May following the short rains, but on a very low level alongside bamboo leaves. Bamboo shoots, which were eaten with bamboo young leaves, were extensively eaten in October and November and later alongside bamboo branchlets in December as the shoots grew into young bamboo culms. *Hypericum revolutum* flowers were abundant between January and March and were an important food at this time and in February the following year when this tree flowered again (Fig. 2). The monkeys were observed feeding on only two shrub species: *Rhamnus prinoides* fruits (1.2 %) and *Clerodendrum* sp. pith which was eaten only in January 2003 (0.4 %).

Bamboo has a relatively high protein content (22 % of dry matter), but it is a very poor source of sugars (just trace amounts) and its lipid content is low (2 %). Since bamboo was eaten in every month of the year and typically at high levels and is an important source of protein, it is probably vital to the survival of golden monkeys in these mountain forests. The golden monkeys obtained their sugars from the few fruits that were available (e.g., *M. lanceolata* 18 % sugar, *G. coffeoides* 12 %), from flowers (*H. revolutum* 29 %), and from the leaves of *Nuxia congesta* (19 %). No group had a food item in their top 10 most frequently eaten foods that had cyanogenic glycocides, while 50 % of these foods contained alkaloids and 30 % had high saponin levels. There were no correlations between any of the nutritional components and foraging effort (the number of point samples observed feeding on an item/all feeding point samples).

Ranging

The group observed in 2003 ranged over 68 ha (272 quarter ha cells) and fed in 241 cells [$n = 11{,}423$ feeding records made in 3,435 scans, during 14 months covering 105 days(Twinomugisha and Chapman 2008)]. The number of feeding events varied substantially among cells (range, 1–505). The evaluation of habitat preferences was facilitated by the fact that the golden monkeys ate so few species of plants. For the purpose of evaluating range use, five plant species were considered: bamboo 59.9 %, *M. lanceolata* 18.7 %, *H. revolutum* 6.8 %, *G. coffeoides* 2.1 %, and *I. mitis* 1.4 %. Together, along with invertebrates (7.5 %), these items constituted 96.4 % of the monkeys foraging effort over the 14 months. To quantify how food availability influences habitat selection, we examined density of food trees, abundance of shrub and vine food plants and bamboo culm density, and phenology of food plants.

The group tended to concentrate its activity in the northwestern part of its range and several other specific areas (Fig. 3a). The group less frequently used the south of its home range, which had higher cumulative basal area of all five major food plants. However, the southern part of the home range consisted almost entirely of bamboo, while the northern part was mixed tree and bamboo and the regenerating zone (Fig. 3b). The monkeys never used this regenerating wooded grassland in 2003. Excluding bamboo basal area from the graphical presentation reveals that the pattern of range use generally follows the distribution of food tree basal area and range use was most closely depicted by the basal area of only three food tree species (*H. revolutum, M. lanceolata*, and *G. coffeoides*; Fig. 3c). There was a higher food tree species basal area in the north compared to the south of the home range, which corresponds to the group's range use (Fig. 3a, c). The distribution of fruiting *M. lanceolata* alone suggests that home range use is strongly influenced by this one species.

A question arises from evaluating this graphical analysis as to whether feeding is preferred within the vicinity of *M. lanceolata* or if areas are selected to allow the golden monkeys to feed both on bamboo and *M. lanceolata* and possibly other food tree species for a balanced diet. The distribution pattern of bamboo was negatively correlated with that of food tree species (*H. revolutum*, $r = -0.150$, $p < 0.001$, *M. lanceolata,* $r = -0.513$, $p < 0.001$, *G. coffeoides,* $r = -0.268$, $p < 0.001$), thus it appears that food tree abundance is critical in determining range use; however, given the ubiquitous nature of bamboo it was relatively easy for animals to switch between feeding on trees to feeding on bamboo.

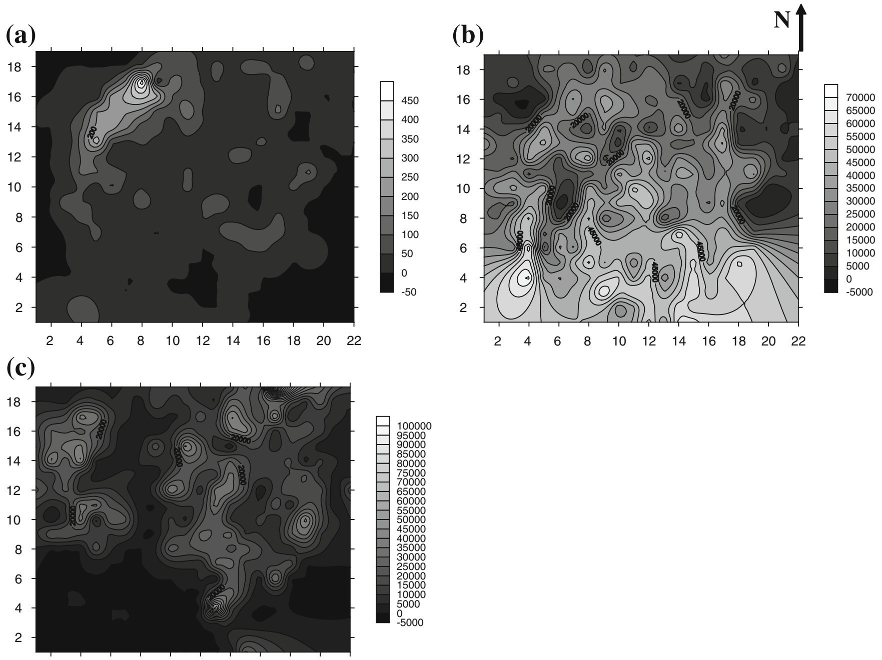

Fig. 3 Contour maps of home range area of one group of golden monkey (*Cercopithecus mitis kandti*) in Mgahinga Gorilla National Park, Uganda, followed from January 2003 to February 2004. Maps show **a** feeding intensities (number of feeding records in grid cells) in different parts during the study, **b** bamboo basal area (*Arundinaria alpina*), and **c** the basal area of three food tree species (*H. revolutum, M. lanceolata*, and *G. coffeoides*) which show a close pattern between food plant distributions and feeding by the group

Demography

The infant to adult female ratio was contrasted among different subspecies of *C. mitis* (Table 4). Golden monkey groups had a lower infant to adult female ratio than *C. m. stuhlmanni*, *C. m. erythrarchus*, or *C. m. labiatus* groups, suggesting that fewer infants are born into golden monkey groups.

Discussion

Both density estimates and sighting rates suggest that while golden monkey population in Mgahinga has received increased protection over the last two decades, their population has declined. These results are supported by the observation that golden monkey groups in Mgahinga had a lower infant to adult female ratio than any other *C. mitis* subspecies for which comparable data exists, suggesting that fewer infants are born into these groups. The information collected on the diet and range use of the golden monkeys provides clues as to why this decline has occurred and offers insights into conservation measures needed to reverse these declines.

The density and species richness of fruiting food trees at Mgahinga is very low, which is typical of high altitude habitats. Despite this fact, the golden monkeys appeared to cope well. Some groups focused their feeding efforts on a few fruiting species, while other groups relied on flowers and leaves and all groups obtained the majority of their protein from bamboo. Twinomugisha et al. (2006) demonstrated that the overall nutritional characteristics of the foods used by the Mgahinga golden monkeys living at a high elevation were not different from those foods used by groups of blue monkeys in Kibale National Park, Uganda, a lower elevation forested park with higher tree diversity. Results indicate that golden monkeys can substitute foods and still obtain a balanced diet. This suggests that a poor diet is not the cause of the population decline. However, it may be important to consider that while the differences in the nutrient content of foods from Kibale

Table 4 Comparison of the infant to female ratio of populations of *C. mitis*

Species	Infant: adult female ratio	Source
C. m. stuhlmanni (Kibale, Uganda)	0.2043	Butynski (1990), Rudran (1978a, b)
C. m. stuhlmanni (Kakamega, Kenya)	0.4225	Cords (1986)
C. m. stuhlmanni (all)	0.2988	Average of above studies
C. m. labiatus	0.5000	Lawes et al. (1990)
C. m. erythrarchus	0.3333	Macleod (2000)
C. m. kandti	0.1282	This Study

and Mgahinga were not statistically different, small differences may be biologically meaningful. Also, there may be differences in nutrients (e.g., mineral content) that were not measured that could impact the Mgahinga population. Furthermore, the nutritional study was done at what was possibly the end of the documented decline. If the nutritional study was done when the population was starting to decline, their diet may have been found to be nutritionally poor.

The observations on the nutritional ecology of the golden monkeys do provide suggestions for the future management of this high altitude population. In general, fruits are known to provide an easily assimilated source of sugars and energy, but have been suggested to supply inadequate amounts of protein (Gaulin 1979). This generalization may explain why some populations of *C. mitis* appear to select foods based on their protein content (Beeson 1989; Lawes 1991). However, none of the groups studied here selected foods high in protein (see discussion of bamboo below). Golden monkeys at Mgahinga consistently fed on bamboo, which has a relatively high protein content (22 % of dry matter), but little sugar. Bamboo was eaten in every month of the year and is an important source of protein that may be vital to the survival of golden monkeys in these high altitude mountain forests. The importance of bamboo is suggested by the fact that in Mgahinga there were higher sighting rates and densities of golden monkeys in the bamboo zone and in forests with bamboo vegetation types than in other habitats. In contrast, the golden monkeys obtained their sugars from the few fruits that were available, from flowers, and from the leaves of *Nuxia congesta*. *Hypericum revolutum* flowers were a particularly important source of sugars (29 % of dry weight) and were available and eaten year round. While, bamboo may be a critical source of protein for the golden monkey, it is very abundant in the habitat, thus it is likely that the availability of the few trees is the critical resource and management should be designed to promote both tree and bamboo growth.

We used a detailed evaluation of the golden monkeys' range use in relation to the spatial and temporal variation of food resources to demonstrate that the distribution of the food trees had a strong positive influence on their range use. Thus, while the ubiquitous bamboo is an important resource for the golden monkey being the leading source of protein and is used extensively throughout the year, the ranging data support the nutritional ecology research in suggesting golden monkey require a combination of resources including food items obtained from trees, vine, and shrubs, in addition to bamboo, to meet all of their nutritional requirements (Twinomugisha and Chapman 2008).

Neither the nutrition nor ranging datasets provide clues as to why the golden monkey population has declined. We offer a relatively simple suggestion for their decline based on changes in habitat selection since 1998. While there were sightings of monkeys in the seven vegetation types in 1998, there were no sightings in three of them in 2003. Similarly, small groups were seen at high elevations in 1989 and 1998, but not in 2003. One possible explanation for this change in distribution is that as the population density of golden monkeys has declined, animals are able to restrict their ranging to only the most preferred habitats. If this is the case, it suggests that prior to 2003 animals were occupying sub-optimal habitats. We suggest that in the 1980s and 1990s the golden monkey density may have been above that which could have been supported by the environment—this is suggested by the abundance of animals in less preferred habitats. If groups from forests outside the park immigrated to the park and sought protection as their original forests were destroyed, this may have pushed the density above that which the habitat could support over the long term. Over the last 14 years, their population may have returned to the level at which the environment could support them. If management recommendation (e.g., evaluation of whether this population was above that thought to be viable from a genetics perspective) was made on the initial population determination, inappropriate management recommendations would have been made. This illustrates the importance of long-term monitoring.

Management Recommendations

Illegal extraction of bamboo and trees pose a serious threat to the conservation of the golden monkey at the high altitude Mgahinga site. Bamboo is the most sought after item by the local community and this extraction may eventually negatively affect its growth leading to poor yield or even a retreat in coverage. We suggest this because in similar bamboo stands on Mt. Elgon, Uganda, Scott (1994) found that bamboo culm size decreased with increasing harvest intensity. The results presented here, however, suggest that tree cutting will have a more significant impact than the bamboo harvest. We suggest restoration in the regenerating zone would be a profitable conservation strategy to promote golden monkey populations and, given the slow rate of regeneration, active intervention and planting will likely be required. The restoration efforts should aim for regenerating a habitat that is a mixture of bamboo and trees, particularly *M. lanceolata* and *H. revolutum*. Such an active reforestation program could add an additional 10.1 km^2 of preferred habitat, which would result in a 75 % increase in bamboo/tree vegetation and facilitate golden monkey population recovery.

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Part III
High Altitude Apes

High Altitude Diets: Implications for the Feeding and Nutritional Ecology of Mountain Gorillas

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Introduction

Though the majority of primates live in tropical habitats, several species partially or exclusively range in high altitude regions of Africa, Asia, and Madagascar (Blanco and Rahalinarivo 2010; Iwamoto and Dunbar 1983; Kirkpatrick and Grueter 2010; Mendiratta et al. 2009; Watts 1998; Whiten et al. 1987). The differences among the diets of high and low altitude primates are likely due to characteristics in their environment. It has been generally accepted that plant species diversity and density decreases with increasing altitude (Aiba and Kitayama 1999; Hamilton 1975; Pellissier et al. 2012; Proctor et al. 2007; Rahbek 1995; Sharma et al. 2009; Vázquez and Givnish 1998; Zhuang et al. 2012). The number of species of understory herbs, shrubs, and vines decreased as altitude increased along the altitudinal gradient from Mexican seasonal dry forest to cloud forest (Vázquez and Givnish 1998). African forests at higher altitudes have fewer fruiting trees, fewer large buttressed trees and lianas, and lower fruit availability, compared to lower altitude forests (Hamilton 1975; Proctor et al. 2007; Schmitt et al. 2010). A similar pattern is seen in Asia, where lower altitudes are characterized by larger numbers of fruiting trees, and higher altitudes are more likely to be composed of herbs and shrubs (Zhuang et al. 2012).

Primates in these high altitude habitats show dietary flexibility in response to fluctuations in the availability of food in different altitudes. For example, the diet

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of the snub-nosed monkey varies dramatically among subspecies at different altitudes. Black-and-white snub-nosed monkey (*Rhinopithecus bieti*, 3,500–4,250 m) fallback foods in winter include bark and nuts (Xiang et al. 2007), while those of the lower altitude gray snub-nosed monkeys (*Rhinopithecus brelichi*, 800–2,570 m) and golden snub-nosed monkeys (*Rhinopithecus roxellana*, 1,700–2,630 m) include leaf buds (Xiang et al. 2012) and lichen (Yiming 2006), respectively. Multiple macaque species at high altitudes also demonstrate dietary plasticity, relying on lower quality foods at higher altitude (Mehlman 1988; Ménard 2002). Japanese macaques (*Macaca fuscata*) in low altitude areas (0–399 m) of Yakushima Island ate more seeds, fruits and animal matter, and less fungi and fibrous foods than those at high altitude (800–1,199 m) (Hanya et al. 2003). Mouse (*Microcebus* spp.) and dwarf (*Cheirogaleus spp.*) lemurs practice hibernation in low temperature months when food at high altitude is especially scarce (Blanco and Rahalinarivo 2010; Schmid and Ganzhorn 2009). While some species become generalists, or even hibernate, when faced with high altitude challenges, others make subtler adjustments. Chimpanzees in higher altitude Kahuzi (as high as 2,600 m) eat and have availability of fewer fruiting tree species than chimpanzees at lower altitude Lopé (200–500 m) (Basabose 2002).

The nutritional quality of potential primate foods also varies according to altitude. In general, the increased availability of fruit provides a rich energy source at lower altitudes, but the quality of these food sources may vary in relation to altitude. The protein content per leaf area increases with altitude due to increased nitrogen as a result of increased precipitation and cooler temperatures (Friend et al. 1989; Hikosaka et al. 2002; Hodkinson 2005; Kitayama and Aiba 2002; Körner 1989). In addition, higher altitude plants typically have lower levels of lignification because of cooler temperatures and carbon limitation (Guo et al. 2012; Richardson 2004). Herbaceous leaves and stems from a montane forest in the Virunga mountain range contained less fiber and tannins than herbaceous leaves and stems from lower altitude tropical rainforests in Cameroon, Uganda and southern India (Waterman et al. 1983). Near absence of condensed tannins in the afro-montane samples also suggests that montane vegetation is more digestible than lowland evergreen vegetation (Waterman et al. 1983).

However, it is not always the case that higher altitudes have more nutritious plants; in cloud forests on large mountains (1,500–3,300 m), there is typically a decrease in nitrogen and an increase in lignin because leaves tend to become more xeromorphic, or thicker, smaller, and harder, in order to adapt to the harsh windy conditions (Bruijnzeel and Veneklaas 1998; Tanner et al. 1998).

A study of colobus monkeys (*Colobus angolensis*) in the high altitude Nyungwe forest, Rwanda, suggests that large group sizes persist in this location because the leaves are higher quality (protein-to-fiber ratio) than those at lower altitude sites where colobus groups are smaller (Fimbel et al. 2001). Gramnivorous geladas are restricted to high altitude areas (1,500–4,000 m) in Ethiopia that correspond to where grasses are higher in protein (Dunbar 1998; Mau et al. 2009). Protein content of grasses in lower altitude grasslands in East Africa are low (2.2–6.9 % CP) compared to that of the gelada's range (Bole, 2,100 m) where protein is 12.5 %. At altitudes close to the limit of the gelada upper range (3,250–3,900 m), protein content was 7 %, indicating that protein content may relate to gelada distribution and survival (Dunbar 1992). Protein concentrations of 7 % or less are unlikely to meet the protein requirements of primates (Oftedal 1992).

Gorillas (*Gorilla* spp.) are folivore-frugivores that live at a variety of altitudes across Africa. The well-studied mountain gorillas (*Gorilla beringei beringei*) in the Virungas live at altitudes of 2,000–3,600 m, while the mountain gorillas of Bwindi live at altitudes of 1,160–2,607 m. The eastern lowland gorillas (*Gorilla beringei graueri*) in the Democratic Republic of Congo live at 600–2,500 m, and the western lowland gorillas (*Gorilla gorilla gorilla*) live in west Africa at 100–700 m (Yamagiwa et al. 2003). The Cross River gorillas (*Gorilla gorilla diehli*) are found at 80–2,000 m in Nigeria and Cameroon but are the most endangered of all apes (Oates et al. 2007). All gorillas consume fruit when it is seasonally available in their habitats (Doran and McNeilage 1998; McNeilage et al. 2001; Remis 1997; Stanford and Nkurunungi 2003). Western gorillas are generally more frugivorous than eastern gorillas (Doran and McNeilage 1998; Goldsmith et al. 2003), and some mountain gorillas eat little or no fruit because it is not available in their high altitude habitat (McNeilage et al. 2001; Watts 1984).

Mountain gorillas in the Bwindi Impenetrable National Park, Uganda are opportunistic frugivores that eat fruit when it is seasonally available (Goldsmith et al. 2003; Robbins and McNeilage 2003; Rothman et al. 2006b, 2011; Stanford and Nkurunungi 2003). Even when fruit is available, they consume a diverse daily diet of leaves, supplemented with bark, pith, and stems (Stanford and Nkurunungi 2003). Nutritionally, Bwindi gorillas consume a diet that is rich in protein (crude protein (CP): 18 %; available protein (AP): 14 %), high in fiber (neutral detergent fiber (NDF): 43 %), low in fat (2 %), and moderate in nonstructural carbohydrates (19 %) (Reiner et al., in review; Rothman et al. 2007, 2008a). The Bwindi gorilla diet varies seasonally (Rothman et al. 2008b), whereby they prioritize the consumption of nonprotein energy (carbohydrates and fats), and consume a diet high in protein (Rothman et al. 2011).

Here, as an example of a high altitude primate, we describe the diversity of the diet of the Bwindi gorillas over 1 year in terms of its botanical composition. We then determine the plant parts from which the Bwindi gorillas obtain their macronutrients. We test the hypothesis that leaves provide the most protein and fiber in the gorilla diet annually, while fruits provide the most nonstructural carbohydrates in the overall diet on a weight basis. We describe the intraspecific variability in nutritional components in the herbaceous leaves that gorillas eat. Finally, we compare the nutrients within gorilla foods to those at other eastern, mountain, and western sites, and predict that generally the foods of Bwindi gorillas will be higher in protein and lower in fiber than gorillas living in lowland areas.

Methods

Study Site

Bwindi Impenetrable National Park is a rugged, mountainous rain forest that was initially designated as a Forest Reserve in 1932 but was upgraded to a national park in 1991 (Butynski and Kalina 1993). BINP is located in the south-western Kigezi region of Uganda, 0°53′−1°08′S, 29°35′−29°50′E, and contains both medium altitude and montane forest.

We collected data during August 2002–July 2003 in Ruhija which is in a high-altitude region of the park, between 2,100 and 2,500 m. Annually, there are bimodal rains in Uganda; the dry months are December to February and June to August, while the wet months are September to November and March to May. Annual rainfall at Bwindi typically ranges from 1,130 to 2,390 mm. The annual rainfall for the study period was 1,436 mm. The daily mean minimum temperature at Ruhija was 13.6 ± 0.41 °C SD (range: 12.8–14.1 °C), and the mean maximum temperature was 16.7 ± 0.65 °C (range: 15.5–17.7 °C).

The behavioral data sampling regime is outlined in other reports (Rothman et al. 2007, 2008b). Briefly, we followed the Kyagurilo group of gorillas for 4 h per day for 319 days. These 4 h periods ranged from 8:00 to 18:00 h, but on most days, we observed the animals between 09:00 and 14:00 h due to the logistics of traveling in the field. We could not follow the gorillas for longer periods due to regulations of the Uganda Wildlife Authority. At the beginning of the study, there were 14 group members: two silverbacks, six females, four juveniles and two infants. During the study an infant was born, bringing group membership to 15.

As described in Rothman et al. (2007), we used a similar method to that of Watts (1984) to calculate food intake on a wet weight basis for each individual using 30 min focal animal sampling. We calculated the proportional wet-weight intake of each diet item for each independent individual (N = 12). Each individual was observed for as long as possible while feeding until it was out of view. Similar to Watts (1984), the time when the animal started and ended feeding represented a timed feeding bout; however, instead of using feeding rates and times, we counted the actual number of diet items and the amounts eaten during these bouts. Each animal was observed at least 6 days per month and observer biases were minimized by having JMR and the two field assistants observe the same animal on 3 days per month. JMR and field assistants collected these focal observations on 319 days and totalled 1,318 h (Rothman et al. 2008b). The gorillas spent approximately 55 % of their time feeding (Rothman et al. 2007). On a monthly basis, plant collections of each individual diet item (i.e., a single leaf) in the gorilla feeding area were weighed (N = 50) and an average was calculated for each month (Watts 1984). To obtain an estimate of diet quality over the year, these monthly unit weights were averaged for the year (Rothman et al. 2007, 2008b). We used the unit weight to estimate the wet weight contribution of each ingredient to the total daily diet, and then we converted this to dry weight (Rothman et al. 2012).

We collected foods eaten by gorillas in the same locations where they were seen feeding in the same months to account for intraspecific variability in nutritional composition (Chapman et al. 2003; Rothman et al. 2009, 2012). Furthermore, we processed foods similarly to the way the gorillas processed them before feeding. For example, if the gorilla ate the pith and removed the outer peel or bark, we also discarded the outer peel/bark. We identified all foods with the assistance of Robert Baryigya and the herbarium at the Institute of Tropical Forest Conservation (ITFC). When a sample could not be identified at ITFC, we took the sample to Makerere University, Uganda where it was identified by herbarium manager Tony Katende. We left voucher specimens at ITFC and also have voucher specimens that are held at Hunter College. We collected 327 plants for nutritional analysis from 82 species. As described in other reports (Rothman et al. 2007, 2008a, b), we dried samples in the field at <22 °C in darkness, and we ground them in a Wiley Mill through a 1 mm screen. Details on the protocols for nutritional analysis are presented in previous reports (Rothman et al. 2007, 2008a, b). Briefly, JMR analyzed samples in the Department of Animal Science at Cornell University, USA and at Hunter College, USA. We analyzed samples for CP, AP, NDF, acid detergent fiber (ADF), acid detergent lignin (ADL), total nonstructural carbohydrates (TNC), and fat (CF). For some nutritional analyses, we use near infrared spectroscopy (Rothman et al. 2009).

