CHAPTER TWENTY-THREE

New Perspectives in the Study of Mesoamerican Primates: Concluding Comments and Conservation Priorities

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INTRODUCTION

The monkeys of Mesoamerica represent an ecologically diverse and successful radiation of non-human primates that inhabit the tropical and subtropical forests from Mexico south and east into Guatemala, Belize, Honduras, Nicaragua, Costa Rica, and the border between Panama and Colombia. This includes a maximum of 9 species and as many as 21 subspecies (Rylands *et al.*,

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this volume). Although howlers, capuchins, spider monkeys, night monkeys, squirrel monkeys, and tamarins represent only a small proportion of the enormous biodiversity of the Mesoamerican region, they are an important component of the community of arboreal mammals in tropical forests, accounting for approximately 61% of the 55 recognized taxa (15 rodent taxa, 13 marsupial taxa, 4 carnivore taxa, and 2 sloth taxa) (Reid, 1997; Emmons, 1990). Further, populations of these species are likely to play a critical role in the recycling of matter, nutrients and energy in the ecosystem (Estrada and Coates-Estrada, 1993). Primates also serve as pollinators and seed dispersers of tropical plants, and in forest regeneration (Lambert and Garber, 1998). Moreover, as outlined by Ford (this volume), the biogeography and dispersal of primates into Mesoamerica occurred as part of a complex set of geological, climatic, ecological, and evolutionary events that have shaped the history of Mesoamerica over the past million years. Different primate lineages entered Mesoamerica at different times, and therefore represent distinct colonization and speciation events.

The study of Mesoamerican primates also holds special significance for the discipline of primatology. From 1931 to 1933, Clarence Raymond Carpenter conducted the first long-term field study of a primate in the wild. Carpenter (1934: 6) studied the "behavior, social relations, and ecology of howling monkeys" (*Alouatta palliata*) on Barro Colorado Island, Panama. Writing the Foreword to Carpenter's (1934) monograph, Robert Yerkes predicted, "Looking forward, it is certain that Doctor Carpenter's contribution may be counted on to command the attention and stir the enthusiasm of other investigators" (Carpenter, 1934: 4). This has certainly been the case. Over the past 70 years, the efforts of many dedicated researchers have contributed importantly to our understanding of the distribution, ecology, behavior, and conservation of Mesoamerican primates.

STUDIES OF MESOAMERICAN PRIMATES

The primary goal of this volume was to integrate and synthesize current information on primates in the Mesoamerican region and examine how anthropogenic factors (such as deforestation, agriculture, and habitat change) as well as natural disturbances (such as hurricanes) affect the current distribution, demography, behavioral ecology, and conservation status of individual taxa. During much of the 20th century, several areas of Mesoamerica have been characterized by political instability, civil war, poverty, and devastating natural and human-induced habitat destruction. For countries such as El Salvador, Guatemala, Honduras, and Nicaragua, only now are we beginning to collect surveys and basic scientific information on their remaining primate populations. El Salvador maintains the highest human population density of any country in Central America, poverty is extreme, and much of the original forests has been cut (see Estrada *et al.*, Chapter 1). The country's entire populations of howler monkeys and capuchins may now be extinct. Spider monkeys continue to exist in El Salvador, but their density, habits, and viability are poorly known. However, recent efforts by local biologists are beginning to provide information about the current distribution of spider monkey populations in that country (Morales, 2002).

The countries of Mexico, Belize, Costa Rica, and Panama, are the sites of the five long-term primate field study sites in Mesoamerica: Los Tuxtlas, Mexico (*A. palliata* and *Ateles geoffroyi*), Baboon Sanctuary, Belize (*Alouatta pigra*), Santa Rosa, Costa Rica (*Cebus capucinus*, *A. geoffroyi*, and *A. palliata* at the site), Hacienda La Pacifica, Costa Rica (*A. palliata*), and Barro Colorado Island, Panama (*A. geoffroyi*, *C. capucinus*, *Saguinus geoffroyi*, and *A.palliata*). While these long-term study sites have provided detailed behavioral, ecological, and demographic data for primate populations that span decades, they have focused principally on three primate species: mantled howlers, black howlers, and white-faced capuchin monkeys. These taxa, however, are among the least endangered Mesoamerican primates, and given the number of studies that have focused on them (Estrada *et al.*, Chapter 1), it is not surprising that this volume is heavily weighted to studies of these three species.