Results

Description of the Bwindi Gorilla Diet

Over the 1 year study, this Bwindi gorilla group ate a diverse diet of over 148 plant parts from 103 species (Table 1). We could not identify two species of herbs where the leaves were eaten. The gorillas ate food items from 23 herbaceous species including a thistle, 21 lianas, 9 shrub species, 31 trees including a tree fern, 5 species of epiphytes including an epiphytic cactus and fern, 2 fungi and 3 species of plant parasites. We estimated that 10 different species of decaying wood were consumed, but we could not confirm their taxonomic identity. The gorillas ate tree bark or herbaceous peel from 17 species, fruit from 30 species, 4 species of flowers, leaves from 57 species, and pith from 6 species. They did not eat any insects and two individuals engaged in coprophagy once during the study. We observed soil eating on two occasions. Although the gorillas ate over 148 plant parts from over 103 species, only 17 plant parts comprised more than 1 % of the wet weight mass of the diet over the year (Table 1). These 17 plant parts (8 species of herbaceous leaves, one species of tree leaves, two species of pith, one species of herbaceous stem or peel, three species of fruit and decaying wood pieces) comprised 96.1 % of the diet (Rothman et al. 2007), with the other 132 remaining plants together composing less than 4 % of the annual diet. On a mass basis,

Table 1 Foods eaten by Bwindi gorillas

Food	Family	Life form	Plant part
Acalypha ornata	Euphorbiaceae	Herb	B, L
Achyranthes aspera	Amaranthaceae	Herb	L
Adenia gummifera	Passifloraceae	Liana	L
Alchornea hirtella	Euphorbiaceae	Shrub	L,F
Allophylus abyssinicus	Sapindaceae	Tree	F, L
Allophylus macrobotrys	Sapindaceae	Tree	L
Allophylus sp.	Sapindaceae	Tree	F
Ancistrorhynchus clandestinus	Orchidaceae	Epiphyte	L
Angraecum infundibulare	Orchidaceae	Epiphyte	L, R
Arundinaria alpina	Poaceae	Grass	YS
Baissea sp.	Apocynaceae	Liana	L
Basella alba	Basellaceae	Liana	L
Carpodinus glabra	Apocynaceae	Liana	B, L
Carduus kikuyorua	Asteraceae	Thistle	L
Cassipourea ruwenzoriensis	Rhizophoraceae	Tree	F
Chrysophyllum albidum	Sapotaceae	Tree	F
Chrysophyllum gorungosanum	Sapotaceae	Tree	F
Clematis sp.	Renunculaceae	Liana	L
Combretum fuscum	Combretaceae	Liana	L
Crassocephalum sp.	Asteraceae	Herb	P
Cyathea manniana	Cyatheaceae	Tree Fern	P
Cyperus renschii	Cyperaceae	Grass	YS
Desmodium repandum	Fabaceae	Liana	L
Diaphanathe subsimplex	Orchidaceae	Epiphyte	L
Dicliptera sp.	Acanthaceae	Herb	L
Dolichos sericeus	Phaseoleae	Liana	L
Dombeya goetzenii	Sterculiaceae	Tree	B, L
Droguetia iners	Urticaceae	Herb	L
Drypetes sp.	Euphorbiaceae	Tree	F
Englerina woodfordioides	Loranthaceae	Parasitic Plant	B, L, S
Ficus asperifolia	Moraceae	Tree	B, L, F
Ficus densistipulata	Moraceae	Tree	L
Ficus exasperata	Moraceae	Tree	B, L, F
Ficus ingens	Moraceae	Tree	B, L, F
Ficus natalensis	Moraceae	Tree	B, L, F
Ficus spp. (Unidentified *Ficus*)	Moraceae	Tree	L, F, B
Ficus conraui	Moraceae	Tree	L, F
Laportea ovalifolia	Urticaceae	Herb	L
Galiniera coffeoides	Rubiaceae	Shrub	F, L
Galium thunbergianum	Rubiaceae	Herb	L
Gandoderma australe	Ganodermataceae	Fungus	Whole
Ganoderma sp.	Ganodermataceae	Fungus	Whole
Gouania longispicata	Rhamnaceae	Liana	L
Helichrysum nudifolium	Compositae	Herb	L
Helichrysum schimperi	Compositae	Herb	L

(continued)

Table 1 (continued)

Food	Family	Life form	Plant part
Ilex mitis	Aquifoliaceae	Tree	B
Ipomoea involcrata	Convolvulaceae	Liana	B, L, S, Fl
Isoglossa sp.	Acanthaceae	Herb	L, Fl
Jasminum abyssinicum	Oleaceae	Liana	L
Jasminum schimperi	Oleaceae	Liana	L
Justicia glabra	Acanthaceae	Herb	L, Fl
Kosteletzkya grantii	Malvaceae	Herb	L
Landolphia buchananii	Apocynaceae	Liana	L
Lasanthus sersecusis	Gentianaceae	Tree	L
Maesa lanceolata	Primulaceae	Tree	L,F
Mimulopsis arborescens	Acanthaceae	Herb	L, P
Mimulopsis solmsii	Acanthaceae	Liana/Shrub	L, B
Momordica foetida	Cucurbitaceae	Liana	L, F
Momordica pterocarpa	Cucurbitaceae	Liana	L, F
Myrianthus holstii	Moraceae	Tree	L, F, B
Mystroxylon aethiopicum	Celastraceae	Tree	B
Mystroxylon aethiopicum	Celastraceae	Tree	F
Olea capensis	Oleaceae	Tree	F
Olea capensis	Oleaceae	Tree	L
Olinia rochetiana	Oliniaceae	Tree	F
Oncinotis sp.	Apocynaceae	Liana	W
Periploca linearifolia	Asclepiadaceae	Liana	L
Pilea holstii	Urticaceae	Herb	L, S
Pilea holstii	Urticaceae	Herb	S
Piper capense	Piperaceae	Herb	P
Pleopeltis macrocarpa	Polypodiaceae	Epiphyte	L
Podocarpus milanjianus	Podocarpaceae	Tree	F
Polystachya adansoniae	Orchidaceae	Epiphyte	L
Polystachya cultriformis	Orchidaceae	Epiphyte	L
Polystachya spatella	Orchidaceae	Epiphyte	L
Pseudodrynaria coronans	Polypodiaceae	Epiphytic Fern	P
Rapanea rhododendroides	Myrsinaceae	Tree	L
Rawnsonia lucida	Lepidoptera	Tree	F
Rhipsalis baccifera	Cactaceae	Epiphytic Cactus	W
Rubus sp.	Rosaceae	Shrub	L, F, S
Rubus steudneri	Rosaceae	Shrub	L, F, S
Rytigynia bugoyensis	Rubiaceae	Shrub	L
Rytigynia kigeziensis	Rubiaceae	Shrub	L, F, Fl
Rytigynia ruwenzoriensis	Rubiaceae	Shrub	L
Salacia elegans	Celastraceae	Liana	L
Sarcorhynchus bilobatus	Orchidaceae	Epiphyte	L, R
Schefflera sp.	Araliaceae	Herb	L
Smilax anceps	Smilacaceae	Liana	L, F
Solanum welwitschii	Liliaceae	Liana	L
Strombosia scheffleri	Olacaceae	Tree	F

(continued)

Table 1 (continued)

Food	Family	Life form	Plant part
Symphonia sp.	Clusiaceae	Tree	F
Syzygium guineense	Myrtaceae	Tree	F
Tapinanthus sp.	Loranthaceae	Parasite	L, S
Teclea nobilis	Rutaceae	Tree	F
Triumfetta tomentosa	Tiliaceae	Shrub	L
Urera cameroonensis	Urticaceae	Liana	B
Urera hypselodendron	Urticaceae	Liana	L,B
Vernonia iodocalyx	Compositae	Herb	P
Vernonia lasiopus	Compositae	Herb	L
Vernonia pteropoda	Compositae	Herb	B
Vernonia tufnelliae	Compositae	Herb	B
Vigna parkeri	Leguminosea	Liana	L
Xymalos monospora	Monimiaceae	Tree	L, B, F

nonwood vegetative foods comprised 80.8 % and fruits comprised 15.3 % annually. Seasonally, the diet varied from 0 to 60 % fruit on a mass basis (Rothman et al. 2008b, 2011).

Nutritional Contributions of Different Plant Parts

Herbaceous leaves composed the bulk of the Bwindi gorilla diet and they also contributed the majority of the protein, fiber, and nonstructural carbohydrates in the diet (Table 2). Surprisingly, fruit contributed a large portion of the fiber in the diet; even though fruit comprised just 15 % of the diet annually, fruits contributed 20–21 % of all fiber (NDF, ADF, ADL) in the diet. Wood also contributed a substantial portion of the fiber in Bwindi diets, though it is likely eaten for its sodium content (Rothman et al. 2006c). Herbaceous leaves, not fruit, contributed the most sugars and other easily digestible carbohydrates to the diet (65 %). Pith contributed few macronutrients to the diet, probably because it is so high in moisture (Rothman et al. 2006a). Fruits contributed the most fat, but fat in the

Table 2 Contributions of different foods eaten by Bwindi gorillas to their overall macronutrient consumption (% dry matter basis)

	Avail P	NDF	ADF	ADL	TNC	CF
Herb leaves	74.5	37.4	32.2	42.9	65.1	16.5
Tree leaves	13.0	14.4	14.3	10.9	3.9	0.6
Fruit	5.8	20.8	21.8	20.3	12.5	80.2
Peel	5.3	5.6	6.7	3.2	1.0	2.0
Pith	0.4	2.6	2.9	2.0	3.1	0.7
Wood	0.9	19.1	22.1	20.8	14.3	0.0

overall Bwindi diet is low (Reiner et al., in review). The results of our nutritional analyses by plant part are presented in Table 3 in comparison to gorilla foods at other sites.

Intraspecific Variability in Nutritional Composition of Staple Foods

Over 7 months of the study we collected and subsequently analyzed five of the herbaceous leaf species from the same site to investigate monthly intraspecific variability in the vegetative portion of the gorilla diet. The nutrients in these foods were variable in different months from the same site (Fig. 1), for example, TNC varied from 15 to 35 % in *Basella alba* leaves, and CP varied from 23 to 37 % in *Urera hypseledendron* leaves. There were no apparent monthly trends that applied to all species.

Discussion

Gorillas have a diverse diet that incorporates a wide range of plant species and parts. Although there are differing sampling methods, Bwindi gorillas appear to eat a lower diversity of foods compared to some western sites (mean diversity is 148 species; Rogers et al. 2004), and a higher number of species than mountain gorillas in the Virungas (Rogers et al. 2004; Watts 1984) as would be expected at a higher altitude. However, only about 11 % of the species that they ate actually contributed more than 1 % of the overall mass of their diet annually. This indicates that although the gorillas eat a wide variety of plant parts and species in their diets, the major macronutrients are gained from just a few food parts and species. The other sparsely eaten dietary components probably provide important micronutrients, fatty acids, amino acids or other important compounds, or serve to help detoxify the toxins in the diet (Dearing et al. 2000; Milton 1999). For example, decaying wood contributes 4 % of the diet, but contributes >95 % of sodium (Rothman et al. 2006c). It is also possible that some of these plants are simply not widely available otherwise they would be eaten more often; we suggest this is the case because many of the herbaceous leaves were higher in TNC than staple foods and gorillas prioritize energy (Table 3; Rothman et al. 2007, 2011). The types of staple foods in their diets during this study were consistent with other studies of Bwindi gorillas at the same site, suggesting that there is stability in these particular food items (Ganas et al. 2004; Robbins et al. 2006; Stanford and Nkurunungi 2003). The Bwindi gorillas also tend to incorporate staple herbaceous foods in their diet regardless of whether fruit is eaten (Robbins et al. 2006), though the amounts of fruit and leaves are quite variable seasonally (Rothman et al. 2008b, 2011).

Table 3 Nutritional composition of foods eaten by gorillas at study sites across Africa

Subspecies	*Gorilla g.gorilla*				*Gorilla b.graueri*		*Gorilla b.beringei*				
Site[1]	Campo, Cameroon[3]	Lope, Gabon[4]	Bai Hokou, CAR[5]	Bai Hokou, CAR[6]	Mondika, CAR/ Congo[7]	Kahuzi, DRC[8]	Tshibinda, DRC[9]	Karisoke, Rwanda[10]	Karisoke, Rwanda[11]	Bwindi, Uganda (Ruhija)[12]	Bwindi, Uganda (Buhoma)[13]
No of species in the diet[2]	50	134	>200	138	25	121[14]	>104	75[15]	9	82	140[16]
No. parts analyzed	36	95	31	68	25	14	39	33	9	327	25
Altitude (m)	200	200–500	400	400	400	2,050–2,350	2,000–2,500	2,680–3,710	2,700–4,500	1,190–2,607	1,450–1,800
Forest type	Lowland evergreen	Lowland rain forest	Semideciduous rain forest	Semideciduous rain forest	Semi-evergreen forest	Montane forest	Montane forest	Montane rainforest	Tropical montane forest	Rugged montane rainforest	Rugged montane rainforest
Herb density	1.1 shrubs or herbs/ 100 m[17]	7.7 stems/m^2 [18]	1.1 stems/m^2 [19]	1.1 stems/m^2 [19]	0.78 stems/m^2 [20]	1.03 stems/ m^2 [21]	1.0 stems/m^2 [21]	8.8 stems/m^2 [15]	8.8 stems/m^2 [15]	10.6 stems/m^2 [16]	4.36 stems/m^2 [16]
Herb leaves											
TNC	26.9	NA	10.9	NA	NA	NA	NA	NA	21.1	38.1	NA
NDF	41.6	NA	63.3	67.2	NA	NA	NA	NA	45.5	35.9	35.3
ADF	37.6	29.9	44.8	49.5	NA	NA	NA	35.5	NA	23.9	17.3
ADL	15.0	NA	NA	18.3	NA	NA	NA	NA	NA	9.5	4.4
Fat	5.5	2.1	0.5	NA	NA	NA	NA	NA	NA	1.0	1.9
Protein	19.4	19.5	16.4	17.2	NA	26.1	24.2	15.5	20.2	19.2	26.6
Tree leaves											
TNC	34.3	NA	14.3	NA	14.5	NA	NA	NA	NA	33.0	NA
NDF	43.2	NA	58.2	69.3	55.8	NA	NA	NA	NA	42.1	NA
ADF	44.1	30.5	44.6	54.7	NA	NA	NA	NA	NA	29.7	NA
ADL	23.0	NA	NA	31.8	17.6	NA	NA	NA	NA	11.5	NA
Fat	4.2	2.6	0.6	NA	2.8	NA	NA	NA	NA	1.0	NA
Protein	13.5	16.5	20.2	17.0	18.7	6.2	36.4	NA	NA	16.7	NA
Herb stems/ herb peel											
TNC	24.9	NA	11.2	NA	0.6	NA	NA	NA	19.8	30.5	NA
NDF	54.4	NA	80.4	67.4	62.4	NA	NA	NA	58.5	58.2	61.6
ADF	41.6	44.6	54.5	49.2	NA	NA	NA	49.3	NA	45.6	52.3
ADL	9.4	NA	NA	26.0	11.0	NA	NA	NA	NA	9.0	8.1
Fat	3.3	1.3	0.3	NA	3.0	NA	NA	NA	NA	1.0	0.6
Protein	7.2	5.1	3.4	16.9	16.4	NA	NA	6.2	9.2	7.8	13.0

(continued)

Table 3 (continued)

Subspecies	*Gorilla g.gorilla*				*Gorilla b.graueri*		*Gorilla b.beringei*				
Site[1]	Campo, Cameroon[3]	Lope, Gabon[4]	Bai Hokou, CAR[5]	Bai Hokou, CAR[6]	Mondika, CAR/ Congo[7]	Kahuzi, DRC[8]	Tshibinda, DRC[9]	Karisoke, Rwanda[10]	Karisoke, Rwanda[11]	Bwindi, Uganda (Ruhija)[12]	Bwindi, Uganda (Buhoma)[13]
Fruits											
TNC	20.1	NA	10.7	NA	42.9	NA	NA	NA	NA	45.0	NA
NDF	64.6	NA	78.7	59.3	44.5	NA	NA	NA	NA	37.3	32.7
ADF	44.8	23.9	65.4	45.3	NA	NA	NA	NA	NA	26.8	20.1
ADL	26.9	NA	NA	24.9	13.4	NA	NA	NA	NA	12.2	7.5
Fat	6.2	4.0	0.8	NA	1.3	NA	NA	NA	NA	5.0	6.1
Protein	6.2	6.1	5.7	8.4	7.4	7.5	17.3	NA	NA	10.9	8.1

[1] All data are presented as a percentage of dry matter aside from the Mondika site where data are presented on an organic matter basis

[2] Items in the total diet aside from Mondika where the important preferred foods and fallback foods are considered by Doran- Sheehy et al. (2009), and in the Virungas where only staple foods are considered by Rothman et al. (2007)

[3] Calvert (1985)

[4] Rogers et al. (1990)

[5] Popovich et al. (1997)

[6] Remis et al. (2001)

[7] Doran-Sheehy et al. 2009 (number of important foods)

[8] Casimir (1975)

[9] Goodall (1977)

[10] Waterman et al. (1983)

[11] Rothman et al. (2007)

[12] this study

[13] Ganas et al. (2008)

[14] Yamagiwa and Mwanza (1994)

[15] Watts (1984)

[16] Ganas et al. (2004)

[17] Tchouto et al. (2006)

[18] Rogers and Williamson (1987)

[19] Goldsmith et al. (2003)

[20] Rogers et al. (2004)

[21] Basabose (2002)

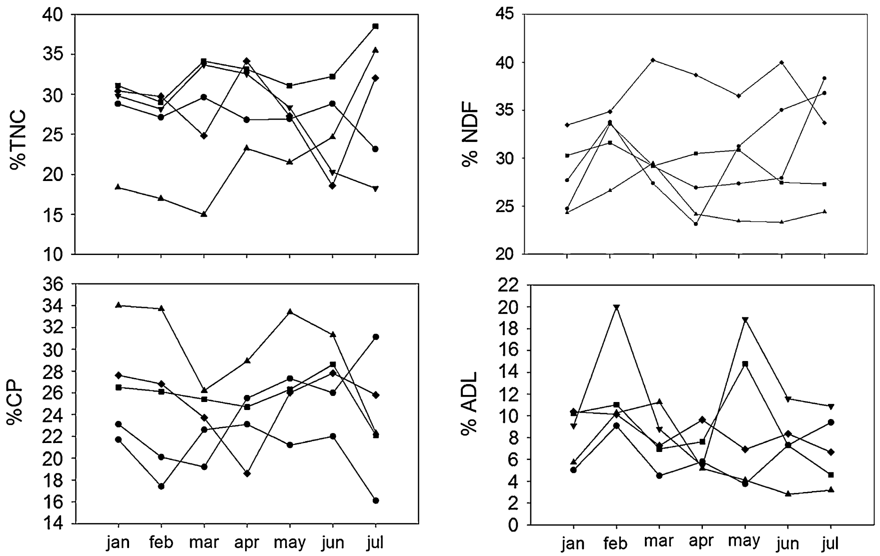

Fig. 1 Intraspecific variability in the nutritional components of five staple herbaceous leaf species over 6 months (●—*Carduus* sp. ■—*Ipomea* spp. ◆—*Triumfetta tomentosa* ▲—*Basella alba* ▼—*Urera hypseledendron*)

Gorillas receive most of their available protein, sugar, and fiber from the herbaceous component of their diets. They also receive a substantial portion of their fiber from wood and fruit; fruits in the Bwindi gorilla diet are similar in their fiber content to leaves, suggesting that 'fibrous' foods are not always leaves and pith as sometimes indicated in the ape literature (Ganas et al. 2004; Rogers et al. 2004; Stanford and Nkurunungi 2003). In addition, the herbaceous leaves provided most of the sugar in the annual diet. These findings are similar to a study on folivorous colobus monkeys in Kibale in which fruits and leaves were similar in their sugar contents (Danish et al. 2006). Western gorillas in the Central African Republic also eat fibrous fruits, particularly during seasons of low food availability (Remis et al. 2001), and fruits eaten by gorillas in Campo, Cameroon were also similar in TNC to leaves (Calvert 1985). The large body size of gorillas is a dietary adaptation that offers an opportunity to eat fibrous foods, especially in periods of food scarcity (Remis 2000; Remis et al. 2003; Doran et al. 2009).

Our hypothesis that gorilla herbaceous leaves in higher altitudes would be of higher quality (higher in TNC and CP, and lower in NDF, ADF, ADL) was partially supported (Table 3). Foods eaten by gorillas in Bwindi were higher in TNC and similar in CP to those in CAR and Campo, Cameroon, and, similar to those in the Virungas (Rothman et al. 2007) which are also higher in altitude. Bwindi fruits were also higher in TNC than those at other sites. However, fiber contents were similar among the different gorilla sites. Bwindi gorillas prioritize energy and consume a surplus of protein (Rothman et al. 2011), so they may be selecting high TNC leaves. In a study of mountain baboons (*Papio ursinus*) where two groups were separated by 400 m in altitude, baboons were similarly constrained because of seasonal differences in food supply and ate diets composed of different plant parts; however, individuals obtained the same nutrient yield (Byrne et al. 1993). The staple foods of the gorilla diet in the Virungas and Bwindi are similar in nutritional composition, even though their diets are different compositionally (Rothman et al. 2007). Other studies have also found that primate diets can vary compositionally but not nutritionally (Conklin-Brittain et al. 1998; Ryan et al. 2013; Twinomugisha et al. 2006). We hope that upcoming new nutritional data from western gorilla sites will be informative for interspecific comparisons of nutrient intake (Jessica Lodwick, personal communication, Shelly Masi, personal communication).

Our results demonstrate that there is considerable intraspecific variability in the nutritional composition of herbaceous leaves eaten by Bwindi gorillas (Rothman et al. 2009, 2012). Thus, a particular food item could be high quality (high TNC, high CP and low NDF, ADL) in some months and low quality in another. It is well known that the nutrient content of a single plant species can vary over different spatial and temporal scales in primate studies (Barton et al. 1993; Rothman et al. 2012). For example, young leaves of the same species eaten by colobines in Kibale National Park, Uganda varied in protein content from 22 to 47 % (Chapman et al. 2003), and the fat content of a single species of ripe fruit in this forest varied seasonally from 0.3 to 30.0 % (Worman and Chapman 2005). Sun-exposed leaves had more protein than shaded leaves in Madagascar (Ganzhorn 1995), and the nutritional value of tamarind leaves and fruits eaten by ring-tailed lemurs (*Lemur catta*) varied according to forest type (Mertl-Millhollen et al. 2003).

This variability has important implications for sampling biases. If samples are not collected from the same site where a primate is feeding at the same time then it may not be representative of the nutrients in the food item ingested at that time (Rothman et al. 2012). Furthermore, it has been demonstrated that the nutrients in primate foods vary diurnally in relation to time of day (Ganzhorn and Wright 1994). For example, chimpanzees (*Pan troglodytes*) feed on leaves later in the day when they are higher in nonstructural carbohydrates and sugar (Carlson et al. 2013). Here, we collected foods from the exact site where the gorillas were feeding, thus all of these leaves were acceptable and eaten by them. It would be interesting to investigate whether the gorillas avoid eating the same species of food because it differs in nutritional composition. Studies of captive western gorillas demonstrate that they are able to discern solutions that have sugars and tannins, and that they use sweetness as a criteria for food selection (Remis and Kerr 2002).

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Preliminary Data on the Highland Sumatran Orangutans (*Pongo abelii*) of Batang Toru

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Introduction

Orangutans are the only great apes occurring in Asia (Caldecott and Miles 2005) and knowledge of their behavioral ecology comes from a number of long-term studies on Sumatra and Borneo (Wich et al. 2009). Although these studies provide a relatively good geographical coverage (except for the lack of studies on *Pongo pygmaeus pygmaeus* in northwest Kalimantan and Sarawak), their altitudinal coverage is limited. Previous survey work indicated that orangutans on Sumatra were rare above 1,000 m and in Borneo above 500 m (Wich et al. 2008). Partly as a result of this, all long-term studies on orangutan behavior and ecology have occurred in areas below 1,000 m (Wich et al. 2009). There are several additional reasons why orangutans have almost exclusively been studied below 1,000 m [exceptions are two short studies in Agusan (Fox and bin'Mohammad 2002) and Sibual-Buali (Djojoasmoro, unpublished data), Sumatra]. First, access is easier to lowland than highland areas and as a result the logistics and expenses of having a research site at higher elevation pose considerable challenges. Second, researchers often establish sites at locations where orangutan densities are high, and at higher elevations densities are often lower (van Schaik et al. 1995), although there are exceptions where densities are very high in highland areas (Husson et al. 2009;

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Wich et al. 2004a). These low densities make such areas less attractive for researchers that often have to obtain sufficient data in a short time frame. Third, the prevailing view that orangutans are a lowland species probably led to fewer studies in highland areas. Although these are very understandable, there are three important reasons to include populations at higher elevations in long-term studies. First, orangutans at higher elevations might add to the known geographic variation of the species (Wich et al. 2009), and thus enlarge our understanding of the flexibility of the taxon. Such understanding of their flexibility is not only of pure academic interest, but will also allow us to better assess suitability of habitats for reintroduction of orangutans in Sumatra and Borneo, the potential of highland areas for these reintroduction efforts, and provide input for population and habitat viability analyses. This is of importance since large numbers of orangutans continue to be taken in by quarantines and await reintroduction to the wild (Russon 2009). Second, deforestation of lowland forest in areas where orangutans live is continuing at a rapid pace (Gaveau et al. 2009; Wich et al. 2011a), and may make the populations occurring at higher elevations increasingly important for conservation of the taxon. Third, new unpublished survey data indicate that in many areas of the Leuser Ecosystem, Sumatran orangutans occur up to 1,500 m (Wich, unpublished data), and therefore, there are relatively large areas where orangutans occur above 1,000 m for which no long-term behavioral or ecological data are available.

Here, we report on a new orangutan study site in the southernmost range (the Batang Toru area) of the Sumatran orangutan [Fig. 1 (Wich et al. 2008)]. Orangutans in this area were first re-discovered in 1997 (Meijaard 1997) and subsequent surveys indicated their presence over a relatively large area in that region (Wich et al. 2003). To obtain some preliminary insights on whether this population and the area where they live differ from other orangutan populations and habitats, we will compare the Batang Toru data with data from other sites (Wich et al. 2009), with a focus on the Ketambe field site on Sumatra, where a long-term study has been conducted in dry land forest [e.g., (Wich et al. 2004b)].

The Batang Toru population is remarkable for several reasons. First, it is isolated from the other populations in Sumatra, and is the only population remaining south of the Toba lake (Wich et al. 2008). Orangutans were once much more common south of Lake Toba, but a combination of hunting, habitat loss and (potentially) disease has led to their disappearance from those areas (Rijksen and Meijaard 1999; Wich et al. 2003). Although a systematic set of surveys is needed to determine the precise number of orangutans in the Batang Toru area, a rough estimate hovers between 400 and 600 individuals for both forest blocks combined, and therefore holds a viable population for at least the western block, where the majority of the orangutans occur (Wich et al. 2008; Marshall et al. 2009b). Second, the orangutan population here is interesting because it appears to be genetically very distinct when examining mtDNA and has a very deep divergence time (3.5 MYA) from the populations north of the Toba Lake (Nater et al. 2011). For Y-chromosomal markers, there was much less divergence between the Sumatran sites (Nater et al. 2011). These results are likely due to male dispersal over large distances, whereas females appear to disperse over much smaller distances

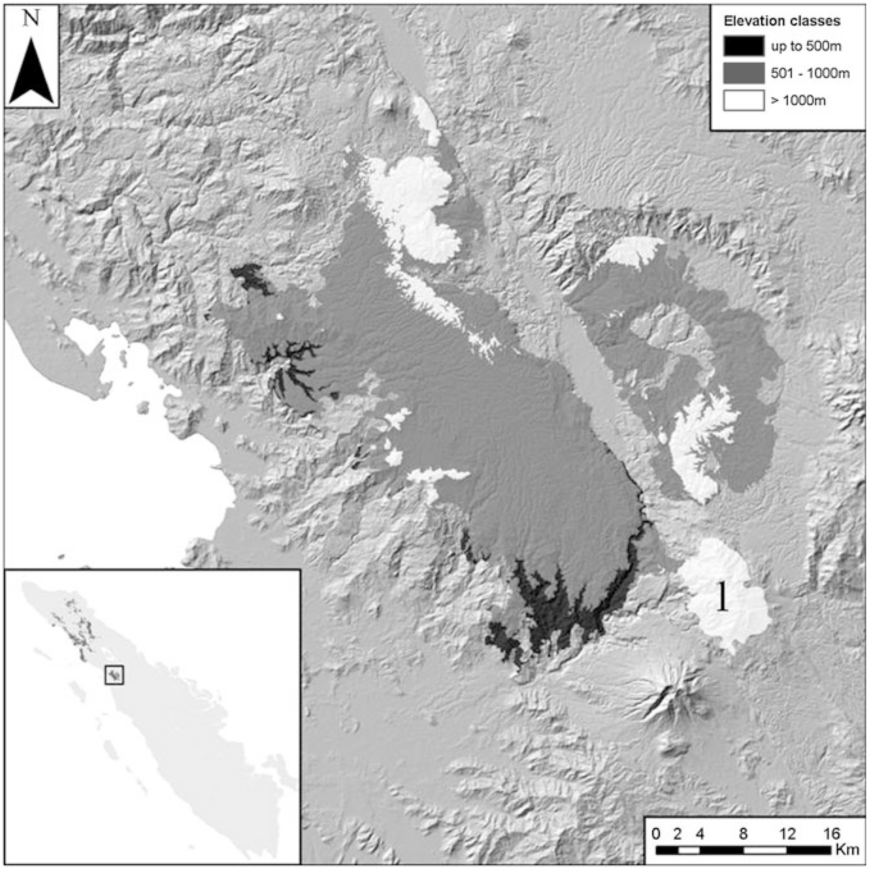

Fig. 1 Map of the orangutan distribution in the two forest blocks for several elevation classes. Number 1 in the map indicates the Sibual-buali protected area, which is normally not considered to be part of the Batang Toru forest blocks. However, since the area does contain orangutans it has been included here for the sake of completeness on orangutan distribution in this area

(Nater et al. 2011). As a consequence of these genetic results, it would be very interesting to investigate whether female orangutans in Batang Toru behave more like Bornean or Sumatran orangutans. Such comparisons are of interest to comprehend the factors behind the geographic variation found in orangutan behavioral ecology (van Schaik et al. 2009b; Wich et al. 2009; Krützen et al. 2011). For at least one important behavior, tool use to obtain seeds from *Neesia* sp fruits, the orangutans in Batang Toru seem to behave as some other Sumatran populations (van Schaik 2009), but more data are needed to determine the overall pattern. Third, a relatively large part of this population resides above 1,000 m, with most of the study area at an elevation close to 1,000 m. This makes it the only orangutan highland population that is being studied at the moment. As mentioned above, there is a strong need to increase our knowledge of highland orangutan populations since forest below 1,000 m is disappearing fast and conserving Sumatran orangutans in the future will depend heavily on highland populations if the current trend of forest loss is not reversed (Wich et al. 2011a). It is especially paramount to determine whether such highland populations are viable without the surrounding lowland forests. In the Ketambe, area orangutans that have home ranges covering a range of altitudes tend to follow the shifts in fruiting peaks along an altitudinal range (Buij et al. 2002). Further study of potential source-sink dynamics (e.g., Dias 1996) in orangutan populations is becoming increasingly urgent, because of loss of lowland forest and the need to assess whether highland populations can persist without lowland areas.

Methods

General Batang Toru Area Description

The forests in the Batang Toru area are split into two (west and east) blocks (Fig. 1). The valley that separates the two blocks contains the Batang Toru River, after which the forest blocks are named. The elevation of the area ranges from 120 m a.s.l along the Batang Toru river up to 1,800 m a.s.l in the eastern block (Usher, unpublished report).

The area is dissected by ravines and, in general, consists of steep incised terrain. The orangutan distribution covers 84,370 ha in the western block and 24,851 ha in the eastern block [updated from Wich et al. (2008)]. The Sibual-buali protected area (*Cagar Alam Dolok Sibual-buali*), located south of Batang Toru, covers an additional 5,528 ha of forest that contains a small number of orangutans that might be isolated from the main west forest block. Mean orangutan density in the area has been estimated using nest counts to be 0.23 ind/km^2 (Wich et al. 2011b), which is low compared to many other areas in Sumatra where densities range from 0.30 to 10.18 (Wich et al. 2004a; Husson et al. 2009).

Study Area

The research camp is located at an elevation of 908 m a.s.l (1° 41 9.1″ N/98° 59 38.1″ E). The study area (Fig. 2) ranges from an elevation of 850 to 1,100 m. Research started in 2006 and is ongoing.

Because of relatively low orangutan densities in the area (Wich et al. 2011b), a large amount of effort had to be invested in locating and habituating orangutans. So far a minimum of at least 17 different individuals have been identified, and 6 of these have been semi-habituated and followed for behavioral data. A total of 137 follow hours have been logged during 20 days from June to October 2011. During

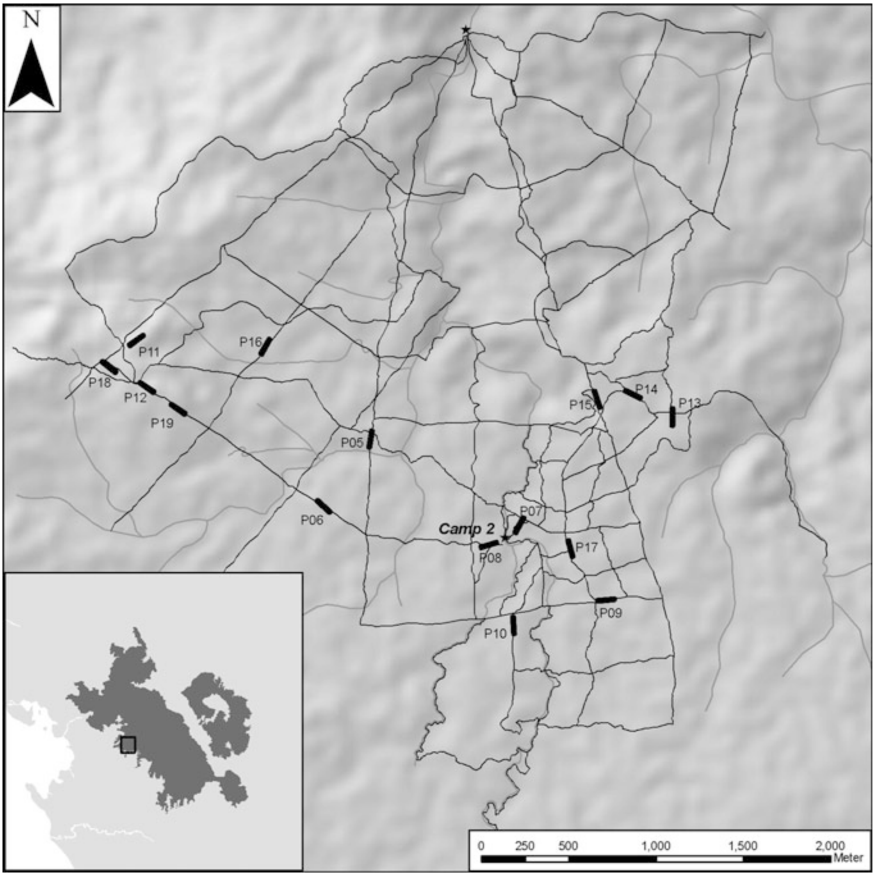

Fig. 2 Map of the study area. The numbers indicate the locations of the botanical/phenology plots. The trail system is indicated by the *black lines* and the rivers by *gray lines*. The current research camp is indicated by camp 2 because there was an earlier camp called camp 1. Since camp 1 is not active anymore it is not indicated on the map

follow hours, orangutan behavioral data are recorded using standardized field methods based upon the San Anselmo standardization (van Schaik 1999, 2003). Individual orangutans were followed from dawn to dusk (i.e., from night nest to night nest) when possible, with behavioral (e.g., feeding, moving, type of locomotion) and ecological (e.g., tree species) variables being recorded at 2-min intervals using focal animal sampling (Martin and Bateson 1993).

Initial assessments of the floristic composition of the Batang Toru study area have resulted in the differentiation of three main forest types (i.e., heath forest, lowland forest, and mixed dipterocarp forest: Table 1), which generally follow Whitten et al. (1987). Heath forest is the most divergent of the forest types, and is characterized by an overwhelming majority of Sapotaceae (36.6 %) and

Table 1 Heath forest, lowland forest, and mixed dipterocarp forest

Rank	Heath		Lowland		Mixed	
	Family	%	Family	%	Family	%
1	Sapotaceae	36.6	Sapotaceae	11.3	Myrtaceae	9.3
2	Myrtaceae	20.3	Myrtaceae	8.6	Lauraceae	7.4
3	Anacardiaceae	7.4	Theaceae	7.9	Fagaceae	7.4
4	Lauraceae	5.0	Anacardiaceae	7.4	Rubiaceae	7.1
5	Icacinaceae	5.0	Myrsinaceae	6.8	Ulmaceae	6.6
6	Fagaceae	3.8	Lauraceae	6.3	Flacourtiaceae	6.4
7	Podocarpaceae	2.8	Icacinaceae	6.1	Sapotaceae	5.2
8	Casuarinaceae	2.6	Fagaceae	5.2	Annonaceae	5.2
9	Araucariaceae	2.4	Moraceae	2.9	Burseraceae	4.4
10	Guttiferae	2.0	Aquifoliaceae	2.7	Myristicaceae	4.2
Total %		87.9		62.5		63.2
Dipterocarpaceae	Not present		Not present		Present	
Shannon-Weiner_Family	2.07 ± SD 0.37		2.76 ± SD 0.14		2.87 ± SD 0.06	
Total # Families	16.4 ± SD 4.6		23.4 ± SD 2.7		23.2 ± SD 2.1	
Shannon-Weiner_Species	2.87 ± SD 0.48		3.10 ± SD 0.20		3.45 ± SD 0.22	
Total # Species	34.0 ± SD 10.6		36.8 ± SD 8.6		43.6 ± SD 8.4	
pH Topsoil	2.62 ± SD 0.15		3.12 ± SD 0.16		3.35 ± SD 0.15	

Note In each plot three pH topsoil measurements were made

Myrtaceae (20.3 %) tree species, a low diversity of tree families (Shannon-Weiner Index = 2.07 ± SD 0.37), a lack of dipterocarp trees, and relatively poor topsoil quality (pH = 2.62 ± SD 0.15). The lowland forest type is characterized by a reduced percentage of Sapotaceae (11.3 %) and Myrtaceae (8.6 %) tree species compared to the heath forest type, a moderate diversity of tree families (Shannon-Weiner Index = 2.76 ± SD 0.14), a lack of dipterocarp trees, and moderate top soil quality (pH = 3.12 ± SD 0.16). Lastly, the mixed dipterocarp forest type is differentiated by a reduced frequency of Sapotaceae tree species compared to both heath and lowland forest types, a high diversity of tree families (Shannon-Weiner Index = 2.87 ± SD 0.06), the presence of dipterocarp trees, and a higher top soil quality (pH = 3.35 ± SD 0.15).

To monitor potential food availability for orangutans, a total of 15 plots of 0.1 ha size (10 × 100 m) were laid out in the three main forest types: Heath forest plots 5, 6, 7, 8, 10; lowland forest plots: 9, 14, 15, 16, 17; and mixed forest plots: 11, 12, 14, 18, 19. In these plots, all trees larger than 10 cm diameter at breast height (DBH) were identified by botanical experts from the Forest Research Institute in Pekanbaru, Riau, Sumatra. Phenology data have been collected on a monthly basis since Jan 2009 from approximately 1,562 trees (since plots are re-measured at the end of each year, and trees die, the total number of trees is somewhat variable).The number of flowers and fruit items was scored along the following scale: ($1 = 0 < 10$; $2 = 11 < 50$; $3 = 51 < 100$; $4 = 101 < 500$; $5 = 501 < 1{,}000$; $6 = 1{,}001 < 5{,}000$; $7 = 5{,}001 < 10{,}000$; $8 => 10{,}001$). In this chapter, we only present fruit availability results expressed as the percentage of trees carrying fruits per month.

Statistics

To analyze rainfall and phenological data, circular statistics were applied (Janson and Verdolin 2005; Jammalamadaka and SenGupta 2001; Batschelet 1981). In order to identify which plots displayed similar botanical compositions, hierarchical cluster analyses were undertaken for both tree family and species. We chose to use these as preliminary analyses here instead of doing an analysis of the phylogenetic structure of the tree community (Vamosi et al. 2009), which we aim to undertake in the future once all species have been identified to their scientific name. Total percentages for each tree family or species were first calculated for each plot, and then clusters were then formed using single-linkage or nearest-neighbor clustering (Shaw 2009). Cluster analyses and dendrograms were performed using SPSS 16.0.0.

Results

Rainfall

Mean annual rainfall at the site was 3,629 mm (range 3,225–3,792 mm), based on two full years of data plus an additional two almost full years. The site may receive slightly more rainfall than the Ketambe research area, which has a mean annual rainfall of 3,241 mm (range 2,696–3,782 mm). To examine whether rainfall was distributed randomly through the year or had a clear single directionality, we made circular plots and employed circular statistics (Janson and Verdolin 2005; Jammalamadaka and SenGupta 2001; Batschelet 1981). The circular plots indicate that in Batang Toru, rain has two peak periods (March and December), similar to Ketambe (Fig. 3). The circular statistics did not show a significant single directionality at Ketambe (Rayleigh test $Z = 0.116$, $r = 0.097$, $P > 0.5$) or Batang Toru (Rayleigh test $Z = 0.148$, $r = 0.148$, $P > 0.5$).

Botanical Plots

The botanical identification work at Batang Toru revealed that there are at least 239 tree species in the 1.5 ha that were covered by plots, and that these plots contain a total of 1,562 trees. A total of 70 trees were not identified at the time of writing, so the actual number of species is likely to be higher than 239. To determine the number of species that can be classified as orangutan food we used the orangutan food list for all sites where orangutans occur (Russon et al. 2009), and combined this with the preliminary diet list from Batang Toru. This yielded a conservative estimate of 68 tree species that can be considered orangutan food, of which 61 species are known to provide fruits that orangutans feed upon. The Batang Toru diet list contained several species that were not included on the Russon et al. (2009) orangutan food list. These were *Gymnostoma sumatrana* (Casuarinaceae), *Gomphia serrata* (Ochnaceae), and three species from the family Podocarpaceae, *Nageia neriifolium*, *Dacrydium beccarii*, and *Dacrycarpus imbricatus*. Of these species, three rank within the top 12 species with the highest basal area in the plots (Table 2). The total basal area of orangutan food trees for Batang Toru (259,127 cm^2/ha) was somewhat less than Ketambe (290,069 cm^2/ha).

To examine whether family and/or species composition differed for the three habitat types a cluster analysis was conducted. The analysis based on families shows that heath plots cluster well together, but that lowland and mixed plots do not cluster separately (Fig. 4a). The cluster analysis based on species clustered all plots save one (heath 10) of the same type close together (Fig. 4b).

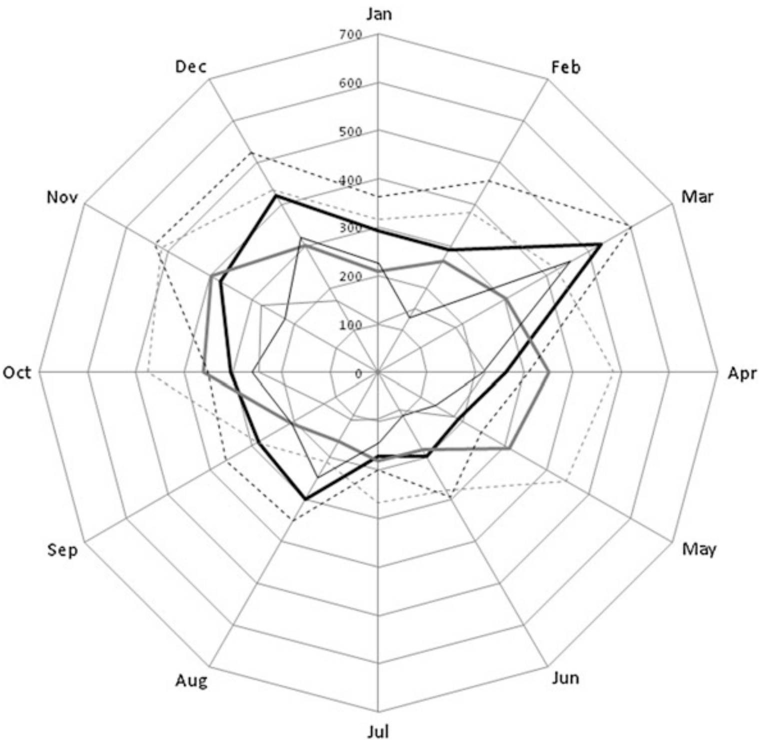

Fig. 3 Circular plots for rainfall in Batang Toru and Ketambe. Batang Toru data are presented in *black* and Ketambe in *gray*, respectively. The *thick solid line* represents mean rainfall, the *thin solid line* represents one standard deviation below the mean and the *dashed lines* represent one standard deviation above the mean. For Batang Toru, the years 2008–2011 were used, whereas for Ketambe rainfall data came from 1972 to 1984

Phenology

Because the main interest of the phenology comparison was to compare production between Batang Toru and Ketambe, no result for the three habitat types are presented here. Monthly fruit availability in Batang Toru was highest during the months of August to October and also showed a peak in April (Fig. 5). The mean percentage of trees carrying fruit was 6.3 % (mean monthly range 4.0–7.9 %). Fruit availability at Ketambe was consistently higher than at Batang Toru (Fig. 5) and showed a mean monthly percentage of trees carrying fruit of 12.6 % (mean monthly range 8.0–16.7 %). The circular statistics did not show a significant single directionality at Batang Toru (Rayleigh test $Z = 0.090$, $r = 0.101$, $P > 0.5$) or Ketambe (Rayleigh test $Z = 0.342$, $r = 0.167$, $P > 0.5$).

Table 2 The total basal area of orangutan food trees for Batang Toru

Basal area ranking	Basal area (cm^2/1.5 ha)	Tree species (family)
1	56,405	*Campnosperma auriculatum* (Anacardiaceae)
2	48,231	*Palaquium rostratum* (Sapotaceae)
3	45,458	*Madhuca laurifolia* (Sapotaceae)
4	27,188	*Gymnostoma sumatrana* (Casuarinaceae)
5	22,212	*Schima walichii* (Theaceae)
6	17,163	*Unknown sp.*
7	16,253	*Tristaniopsis whiteana* (Myrtaceae)
8	14,520	*Garcinia hombroniana* (Clusiaceae)
9	14,210	*Palaquium hexandrum* (Sapotaceae)
10	13,834	*Polyalthia sumatrana* (Annonaceae)
11	13,195	*Dacrydium beccarii* (Podocarpaceae)
12	13,166	*Agathis borneensis* (Araucariaceae)

Note basal area was summed for all individual trees in all plots to obtain the number in the table

Orangutan Activity Pattern

Very preliminary activity pattern data showed that at Batang Toru 47.8 % (SD = 14.4) of the time was spend on feeding, 20.8 % (SD = 12.4) on resting, 29.9 % (SD = 13.1) on moving, and 1.6 % (SD = 1.5) on other activities, such as nest building and social activities (Fig. 6).

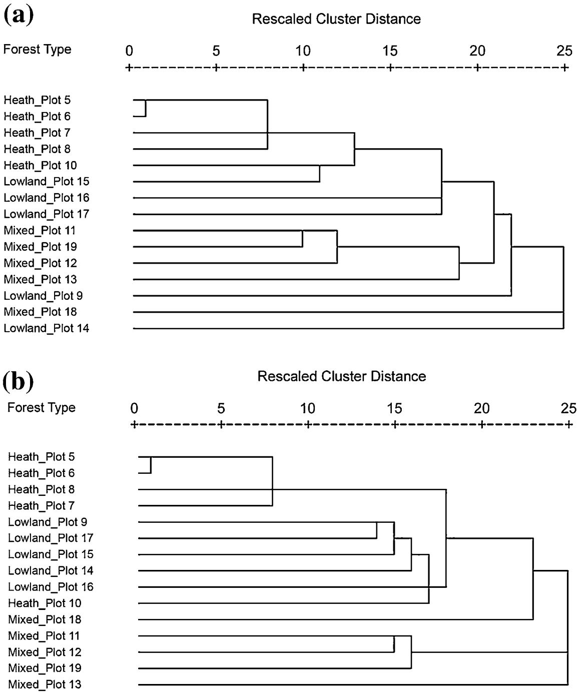

Fig. 4 (**a**) dendogram for the different vegetation types based on tree family composition per plot, (**b**) dendogram for the different vegetation types based on species composition per plot

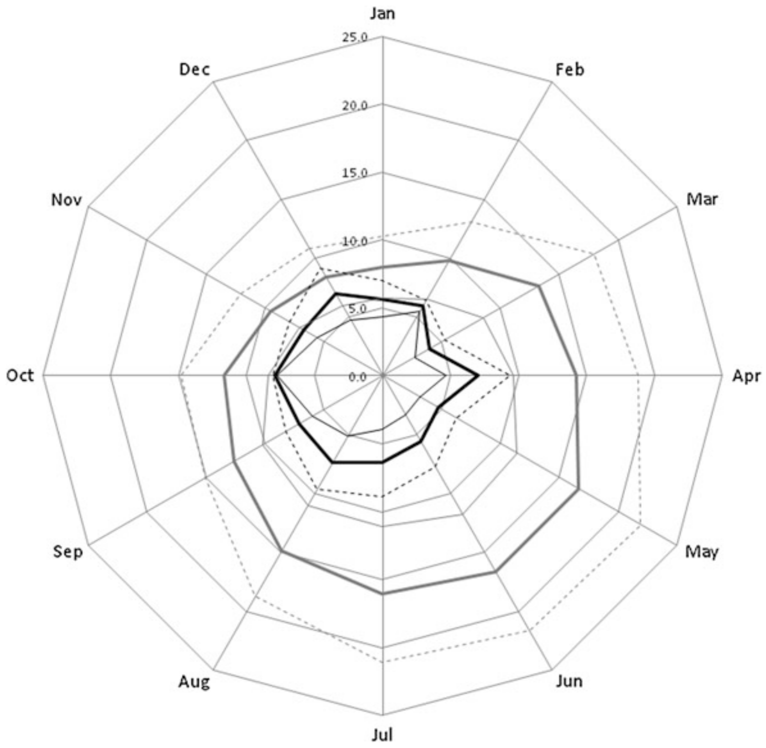

Fig. 5 Circular plots for the mean monthly percentage of trees carrying fruit in Batang Toru and Ketambe. Batang Toru data are presented in *black* and Ketambe in *gray*, respectively. The *thick solid line* represents mean rainfall, the *thin solid line* represents one standard deviation below the mean and the *dashed lines* represent one standard deviation above the mean. For Batang Toru data were used from 2009 to 2011, whereas for Ketambe data were for 1988–2001

Orangutan Diet

Orangutans in Batang Toru fed on fruit for the vast majority of their feeding time (Fig. 7). A total of 73.7 % (SD = 24.8) of feeding time was spend on fruits, while only 8.4 % (SD = 7.1) of feeding time was spent on the second highest item [other, which was mainly made up of pith and stem (7.7 %)] and 6.8 % (SD = 6.6 %) on the third highest (leaves).