Despite many decades of research throughout the Mesoamerican region, several questions concerning primate behavior, ecology, and conservation remain unanswered. In the case of *A. palliata*, *A. pigra*, and *Cebus*, long-term studies have been conducted in only a small number of localities (long-term studies of *C. capucinus* have been concentrated in the dry tropical forests of Costa Rica) and therefore, we have limited information on variability in ecology and behavior across a spatial scale encompassing the range of habitats exploited by these species. Moreover, only two of these long-term study sites (Los Tuxtlas, Mexico and Santa Rosa National Park, Costa Rica) represent large, continuous forested areas. In contrast, the Community Baboon Sanctuary in Belize and Hacienda La Pacifica in Costa Rica consist of fragmented forests and/or linear strips of vegetation along rivers. Barro Colorado, Panama is a relatively small island (1600 ha) and lacks the normal range of predators found on the mainland. Clearly, there is a need to study Mesoamerican primates in areas of continuous forests.

For species such as *Saimiri oerstedii* (Boinski, 1987a,b; 1994), *S. geoffroyi* (Dawson, 1975; Garber, 1980, 1984a,b), and *A. geoffroyi* (Coelho *et al.*, 1976; Cant, 1986; Chapman, 1987, 1988a,b; Milton, 1981a,b) we have data for only a single group over the course of 1 year, or studies of a few groups over shorter periods. In the case of *Aotus zonalis*, there exist virtually no published studies and we continue to lack even the most basic natural history information (Moynihan, 1964; Thorington *et al.*, 1976). Even for those species for which we have detailed information, we know very little about dietary and habitat flexibility, and how these species respond to changing environmental conditions associated with human disturbance.

Recent studies of fragmented landscapes (Murcia, 1995; Restrepo *et al.*, 1999) indicate that edges represent dynamic components of an ecosystem, and that edge effects change over time. For example, Restrepo *et al.* (1999) have described changes in fruit abundance, leaf area, water availability, soil fertility, temperature, and humidity not only between edges and interior habitats, but also between older and younger edges. In other cases, however, edges and interior forest zones may contain similar plant species. Williams-Linera (1990) reports that in a lowland rainforest in Panama, there were no significant differences in tree or seedling species composition in the forest edges and the forest interiors. Given that edge effects are neither uniform nor standard, from site-to-site (Murcia, 1995), it is difficult to predict exactly how a primate species will respond to the specific conditions of a forest fragment (edge plus interior), and the effect that factors such as the distribution of resting or refuse sites, gaps in the forest canopy, suitable routes for arboreal travel, and exposure to predators have on the ability of individual primate species to survive in human-disturbed forest landscapes (Chapman and Peres, 2001)

Aotus, Saimiri, and Saguinus

The Mesoamerican primates that we know least about, *Aotus*, *Saimiri*, and *Saguinus*, are small-bodied platyrrhines that differ significantly in behavioral ecology, social organization, mating systems, and life history strategies. *Aotus* is reported to live in pair-bonded nuclear family social groups and is the only species of higher primates to adopt a nocturnal lifestyle (Wright, 1981). For their body mass (approximately 900–1000 g), night monkeys are characterized by an extremely short gestation period (133 days), females give birth once per year to a single infant, and adult males (presumably fathers) help care for the young

(Garber and Leigh, 1997). Moreover, *Aotus* is reported to occupy small home ranges of 4–10 ha (Wright, 1989). Given the limited quantitative data available, patterns of habitat preference and diet in Mesoamerican night monkeys are poorly understood. Hladik *et al.* (1971) examined the stomach contents of *Aotus* from Panama. These authors report that fruits (65%), foliage (30%), and insects (5%) account for the majority of the night monkeys' diet. There are no published studies concerning the ability of Mesoamerican night monkeys to exploit disturbed forests. However, Wright (1981: 214) cites Cassidy (pers. comm.) indicating that *Aotu*s was found to inhabit "shady trees adjacent to coffee plantations in Colombia."