As mentioned earlier, orangutans in the Batang Toru forest have been observed to feed on a number of fruit species, which where previously unrecorded in the diet of Sumatran orangutans. These include species from three genera from the family of the Podocarpaceae, mainly known for its Southern Hemisphere conifers, consisting of *Nageia, Dacrydium*, and *Dacrycarpus*. The tiny cones (<10 mm) of the latter two species (*Dacrydium beccarii* and *Dacrycarpus imbricatus*) have two to five fused scales, of which only one, rarely two, are fertile, each fertile scale with

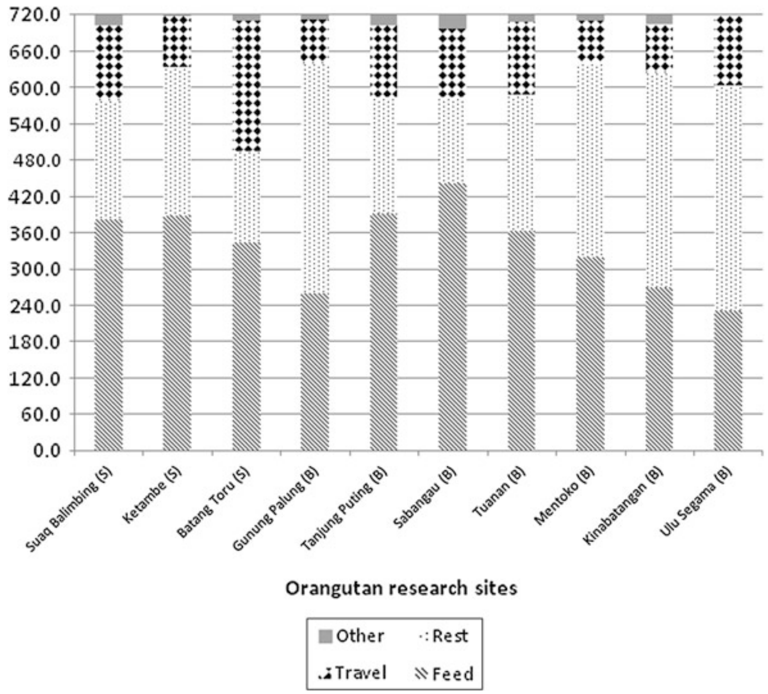

Fig. 6 Time budgets for a number of orangutan populations [based on (Morrogh-Bernard et al. 2009)]. Sites are presented from the west to the east of the orangutan distribution on Sumatra and Borneo. (*S*) Sumatra and (*B*) Borneo

one apical seed. At maturity, the scales become berry-like, swollen, brightly red colored and fleshy. Both species are highly favored by the Batang Toru orangutans. In May 2010, a large number of *Dacrydium beccarii* trees in the study area fruited and attracted a minimum of 17 different orangutan individuals into a small area (<1 km^2), where they predominantly fed on the tiny fruits of this species over a period of several weeks, frequently gathering in feeding parties. The small fruits of *Dacrycarpus imbricatus* seem highly favored as well. Another species of interest in the family Podocarpaceae fed upon by the orangutans is the species *Nageia nerifolii*, with a drupelike seed also sessile on a succulent epimatium. The Batang Toru orangutans also feed on the tiny wind dispersed seeds of *Gymnostoma sumatrana* (Casuarinaceae), a common canopy species in the study area. The fruit of this species is a woody, intricate round structure superficially resembling a conifer cone made up of numerous carpels, each containing a single seed with a small wing. Orangutans have been observed to suck out the tiny winged seeds from the different openings in a cone. Another species with interesting fruit that seems favored by orangutans in Batang Toru is *Agathis borneensis* (Araucariaceae), a large conifer. The large (10–13 cm) oval fruits/cones of this species contain hundreds of small wind-dispersed seeds also called *samaras* (“winged nuts”). The

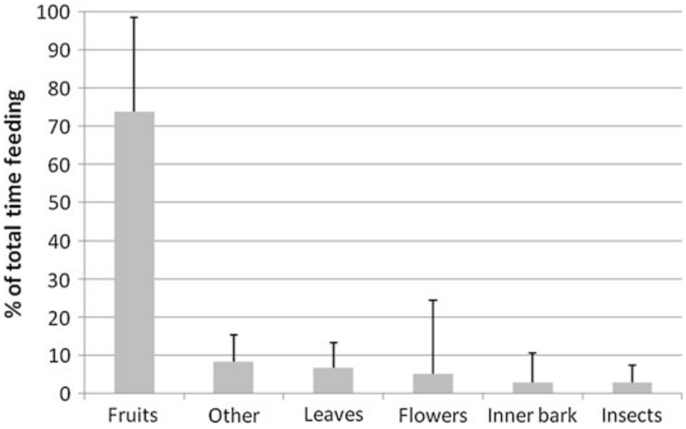

Fig. 7 Mean percentage of various food items in the diet, with one standard deviation above the mean shown. Standard deviations were calculated from the daily means

orangutans peel apart the soft scales of the cones which cover/encapsule these winged seeds. The weight of 1,000 seeds has been listed to be 20–25 g (Wageningen University, Agathis Factsheet: http://webdocs.dow.wur.nl/internet/fem/uk/trees/agaborf.pdf). It is interesting that orangutans seem to favor these species that have mostly very small seeds/fruits, and fed, on these while larger fruits were also available.

Discussion

Initial analyses indicate that the highland area that is home of the study population contains three forest habitat types of which the heath type appears to be very different from the mixed and lowland types based on both family and species cluster analyses. Although in the species cluster analysis one heath plot was clustered between other habitat types, the overall clustering does seem to support these three habitat types. It is not known at present whether orangutans prefer one habitat type over the other, but nest surveys in the area indicate that nests are found in all three areas (Fredriksson, unpublished data). Future mapping of the study area for these habitat types needs to be conducted so that orangutan nest locations can be examined in relationship with the three habitat types. Furthermore, it would be interesting to examine whether or not fruit productivity varied among the three habitat types, and if so, how differences in fruit productivity may impact orangutan densities and their behavioral ecology.

Overall, fruit production in the study area was well in the range of other orangutan study sites, but lower than both Ketambe and the peat swamp forest of Suaq Balimbing (Wich et al. 2011c). Although a study of fallen fruit on fruit trails at different elevations in Sumatra shows that there is less fruit on fruit trails at higher elevations (Djojosudharmo and van Schaik 1992), this does not necessarily indicate a lower fruit production at higher elevations. Greater study of fruit production at different elevations will be important to assess production differences by altitude. The examination of botanical plots yielded a slightly lower value for the overall basal areas of orangutan food trees in Batang Toru than Ketambe. It is important to realize that a simple crude orangutan food tree basal area comparison does not incorporate orangutan food preferences, and various other data that are ideally obtained for such comparisons (Marshall et al. 2009a). These results should therefore be treated with caution until a more refined analyses has been conducted after more data on orangutan feeding ecology have been collected at Batang Toru. Although mean orangutan density in the two Batang Toru forest blocks is low (0.23 ind/km^2), the density in the study area ranges from 0.19 to 0.74 ind/km^2 [based on data from Wich et al. (2011b)], which falls within the values (0.11–10.81) reported for Borneo and Sumatra for unlogged sites (Husson et al. 2009), but remains on the very low side. This is partly due to the higher elevation of the study area and subsequent lower food availability compared to many of the other sites. The relatively high orangutan density in the study area compared to the rest of the Batang Toru area indicates that the study area might be a relatively rich area in terms of fruit production, as compared to other parts of the Batang Toru forest blocks.

The preliminary time budget data indicate that percentage feeding time is well within the range found in other studies on Sumatra and Borneo [Fig. 6, (Morrogh-Bernard et al. 2009)]. However, the percentage of travel is highest of all studies so far and the percentage resting is second lowest after the Sabangau population in the peat swamps of Central Kalimantan (Morrogh-Bernard et al. 2009). This could indicate a need for orangutans in Batang Toru to travel between dispersed food trees. Alternatively, it could be an effect of the semi-habituated state of the orangutans, although under this hypothesis one would predict the percentage feeding to be low as well, which it is not. A third possibility is that these figures are the result of a sampling error due to the limited sample size. Once more data are available, it will be possible to distinguish the various options. The preliminary diet data indicate that the percentage feeding on fruit in the Batang Toru study population is high when compared to the reported percentages from others sites, but within their range of monthly reported values [Table 3 (Morrogh-Bernard et al. 2009)]. The other diet item percentages also fall within the range of those reported from other sites.

When the study in Batang Toru started, several wooden sticks were found sticking out of *Neesia* sp. fruits, indicating that orangutans had been using these sticks to pry out the seeds from the *Neesia* sp. fruits (van Schaik et al. 2009a; van Schaik 2009). This finding is of high interest because it indicates that there is a gap in the distribution of this type of tool use from the northern populations to Batang Toru, which strengthens the cultural explanation for this behavior (van Schaik 2009). Since this initial finding, unfortunately no additional *Neesia* feeding has been observed in the area, and it is thus not yet known whether there are subtle differences in tool use technique between the Batang Toru population and others.

Table 3 Range of monthly reported values

Site and range	Fruits	Flowers	Leaves	Bark	Invertebrates	Other
Suaq Balimbing (S)						
Mean	66.2	–	15.5	1.1	13.4	3.8 (inc. fl)
Low fruit–high fruit	62.7–69.6	–	18.3–12.7	0.8–1.4	14.6–12.2	3.6–4.1
Ketambe (S)						
Mean	67.5	3.5	16.4	2.7	8.8	1.3
Monthly range	57.5–71.5	–	10.6–20.1	2.2–3.3	5.7–11.7	–
Batang Toru (S)						
Mean	73.7	5.3	6.8	2.9	2.9	8.4
Sabangau (B)						
Mean	73.8	9.0	5.1	1.5	8.6	2.0
Monthly range	24.4–91.9	0.0–60.2	0.3–17.4	0.0–9.1	0.7–28.0	0.1–4.9
Tuanan (B)						
Mean	68.6	5.9	17.2	1.0	6.3	0.6
Monthly range	26.3–88.0	0.0–5.1	4.5–49.5	0.0–5.9	0.3–24.1	0.0–2.5
Tanjung puting (B)						
Mean	60.9	3.9	14.7	11.4	4.3	4.0
Monthly range	16.4–96.1	0.0–41.1	0.0–39.6	0.0–47.2	0.0–27.2	0.0–21
Gunung Palung (B)						
Mean	70.0	5.1	13.4	4.9	3.7	2.9
Monthly range	25.8–99.0	0.0–49.6	0.1–41.1	0.0–30.9	0.0–14.0	0.0–9.2
Kinabatangan (B)						
Mean	68.0	1.3	22.9	6.7	1.2	–
Mentoko (B)						
Mean	53.8	–	29.0	14.2	0.8	2.2 (inc. fl)
Monthly range	25.7–89.0	–	5.3–55.6	0.0–66.6	0.0–11.1	0.0–2.5
Ulu Segama (B)						
Mean	51.5	–	35.6 (inc. fl)	11.2	2.1	–
Monthly range	10.0–90.0	–	8.3–75.0	0.0–36.7	0.0–8.3	–

Note Mean values and ranges are presented. For Suaq Balimbing monthly ranges were not available, but low and high fruit availability values were available so these are reported. Values obtained from Morrogh-Bernard et al. (2009). For Batang Toru the ‘other’ category contains pith and stem. Due to the preliminary nature of the Batang Toru data, monthly ranges are not yet known, but in the main text we provide standard deviations based on the daily means for fruit and leaves. The other SD values are: Flowers (19.1), bark (7.7), and invertebrates (4.7). For some food items, data was not available from some of the field sites. (*S*) Sumatra and (*B*) Borneo

The two main threats to the orangutans in Batang Toru are habitat loss and hunting (Wich et al. 2003, 2011a, b). Habitat loss (overall forest loss 2001–2010 4.3 %: Usher, unpublished report) is occurring at a relatively low rate compared to other areas in Sumatra and the rest of Indonesia [Usher, unpublished report (Wich et al. 2011a)], but nevertheless continues at a steady pace. Land clearing is most prevalent close to a gold mine that has recently started active operations at the southern edge of the Batang Toru forest. At present, only 25,000 ha of the whole Batang Toru forest block is designated as protected forest or as a nature reserve (Usher, unpublished report), while the remainder has no protected status and is primarily allocated as production forest, although only one active logging concession license has been handed out (Wich et al. 2011a). Efforts are underway to lobby for a change of status for the unprotected forest in the Batang Toru area to protected forest, and the establishment of a collaborative management system among the three local district governments where this forest is located. Water from one of the catchments that flows from the Batang Toru forest is currently used for a large hydro-electric dam, and another hydro-electric scheme is planned at the southern boundary of the forest, highlighting the importance of the ecosystem services provided by this forest area, and the need for collaborative management because the catchment area and hydro-electric plants are in different districts.

The Batang Toru area is also unique in Sumatra, because it is the only area where hunting of orangutans in the forest occurs (Wich et al. 2003, 2011a). In other areas of Sumatra, orangutans are killed mainly at the forest-agriculture interface (Wich et al. 2011a; Campbell-Smith et al. 2010, 2011), whereas in Batang Toru hunting also occurs by hunters that go into the forest. In most cases, these hunters are probably not actively targeting orangutans from the outset, but more focused on ungulates (e.g., *Rusa unicolor*, *Sus scrofa*) and other commercially traded species like pangolin (*Manis javanica*), cave and fruit bats (*Pteropus vampyrus*), and various song birds. Local hunters do not use blowpipes or arrows, and few, if any, own firearms apart from air rifles. Most hunters are limited to dogs and spears or snares. Thus, successful hunting of orangutans is largely opportunistic. However, if an orangutan is encountered, some hunters will try to hunt it for food (Usher, unpublished report). This is in addition to the killing and often eating of orangutans considered a threat to crops and people at the forest edge. This differs from the other areas in Sumatra where orangutans are killed, but not eaten, because they are perceived as a pest or they are feared along the forest edge (Campbell-Smith et al. 2010). It is likely that hunting pressure is more severe in the northwestern half of the Batang Toru forests, where the majority of the population is Christian and has no taboo on eating primates. While the predominantly Muslim population along the southeastern borders does kill primates, this appears to be primarily related to crop raiding, and not for consumption. Although it is not known how many orangutans are killed each year in the Batang Toru area, orangutan populations quickly spiral toward local extinction when they are hunted, even if those rates are low (Marshall et al. 2009b). It is, thus, crucial that campaigns to stop orangutan killing are continued, and that proper law enforcement occurs so that the illegal killing of orangutans is put to a halt.

As mentioned earlier in this chapter, there are two blocks of forest that are part of the Batang Toru area, and one area that is adjacent to the Batang Toru area, which still contains orangutans (Sibual-Buali area, Fig. 1). At present, these three blocks are not connected by forest and it is probably unrealistic to strive for a connection between the western and eastern block, because they are divided by a provincial paved road, which is bordered by human settlements. In other areas, the forest blocks are also separated by extensive rice fields. However, the western block and the Sibual-Buali area were connected until fairly recently. In 2001, there was only a small unpaved road that cut through the forest connecting these two areas. Orangutan nests were observed close to the road on both sides, indicating that orangutans were possibly still crossing the road (Wich and Geurts, pers. obs). The maintenance of potential corridors between these forest blocks also needs to be considered a conservation priority. Although orangutan numbers in the Sibual-buali area are low, connecting the two forest areas is important in boosting the overall orangutan population size, and also in maintaining maximum genetic diversity of this unique population, which is already isolated from all other Sumatran orangutans.

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Modern Human Biological Adaptations to High-Altitude Environments in the Andean Archaeological Record

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Introduction

Modern humans are the most geographically widespread primate species inhabiting every terrestrial ecosystem of our planet. While cultural and technological innovations enable us to live worldwide, biological adaptations to specific environments also are important in allowing humans to live across the globe. High-altitude regions of 2,500 m and higher are among the most challenging ecosystems to inhabit with cold ambient temperatures, limited food availability, and reduced barometric pressure of atmospheric oxygen (Pawson and Jest 1978; Beall et al. 2012). Despite the physiological challenges of living at high altitudes, modern humans have inhabited high-altitude regions for millennia: since as early as 30,000 years ago on the Tibetan Plateau (Madsen et al. 2006; Aldenderfer 2011) and by 11,000 years ago in the South American Andes (Aldenderfer 1999; Aldenderfer and Flores Blanco 2011). The longevity of human settlement in different high-altitude regions and the physiological challenges of living at high elevations suggest that human populations indigenous to high altitudes have developed biological adaptations to survive and reproduce in these harsh environments.

Our knowledge of human biological responses to high-altitude environments derives from studies of living populations indigenous to highland regions, predominantly highland Quechua and Aymara populations from the Andes compared with closely related lowland groups and Europeans who have migrated to the highland Andes and indigenous highland Tibetan populations compared with Han Chinese migrants to the Tibetan Plateau (e.g., Baker 1978; Moore et al. 1998; Frisancho 1993; Beall 2001, 2007b; Brutsaert 2010; Beall et al. 2012). These studies demonstrate that modern humans have developed a multitude of responses to the stress of living at high altitudes including short-term physiological adjustments, developmental acclimatization traits that require childhood growth and

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lifelong exposure in high-altitude environments, and natural selection over many generations in specific populations (Harrison et al. 1969; Frisancho et al. 1973, 1995, 1997; 1999; Baker and Little 1976; Baker 1978; Beall et al. 1977, 1997, 1998, 1999, 2004, 2010, 2012; Gupta and Basu 1981; Greksa et al. 1984, 1985; Greksa 1986, 1990; Frisancho and Greksa 1989; Greksa and Beall 1989; Moore 1990; Curran et al. 1998; Moore et al. 1998, 2001; Brutsaert et al. 1999a, b, 2005; Beall 2001, 2006, 2007a, b; Garruto et al. 2003; Bennett et al, 2008; Julian et al. 2009, 2011; Brutsaert 2010; Hoit et al. 2011; Kiaymu et al. 2012). Decades of scholarship demonstrate that human biological responses to high-altitude environments are multi-faceted involving many physiological traits that manifest across the life cycle, including enhanced maternal oxygen transport that buffers fetal growth from hypoxic conditions (e.g., Moore 1990; Moore et al. 1998, 2001; Lopez Carmelo et al. 2006; Bennett et al. 2008; Julian et al. 2009, 2011); physiological and morphological traits that enhance oxygen delivery and transport in response to hypoxia at different stages of childhood, adolescence, and adulthood (e.g., Frisancho et al. 1973, 1995, 1997, 1999; Frisancho and Greksa 1989; Greksa and Beall 1989; Greksa 1990; Schoene et al. 1990; Beall et al. 1997, 1998, 1999, 2004, 2010, 2012; Curran et al. 1998; Brutsaert et al. 1999a, b, 2004, 2005; Weitz et al. 2002, 2004; Garruto et al. 2003; Hoit et al. 2011; Kiyamu et al. 2012); and growth patterns in stature and body proportions that are responses to cold climatic conditions and nutritional stress (e.g., Harrison et al. 1969; Frisancho and Baker 1970; Clegg et al. 1972; Bharadwaj et al. 1973; Beall et al. 1977; Frisancho 1978; Mueller et al. 1978, 1980; Stinson and Frisancho 1978; Palomino et al. 1979; Stinson 1980, 1982, 1990, 2009; Gupta and Basu 1981; Greksa et al. 1984, 1985; Greksa 1986; Leonard 1989; Leonard et al. 1990, 1995, 2000; Post et al. 1997; Dittmar 1998; Weitz et al. 2000; Pawson et al. 2001; Weitz and Garruto 2004; Tripathy and Gupta 2005, 2007; Bailey et al. 2007; Pawson and Huicho 2010). Recent scholarship has also shown that human biological responses to high-altitude environments are not uniform across all populations with multiple independent natural selection events occurring in specific highland human groups in recent human evolutionary history (e.g., Williams-Blangero et al. 1993; Moore et al. 1998; Beall 2001, 2006, 2007a, b; Beall et al. 2004, 2010, 2012; Bigham et al. 2008, 2010; Simonson et al. 2010; Yi et al. 2010; Scheinfeldt et al. 2012). Given the length of time that humans have occupied high-altitude environments and that many biological responses to high-altitude stressors require either lifelong exposure to high elevations or genetic adaptations that develop over many generations, ancient humans from highland regions also should have developed many of the same biological responses to high-altitude environments that are evident in living groups.

This chapter synthesizes work that compares the skeletal morphology of lowland and highland human populations from archaeological contexts in the Andes to identify biological responses to the environmental stressors of high-altitude regions in the ancient past (Weinstein 2005, 2007). While there are many biological responses to high-altitude stressors that develop across the human life cycle, the vast majority of these physiological traits are not identifiable in skeletal remains. Thus, the focus of my work is to compare modern human skeletons from lowland and highland regions in the Andes to identify responses to cold stress, nutritional stress, and high-altitude hypoxia that can be detected from human skeletal morphology. I argue that, similar to studies of physiological responses and genetic traits in living human populations at high altitudes, variations in human skeletal morphology in response to high-altitude environmental stressors are not uniform across all populations. I show that the variability in skeletal morphology in response to high-altitude stressors reflects both population history and the severity of the local environmental conditions in the Andes. Below I briefly outline human population history in the Andes. I discuss what is known about living human biological responses to three high-altitude stressors: cold climatic conditions, limited nutrition, and high-altitude hypoxia based on studies of living human populations. I then apply what is known about the biological responses to high-altitude environments in living humans to interpret the morphology of modern human skeletal remains from archaeological contexts in the highland Andes.

Geography and Population History of the Andes

At an average elevation of 4,000 m, the Andes encompass two mountain chains, the Western and Eastern Cordilleras, which run along the western coast of South America from Colombia southward through Tierra del Fuego, with the Altiplano, a highland plain that exceeds 4,000 m in elevation, situated in between these two ranges. The Andes extend longitudinally from the Pacific Ocean eastward to the tropical lowlands of Ecuador, Peru, and Bolivia. Millions of people currently live at high elevations in the Andes, including indigenous Quechua and Aymara groups, people of European descent, and many of mixed ancestry. The rich Andean archaeological record reveals long-term human settlement in highland and coastal regions of the Andes dating back to the end of the Pleistocene, the development of highland Andean agropastoralism based on farming and camelid herding and coastal marine-based diets, long-distance trade networks, and the rise of complex societies across this immense landscape (Moseley 2001).

Evidence from archaeology and craniodental morphological variation indicate that humans first colonized South America during the late Pleistocene and rapidly settled into diverse ecosystems, including the highland Andes (e.g., Greenberg et al. 1986; Roosevelt et al. 1996; Aldenderfer 1999; Powell and Neves 1999; Dillehay 2000; Neves et al. 2007; Rothhammer and Dillehay 2009; Aldenderfer and Flores Blanco 2011; Hubbe et al. 2011). While geneticists disagree on South American population history subsequent to that initial dispersal, studies of mtDNA haplogroups, microsatellites, and Y-chromosome and autosomal sequences indicate that Andean populations are quite homogenous with increasing gene flow through time (Tarazona-Santos et al. 2001; Fuselli et al. 2003; Lewis et al. 2007; Lewis and Long 2008; Scilar et al. 2012). Analysis of ancient mtDNA haplogroups from the south-central Andes shows an escalation of gene flow across highland and lowland regions during the Middle Horizon (1600–1000 B.P.) and Late

Intermediate Period (1000–500 B.P.), time periods that witnessed increasing geopolitical and economic complexity (Moraga et al. 2005). Mitochondrial DNA data also reveal genetic continuity in the south-central Andes for at least the last 1,000 years (Lewis et al. 2007a), which suggests that physiological traits that have an underlying genetic basis in living highland Aymara and Quechua groups, such as many of those traits associated with high-altitude adaptations, were likely to have been present in their ancestors.

Cold Stress at High Altitudes

High-altitude regions typically have cold climates with nighttime temperatures falling below freezing year-round even in the areas of the highland Andes that fall within tropical latitudes (Pawson and Jest 1978). Cold climatic conditions can lead to natural selection as outlined by Bergmann's (1847) and Allen's (1877) rules, which describe patterns of eco-geographic variations in body size and proportions among closely related populations of geographically dispersed endothermic species that inhabit a wide range of climatic zones across different latitudes. According to these eco-geographic rules, populations from cold climates and high latitudes tend to be heavier with short appendages compared with their conspecifics from warmer climates and tropical latitudes. Heavier individuals with shorter limbs have smaller surface area to body mass ratios and are better equipped at conserving heat under the stress of cold climatic conditions. Conversely, a larger surface area to body mass ratio enables taller, thinner individuals to shed body heat under hot climatic conditions (e.g., Calder 1984; Schmidt-Nielson 1984). These eco-geographic rules explain variation in body size and proportions among numerous mammalian, avian, and other vertebrate species that inhabit a wide range of latitudes and climatic zones including different altitudes (e.g., Searcy 1980; Aldrich and James 1991; Graves 1991; Ashton et al. 2000; de Queiroz and Ashton 2004). Bergmann's and Allen's rules explain clinal variation in body size and appendage lengths in many nonhuman primate species (e.g., Albrecht 1980; Anderson 1982; Dunbar 1990; Albrecht et al. 1990; Fooden and Albrecht 1993, 1999; Paterson 1996; Fooden 1997; Weinstein 2011), modern humans from living and archaeological contexts (e.g., Newman 1953, Roberts 1953, 1978; Newman and Munro 1955; Crognier 1981; Jacobs 1985; Stinson 1990; Ruff 1994; Katzmarzyk and Leonard 1998; Holliday and Ruff 2001; Weinstein 2005; Auerbach 2007, 2010; Temple et al. 2008; Leonard and Katzmarzyk 2010; Cowgill et al. 2012) and in fossil hominins dating to the Pleistocene epoch (e.g., Trinkaus 1981; Ruff 1994, 2002b, 2010; Ruff and Walker 1993; Ruff et al. 1997; Holliday 1997, 1999; Rosenberg et al. 2006). While evidence suggests that limb lengths are affected by nutritional and other ecological conditions during growth and development (e.g., Bogin and Varela-Silva 2010; Leonard and Katzmarzyk 2010), the strong association of variations in limb proportions with latitude and other eco-geographic variables including altitude in a large sample of immature human skeletons from diverse geographic regions attests to the power of climatic conditions as a natural selective force shaping body size and shape in different human populations (Cowgill et al. 2012).

Living human populations indigenous to the Andes vary in body size and proportions in ways that are correlated, in part, with climatic conditions associated with different altitudes. Similar to other human groups from cold climates and high altitudes (e.g., Tripathy and Gupta 2007), highland Aymara and Quechua have short limbs relative to stature compared with lowland Andean populations of similar ancestry and comparable socioeconomic status (Stinson and Frinsancho 1978; Palomino et al. 1979; Stinson 2009) and with other South American populations (Stinson 1990; Katzmarzyk and Leonard 1998; Leonard and Katzmarzyk 2010). Given that mtDNA variation among ancient human skeletons and extant populations indicate genetic continuity in the south-central Andes for at least the past 1,000 year (Lewis et al. 2007a), and that the eco-geographic patterns of variation in body proportions reflect natural selection to climatic conditions (e.g., Cowgill et al. 2012), it is reasonable to expect ancient human populations from the highland Andes to exhibit body sizes and proportions that are indicative of a cold adaptation similar to their living descendants. Human skeletons from highland Andean archaeological contexts should exhibit small intralimb length proportions with short distal limb segments of both the upper and lower limb relative to its proximal limb segment in patterns that signify a cold adaptation as predicted by Allen’s rules.

Nutritional Stress at High Altitudes

High-altitude regions also have limited energy in that fewer flora and fauna thrive at higher elevations compared to lowland areas. Limited energy can lead to nutritional stress, which results in delayed growth and short adult stature in living human populations, including highland Andeans compared with lowland Andean groups and with European migrants to high altitudes (e.g., Frisancho and Baker 1970; Beall et al. 1977; Frisancho 1978; Mueller et al. 1978, 1980; Greksa et al. 1984, 1985; Greksa 1986; Stinson 1980, 1982, 1990, 2009, 2012; Pawson et al. 2001; Pawson and Huicho 2010). Human biologists initially hypothesized that chronic exposure to high-altitude hypoxia was the primary cause of the delayed childhood growth and short adult stature in highland populations (e.g., Frisancho and Baker 1970). Later work, however, revealed that limited nutrition during childhood and adolescence associated with poor socioeconomic conditions more profoundly influenced the small body sizes in indigenous highland Andean groups (Stinson 1980, 1982, 1990; Greksa et al. 1984, 1985; Greksa 1986; Leonard 1989; Leonard et al. 1990, 1995, 2000; Katzmarzyk and Leonard 1998; Pawson et al. 2001; Stinson 2009; Leonard and Katzmarzyk 2010; Pawson and Huicho 2010). In highland Peru and in Ecuador, individuals with low socioeconomic status experience annual seasonal shortages of adequate food resources leading to delayed growth during childhood and adolescence and short adult stature (e.g., Leonard 1989; Leonard et al. 1990, 1995, 2000). Improved infrastructure in highland Peru led to improved childhood growth during the 1980s followed by a reemergence of growth stunting during the 1990s in response to disrupted food supply in the context of sociopolitical crises in this region (Pawson et al. 2001; Pawson and Huicho 2010). Secular increases in body weight, stature, and BMI in indigenous Aymara children of highland Bolivia and Chile during the past four decades are similarly associated with improved socioeconomic and nutritional conditions (Post et al. 1997; Dittmar 1998). Similar to the Andes, secular increases in childhood growth also account for improved nutrition and health in highland populations from Ethiopia and the Himalayas (e.g., Harrison et al. 1969; Clegg et al. 1972; Bharadwaj et al. 1973; Gupta and Basu 1981; Weitz et al. 2000; Weitz and Garruto 2004; Bailey et al. 2007; Tripathy and Gupta 2007).

Among living human populations suffering from mild to moderate chronic undernutrition, limb lengths tend to be short relative to stature in patterns that differ from those of climatic adaptations (e.g., Bogin 1999; Stinson 2009, 2012; Bogin and Varela-Silva 2010). When undernourished groups experience improved diets, lower limb lengths tend to increase relative to stature. Thus, living human populations experiencing both mild undernutrition and improved diets demonstrate the plasticity of the body in response to nutritional conditions. It is reasonable to expect that limited nutrition also affected human populations from the highland Andes in the ancient past, a pattern that should be reflected in variations in limb lengths compared with body size in human populations from different altitudes.

High-Altitude Hypoxia

All organisms experience hypoxic stress, when bodily tissues receive insufficient amounts of oxygen, with increasing elevation. Unlike other environmental stressors of high-altitude regions, high-altitude hypoxia is chronic and universal and cannot be lessened with behavioral or cultural modification. Hypoxic conditions result from a progressive reduction in the partial pressure of atmospheric oxygen with increasing altitude. Humans experience the adverse effects of high-altitude hypoxia at 2,500 m during rest and at 2,000 m during physical activity (Frisancho 1993). Human populations living at high altitudes exhibit respiratory, cardiovascular, and hematological traits that function to enhance oxygen delivery from the atmosphere to body tissues (e.g., Baker and Little 1976; Baker 1978; Greksa 1990; Beall 2001; Brutsaert 2010; Beall et al. 2012). Pulmonary ventilation in high-altitude natives from the Andes and the Tibetan Plateau is low compared to lowland populations who migrate to high altitudes (e.g., Frisancho et al. 1999; Beall et al. 1997, 2012; Beall 2001; Brutsaert 2010), although the underlying physiology of hypoxic ventilatory responses differ in highland Andean and Tibetan populations suggesting the work of natural selection in both highland groups (Brutsaert et al. 2005; Beall et al. 1997, 2012; Beall 2007a, b). Highland groups have larger lung volumes, as measured by vital capacity, residual volume, and total lung capacity, compared with sea-level inhabitants and adult migrants to high altitudes (e.g., Frisancho et al. 1973; Greksa and Beall 1989; Frisancho et al. 1997; Brutsaert et al. 1999a, 2004; Brutsaert 2010; Beall et al. 2012; Kiyamu et al. 2012). High-altitude natives also have higher red blood cell counts, elevated hemoglobin concentrations, and increased oxygen saturation of arterial hemoglobin compared with lowland populations (e.g., Schoene et al. 1990; Beall 2001, 2006; Garruto et al. 2003; Brutsaert 2010; Beall et al. 2012), physiological traits that show different phenotypic variance in highland Tibetan and Andean groups indicating that these traits have been shaped by natural selection over the course of Tibetan and Andean population history (Beall et al. 1998, 1999, 2010, 2012; Bigham et al. 2010; Simonson et al. 2010; Yi et al. 2010). The aerobic capacity of high-altitude natives is elevated and significantly greater than that of adult migrants to highland regions, which indicates more efficient oxygen use under physically strenuous conditions (e.g., Frisancho et al. 1995; Curran et al. 1998; Brutsaert et al. 1999b; Brutsaert 2010). High-altitude inhabitants also exhibit enlarged chests relative to stature. Anteroposterior and transverse chest diameters, chest circumferences at multiple levels of the thorax, and sternal length and breadth are larger in indigenous highland peoples than closely related lowland groups, although this pattern is stronger and more consistent in highland Andean populations than in highland Tibetans (e.g., Frisancho et al. 1973; Beall et al. 1977, 2012; Beall 1981; Eckhardt 1985; Greksa and Beall 1989; Kramer 1992; Brutsaert et al. 1999a; Weitz et al. 2004; Brutsaert 2010).

Developmental acclimatization explains much of the cardiovascular, respiratory, and hematological responses to high-altitude hypoxia. Individuals born and raised at high altitudes, regardless of ancestry, develop enhanced oxygen-transport traits compared with lowland individuals who migrate to high elevations as adults (e.g., Greksa and Beall 1989; Greksa 1990; Garruto et al. 2003; Beall et al. 2012). Children of European ancestry raised in highland Peru and Bolivia, for example, acquire enlarged lung volumes, as measured by forced vital capacity and residual lung volume, that are similar to highland Aymara and Quechua children (Greksa et al. 1985; Frisancho and Greksa 1989; Greksa and Beall 1989; Frisancho et al. 1997; Brutsaert et al. 1999a, b, 2004; Brutsasert 2010). Similarly, Han Chinese populations that migrate to high-altitude regions in Qinghai Province, China develop enhanced lung volumes over the course of childhood and adolescence (Weitz et al. 2002). Individuals from sea level who reside at high altitudes during childhood also develop aerobic capacities that are nearly equal to native highlanders depending on age of migration and length of residence (Frisancho and Greksa 1989; Frisancho et al. 1995; Brutsaert et al. 1999b; Brutsaert 2010).

Although developmental acclimatization explains much of human adaptability to high-altitude hypoxia, differences in age of development and genetic and phenotypic variation of enhanced oxygen-transport traits in indigenous highland Andeans and Tibetans suggest that these populations have undergone natural selection for different adaptive pathways in response to chronic exposure to high-altitude hypoxia over the course of millennia. Highland Tibetans, for example, have undergone natural selection for ventilation rates, hemoglobin concentration, and oxygen saturation of arterial hemoglobin (e.g., Beall et al. 1998, 2004, 2012; Beall 2001, 2006, 2007a, b; Bigham et al. 2008). Similarly, recent work among highland Amhara populations in Ethiopia show elevated pulmonary arterial pressure that differs from the pulmonary arterial responses of highland Andeans and Tibetans (Hoit et al. 2011). Moreover, Amhara populations from highland Ethiopia show evidence for positive selection for hemoglobin concentration in response to high-altitude hypoxia in genetic loci that differ from those of highland Himalayan and Andean populations (Scheinfeldt et al. 2012).

Highland Andean populations have responded to high-altitude hypoxia through selection for anteroposteriorly and mediolaterally enlarged chests relative to stature (Beall et al. 1977, 2012; Beall 1981, 2001; Greksa and Beall 1989; Frisancho et al. 1997; Brutsaert et al. 1999a, 2004). Chest widths and depths relative to stature are larger and develop at earlier ages in highland Peruvian Quechua compared with highland groups from Nepal (Beall 1981; Greksa and Beall 1989). The degree of phenotypic variance in chest size in highland Aymara and Quechua compared with highland Tibetans suggests strong directional selection for this trait in Andean populations (Eckhardt 1985; Kramer 1992; Williams-Blangero et al. 1993). Highland Quechua children develop larger chests relative to stature at earlier ages than highland Aymara children (Stinson 1980; Greksa et al. 1984). Thus, an enlarged chest, as measured by anteroposterior and transverse chest diameters, appears to be specific to Andeans in response to high-altitude hypoxia and cannot be acquired through processes of developmental or adult acclimatization (Greksa and Beall 1989; Frisancho et al. 1997).

Beall (2001, 2007a, b) cogently argues that oxygen-transport traits with genetic or phenotypic variance specific to highland Andean and other high-altitude human populations developed over many generations through natural selection. Given the length of time that Andean populations have inhabited high-altitude regions and that their living descendants developed enlarged chests in response to chronic exposure to high-altitude hypoxia, ancient highland Andeans also ought to exhibit morphological evidence for enlarged chests. Skeletal elements of the thorax, specifically the sternum, clavicle, and ribs, should correspond to greater chest width and depth in ancient human skeletons from high altitudes in the Andes compared with their lowland neighbors.

Goals of This Study

Based on the well-documented biological responses of living Andeans indigenous to high-altitude environments and the great time depth of human settlement in the highland Andes, I examine evidence for the presence of biological adaptations to high altitudes in the Andean archaeological record. Using previously published work (Weinstein 2005, 2007). I synthesize comparisons of body size and proportions of the thorax and limbs in four groups of human skeletons from Andean coastal and highland regions to identify biological adaptations to the environmental stressors of high altitudes in the ancient past. Specifically, I demonstrate that instances of cold stress, limited nutrition, and high-altitude hypoxia are evident among some of the highland human skeletons to varying degrees of magnitude.

Materials and Methods

Human Skeletal Samples

Human skeletons from different altitudes in the Andes are ideal for testing hypotheses about the presence of biological adaptations to high-altitude environments in the archaeological record. The South American Andes encompasses multiple elevations within short geographic distances. Lowland regions along the Pacific coast have mild tropical to subtropical climates while climatic conditions at high altitudes have dramatic daily fluctuations in ambient temperature with nighttime temperatures often falling below freezing year-round (Pawson and Jest 1978). Human populations first settled coastal and highland regions in the Andes at 11,000 years BP (Aldenderfer 1999; Aldenderfer and Flores Blanco 2011). In general, coastal populations exploited the rich marine resources of the Pacific Ocean for millennia (Moseley 2001). Highland populations, in contrast, practiced an agropastoral subsistence strategy that required "verticality," a land-use pattern that simultaneously exploits three elevational zones: the Altiplano above 4,000 m for camelid herding, mountainous valleys at 2,500–4,000 m for the cultivation of tubers and hardy grains, and elevations between 2,000–2,500 m for the cultivation of maize and other less resilient crops (Murra 1972; Moseley 2001). The absence of marine resources in highland sites and vice versa suggests that coastal and highland Andean groups maintained largely separate populations until at least 3,500 years BP (Moseley 2001). Thus, the Andean archaeological record documents dietary variation and population interactions between coastal and highland settlements through time.

To identify the presence of human biological adaptations to cold stress, limited nutrition, and hypoxia in high-altitude regions in the ancient past, I compare four sex-specific samples of adult human skeletons from the Andes: two lowland samples from the Pacific coast, and two highland samples (Table 1). Time, dietary variation, and population history are important factors that may influence variation in body size and proportions. The first coastal sample is from Arica, Chile, and dates to two temporal periods. The earlier Archaic period individuals date to 3210–1720 B.C.E. (Allison et al. 1984; Standen et al. 1984, 1997; Focacci and Chacón 1989). Skeletal remains of fish, shellfish, marine birds, and mammals indicate that these individuals subsisted primarily on the rich marine resources of the Pacific Ocean (Bird 1943; Llagostera 1989; Villaxa and Corrales 1993;

Table 1 Sample sizes and compositions

	Males	Females	Dates[a]	Alt.[b]	Location[c]
Machu Picchu and Cuzco, Peru	22	19	Fifteenth century	2,000–3,800	FMNH, YPM
San Pedro de Atacama, Chile	42	60	250–1240 C.E.	2,500	MSPA
Arica, Chile	54	69	3210–1720 B.C.E. 750–1250 C.E.	<100	SMA
Ancón, Peru	52	28	1000–1476 C.E.	<100	FMNH

[a] See text for citations of dates and sites

[b] Elevation in meters above sea level

[c] SMA = Museo Arqueológico San Miguel de Azapa, Universidad de Tarapacá, Arica, Chile; MSPA = Museo R.P. Le Paige, San Pedro de Atacama, Chile; FMNH = Field Museum, Chicago, Illinois; YPM = Peabody Museum of Natural History, Yale University, New Haven, Connecticut

Arriaza 1995). The later individuals date to 750–1250 C. E. and had a varied diet based on the cultivation of maize, beans, and tubers, and the harvesting of marine resources (Berenguer and Dauelsberg 1989; Arriaza et al. 1995; Langsjoen 1996; Standen et al. 1997). I pooled the Arica individuals from these two temporal periods into one sample because limb lengths and proportions do not vary between individuals (Weinstein 2001). The second lowland sample is from Ancón, Peru, along the central Andean coast dating to 1000–1476 C.E. and had a diet based on marine resources and agriculture (Moseley 2001).

The first highland sample is from San Pedro de Atacama at 2,500 m and dates to 250–1240 C.E. with a diet and subsistence strategy based on agropastoralism (Costa 1988; Llagostera et al. 1988; Neves and Costa 1998; Neves et al. 1999). The second highland sample is comprised of human skeletons from Machu Picchu (2,000–2,850 m) and Cuzco (3,500–3,800 m) and date to the fifteenth century (Eaton 1916; Burger and Salazar 2003). Stable isotope analysis of human bone and dental pathological conditions indicate that these individuals consumed a diet high in maize (Burger et al. 2003; Verano 2003).

Osteometric Measurements

Living human populations from the highland Andes exhibit small intralimb length proportions for the upper and lower limbs in response to cold climates; short limbs, short stature, and small body weights in response to undernutrition; and enlarged chests and lung volumes in response to high-altitude hypoxia. I compare these morphological features in human skeletons from high and low altitudes to test whether the highland individuals also exhibit evidence of adaptations to high-altitude environments. Table 2 lists the osteometric variables and their definitions that I use to compare these morphological features. I discuss the rationale for choosing these specific variables elsewhere (Weinstein 2005, 2007). The highland human skeletons ought to exhibit small intralimb proportions in response to cold

Table 2 Osteometric variables and their definitions

Limb Variables	Definition	Source
HUM	Maximum length of the humerus	Martin (1928)
RAD	Maximum length of the radius	Martin (1928)
FEM	Maximum bicondylar length o the femur	Martin (1928)
TIB	Maximum length of the tibia	Martin (1928)
FHB	Average of A–P and S–I dm of femoral head	Grine et al. (1995)
Body mass (kg)	Average of the following equations:	Source
	2.268 × FHB—36.5	Grine et al. (1995)
	2.239 × FHB—39.9	McHenry (1992)
	2.741 × FHB × 54.9 (males)	Ruff et al. (1991)
	2.426 × FHB—35.1 (females)	Ruff et al. (1991)
Intralimb proportions	Definition	
Upper limb	RAD/HUM	
Lower limb	TIB/FEM	
Chest Variables	Definition	Source
MANLG	Manubrium length from the suprasternal notch to its most distal end along midline	Weinstein 2007
MANBR	Manubrium breadth from right and left points inferior to the clavicular notch and superior to the first costal notch	Weinstein 2007
STRLG	Length of the corpus sterni from its most superior midline point to its most distal point excluding the xyphoid process	Weinstein 2007
STRBR	Breadth of the corpus sterni at the level of the fourth sternebrae	Weinstein 2007
CLAV	Maximum length of the clavicle	Martin (1928)
DOR	Dorsal vertebral body height: summed length of the dorsal surfaces of the vertebral bodies T11-L5	Franciscus and Churchill (2002)

(continued)

Table 2 (continued)

Limb Variables	Definition	Source
Rib curvatures and areas	Definition	Source
R#TVC	The straight line distance of ribs 1–12 from its more proximal point on the rib tubercle to its most ventral end of the rib shaft	Franciscus and Churchill (2002)
R#TVS	The subtense of the tuberculo-ventral chord to the most lateral aspect of the shft for ribs 1–12	Franciscus and Churchill (2002)
R#AREA	The area encompassed by each rib (1–12) based on the following equation: $[0.5\prod][(0.5R\#TVC)(R\#TVS]$	Franciscus and Churchill (2002)
R#CHORD	The straight line distance of the most proximal point on the head of ribs 1–12 to its most distal point along the rib shaft	Weinstein (2001)
R#ARC	The absolute length of ribs 1–12 from its most proximal point on the rib head to its most distal point along the rib shaft	Weinstein (2001)
R#CURV	The degree of curvature of each rib 1–12: R#CHORD/R#ARC	Weinstein (2001)

climatic conditions, short limbs and small body sizes in response to nutritional stress, and enlarged chests as evidenced by longer ribs with large areas and open curvatures in response to high-altitude hypoxia. I estimate body mass for each individual based on femoral head breadth (FHB) using the average of three regression equations of FHB against known body weight in reference samples developed by Ruff and colleagues (1991), McHenry (1992), and Grine and colleagues (1995) (Table 3), a method to reconstruct body mass that has been used by others working with human skeletons from the Andes (Pomeroy and Stock 2012).

Statistical Analyses

I compare intralimb length proportions, limb lengths to body mass, chest proportions, and rib areas and curvatures to body mass in sex-specific groups across the four samples using ratios of log-transformed indices according to the methods described in Ruff (2002a). I calculate each index as $\log(Y/X^b)$, where Y is the dependent variable in the regression model, X is the independent variable, and b is the predicted slope if the independent and dependent variables scale isometrically (Ruff 2002a). In the case of intralimb length proportions, the predicted isometric slope is 1.0 (Table 4), whereas in the indices of body mass versus limb lengths, the predicted isometric slope is 0.333 (Table 5). The log-transformed indices of chest proportions compare manubrium length (MANLG) versus manubrium breadth (MANBR), sternal body length (STRLG) versus sternal body breadth (STRBR), body mass versus clavicle length (CLAV), and lower vertebral body height (DOR) versus CLAV (Table 6). With the exception of body mass versus CLAV, where the predicted isometric slope is 0.333, all the other chest proportion indices have a predicted isometric slope of 1.00. The highland individuals ought to exhibit skeletal evidence of enlarged chests via longer clavicles and wider sterna compared with their lowland counterparts. I also use log-transformed indices to compare rib areas (R#AREA) (Tables 7, 8) and rib curvatures (R#CURV) relative to body mass (Tables 9, 10). Both R#AREA, which represents the area encompassed within each rib, and R#CURV, which quantifies the degree of curvature of each rib, are dependent variables against body mass as the independent variable with a predicted isometric slope of 0.667. Rib areas should be larger and rib curvatures should be more open in the highland individuals as a consequence of adaptations to high-altitude hypoxia compared with lowlanders. As in Ruff (2002a), I compare mean log (Y/X^b) indices between sex-specific samples using ANOVA and Tukey multiple comparison tests. I consider group means as significantly different at $P \leq 0.05$.

Results

Comparisons of body mass in the four sex-specific groups juxtapose highlanders, who tend to be lighter, from lowlanders, who tend to be heavier

Table 3 Mean body mass in kg ± 1 SE[1]

Sample	Males	Females
Machu Picchu and Cuzco	58.60 ± 1.53	49.96 ± 1.13
Atacama	61.34 ± 0.76	52.74 ± 0.59
Arica	62.27 ± 0.75	55.13 ± 0.60
Ancón	66.36 ± 0.83	56.83 ± 1.00
Scheffe's test[2]	Ancón > Machu Picchu/Cuzco, Atacama, and Arica	Machu Picchu/Cuzco and Atacama < Arica and Ancón

[1] Mean and standard error of body mass estimates are based on the average of the three regression equations for each individual (Ruff et al. 1991; McHenry 1992; Grine et al. 1995)

[2] Scheffe's test results compare mean body mass between two samples. Inequality indicates significant different ($P \leq 0.05$) in direction shown

Table 4 Log-transformed indices of intralimb proportions

Ratio	Site	n	Mean	SE	Tukey test results[1]
Males log (RAD/HUM)	MP/C[2]	13	−0.282	0.045	MP/C < Atacama, $P = 0.003$;
	Atacama	44	−0.244	0.035	MP/C < Arica, $P = 0.001$;
	Arica	38	−0.244	0.039	MP/C < Ancón, $P = 0.02$
	Ancón	52	−0.251	0.028	
Males log (TIB/FEM)	MP/C	18	−0.181	0.026	MP/C < Atacama, Arica and
	Atacama	38	−0.154	0.019	Ancón, $P \leq 0.001$
	Arica	48	−0.153	0.029	
	Ancón	51	−0.155	0.026	
Females log (RAD/HUM)	MP/C	10	−0.293	0.046	MP/C < Atacama and Arica,
	Atacama	56	−0.263	0.030	$P = 0.02$;
	Arica	56	−0.262	0.029	MP/C < Ancón, $P = 0.004$
	Ancón	28	−0.256	0.027	
Females log (TIB/FEM)	MP/C	12	−0.182	0.025	MP/C < Atacama, $P = 0.02$
	Atacama	54	−0.161	0.023	MP/C < Arica, $P = 0.002$
	Arica	66	−0.155	0.023	MP/C < Ancón, $P < 0.001$
	Ancón	28	−0.145	0.023	

[1] Only pairwise comparisons that are significant at $P \leq 0.05$ are listed

[2] On this table and all subsequent tables, MP/C stands for Machu Picchu and Cuzco

(Weinstein 2005, 2007; Table 3). Body mass steadily decreases with increasing altitude in males with Ancón lowlanders as the heaviest, followed by Arica lowlanders, Atacama highlanders, and Machu Picchu/Cuzco highlanders as the lightest. The difference between the Ancón lowlanders and the other three groups is statistically significant (Table 3). The progressive decrease in body mass with increasing altitude is even more pronounced in females in which differences between the lighter highlanders and the heavier lowlanders are statistically significant (Table 3).

Comparisons of intralimb length proportions reveal two patterns (Weinstein 2005; Table 4). First, Atacama highlanders have upper (HUM/RAD) and lower (FEM/TIB) intralimb length proportions that are indistinguishable from the two lowland groups (Table 4). Second, Machu Picchu/Cuzco highlanders have significantly shorter upper and lower intralimb length proportions compared with the other three samples (Table 4).

Limb lengths relative to body mass also vary across an altitudinal gradient, although in a pattern different from that of intralimb length proportions (Weinstein 2005; Table 5). The two highland samples tend to have long limbs for their small body sizes, whereas the two lowland samples tend to have shorter limbs for their larger body sizes, a contrast that is most apparent in the Atacama highlanders compared with the Ancón and Arica lowlanders (Table 5). Limb lengths relative to body mass in Machu Picchu/Cuzco highlanders tend to cluster near the smallest Atacama highlanders, but statistically differ in comparisons with Ancón lowlanders only (Table 5).

Comparisons of chest proportions reveal that Atacama highlanders tend to have wider chests than the two lowland groups whose chest proportions tend to cluster together (Weinstein 2007; Table 6). Atacama highlanders have the widest manubria based on the log-transformed index of MANBR/MANLG and the longest and most narrow sternal bodies based on the log-transformed index of STBR/STLG, whereas Arica and Ancón lowlanders have narrow manubria and short and wide sternal bodies (Table 6). Mean values of indices of clavicular length to body mass and DOR also juxtapose Atacama highlanders with the two lowland groups with varying degrees of statistical significance (Table 6). Machu Picchu/Cuzco highlanders exhibit chest proportions with the greatest range of variation with males approximating those of Atacama males, whereas a few Machu Picchu/Cuzco females tend to resemble lowlanders (Table 6).