Saguinus geoffroyi (adult body mass 450–500 g) lives in small multimale–multifemale groups (6–10 individuals) that are characterized by cooperative infant care, polyandrous and polygynous matings, the production of twin offsprings, female reproductive suppression, and the potential for a group's sovereign breeding female to give birth twice per year (Garber and Leigh, 1997). However, on a mainland site (Agua Clara, Panama) located approximately 5 km from Barro Colorado Island, Garber (pers. comm.) found that females tended to give birth only once per year, and that it was not uncommon for a female to lose one of her twin infants during the first few months of life.

Panamanian tamarins have home ranges of 10–30 ha (Dawson, 1975; Garber, 1984a) and, in addition to consuming ripe fruits in the canopy, and resources such as plant exudates and small vertebrates found on the trunks of large trees, spend approximately 70% of their foraging time searching for insects (large-bodied orthopterans) (Garber, 1984a,b). Garber (1984a) reports, that in a dry tropical forest in Panama, tamarins restricted much of their insect foraging behavior to areas of disturbed secondary vegetation such as forest edges and tree fall gaps. In this regard, Panamanian tamarins may be able to survive in forest fragments characterized by a high ratio of forest edge to forest interior.

Saimiri oerstedii (adult body mass 650–900 g) lives in the largest social groups of any Mesoamerican primate (40–65 individuals) and utilizes home ranges of 76–110 ha (Boinski, 1987c; Janson and Boinski, 1992). These groups may contain as many as 14 reproductively adult females. Squirrel monkeys are characterized by an extremely short breeding season in which males attain a "fatted"state immediately prior to mating (associated with hormonally mediated water retention), birth synchrony within groups, and an elongated period of juvenile development (Boinski, 1987a; Janson and Boinski, 1992). Infant *Saimiri* weigh approximately 20% of their mother's weight at birth (the largest of any anthropoid primate), achieve 95% of adult brain size at 3 months of age, and have an interbirth interval of up to 2 years (Garber and Leigh, 1997). Whereas male night monkeys and tamarins reach full adult reproductive maturity by 2–2.5 years of age, male *Saimiri* may not reach full adult body mass until 4–5 years of age (Boinski, 1992). Costa Rican squirrel monkeys devote approximately 90% of their foraging time to the pursuit and capture of insect prey (Boinski, 1986). Given the energetic requirements of large group size, large home range size, and a slow life history, forest fragmentation is likely to impact populations of *Saimiri* more severely than *Saguinus* or possibly *Aotus.* Recent studies of *Saimiri* in fragmented landscapes in Costa Rica indicate, however, that populations of squirrel monkeys can persist in small forest patches or across linear strips of vegetation (J. Saenz, pers. comm.). How this affects diet, group size, group cohesion, and reproductive success is unclear.

In short, field research on *Aotus*, *Saimiri*, and *Saguinus* is sorely needed in order to examine the natural history, ecology, and behavior of these taxa. Moreover, deforestation in Costa Rica and Panama, where populations of these primates are found, has reduced the original forest cover to about 40% and 39%, respectively (Estrada *et al.*, Chapter 1). Although these two countries still contain large extensions of forest cover in proportion to their territory, current deforestation rates in Costa Rica are estimated at −0.77% per year, and in Panama these are −1.65% per year (see Estrada *et al.*, Chapter 1). Thus, lack of information about the current distribution, basic ecology, and behavior of populations of *Aotus*, *Saimiri*, *and Saguinus*, coupled with gradual and rapid modifications of landscapes in Costa Rica and Panama by human activity, make the task of identifying specific conservation recommendations exceedingly difficult.

Ateles

Ateles geoffroyi is the largest bodied Mesoamerican primate (adult body mass is 7.5–8.2 kg; Ford and Davis, 1992). Although it is widely distributed from the Yucatan peninsula into Panama, 60% of all published reports come from sites in Mexico and Costa Rica (Estrada *et al.*, Chapter 1). Given their rapid speed of travel (tail-assisted suspensory locomotion), fission–fusion social system, and large home range (several hundred hectares), long-term field studies of *A. geoffroyi* have yet to be conducted. Geoffroy's spider monkey is highly frugivorous (ripe fruits account for >70% of feeding time; Chapman, 1987).