While all modern humans share a barrel-shaped thoracic morphology (Jellema et al. 1993; Franciscus and Churchill 2002; Weinstein 2007), there are subtle, yet important, variations in rib areas and curvatures in these four groups. Among males, mean values of rib areas relative to body mass are largest in Atacama highlanders at all levels of the thorax, smallest in Ancón lowlanders, and considerably variable in Machu Picchu/Cuzco highlanders and Arica lowlanders (Table 7). Machu Picchu/Cuzco males approach Atacama highlanders in mean rib area at ribs 2–4; statistically exceed Ancón lowlanders at ribs one, four, and six; and steadily decline in area beginning at rib five with statistically smaller values than Atacama and Arica males at ribs 6–7 and with Atacama males only at ribs 8–9 (Table 7). Mean values of rib areas relative to body mass in Arica males are nearly as high as Atacama highlanders at ribs 1–2, fall below Machu Picchu/Cuzco males and significantly below Atacama males at ribs 3–4, rise at ribs 6–7, followed by a slight decline at ribs 8–10 (Table 7). Given that males from both highland groups have the smallest body masses (Table 3), their relatively large rib areas at all levels of the thorax in Atacama highlanders and at the superior ribs in Machu Picchu/Cuzco highlanders suggest that males in these groups have especially large thoraces when compared with larger-bodied lowlanders. Mean rib areas relative to body mass in females illustrate a similar contrast between Atacama highlanders and Ancón lowlanders (Table 8). Arica females exhibit mean values of rib areas relative to body mass that are nearly as large as Atacama highlanders and

Table 5 Log-transformed indices of limb lengths against body mass estimates

Ratio	Site	n	Mean	SE	Tukey test results[1]
Males log (HUM/mass$^{0.333}$)	MP/C	10	2.970	0.021	Ancón $<$ MP/C, $P = 0.006$
	Atacama	40	2.968	0.051	Ancón $<$ Atacama and Arica,
	Arica	42	2.953	0.054	$P \leq 0.001$
	Ancón	51	2.909	0.060	
Males log (RAD/mass$^{0.333}$)	MP/C	10	2.715	0.077	Ancón $<$ MP/C, $P = 0.035$
	Atacama	41	2.725	0.053	Ancón $<$ Atacama and Arica
	Arica	39	2.710	0.060	$P < 0.001$
	Ancón	51	2.659	0.062	
Males log (FEM/mass$^{0.333}$)	MP/C	16	3.290	0.055	Ancón $<$ MP/C and Atacama
	Atacama	39	3.295	0.050	$P \leq 0.001$
	Arica	49	3.258	0.050	Arica $<$ Atacama, $P = 0.005$
	Ancón	51	3.235	0.051	
Males log (TIB/mass$^{0.333}$)	MP/C	15	3.103	0.054	Arica $<$ Atacama, $P = 0.038$
	Atacama	39	3.138	0.054	Ancón $<$ Atacama, $P < 0.001$
	Arica	47	3.105	0.059	
	Ancón	51	3.080	0.058	
Females log (HUM/mass$^{0.333}$)	MP/C	9	2.992	0.051	Ancón $<$ MP/C, Atacama, and
	Atacama	53	2.990	0.048	Arica, $P < 0.001$
	Arica	61	2.954	0.054	Arica $<$ Atacama, $P = 0.001$
	Ancón	28	2.904	0.058	
Females log (RAD/mass$^{0.333}$)	MP/C	8	2.717	0.043	Ancón $<$ MP/C, Atacama, and
	Atacama	55	2.726	0.050	Arica, $P \leq 0.01$
	Arica	58	2.692	0.056	Arica $<$ Atacama, $P = 0.005$
	Ancón	28	2.649	0.062	
Females log (FEM/mass$^{0.333}$)	MP/C	12	3.318	0.047	Ancón $<$ MP/C, Atacama, and
	Atacama	54	3.321	0.049	Arica, $P \leq 0.002$
	Arica	68	3.281	0.049	Arica $<$ Atacama, $P < 0.001$
	Ancón	28	3.240	0.064	
Females log (TIB/mass$^{0.333}$)	MP/C	10	3.151	0.047	Ancón $<$ MP/C and Atacama,
	Atacama	52	3.160	0.053	$P \leq 0.022$
	Arica	66	3.124	0.052	Arica $<$ Atacama, $P = 0.002$
	Ancón	28	3.094	0.060	

[1] Only pairwise comparisons that are significant at $P \leq 0.05$ are listed

Table 6 Log-transformed indices of chest proportions

Ratio	Site	n	Mean	SE	Tukey test results[1]
Males log (MANBR/MANLG)	MP/C[2]	5	0.24	0.07	
	Atacama	33	0.36	0.03	
	Arica	26	0.26	0.03	
	Ancón	15	0.29	0.04	
Males log (STBR/STLG)	MP/C	4	−0.98	0.10	Atacama < Arica and Ancón; $P \leq 0.001$
	Atacama	36	−1.15	0.03	
	Arica	26	−0.94	0.04	
	Ancón	16	−0.86	0.05	
Males log (CLAV/$M^{0.333}$)	MP/C	9	3.64	0.02	Arica and Ancón < Atacama; $P = 0.03$
	Atacama	37	3.65	0.01	
	Arica	34	3.62	0.01	
	Ancón	20	3.61	0.01	
Males log (CLAV/DOR)	MP/C	10	−0.10	0.02	
	Atacama	35	−0.08	0.01	
	Arica	23	−0.13	0.02	
	Ancón	19	−0.13	0.01	
Females log (MANBR/MANLG)	MP/C	4	0.26	0.06	Arica < Atacama $P < 0.001$
	Atacama	47	0.32	0.02	
	Arica	33	0.20	0.02	
	Ancón	8	0.26	0.04	
Females log (STBR/STLG)	MP/C	5	−1.00	0.08	Atacama < Arica and Ancón; $P < 0.001$
	Atacama	48	−1.13	0.03	
	Arica	28	−0.90	0.03	
	Ancón	8	−0.83	0.06	
Females log (CLAV/$M^{0.333}$)	MP/C	3	3.50	0.03	MP/C < Atacama $P = 0.01$
	Atacama	51	3.62	0.01	
	Arica	49	3.56	0.01	Arica and Ancón < Atacama, $P < 0.001$
	Ancón	13	3.54	0.02	
Females log (CLAV/DOR)	MP/C	2	−0.18	0.05	Arica < Atacama $P < 0.001$
	Atacama	45	−0.13	0.01	
	Arica	36	−0.19	0.01	
	Ancón	12	−0.14	0.02	

[1] Only pairwise comparisons that are significant at $P \leq 0.05$ are listed

Table 7 Log-transformed indices of rib areas in males[1]

Ratio	Site	N	Mean	SE	Tukey test results[2]
Log ($R1RA/M^{0.667}$)	MP/C	9	4.41	0.08	MP/C < Arica and Atacama, $P < 0.001$
	Atacama	30	4.82	0.04	Ancón < MP/C, $P = 0.04$
	Arica	30	4.77	0.04	Ancón < Arica and Atacama, $P < 0.001$
	Ancón	17	4.14	0.06	
Log ($R2RA/M^{0.667}$)	MP/C	6	5.92	0.07	Ancón < Atacama, $P < 0.001$
	Atacama	21	6.01	0.04	Ancón < Arica, $P = 0.03$
	Arica	23	5.90	0.04	
	Ancón	17	5.74	0.04	
Log ($R3RA/M^{0.667}$)	MP/C	6	6.40	0.05	Arica and Ancón < Atacama, $P < 0.001$
	Atacama	21	6.47	0.03	
	Arica	12	6.31	0.03	
	Ancón	17	6.28	0.03	
Log ($R4RA/M^{0.667}$)	MP/C	4	6.62	0.05	Ancón < Arica and MP/C, $P = 0.02$
	Atacama	21	6.67	0.02	Arica < Atacama, $P = 0.05$
	Arica	12	6.57	0.03	Ancón < Atacama, $P < 0.001$
	Ancón	17	6.45	0.03	
Log ($R5RA/M^{0.667}$)	MP/C	6	6.63	0.06	Ancón < Atacama and Arica, $P < 0.001$
	Atacama	25	6.75	0.03	
	Arica	14	6.70	0.04	
	Ancón	16	6.47	0.04	
Log ($R6RA/M^{0.667}$)	MP/C	8	6.63	0.04	MP/C < Atacama, $P = 0.01$
	Atacama	22	6.77	0.02	MP/C < Arica, $P = 0.04$
	Arica	12	6.75	0.03	Ancón < MP/C, $P = 0.05$
	Ancón	16	6.51	0.03	Ancón < Arica and Atacama, $P < 0.001$
Log ($R7RA/M^{0.667}$)	MP/C	7	6.54	0.04	MP/C and Ancón < Atacama and Arica $P < 0.001$
	Atacama	29	6.72	0.02	

(continued)

Table 7 (continued)

Ratio	Site	N	Mean	SE	Tukey test results[2]
	Arica	13	6.74	0.03	
	Ancón	15	6.49	0.03	
Log (R8RA/$M^{0.667}$)	MP/C	6	6.51	0.04	MP/C < Atacama, $P = 0.02$
	Atacama	26	6.66	0.02	Ancón < Arica and Atacama, $P < 0.001$
	Arica	21	6.62	0.02	
	Ancón	16	6.44	0.03	
Log (R9RA/$M^{0.667}$)	MP/C	6	6.41	0.05	MP/C < Atacama, $P = 0.03$
	Atacama	26	6.56	0.02	Ancón < Atacama, $P < 0.001$
	Arica	17	6.50	0.03	Ancón < Arica, $P = 0.02$
	Ancón	17	6.37	0.03	
Log (R10RA/$M^{0.667}$)	MP/C	1	6.04	0.18	Arica < Atacama, $P < 0.001$
	Atacama	27	6.36	0.04	
	Arica	24	6.17	0.04	
	Ancón	9	6.20	0.06	

[1] This index is not reported for ribs 11 and 12

[2] Only pairwise comparisons that are significant at $P \leq 0.05$ are listed

Table 8 Log-transformed indices rib areas in females

Ratio	Site	N	Mean	SE	Tukey test results[a]
Log ($R1RA/M^{0.667}$)	MP/C	6	4.08	0.09	MP/C and Ancón < Atacama and Arica $P < 0.001$
	Atacama	47	4.79	0.03	
	Arica	43	4.79	0.03	
	Ancón	13	4.17	0.06	
Log ($R2RA/M^{0.667}$)	MP/C	0	–	–	Ancón < Atacama, $P = 0.03$
	Atacama	32	5.93	0.03	Ancón < Arica, $P = 0.04$
	Arica	28	5.92	0.03	
	Ancón	7	5.77	0.06	
Log ($R3RA/M^{0.667}$)	MP/C	1	6.28	0.12	Ancón < Atacama, $P = 0.01$
	Atacama	31	6.39	0.02	Ancón < Arica, $P = 0.05$
	Arica	21	6.37	0.03	
	Ancón	11	6.25	0.04	
Log ($R4RA/M^{0.667}$)	MP/C	1	6.19	0.09	MP/C and Ancón < Atacama and Arica $P < 0.001$
	Atacama	34	6.61	0.02	
	Arica	23	6.58	0.02	
	Ancón	12	6.42	0.03	
Log ($R5RA/M^{0.667}$)	MP/C	0	–	–	Ancón < Atacama and Arica, $P < 0.001$
	Atacama	34	6.70	0.01	
	Arica	23	6.68	0.02	
	Ancón	10	6.50	0.03	
Log ($R6RA/M^{0.667}$)	MP/C	0	–	–	Ancón < Atacama and Arica, $P < 0.001$
	Atacama	35	6.75	0.01	
	Arica	22	6.71	0.02	
	Ancón	11	6.55	0.02	
Log ($R7RA/M^{0.667}$)	MP/C	0	–	–	Ancón < Atacama and Arica, $P < 0.001$
	Atacama	38	6.71	0.02	

(continued)

Table 8 (continued)

Ratio	Site	N	Mean	SE	Tukey test results[a]
	Arica	23	6.66	0.02	
	Ancón	11	6.51	0.03	
Log ($R8RA/M^{0.667}$)	MP/C	0	–	–	Ancón < Atacama and Arica, $P < 0.001$
	Atacama	39	6.64	0.02	
	Arica	23	6.60	0.02	
	Ancón	11	6.47	0.03	
Log ($R9RA/M^{0.667}$)	MP/C	1	6.18	0.12	MP/C < Atacama, $P = 0.01$
	Atacama	40	6.54	0.02	MP/C < Arica, $P = 0.04$
	Arica	27	6.50	0.02	Ancón < Atacama and Arica, $P < 0.001$
	Ancón	9	6.27	0.04	
Log ($R10RA/M^{0.667}$)	MP/C	1	5.91	0.15	Arica < Atacama, $P = 0.01$
	Atacama	39	6.29	0.02	Ancón < Atacama, $P < 0.001$
	Arica	33	6.18	0.03	Ancón < Arica, $P = 0.02$
	Ancón	2	5.84	0.11	

As in Table 9, this index is not reported for ribs 11–12

[a] Only pairwise comparisons that are significant at $P \leq 0.05$ are listed

Table 9 Log-transformed indices of rib curvatures in males

Ratio	Site	N	Mean	SE	Tukey test results[a]
Log ($R1CURV/M^{0.667}$)	MP/C	9	1.37	0.04	Ancón < Atacama, $P = 0.01$
	Atacama	30	1.38	0.02	
	Arica	30	1.33	0.02	
	Ancón	17	1.27	0.03	
Log ($R2CURV/M^{0.667}$)	MP/C	6	1.15	0.04	Ancón < Atacama, $P = 0.01$
	Atacama	21	1.17	0.02	Ancón < Arica, $P < 0.001$
	Arica	23	1.18	0.02	
	Ancón	17	1.06	0.02	
Log ($R3CURV/M^{0.667}$)	MP/C	6	1.20	0.04	Ancón < MP/C, $P = 0.02$
	Atacama	22	1.23	0.02	Ancón < Arica and Atacama
	Arica	12	1.21	0.03	$P < 0.001$
	Ancón	17	1.08	0.02	
Log ($R4CURV/M^{0.667}$)	MP/C	4	1.28	0.05	Ancón < Atacama, $P = 0.01$
	Atacama	22	1.29	0.02	
	Arica	12	1.27	0.03	
	Ancón	16	1.18	0.03	
Log ($R5CURV/M^{0.667}$)	MP/C	6	1.37	0.03	Ancón < MP/C, $P = 0.01$
	Atacama	25	1.37	0.02	Ancón < Atacama, $P < 0.001$
	Arica	14	1.32	0.02	Ancón < Arica, $P = 0.05$
	Ancón	15	1.24	0.02	
Log ($R6CURV/M^{0.667}$)	MP/C	8	1.45	0.03	Ancón < MP/C and Atacama
	Atacama	23	1.42	0.02	$P < 0.001$
	Arica	12	1.38	0.03	Ancón < Arica, $P = 0.04$
	Ancón	16	1.28	0.02	
Log ($R7CURV/M^{0.667}$)	MP/C	6	1.48	0.04	Ancón < MP/C and Arica
	Atacama	29	1.48	0.02	$P = 0.01$

(continued)

Table 9 (continued)

Ratio	Site	N	Mean	SE	Tukey test results[a]
	Arica	14	1.44	0.02	Ancón < Atacama, $P < 0.001$
	Ancón	14	1.34	0.02	
Log (R8CURV/M$^{0.667}$)	MP/C	6	1.52	0.03	Ancón < MP/C, $P = 0.05$
	Atacama	26	1.53	0.02	Ancón < Atacama, $P < 0.001$
	Arica	21	1.48	0.02	
	Ancón	16	1.42	0.02	
Log (R9CURV/M$^{0.667}$)	MP/C	6	1.55	0.03	Ancón < MP/C, $P = 0.01$
	Atacama	26	1.54	0.02	Ancón < Atacama and Arica $P < 0.001$
	Arica	17	1.51	0.02	
	Ancón	17	1.42	0.02	
Log (R10CURV/M$^{0.667}$)	MP/C	5	1.58	0.04	Ancón < Atacama and Arica $P < 0.001$
	Atacama	29	1.57	0.02	
	Arica	24	1.57	0.02	
	Ancón	18	1.48	0.02	
Log (R11CURV/M$^{0.667}$)	MP/C	8	1.64	0.03	Ancón < Atacama, $P < 0.001$
	Atacama	30	1.66	0.02	Ancón < Arica, $P = 0.01$
	Arica	23	1.65	0.02	
	Ancón	16	1.56	0.02	
Log (R12CURV/M$^{0.667}$)	MP/C	6	1.77	0.04	
	Atacama	28	1.75	0.02	
	Arica	17	1.74	0.02	
	Ancón	14	1.68	0.02	

[a] Only pairwise comparisons that are significant at $P \leq 0.05$ are listed

Table 10 Log-transformed indices of rib curvatures in females

Ratio	Site	N	Mean	SE	Tukey test results[a]
Log (R1CURV/$M^{0.667}$)	MP/C	6	1.65	0.04	Atacama, Arica, and Ancón < MP/C
	Atacama	47	1.47	0.02	$P < 0.001$
	Arica	43	1.43	0.02	
	Ancón	13	1.41	0.03	
Log (R2CURV/$M^{0.667}$)	MP/C	0	–	–	
	Atacama	32	1.31	0.02	
	Arica	28	1.29	0.02	
	Ancón	7	1.25	0.04	
Log (R3CURV/$M^{0.667}$)	MP/C	1	1.49	0.10	
	Atacama	31	1.34	0.02	
	Arica	21	1.33	0.02	
	Ancón	11	1.28	0.03	
Log (R4CURV/$M^{0.667}$)	MP/C	1	1.65	0.09	Atacama < MP/C, $P = 0.04$
	Atacama	32	1.40	0.02	Arica < MP/C, $P = 0.02$
	Arica	23	1.38	0.02	Ancón < MP/C, $P = 0.01$
	Ancón	12	1.34	0.03	
Log (R5CURV/$M^{0.667}$)	MP/C	0	–	–	
	Atacama	34	1.46	0.01	
	Arica	23	1.41	0.02	
	Ancón	10	1.39	0.03	
Log (R6CURV/$M^{0.667}$)	MP/C	0	–	–	
	Atacama	36	1.53	0.03	
	Arica	22	1.48	0.04	
	Ancón	11	1.44	0.06	
Log (R7CURV/$M^{0.667}$)	MP/C	0	–	–	
	Atacama	36	1.55	0.01	

(continued)

Table 10 (continued)

Ratio	Site	N	Mean	SE	Tukey test results[a]
	Arica	22	1.53	0.02	
	Ancón	11	1.50	0.02	
Log (R8CURV/$M^{0.667}$)	MP/C	0	–	–	Ancón < Atacama, $P < 0.001$
	Atacama	38	1.61	0.01	
	Arica	23	1.59	0.01	
	Ancón	11	1.52	0.02	
Log (R9CURV/$M^{0.667}$)	MP/C	1	1.66	0.07	Ancón < Atacama, $P = 0.01$
	Atacama	41	1.63	0.01	
	Arica	27	1.60	0.01	
	Ancón	11	1.55	0.02	
Log (R10CURV/$M^{0.667}$)	MP/C	2	1.67	0.06	
	Atacama	39	1.66	0.01	
	Arica	33	1.65	0.01	
	Ancón	11	1.62	0.02	
Log (R11CURV/$M^{0.667}$)	MP/C	4	1.83	0.04	
	Atacama	40	1.73	0.01	
	Arica	25	1.75	0.02	
	Ancón	10	1.72	0.02	
Log (R12CURV/$M^{0.667}$)	MP/C	2	1.89	0.05	Ancón < Arica, $P = 0.05$
	Atacama	35	1.85	0.01	
	Arica	23	1.87	0.01	
	Ancón	7	1.79	0.03	

[a] Only pairwise comparisons that are significant at $P \leq 0.05$ are listed

significantly larger than Ancón lowlanders at all levels of the thoracic cage (Table 8). Although rib data are available for only one female from Machu Picchu/Cuzco, this individual has significantly smaller rib areas relative to body mass than mean values for both Atacama and Arica females at ribs one, four, and nine (Table 8).

Males from Machu Picchu/Cuzco, Atacama, and Arica have high mean values of rib curvatures relative to body mass indicating more open chests at all levels of the thorax compared with Ancón males, whose values are significantly smaller than at least one other male sample at every rib except for the twelfth (Table 9). Mean values of rib curvatures relative to body mass are nearly equal in both highland male groups at all levels of the thorax, and these two groups slightly, but not significantly, exceed Arica lowlanders at ribs 5–9 (Table 9). Rib curvatures relative to body mass are highest in the few Machu Picchu/Cuzco females with available data, specifically for ribs one, 3–4, and 9–12 (Table 10). Machu Picchu/Cuzco females have the smallest body masses (Table 3), and while this group is missing values at ribs two and 5–8 with most rib data available from only one female, high mean values of curvature relative to body mass in the ribs that are present suggest that chest depth is even larger when controlled for size in this individual (Table 10). Indices of mean rib curvatures relative to body mass are similar in females from highland Atacama and lowland Arica and Ancón (Table 10). Atacama females are the largest of these three groups, followed by Arica females. Ancón females are the smallest, and in addition to the significantly smaller values compared with the Machu Picchu/Cuzco female reported above, this group is also significantly smaller in mean values of rib curvatures relative to body mass compared with Atacama females at ribs 8–9 (Table 10).

Discussion

The results from this study illustrate the variability in human biological responses to environmental stressors of high-altitude regions. I argue that the effects of climatic conditions, nutritional stress, and high-altitude hypoxia are evident in human skeletons from different altitudes in the Andes, albeit with different degrees of magnitude and not in concert. Specifically, in comparison to the two lowland samples, the highland group from San Pedro de Atacama exhibits responses to high-altitude hypoxia via thoracic skeletal morphology, nutritional stress in terms of small body sizes, but no apparent morphological response to cold stress as revealed by intralimb length proportions. In contrast, the highland individuals from Machu Picchu/Cuzco exhibit short intralimb length proportions indicative of adaptations to cold stress, small body sizes that suggest limited nutrition, and highly variable thoracic skeletal morphology suggesting varied responses to high-altitude hypoxia that most likely reflect gene flow in this region. Below, I discuss the affects of each environmental stressor and the role of gene flow on these ancient Andean highland groups.

Intralimb Length Proportions and Climatic Adaptations

Intralimb length proportions vary across an altitudinal gradient in a pattern that reveals the degree of severity of cold stress at different elevations in the highland Andes (Weinstein 2005). Individuals from the highest altitudes, those from Machu Picchu and Cuzco, have the shortest intralimb length proportions, a pattern best explained as a morphological adaptation to cold climates as predicted by Allen's rule. A cold-adapted body form in the Machu Picchu/Cuzco individuals is to be expected given that these individuals were recovered from, approximately, 2,000–3,800 m in elevation where ambient temperatures frequently fall below 0 °C and that living Andeans from high altitudes show similar evidence of morphological adaptations to cold climates (Stinson and Frisancho 1978). Intralimb length proportions in other Inca-period human skeletons from neighboring regions in highland Peru are equally as small as Eskimo/Inuit groups from Arctic climates illustrating further the development of a cold-adapted body shape among some prehistoric highland populations of southern Peru (Weinstein 1998, 2001).

Atacama highlanders, in contrast, have intralimb length proportions that are longer and indistinguishable from individuals from the two coastal sites. At 2,500 m, San Pedro de Atacama is at the lower limit of high altitude. While nighttime temperatures drop substantially at this elevation, climatic conditions at this location in northern Chile do not appear to be cold enough to create a natural selective pressure in these populations. Thus, based on the contrasts in intralimb length proportions between the Machu Piccu/Cuzco highlanders and the Atacama highlanders, climatic conditions in the southern Peruvian highlands appear to be severe enough to favor the selection for a cold-adapted body shape, whereas temperatures in the Atacama Desert of northern Chile do not.

Body Size, Limb Lengths, and Dietary Variation

Results from this study show that the two highland samples have small body sizes based on estimations of body mass while the two lowland groups have larger body sizes. Based on what is known about living highland human populations experiencing nutritional stress, I interpret the contrast between the smaller-bodied highlanders and the larger-bodied lowlanders to reflect a generally poorer quality diet in the highland groups (Weinstein 2005). Studies of living populations at high altitudes suggest that dietary variation and nutritional stress are important in explaining the delayed growth and short stature of highland Andean populations (e.g., Leonard 1989; Leonard et al. 1990, 1995, 2000; Pawson and Huicho 2010). Limb lengths are particularly susceptible to stunting as a result of chronic undernutrition during critical growth periods in childhood and adolescence (Bogin 1999; Stinson 2009, 2012; Bogin and Varela-Silva 2010).

Archaeological evidence infers that the highland and lowland groups differed in their diets and subsistence bases. The larger-bodied lowlanders relied heavily on marine resources as a dietary staple, with an increase in terrestrial resources through time (e.g., Arriaza 1995; Moseley 2001). Individuals from Ancón exhibited rather high frequencies of cribra orbitalia and porotic hyperostosis (personal observation), osteological conditions that are indicative of iron-deficiency anemia (Stuart-Macadam 1992) and that are common in prehistoric Andean coastal groups exposed to parasites from marine-based diets (Walker 1986). The other coastal group from Arica, however, does not exhibit these pathological conditions in high frequency or any other obvious nutritional deficits (personal observation).

Machu Picchu/Cuzco and Atacama highlanders, in contrast consumed a typical highland Andean diet of maize, tubers, hardy grains, and camelid meat that seasonally fluctuated in quality and quantity (e.g., Costa 1988; Núñez 1991; Costa Junquiera and Llagostera 1994; Miller 2003; Burger et al. 2003). While dietary reconstruction based on faunal remains, stable isotopic analysis of human bone, and paleopathological conditions of human skeletal remains do not identify any obvious nutritional deficits in the highland groups, the agropastoral highland diet most likely encompassed a smaller degree of food diversity compared with the marine-based and agricultural diets of coastal groups. Low food diversity can lead to insufficient intake of specific nutrients, and as is the case in living Andean highland populations, delayed growth and short adult stature (Leonard et al. 1990; Bogin 1999).

Thoracic Skeletal Morphology and High-Altitude Hypoxia

An even more interesting picture of biological responses to high-altitude environments emerges with comparisons of thoracic skeletal morphology. Beall (2001, 2006, 2007a, b) argues that the physiological and morphological traits that enhance oxygen delivery in extant highland Andeans and Tibetans are shaped by natural selection and require these groups to have inhabited their respective regions for long periods of time. Results from this study demonstrate that the enlarged thoraces, traits specific to living highland Andean populations that function as an adaptation to high-altitude hypoxia, were also present in some, but not all, highland individuals during Andean prehistory.

Atacama highlanders generally have the widest manubria, the longest clavicles, the largest rib areas, and most open rib curvatures, morphological traits that appear to represent enlarged chests consistent with adaptations to high-altitude hypoxia. Even though San Pedro de Atacama, at 2,500 m in elevation, is at the lower limit of high altitude, hypoxia may be powerful enough at this elevation to require natural selection for enlarged thoraces in inhabitants of this region. The inhabitants of Machu Picchu and Cuzco, in contrast, appear to have endured high-altitude hypoxia differently with a noticeable sex-based difference in thoracic morphology.

Machu Picchu/Cuzco males tend to have narrow sterna, yet long clavicles and superior ribs that are large in area and more open in curvature similar to their highland Atacama counterparts. Machu Picchu/Cuzco females, in contrast, tend to have short clavicles and narrow sterna, indicating narrower and shallower chests similar to lowlanders, yet one individual with ribs that are markedly open in curvature. The sex-based difference in thoracic morphology in the Machu Picchu/ Cuzco sample is enigmatic. Some individuals in this group may have developed respiratory responses to high-altitude hypoxia, while others may have migrated to high altitudes from lower elevations, a scenario that is discussed further below.

Population Interactions and the Effects of Gene Flow

Variation in mtDNA among living and ancient Andean groups indicates that gene flow between densely populated regions increased with time over the last millennium (e.g., Moraga et al. 2005; Lewis et al. 2007a, b). The results of this study suggest, however, that with the exception of the Machu Picchu/Cuzco sample, gene flow had minimal effect on the biological variation observed in these individuals. Analysis of biological distance based on nonmetric cranial and dental traits indicates genetic continuity in Arica populations from the Archaic Period (3000–1000 B.C.E.) through the Late Intermediate Period (1000–1476 C.E.) (Sutter 2000; Sutter and Mertz 2004). Archaeological evidence also indicates continuous human settlement along the central Andean coast beginning at 11,000 years BP and a geopolitical separation between the central coast and the south-central highlands that continued through the Late Intermediate Period (Moseley 2001). Thus, coastal populations appear to be relatively isolated from their highland neighbors, at least in the coastal groups represented in this study. Likewise, archaeological evidence from San Pedro de Atacama and craniometric variation from throughout the south-central Andes suggests that highland populations from the Atacama Desert had strong biological and cultural ties with the highlands to the north and east rather than with the coastal settlements to the west (Núñez 1991; Torres-Rouff 2008; Varela et al. 2008).

The high degree of variability in thoracic skeletal morphology in Machu Picchu/Cuzco highlanders raises the possibility that these individuals may have originated from across the Andes. Population movements across vast distances were ubiquitous during the Inca period, and Andean archaeologists have long speculated about the geographic origins of the inhabitants of Machu Picchu and Cuzco (e.g., Burger et al. 2003; Verano 2003). Carbon and nitrogen stable isotopes extracted from human bone signify dietary variation in the Machu Picchu residents that suggest coastal to highland migrations (Burger et al. 2003; Turner et al. 2009). Verano (2003), in his analysis of artificial cranial deformation styles and nonmetric cranial traits, argues that approximately half of the Machu Picchu males were coastal in origin and half were from highland regions, while all but three females were from the northern coast of Peru. Despite evidence of a cold adaptation as indicated by small intralimb length proportions, the highly variable pattern of thoracic skeletal morphology in the Machu Picchu/Cuzco sample supports the argument that these individuals originated from both coastal and highland Andean regions. Individuals from this group have the greatest range of variation in thoracic skeletal morphology. Males tend to cluster with Atacama highlanders in thoracic morphology in a pattern that suggests the development of respiratory adaptations to high-altitude hypoxia. Females, although small in sample size, resemble Ancón lowlanders in chest proportions indicating no adaptation to high-altitude hypoxia yet one female who differs from this pattern in rib morphology. This sex-specific pattern in thoracic morphology is reminiscent of Verano's (2003) findings that many of the residents at Machu Picchu were not highland in origin and emigrated from lowland regions from elsewhere in the Andes.

Conclusions

Human biological responses to high altitude in the Andean archaeological record are highly variable across short geographic distances and reflect population history in a particular region and the severity of the local environmental conditions. Patterns of variation in intralimb length proportions, body size and limb lengths, and thoracic skeletal morphology reveal that, in addition to gene flow, dietary practices, climatic conditions, and exposure to hypoxia place different natural selective pressures on human populations in the Andes. The adverse effects of high-altitude hypoxia require the selection for an enlarged chest in populations that reside at elevations of 2,500 m. Climatic conditions at this elevation in the Atacama Desert of northern Chile, however, are not cold enough to warrant the selection for a cold-adapted body shape, but do so at higher elevations. Ancient highland Andean subsistence practices further contribute to the small body sizes in highland Andean populations.

Given the varied responses of ancient highland Andeans to high-altitude environments, the biological responses of ancient populations from other highland regions throughout the world ought to be equally as complex. Living highland Tibetans and Ethiopians exhibit physiological responses to high-altitude environments in ways that are markedly different from highland Andeans (e.g., Beall 2001, 2006 2007a, b; Hoit et al. 2011; Scheinfeldt et al. 2012) and suggest that indigenous highland populations from different continents have undergone recent convergent evolution leading to unique biological adaptations in response to living at high altitudes. Identifying biological adaptations to high-altitude regions in the archaeological records of the Tibetan Plateau and the highlands of Ethiopia would add to our growing knowledge of the development of biological adaptations to high altitude in modern humans.

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High Altitude Primates, Extreme Primates, and Anthropological Primatology: Or, There is More to Human Evolution than Tool Use, Culture, or African Apes

Ken Sayers

> Man can inhabit every climate. He lives and multiplies in the northern as well as the southern regions of the earth. But the ape exists with difficulty in temperate countries, and can multiply only in those which are warm. This difference of temperament implies others in organization, which, though concealed, are not the less real.
> Georges Louis Leclerc, Compte de Buffon, "The nomenclature of apes," (1791/1972).

Introduction

Even before the momentous debuts of Darwin, Wallace, or Huxley, it had long been suspected that monkeys and apes, or even more primitive primates, were important in some way—at least in a vaguely articulated way—to defining humanness. As early as 1699, the British physician Edward Tyson had taken scalpel to chimpanzee and noted that, in many characters anyway, it was anatomically more similar to humans than it was to monkeys (Tyson 1699/1972; cited in Huxley 1863; Yerkes and Yerkes 1929). After the introduction of natural selection as a realistic mechanism of evolutionary change, more detailed anatomical work commenced to specifically determine the provenance of humans in the grand scheme of life. The famous conclusions of this work (Huxley 1863; Darwin 1874/1998) proposed apes in general, or specifically African apes, as our closest living relatives, a hypothesis that has of course been borne out by current molecular methods (Glazko and Nei 2003). It is therefore not surprising that recent primate studies—anatomical, physiological, ecological, behavioral, and cognitive—often begin with the premise that the more closely a species is related to

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humans, the more "relevant" it is to questions of human evolution (Wrangham 1987; Rodman 1999; McGrew 2010).

Our very closest living relatives, although certainly relevant to anthropological questions, are not uniquely so. As a matter of fact, the (likely) substantial divergence of extant apes from the last common ancestors (LCAs) we shared with them suggests rather strongly that the increasingly focused attention given to these primates, at the expense of other taxa, has actually hampered attempts to accurately reconstruct hominid behavioral evolution (e.g., White et al. 2009). The relevance of a nonhuman form to human origins should not be implicitly or explicitly measured by genetic distance from humans, and anthropological primatology will be well-served to focus more intensively on broad evolutionary principles that apply widely in the animal kingdom (Tooby and DeVore 1987; Strier 2001; Sayers and Lovejoy 2008). This chapter will examine how vertebrates (primates will be emphasized) living in exceptionally marginal habitats—irrespective of taxa and especially those living at high altitudes—illustrate general ecological principles that have direct bearing on early hominid behavioral, anatomical, physiological, and phylogenetic reconstructions. As foreshadowed by Buffon (1791/1972) in the eighteenth century, these are principles that cannot be satisfactorily elucidated by studying only hominoids (see also Strier 2001).

The approach taken here differs from most current primate-based behavioral considerations of human evolution, which utilize chimpanzee referential models and/or comparisons between an extant ape (or less frequently two or more apes) and hominids/humans. The approach thus requires further justification or, better still, an argument that it is superior to the standard methods.

It is best perhaps to begin with a rhetorical question: why *is* primatology relevant to anthropology? Primate studies, as noted, have long been deemed crucial to understanding humanity; this has, indeed, been the opinion of scholars working in all the traditional "four fields" of the discipline. This obviously includes biological anthropologists, but also cultural anthropologists (Lévi-Strauss 1968; Rodman 1999), archeologists (Oakley 1964; Toth et al. 1993), and linguists (Hockett 1960; Hewes 1973). Indeed, one of the earliest detailed studies of primate behavior—Solly Zuckerman's investigation of baboons in the London Zoo and (much more briefly) in South Africa—was undertaken under the prompting of the cultural anthropologists W.J. Perry and Bronislaw Malinowski and the archeologist and physical anthropologist Grafton Elliot Smith (Zuckerman 1932). Zuckerman was an anatomist, physiologist, and paleoanthropologist in addition to a behaviorist, and his explicit interest in human evolution linked him with later workers important in training or encouraging primatologists, such as Sherwood Washburn (although unlike this worker and most of his students, Zuckerman preferred primate laboratory studies; see Zuckerman 1963; Burt 2006; Sussman 2007).

Some of the most important "anthropological" primate work of the formative years (ca. 1900–1960) was performed by individuals who never claimed to be, or were not initially considered to be, anthropologists. Zuckerman's contemporaries L.T. Hobhouse (a polymath sociologist), Wolfgang Köhler, Robert Yerkes, and

C.R. Carpenter (ostensibly psychologists), and Kinji Imanishi (originally an ecologist/zoologist) are probably the best examples. Hobhouse's (1901), Kohler's (1925) and Yerkes' (e.g., 1916; Yerkes and Yerkes 1929) studies remain the template for many laboratory investigations of comparative primate behavior and cognition, while the work of Yerkes' student Carpenter (e.g., 1934) and Imanishi in Japan (see Imanishi 1965) laid the foundation for virtually all later primate field research. Whether nonhuman primate work is labeled "anthropological," of course, should not depend on what type of department a researcher was trained or studies in, nor whether the project occurs in field or laboratory, and independent of whether the taxon investigated is a hominoid. It should instead be contingent on whether or not the questions asked have relevance to the human condition (Hooten 1955).

It has been suggested that "the function of primatology in anthropology is to elucidate…the origins of human nature using morphological and behavioral comparisons among living nonhuman primates, fossil primates, and humans" (Rodman 1999:312). This is essentially a description of the comparative method (reviewed in Hailman 1998) which seeks to identify homologous or analogous characters via between-species comparisons, and, while essential, is not the sole use of nonhuman primates within anthropology (see below). Regardless, it is interesting to note that over many decades of such work, researchers studying such disparate taxa as baboons (Washburn and DeVore 1961), langurs (Jay 1968), New World monkeys (Kinzey 1987), and prosimians (Jolly 1966) felt justified to pen authoritative reviews on the relevance of primate ecology or behavior to questions in human evolution. With only few exceptions (e.g., Grueter et al. 2012; Koenig and Borries 2012), this is hardly thinkable today, as such work is increasingly becoming limited to those researchers who largely or exclusively study apes (Strier 2001). This is a step backwards, encourages narrow as opposed to broad knowledge of topics and taxa, and remains, ultimately, a serious impediment to the development of our discipline.

It is true that the African apes, particularly chimpanzees and bonobos, are our closest living relatives, and it is thus obvious that they will share more traits with humans than our more distant primate relatives. Rodman (1999:330) opined that "(c)himpanzees and bonobos are particularly important to understanding the origins of human behavior, and it is not surprising that it is chimpanzees that have the most human characters, including limited material culture". While this is true in a genetic and, in some cases, an anatomical sense, it is likely that the differences between humans, chimpanzees, *and other animals* have been overstated, even in relation to such textbook anthropological topics as tool use, cooperative hunting, and cultural learning. In short, numerous animals engage in such behaviors, diminishing the rationale for the intensive study of only chimpanzees in relation to these issues (topics, incidentally, whose importance for human evolution can and should be debated, Sayers and Lovejoy 2008). Perhaps more important, it is likely that the recent focus on African apes in discussions of human origins—to the exclusion of other primates and indeed vertebrates—has lead to numerous misleading characterizations of our early evolution.

The reason is that early hominids/hominins (hereafter, hominids) were not chimpanzees, bonobos, gorillas or orangutans. They were unique species with unique morphologies living in unique habitats with unique selective pressures. Over the past 5 decades, much of the work on African apes, for example, could be considered the relentless pursuit of plesiomorphy—the identification of primitive characters shared by these forms and humans (e.g., Wrangham and Pilbeam 2002). A disproportionate amount of attention has been paid to putative shared behavioral characters that are featured in particular models of human evolution and can often be summed in a simple word or phrase—Man the Hunter, Woman the Gatherer, Man the Language-user, Woman the Tool-maker, Man the Culture-bearer. This, of course, contrasts with traditional phylogenetic analyses, which are particularly concerned with derived characters (Mayr 1982). One end result is that topics for study may be chosen based on popularity or notions of perceived importance, rather than actual importance, resulting ultimately in a more limited knowledge of both human and ape. There is a reason, for example, why we know more today about chimpanzee termite fishing than we know about their overall foraging strategy.

Another ramification of a hominoid-centered approach has been the common view that if chimpanzees or other apes are so close to humans in so many features (but see Latimer et al. 1981; Sayers and Lovejoy 2008), they must be nearly identical to those of emergent hominids (Zihlman 1978; Wrangham and Pilbeam 2002). As it turns out, there is fossil evidence with which to examine such claims, and it strongly suggests that our closest living relatives are considerably divergent from early hominids in not just the oftentimes trivial, overlapping "characters" that populate cladistic reconstructions, but several *fundamental* elements of ecology and behavior (Sayers et al. 2012). This is exemplified by *Ardipithecus ramidus*, which frequented woodland Ethiopian habitats circa 4.4 million years ago (White et al. 2009). All available evidence points to *A. ramidus* being a very primitive hominid in the classic sense (White et al. 2009; Sayers et al. 2012) and, whatever its specific taxonomic affinities, is vital for interpreting earliest hominid evolution. The *A. ramidus* dentition is more generalized than African apes, with less molar shearing surface and comparatively diminutive incisors when compared with chimpanzees or bonobos (Suwa et al. 2009). The postcranium also differs, evincing evidence of a slow-climber lacking the suspensory features of living apes, with incipient characters linked to bipedality (and which would reduce arboreal agility, Lovejoy et al. 2009a).

These traits, first of all, suggest differing foraging strategies between *A. ramidus* and extant apes. The small incisors and flat molars of *Ardipithecus* suggest less efficient processing of fruits and leaves; the overall dental pattern suggests a comparatively greater compromise between many foodstuffs (e.g., less ripe-fruit reliance or leaf exploitation than in chimpanzees, Suwa et al. 2009) and a trend towards a suid-like, ursid-like omnivory that reaches its apex in later *Australopithecus* (Hatley and Kappelman 1980). The postcranial characters of *Ardipithecus*, including relatively short metacarpals and fore and hindlimbs of approximately equivalent length, suggest differences in the time and energetic costs of food collection. These characters, for example, would either exclude or reduce profitability for many types of hunting, both arboreal and terrestrial, seen in extant chimpanzees (Sayers and Lovejoy submitted). Given that even within-species variation in morphology and behavioral attributes can significantly influence individual-specific food profitability (e.g., chimpanzees, Sayers and Menzel 2012), it is likely that differences between the long-lost feeding behavior of *Ardipithecus* and living *Pan* are considerable.

The differences in postcranial anatomy would also make *Ardipithecus* and all later hominids slower and more injury-prone than living apes, and thus more susceptible to predation (e.g., Brain 1981; Hart and Sussman 2005). Given their anatomical constraints, early hominids likely responded behaviorally to such danger in a fashion partially contrasting with that of living apes. While chimpanzees can evade many predators with their locomotor prowess, our immediate ancestors certainly could not. The possible hominid behavioral responses may have included increased group sizes, greater within-group cohesion, cryptic evasion, and/or increases in tool-based predator deterrence and mobbing behavior (see Treves and Palmqvist 2007).

Given that biological fitness is the currency of natural selection, it is also important to stress that *A. ramidus* also likely differed from extant apes in reproductive and social strategies. The combination of a non-honing canine premolar complex and relatively low skeletal and canine dimorphism in *A. ramidus* (Suwa et al. 2009; White et al. 2009) suggests reduced variation in male reproductive success, reduced promiscuity by one or both sexes (especially when considering later hominid characters, see Pusey 2001), and a breeding situation emphasizing female mate choice (likely in favor of less aggressive-looking males) as opposed to overt male–male competition (Lovejoy 2009). In addition, the probable increase in range size that would accompany increasingly terrestrial habits from *Ardipithecus* through *Australopithecus* (due to the arboreal canopy becoming less and less accessible, Lovejoy 1981, 2009) would likely involve a concurrent reduction in territorial behavior (see Mitani and Rodman 1979). As with ecological and morphological characters, attempts to pigeonhole ancestral human mating and social systems into that of an extant ape will likely result in error.

The differences between emergent hominids and living apes detailed above are, once again, anything but trivial; indeed, it is unlikely that a researcher can truly understand human evolution without acknowledging them. Foraging, safety, and reproduction have long been considered to be the three broad categories of activity to which virtually all selective pressure on anatomy, behavior, and ecology are related (for primates, see Zuckerman 1932; Lovejoy 1993). *A. ramidus* almost certainly differed significantly from living apes in all of them; the LCA of *Pan* and *Homo* likely did as well (Lovejoy et al. 2009); and the same can be said for *Australopithecus* and later hominids (Latimer et al. 1981; Sayers and Lovejoy 2008). This does not, of course, make ape work any less relevant or interesting—differences are of course as important as similarities—but does suggest that the hominoid referential view is outmoded and in need of change.

This lengthy but necessary discussion suggests that human origins research is best performed by examining a plethora of species, whether first hand or through the literature. One undoubtedly valuable tool, as noted above, is the comparative method, which uses phylogenetic comparisons to identify homologous and analogous characters. The comparative method has a long history in primatology, particularly with respect to anatomy and physiology (e.g., Huxley 1863), and is essential for accurate reconstruction of primate, including human, evolution.

Several problems or limitations associated with the comparative method, however, should at least be mentioned. First, within primatology, comparisons tend to be based on small numbers of species, particularly humans, chimpanzees, and (for laboratory studies) rhesus macaques, likely obscuring much of the relevant variation in primate evolution. Rhesus macaques, for example, obviously do not accurately capture the characteristics of all Old World monkeys. Second, behavioral characters are frequently vaguely defined or not linked with their proximate causes. As a result, certain behavioral suites with potentially contrasting genetic/physiological/cultural underpinnings may be erroneously lumped together (e.g., chimpanzee and human male aggression, see Sayers et al. 2012). Third, in situations where abilities (e.g., perceptual, cognitive) are being measured, misleading results can be attained when the ecological milieu of the species in question are not adequately considered (i.e., the tests are not "species-fair" or "ecologically relevant," Cook 1993). Lastly, comparisons, for pragmatic reasons, generally consider species as "types," and thus are prone to overlook the considerable, often crucial, variation within species. These caveats are by no means limited to the use of the comparative method within primatology, however, and, if such pitfalls can be avoided, these techniques can provide a powerful tool for identifying many of the important adaptive shifts in primate and human evolution.

Another important source of information, which will receive special consideration here, are broad evolutionary principles again derived from a variety of organisms (and in this respect similar to the comparative method) but which must be applied to specific cases (e.g., *Australopithecus africanus* at time and site *x*) based on the organism's unique characters. These would include well-supported predictions from behavioral genetics, competition theory, niche theory, life history theory, foraging theory, sexual selection, kin selection, movement ecology, game theory, and so on (e.g., Bulmer 1994; Westneat and Fox 2010). These are models that are tested using a wide range of *individuals* (for broad models, individuals across species), and then utilized to predict characteristics of other *individuals*. A wide range of creatures, including primates, provide the raw material for the development of such "strategic models" (Tooby and DeVore 1987) that can be utilized to predict the behavior of our earliest hominid relatives based on their individual anatomy, habitat, etc.

And with this we get to the crux of this chapter and its more specific relevance to this volume. Primates living at high altitudes face unique *problems* that differ in some respects from other primates, and which are broadly similar to those faced by hominids at certain temporal and spatial points during human evolution. In some cases these problems can be defined by elements of the abiotic environment—altitude and its effect on oxygen availability, aridity, temperature—with predictable selective pressures resulting. High altitude and other comparatively marginal environments also are characterized by predictable features of the biological environment, such as particular patterns of resource distribution. Wide-ranging research from evolutionary ecology suggests that responses to such heterogeneity will be similar in certain general ways regardless of taxa, but always tailored to the unique morphology and evolutionary history of the animal. It goes without saying (actually it does not, so the author is saying it) that some environmental and ecological features which covary with elevation are far more quantifiable in theory or actuality than the determinants of such staple primate fodder as tool use or cultural learning.

It is important to recognize that although high altitude organisms are being examined here, the chapter is "about" more than just elevation. Elevation changes, as will be detailed below, mimic changes in latitude, which bring along with it a plethora of predictable environmental changes. A snub-nosed monkey living at 3,500 m elevation may face similar thermoregulatory concerns to what a Neander Valley hominid living at 100 m elevation faced 40,000 years ago—although the monkey does so without the controlled use of fire. Such overlap in selective pressures could be expected to result in certain parallel adaptations in anatomy and physiology. Similarly, an Assamese macaque living at 2,500 m might negotiate patterns of resource seasonality not unlike that Dmanisi hominids negotiated 1.8 million years ago (see Reed and Fish 2005). Certain general rules concerning behavioral responses to food availability could be expected to apply to both organisms, whether or not their actual diets were similar, and despite the fact that the former rarely uses tools. The question is not whether high-altitude nonhuman primates can successfully be used as referential models for early hominids—as with living apes, they certainly *cannot*, at least in a broad behavioral sense—but instead whether they can provide information on how our forebears solved problems in their own unique way. It is argued that they can indeed help provide such information.

High Altitude Habitats, Marginal Habitats, and Primate Anatomy and Physiology

Human Evolution

One of the defining characteristics of the human lineage is the ability to colonize novel habitats, and, in terms of classical life history theory, this is only one of several r-selected features in what is traditionally thought of as the most K-selected of primate groups (MacArthur and Wilson 1967; Lovejoy 1981). Evidence indicates that this ecological flexibility may be quite ancient (Brunet et al. 1995; Potts 2012). Although it is not possible to state unequivocally at which time our direct ancestors first occupied what might be called "high altitude environments," we know that the habitats being exploited were extraordinarily varied at least from the time of *Australopithecus*, and perhaps earlier. At just what elevation a location can be considered a "high altitude environment" is open for discussion, of course, so altitude here will simply be considered a continuous variable, with predictable correlates as it varies. From the perspective of this chapter, altitude is primarily important for setting up the problems that are faced by the organisms living there, some of which (low temperature, aridity) are experienced by some creatures living in habitats that are decidedly *not* high altitude. Whether or not elevation is the same, similar selective pressures would of course tend to promote convergent evolution.

The Miocene hominid *Ardipithecus kadabba* (5.2–5.8 mya, Haile-Selassie 2001; Haile-Selassie et al. 2004) lived in what have been described as "cool, high altitude and/or humid habitats"—based oxygen isotope ratios (WoldeGabriel et al. 2001:177), and associated paleofauna includes abundant cane or mole rats (*Thryonomys* spp.) which today are characteristic of highland settings. Although directly analogous environments have yet to be argued for australopithecines, it is clear that they were also quite plastic in their habitat occupation (Brunet et al. 1995; Bonnefille et al. 2004). By the early to middle Pleistocene, *Homo* was clearly a jack-of-all-trades ecologically, and lived in many biomes, including highland and arid habitats (Wolpoff 1999). Recent work in the Pindus Mountains of Greece has unearthed Middle Paleolithic Mousterian stone tool sites at elevations of up to 2,100 m (Efstratiou et al. 2006, 2011) and modern humans continue this tradition, inhabiting numerous locations above 3,000 m, most spectacularly the permanent Tibetan residences that exist up to approximately 5,000 m (Beall 2006).

Correlates of Increasing Altitude

There are numerous predictable environmental changes with increasing elevation, and these can be related to anatomical, physiological, and behavioral adaptations or responses for the organisms which live there. Most striking, there are changes related to the abiotic or geophysical environment that in turn measurably influence the biological one. At higher elevations, there is a general increase in ultraviolet radiation (UV) and aridity, as well as related reduction in barometric pressure (reducing the amount of oxygen available) and ambient temperatures (Baker 1984).

Ultraviolet Radiation

Ultraviolet radiation, of which exposure increases at higher altitudes, has been argued as the basis for numerous evolutionary adaptations in taxa ranging from microorganisms to humans, and can exert direct effects both on individual organisms and the organic world around them. The evolution of human skin pigmentation patterns, for example, has long been understood as reflecting responses to geographically specific UV exposure, which is involved (on the positive side) in vitamin D production and (on the negative side) in the destruction of folate, a compound integral to DNA synthesis (Jablonski and Chaplin 2010). The Tibetan plateau, for example, receives higher UV than lowland settings at comparable latitudes, and some have related this to the skin pigmentation patterns of the region's human denizens.

While nonhuman mammals and birds are often considered shielded from most negative bodily effects of UV exposure by the protection of hair or feathers—and thus cannot be utilized as direct anatomical analogs for later hominids in this regard—there may be environmental correlates that could potentially influence food distribution, and thus (in similar ways) human and nonhuman foraging strategy. Although these correlates are complex and interrelated with other variables such as temperature and moisture, increased UV levels have been linked with altered susceptibility of plants to predators, parasites, and disease, with reduced plant productivity or chlorophyll content, and with increased leaf thickness (Bornman and Vogelmann 1991; Caldwell et al. 1998). Such effects could potentially contribute to the overall lowering of food and habitat quality at high altitudes, and, if so, would favor increasingly "generalist" dietary selection (see below).

Aridity

Air becomes drier at higher altitudes, or aridity increases, and this again will have an influence on the environment. Plants generally become smaller in size and overall biological productivity is reduced (Cronin 1979). Whereas plants in more humid locales are noted for above-ground competition for light, plants in arid environments often focus their evolutionary energies on underground competition for moisture (Dai et al. 2009). While this again reduces the "typical primate" above-ground plant vegetative and reproductive foodstuffs, and thus again can reduce overall habitat quality and encourage generalist foraging, the biomass of other resources such as underground storage organs (USOs) may increase (Andersen 1987; Wrangham et al. 1999).

The utilization of USOs has been considered by some as a key feature allowing early hominids including *Australopithecus* and *Homo erectus* to occupy increasingly variable habitats, particularly more arid ones, and has even, controversially, been linked with key changes in hominid social structure (Wrangham et al. 1999; Laden and Wrangham 2005). While much has been made of the fact that savanna chimpanzees will on occasion exploit USOs (Hernandez-Aguilar et al. 2007), the same can be said for capuchins (which, like savanna chimpanzees, do so with tools, Moura and Lee 2004), baboons (Altmann 1998), and high-altitude black and white snub-nosed monkeys (Ren et al. 2008) and Himalayan gray langurs (Sayers et al. 2010). Note that these are all primates living in relatively arid habitats (for one exception, see Hockings et al. 2010). The exploitation of USOs, however, should not be the factor that is considered particularly relevant here—either for living nonhuman primates or extinct human ancestors—but instead focus should be placed on the ecological variables that are causally related to such behavior (e.g., habitat quality, the profitability of USOs in comparison with other foods, and the influence of these factors on dietary niche breadth, see below).

Numerous models of human evolution, in addition, highlight the effects of cooling and accompanying aridification and seasonality on the origin, evolution, or extinction of particular animal and plant species (reviewed in Potts 1998, 2012; Wolpoff 1999). Following lead from the classic savanna hypothesis (Dart 1925, 1953), perhaps the most well-known modern version is the turnover-pulse hypothesis, which argues that changes in the physical environment precipitate, in a punctuated fashion, most or all extinction and speciation events (e.g., Vrba 1980, 1993). In relation to human evolution, numerous lines of geophysical evidence, including the fossil record, have been utilized to postulate links between Plio-Pleistocene African climatic shifts with the extinction of woodland species and the concurrent rise of what are considered more open-country forms (e.g., certain hominids). The most critical hypothesized pulses have been placed at: (a) 5.0 mya, which is linked with the origin of classic hominids and by extension pivotal traits such as bipedality, (b) 2.5 million years ago, which is linked with the origins of hyper-robust australopithecines, *Homo*, and modified stone tools, and (c) 0.9 mya, which is linked with the extinction of the robust australopithecines (Vrba et al. 1989).

There are a number of avenues for testing such hypotheses, or for otherwise gathering information relevant to their evaluation. The first, obviously, involves continued examination of the fossil record to document the timing of evolutionary change. The findings that bipedality likely evolved in forested habitats (e.g., White et al. 2009) and that mammalian turnover in the Turkana region during the late Pliocene was more gradual than punctuated (Behrensmeyer et al. 1997), for example, argue against the proposed turnover-pulses at 5.0 and 2.5 mya, respectively. Another obvious avenue is the continued collection and analysis of paleoclimatic data. Current research in this area suggests prolonged periods of environmental variability in Africa from the late Miocene to Pleistocene, leading to an alternative hypothesis which stresses climate fluctuation as opposed to unidirectional changes in aridity (the variability selection hypothesis, reviewed in Potts 2012).

These geological lines of evidence, while important, do not actually inform on the causal processes of evolution. At best they can demonstrate correlation. But how do individual animals, or multiple individuals within a species, actually respond to differences in environmental characteristics, whether they involve aridity, temperature, seasonality, or other factors? How do these responses vary between individuals of closely related species? To answer such queries, increased focus must be placed on extant forms. As Wolpoff (1999:320) noted, while addressing the issue of climate change and causality: "One way to approach this question is to examine how increased aridity and seasonality affects living primates with broad enough geographical ranges to potentially reflect climate variation." Primates ideal for such investigation include (but are not limited to)

Macaca mulatta, *Semnopithecus entellus*, *Alouatta palliata*, *Lemur catta*, and some forms of *Papio*.

All too often paleoanthropologists are quick to link habitat changes with major alterations in hominid anatomy, and the turnover-pulse hypothesis is perhaps only the most familiar modern example. One gets the impression that some of these workers are unaware that many animals possess broad fundamental niches (i.e., are generalists), including the primates listed above and probably most or all hominids. As noted, changes in aridity are associated with changes in habitat characteristics, including food and water availability, but phenotypically-pliable animals can adjust to some new environments simply by altering behavior. A first line of inquiry in relation to climate-determinate models of human evolution is thus to determine the flexible responses of individuals within a species living in different habitat types. Intraspecific comparisons of this type of by no means rare in primatology, but generally involve gross food exploitation (percentage fruits, leaves, etc.), general activity patterns (percent time resting, feeding, etc.), or other crude measures (daily path length, group size, etc.). These variables, unfortunately, provide little information on the proximate mechanisms underlying behavior. In relation to feeding, for example, the data most sorely needed relate to perceptual and psychological models of resources use; e.g., the nutritional value of foods, the physiology of digestion for specific foods, the sensory basis of foraging, the abundance and distribution of specific food types, how distribution is related to movement, and the time taken to handle specific foods (Sayers 2013 and see below). Such information can inform on the plasticity of generalist primates even in cases with little or no underlying genetic or morphological change.

Another important goal of such studies is to elucidate the limits of such flexible responses (i.e., ecological extremes), and any genetic, physiological, or morphological differences that allow these limits to be reached (Bishop 1979). Such data, as noted, are critical for evaluating questions central to climate-determinant models of human evolution. What habitat changes—whether increased aridity or other—would, absent genetic variability allowing pertinent adaptation, promote local extinction? Given (or assuming) the requisite genetic variation, what factors would promote directional, stabilizing, or disruptive selection? Although some data relevant to these questions are available (Cahill et al. 2012), no systematic evaluation of them, in relation to models of human evolution, has yet been performed for any nonhuman primate.

It has been argued that comparing savanna versus forest chimpanzees can inform on the behavior of early hominids which moved into more open or arid habitats (Moore 1996). This is certainly the case when the studies involve general ecological principles (e.g., habitat quality and diet breadth) and indeed the same justification can be applied to the study of any nonhuman primate that inhabits multiple habitat types. One problem is that many savanna/woodland chimpanzee comparisons have focused on singular, tangential investigations of anthropological buzzwords such as tool use, hunting (Pruetz and Bertolani 2007), USOs (Hernandez-Aguilar et al. 2007), and fire (Pruetz and LaDuke 2010). Research should be expanded to include more general—and, as viewed here, more basic—

evolutionary questions, and this necessitates comparative data from myriad nonhuman animals. Early hominids were different in critical ways from living primates, as detailed above, and simplistic referential models should be avoided.

Hypoxia

Perhaps the most famous environmental effect of increasingly higher altitudes is the reduced availability of oxygen, or hypoxia. Responses to low oxygen conditions can be related to phenotypic plasticity (acclimatization), genotypic state, or both. It is interesting to note that even within *Homo sapiens*, different populations have adapted to hypoxia in different ways. The concentration of oxygen in the blood is influenced by both the concentration of hemoglobin—the component of red blood cells that carries oxygen to tissues—and the proportion of hemoglobin that is carrying this element, termed oxygen saturation. A comparison of high altitude human populations in Tibet, Ethiopia, and the Andes shows differences in hemoglobin concentration and oxygen saturation; Andeans and then Tibetans score highest in these measures. The Ethiopian sample, surprisingly, does not differ from populations living at sea level. Also surprisingly, genetic work has indicated differences in the heritability of these features between the groups (Beall 2006).

Similar trends emanate from nonhuman animals living in reduced oxygen conditions, including not only high altitudes, but also, in the case of burrowing forms, underground habitats. Some of these birds and mammals exhibit particular genetic adaptations to hypoxic conditions while others do not, demonstrating again that there is more than one way to skin a hypoxic cat (reviewed in Storz et al. 2010). The high altitude bar-headed goose (*Anser indicus*) of Asia, for example, has increased capillarity in the heart and flight muscles which aid oxygen transport. These characters occur in the goose regardless of whether or not an individual was reared at high elevations, unlike in a fellow high-elevation avian, the Andean coot (*Fulica ardesiaca*, León-Velarde et al. 1993). In relation to environmentally responsive traits, an especially interesting contrast can be made between “adaptive phenotypic plasticity”, which allows colonization of such extreme environments, and “maladaptive plasticity”, which hinders it (Storz et al. 2010:4125). An example of the latter would be physiological changes, such as arterial hypertension, that paradoxically can reduce oxygen transport in lowland forms when acclimatizing to higher elevations. It is expected that organisms with favorable phenotypic plasticity will be more likely to invade hypoxic habitats, with selection potentially acting on the underlying genotype after a population is established.

The physiological or genetic predispositions of most nonhuman primates living in high altitude habitats is little known, but the research performed to date is promising and suggestive that further work will illuminate the shared versus derived aspects of human high altitude adaptation. A study of the hemoglobin of the gelada baboon (*Theropithecus gelada*), which inhabits Ethiopian montane grassland from 1,400 to over 4,000 m elevation (Rowe 1996), revealed higher rates of oxygen binding than the comparatively lowland hamadryas (*Papio hamadryas*) or anubis (*P. anubis*) baboons (Takenaka 1980).

In another study, the ratio of nonsynonymous to synonymous mutations—those which change or do not change the encoded protein—of mitochondrial DNA evinces evidence of positive selection in the NADH dehydrogenase genes of the golden snub-nosed monkey (*Rhinopithecus roxellana*), and in contrast to eight other sampled colobines. The NADH genes are integral to oxidative phosphorylation (adenosine triphosphate production) and are thus crucial for oxygen utilization and energy regulation. Positive selection for them in *R. roxellana* is argued to be related to their cold, high altitude environment, which reaches to over 4,000 m in the coniferous and broadleaf forests of China, and similar to mitochondrial genes in other high altitude forms, including various pikas, antelopes, and camels. Although the hypothesis is intriguing, more comparative data are needed—on both the distribution of NADH bases and its phenotypic/physiological consequences—to adequately evaluate it. Interestingly, the black and white snub-nosed monkey (*Rhinopithecus bieti*) which inhabits elevations at least as high in montane forest (Kirkpatrick 1998), did not show evidence of this positive selection, and it is possible that clues to its remarkable hardiness in relation to heredity and hypoxia may lie in the nuclear genome (Yu et al. 2011).

Temperature and Ecogeographic Rules

The colder temperatures that occur with increasing altitude in some ways mimic the effects of latitudinal changes, and have long been studied in the context of ecogeographic rules. The most famous of these is Bergmann's Rule, which holds that homeotherms in cold climates or higher latitudes are expected to be larger than closely related species, or individuals within the same species, living in warmer locales or lower latitudes (Bergmann 1847). This rule has been examined in a wide range of taxa, using widely different units of analysis—including within species, across species, and even across genera, families, classes, and orders (Meiri 2011). In general the rule holds for many taxa, including birds and mammals (Meiri and Dayan 2003) and some primate genera or families (Harcourt and Schreier 2009), but not across certain groups, such as Malagasy primates (Kamilar et al. 2012). It has been pointed out, however, that Bergmann considered the body size-temperature connection to be the strongest within single species, so it is expected that greater discrepancy will occur at higher taxonomic levels (Meiri 2011).

The most-cited functional explanation for Bergmann's Rule is the hypothesis of its namesake: that it is related to the retention of heat, which is dissipated more slowly in individuals of larger body size, which have decreased relative surface area when compared to smaller individuals (Minkoff 1983). Alternative or complementary hypotheses exist; for example, that body size is actually related to biological productivity, which happens to be correlated with temperature (positively) and latitude (inversely) (Rosenzweig 1968). In primates, this may be relevant to the Jarman-Bell Principle, which relates larger body size to generally decreasing "nutritional quality," which is also (potentially) characteristic of cooler temperatures and higher latitudes (Gaulin 1979).

The two nonhuman primates with the widest geographical and habitat distributions clearly conform to Bergmann's Rule. The first is the gray langur (*S. entellus*), which is distributed throughout Sri Lanka and the Indian subcontinent in habitats ranging from subtropical forest to Himalayan regions approaching or exceeding 4,000 m. The other is the rhesus macaque, which is found throughout much of Asia, from tropical forest to the Himalayan foothills. Both species, without question, increase in body mass with increasing latitude, based on skull data (Albrecht and Miller 1993; Plavcan et al. 2005). No statistics are necessary; in the gray langur, for example, adult members of Himalayan populations weigh about twice as much as those in Sri Lanka (Oates et al. 1994). Bergmann's rule also broadly applies in humans; for many populations, the correlation coefficient between latitude and body breadth, a surrogate measure for mass, is greater than 0.90 (Ruff 1993).

Another famous ecogeographic rule is Allen's Rule, which asserts that within a variable species, or closely related forms, protruding body parts, such as limbs, ears, and tails, will be shorter in colder environments than in warmer ones (Allen 1877). Again, the functional explanation is generally thermoregulatory; shorter protruding parts equate to lower relative surface area and reduced heat dissipation (Minkoff 1983). Studies with mice have shown that individuals reared in cold temperatures have reduced cartilage proliferation in their extremities than those reared in warmer temperatures, and that this appears to be related more to the direct temperature of the appendage than to blood flow (Serrat et al. 2008). While this suggests that Allen's Rule is at least partially a question of phenotypic plasticity, little is known about the genetics underlying this plasticity, or any more direct genetic involvement.

Allen's Rule, like Bergmann's, has been widely applied to humans—particularly in relation to limb lengths—and has found support under a variety of measures (Newman 1953; Ruff 1993). This rule also appears to be generally consistent with observed morphological variation in nonhuman primates, although its success, once again, will vary dependent on the taxonomic levels and geographical range considered, as well as other (often selective) factors. The most detailed information comes from *Macaca*, perhaps the most demographically successful extant primate genus other than *Homo*. A study of the joint diameters and extremity lengths of six macaque species reveals that species from higher altitudes or temperate latitudes tend to have larger joint diameters and shorter limbs, consistent with Bergmann's and Allen's Rules (Weinstein 2011). Again, differences in protruding body parts appear to be at least partially related to the environmental conditions under which an individual is reared; adult Japanese macaques (*Macaca fuscata*) living in the southern United States were characterized by lower body weights and longer limb segments than another group living in the northern United

States (Paterson 1996). All “rules” are meant to be broken, however, and there are exceptions: a detailed study of crab-eating macaques (*Macaca fascicularis*) from Southeast Asia found no relationship between tail length and either temperature or latitude (Schillaci et al. 2009).

Such exceptions notwithstanding, Allen’s Rule is successful enough, and general enough, to be of importance to fundamental questions in hominid evolution. Comparisons of early *Homo* (e.g., KNM-WT 15000) with later, cold-adapted forms such as Neandertals, for example, illustrate predictable differences in limb length that certainly can be linked to the temperatures these forms were exposed to (Ruff 1993).

The study of physiological effects such as those related to Bergmann’s and Allen’s Rules represent more than just an archaic rumination on topics left over from the nineteenth century. Our increasing knowledge of the mechanisms behind the development of extremities, for example, including environmental effects (Serrat et al. 2008), has vital repercussions for the characters that can or should be chosen for phylogenetic analyses and the construction of evolutionary trees. In early hominid taxonomy, for example, a femur or humerus (or insert other bone) may be divided (“atomized”) into dozens of separate characters; a common theme seems to be that if you can measure something, you should include it when generating cladograms (for theoretical discussion, see Gould and Lewontin 1979; Mayr 1983). While some skeletal characters are directly influenced by gene expression, however, others may be by-products of such expression, related to systemic growth factors, indicative of environment or behavior only, or unrelated to anything meaningful (Lovejoy et al. 1999). By including all such “character types” in a reconstruction, there is an increased probability, for example, of counting one genuine character multiple times, and of corresponding error (e.g., taxonomic inflation).

Modern humans, although following Bergmann’s and Allen’s Rules, obviously have many cultural buffers to cold and inclement weather, such as clothing and fire, that nonhumans lack. Nonhuman primates living at high altitude do have, however, some behavioral responses that could potentially (but see Kirkpatrick 1998) be linked to low temperatures, such as the frequent huddling behavior observed in Japanese macaques (“lumping,” Suzuki 1965), Himalayan gray langurs (Bishop 1979; Sayers and Norconk 2008), and black and white snub-nosed monkeys (Kirkpatrick 1998).

Ecological Correlates of Increasing Altitude, and Its Effect on Behavior

As features of the abiotic environment change with increasing altitude, as noted above, features of the biological environment change as well. It is interesting to consider that nearly all of these changes, such as increases in aridity and decreases in temperature, have the sum effect of making a habitat more marginal and seasonal (Cronin 1979). There is less biological productivity on average, and the effects regarding animal behavior can be profound (Pianka 1994). Altitude and its correlates, of course, are only a part of the picture, and other factors, particularly precipitation patterns, will have significant effects on factors such as plant diversity, abundance, and the seasonality of production. The relationships between altitude and precipitation are complex, however, and can vary even over small geographical distances (e.g., Polunin and Stainton 1997).

Many broad surveys of primate ecology often focus solely and explicitly on tropical primates (van Schaik and Brockman 2005), which is not surprising given that the vast majority of extant forms inhabit a narrow belt around the equator. With considerations of human evolution, however, it is paramount to extend these evaluations to primates whose ranges extend outside the tropics. In many cases (e.g., *Macaca*, *Alouatta*, *Semnopithecus*) these are primates which have considerable demographic success and live in a wide variety of habitats, including high altitude and temperate regions. In this respect, they are especially important taxa for comparison and contrast with hominids, which are notable not just for advanced cognition and communication, but also the related—and just as important—ability to occupy an extraordinary range of habitats (Richard et al. 1989; Hart and Sussman 2005). While our current cooperative and technological abilities have allowed us to push the limits of such adaptation, there are, as noted previously, indications that its roots extend back to the dawn of human evolution—certainly at least to gracile *Australopithecus*, which possessed remarkably generalized dentitions and ranged at least from South Africa to present-day Chad in a wide variety of habitat types (Brunet et al. 1995, 2002; Bonnefille et al. 2004). These forms were not specialists in any sense of the word.

And this is why, from an ecological and anthropological perspective, marginal habitat primates are important. They live in environments that, in terms of resource distribution and other factors, were becoming increasingly common throughout human evolution. Particularly common are wide-ranging, demographically successful primates that can be compared and contrasted in a gradation of differing habitat types. Although a book could be written about the numerous repercussions, it is convenient to concentrate here, as an example, on feeding behavior. In general, most foraging animals face essentially the same problems: where to go to find food, what to eat when you get there, and how long to stay before moving on (Pyke et al. 1977; Menzel 1997). And basically, whether you are a praying mantis feeding on fellow insects, a langur harvesting leaves, or a human hunter–gatherer collecting fruit, the rules are the same: acquire the most energy possible given the time you spend foraging.

So, given that the rules are the same, we can expect broadly similar responses to changes in food availability whether the animal in question is hermit crab, howler, or hominid (the alliteration follows Crockett 1987). From a sensorimotor and perceptual perspective, the underlying mechanisms in the primates are expected to be most similar, as both the howler and hominid have, for example, sharp, trichromatic color vision. But, in a given habitat and across taxa, when profitable foods (e.g., high energy/low handling time) are common, an animal is expected to specialize. When they are rare, the diet is expected to expand to include food items that would not be taken under better conditions (Schoener 1971; Charnov 1976;

Sih and Christensen 2001). Profitability, of course, is not only dependent on the physical and chemical characteristics of the food, but on the anatomical and physiological tools that the forager has to collect, remove, and process the nutrients from the item. This, of course, is the primary proximate reason as to why animals of different species living in the same habitat—or even animals within a species that differ in features such as jaw size—have differing diets, although other factors, such as intra or interspecific competition, can also come into play.

Himalayan populations of gray langurs (*S. entellus*) illustrate these principles well. As the northernmost representatives of a form that inhabits an astoundingly diverse range of habitats (Bishop 1979; Koenig and Borries 2001), they approach the "upper limits" of the ecological challenges faced by nonhuman primates (Curtin 1982). In mountainous Nepal, the habitats are very seasonal: during spring there is deciduous leaf flush, flowering and fruiting increases throughout the mild summer monsoon, and overall food availability drops precipitously during the late fall and winter. The langurs, over the annual cycle, have an eclectic diet, including not only leaf parts, but fruits, flowers, USOs, fungi, and other items. During the snowy months of winter, very little food is available, and deciduous leaves are virtually absent (Sayers and Norconk 2008). Such dramatic shifts in food abundance, perhaps more pronounced in high-altitude environments than any other primate habitat, allow questions of diet expansion and contraction to be examined in a remarkably straightforward fashion. As will be noted, the results have direct repercussions on proposed models of early hominid diet.

Quantification of the nutritional content of Himalayan langur foods, item-specific intake rates, and the travel time between patches, illustrates that Himalayan langurs alter their foraging strategy as the encounter rates with profitable foods changes (Sayers et al. 2010). During the lean season of winter, the langurs expand their diet to include nonseasonal foods of low energetic value for the time taken to handle them, including leathery evergreen mature leaves, woody roots, and bark; foods that were routinely ignored only several months earlier. Although Himalayan langurs possess the typical colobine dental and alimentary characters that aid in the digestion of high fiber foods (Kay and Davies 1994), which include those eaten in winter, these items are clearly not preferred, and likely take more time and energy to digest (see Whelan and Schmidt 2007).

The foods taken during such ecological hard times are often today referred to as "fallback foods," but their importance was noted even in the earliest days of optimal foraging theory (Emlen 1966; MacArthur and Pianka 1966; Schoener 1971). They can, without question, lead to substantial evolutionary change, which is exemplified by a phenomenon called Liem's Paradox—the coupling of anatomical specializations (sometimes extreme) for exploiting specific food types with a generalist feeding strategy (Liem 1980; Robinson and Wilson 1998). Generalist colobines such as gray langurs could be argued to be examples of Liem's Paradox, as could certain forms of early hominid (see Sayers 2013). The massive postcanine teeth and heavily anchored jaws of robust australopithecines—instead of being an indication of narrow dietary niche breadth—might instead reflect an adaptation for feeding on low-ranking, mechanically challenging foods when more profitable resources were scarce (Peters and Vogel 2005; Ungar et al. 2008).

Primates living in comparatively marginal habitats, such as those at increasingly high altitudes, face some of the same ecological challenges as did early hominids. It is generally thought that conditions in many areas became progressively more marginal during the African Plio-Pleistocene (e.g., more arid, with reduced above-ground plant biomass); these changes (mimicked by the habitats of high-altitude primates), based on well-tested predictions from foraging theory, would likely result in a broadening of diet (Gaulin 1979). Interestingly, many reconstructions of early hominid diet (including gracile *Australopithecus*, see Teaford and Ungar 2000) trend towards postulating species-specific or specialized foraging strategies for particular hominid taxa. It would be constructive, if not transformative, for hominid diet modelers to examine the differences in foraging strategy that occur between lowland and highland gray langurs, or lowland and highland Japanese macaques (e.g., Suzuki 1965). These are animals within the same species and presumably possessing similar dental anatomy, but which (at least seasonally) feed on strikingly different foodstuffs. It is likely that early hominid diet selection, given the generalist nature of many of these forms, was far more dependent on characteristics of the habitat than putative phylogenetic constraints. As noted, this lesson is perhaps most striking when examining geographically successful primates whose distribution extends to high altitudes.

This does not mean, however, that we can utilize any specific primate, including any high altitude primate, as a strict behavioral referential model (Tooby and DeVore 1987) for our hominid ancestors, as their morphologies are different, and no two habitats are ever identical. Instead, focus should be given toward identifying and quantifying those variables most important to behavior or ecology in a wide range of primate (and other) taxa—in the case of foraging, these would include nutritional and abundance variables, time costs, and the physiology of digestion—and determining their influence on behavior. These lessons can then inform on the reconstruction of early hominid behavior. In cases where paleoenvironmental data is sufficiently detailed—and the above variables can be estimated for hominids at a particular site and time—such an approach could even lead to robust predictive models of early hominid ranging and diet.

Discussion

The reconstruction of hominid evolution is, to say the least, a difficult enterprise, and workers should be willing to take information from wherever they can get it. This includes not only the fossil and archeological records, but also our closest relatives, and our more distant relatives. Nonhuman primates have long been regarded as pivotal for understanding our origins, and rightly so. They are a constant source of information, and their many similarities to (and differences from) ourselves help inform us about what it means to be human. But there is not a particular species that is the "best" model for human evolution; indeed, there is no particular reason for even attempting to identify such a model. All primates—every last one of them—are relevant. Nonprimates, for that matter, are important as well (Sayers and Lovejoy 2008).

Obviously, this does not mean that any particular question in human evolution can be investigated with just any nonhuman animal. An individual interested in the ecological determinants of tool use, for example, might not want to study *Alouatta*, where the instances of such behavior per annum can be counted on one hand, or finger. But there are innumerable questions in human evolution, and in anthropological primatology, even though interest seems to be increasingly given to fewer and fewer such questions. There is more to life than tool use, culture, or African apes. While *Alouatta* might not be the best subject for studies of tool use, it is an excellent one for the investigation of sexual selection (Crockett 1987). Given the many obvious epigamic features of modern humans, it could be argued that this topic is every bit as important to hominid evolution, or even more so. And it is also likely that the elucidation of what variables are important to the ranging and dietary selection of animals generally—robust rules of behavior that usually involve time and energy—will prove far more useful than singular focus on the tools that the odd nonhuman animal uses to extract a particular food.

High altitude and other marginal habitat primates, whether ape or otherwise, are relevant to anthropology for myriad reasons. They evince some—but not all—of the anatomical, physiological, and behavioral adaptations that illuminate the mechanisms by which humans achieved almost unprecedented demographic success. Understanding such adaptations may not open a window to the past, but will undoubtedly illuminate the processes which occurred in the past. Humans are unique, as are chimpanzees, snub-nosed monkeys, and sportive lemurs. When all is said and done, evolution basically comes down to reproduction, and (for multiple breeders) feeding and staying alive to achieve more reproduction. These are problems faced by all animals, and not just our closest relatives. The reconstruction of human evolution should be concerned with elucidating the behavior of unique forms, but with general principles derived from all species.

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