Van Roosmalen and Klein (1988) report that *A. geoffroyi* may be the most "flexible" spider monkey species and is found to exploit a wide range of habitat types including mangrove, primary forest, evergreen forest, semi-deciduous forest, and deciduous forest. *A. geoffroyi* also is found to range from sea level to 2500 m above sea level (Rowe, 1996). Along with *Cebus*, *Ateles* has a "more highly developed and the most fissurated brain" of any Mesoamerican primate (Hershkovitz, 1977: 359) and a slow life history. A female does not produce her first infant until approximately age 7–9, has a long period of gestation (226–232 days), and an interbirth interval of approximately 3 years (Fedigan and Rose, 1995). Due to its large size, palatable meat to humans, and the attractiveness of its infants as pets, *Ateles* is extremely vulnerable to human hunting and capture (Kinzey, 1997; Duarte and Estrada, 2003).

Given its slow life history and reproductive pattern, one might expect *Ateles* to be among the first Mesoamerican primate species to become locally extinct in areas of forest fragmentation or adjacent to human habitation. Although this may often be the case, populations of *Ateles* are found to exist in fragmented landscapes in El Salvador, Honduras, and Mexico. Investigations focusing on the ecological, local, and historical conditions that allow *Ateles* to survive in these areas are a high priority. In a recently published study of a population of spider monkeys inhabiting a highly fragmented landscape in Los Tuxtlas, Mexico, it was shown that larger forest fragments contained larger populations of spider monkeys and that the presence, relative abundance and basal area of emergent fruiting trees appeared to explain the persistence of *Ateles* in such environments (González-Zamora and Mandujano, 2003).

Milton and Hopkins (this volume) provide detailed information on the reintroduction of *A. geoffroyi* into protected forested areas on BCI, Panama. This began more than 40 years ago with the introduction of several juveniles. However, only one male and four females survived the initial reintroduction and have served as the genetic founders of the current population. Their data indicate that for more than 30 years, spider monkey population growth either increased extremely slowly or not at all. This highlights the difficulties that species with a slow life history may have in colonizing new environments. Since the late 1990s the population on BCI has increased to 28 animals. Milton and Hopkins conclude that even in the absence of other large-bodied frugivores, mammalian predators, and being introduced into a productive and protected environment, spider monkey populations require extremely long periods of time to increase to a point where persistence is likely. Conservation policies governing primate reintroductions need to consider a species' life history traits and the minimum population size to maximize the likelihood of success.

Cebus and Alouatta

Despite exhibiting very different adaptive patterns, life history strategies, diets, and foraging behavior, *Cebus* and *Alouatta* represent the most geographically widespread genera of New World monkeys. *Cebus* and *Alouatta* also are among the best-studied primates. Capuchins are highly encephalized, are the only group of platyrrhines that can move their digits independently, possess a pseudo-opposable thumb, are reported to hunt for vertebrates in a coordinated manner, exploit embedded or hidden foods, and may on very rare occasions use a tool to solve a foraging problem (Janson and Boinski, 1992; Garber and Brown, 2004). In the case of *C. capucinus* (adult body mass 2.2–3.2 kg), Fedigan and Rose (1995) and Fragaszy *et al.* (2004) report that females have their first offspring at 6–7 years of age, and are characterized by an interbirth interval of 26.4 months. In contrast, sympatric mantled howlers are considerably larger (4.7–7.5 kg; Glander, this volume), have an earlier age at first reproduction (3.5 years of age), and a shorter interbirth interval (19.9 months). Moreover, adult male white-faced capuchins reach full adult body mass by age 10 (Fragaszy *et al.*, 2004), whereas adult male mantled howlers reach full adult body mass at age 5 (Glander, this volume).

Capuchins and howlers also differ significantly in dietary profile. Mantled howlers are characterized by a slow rate of food passage, and exploit a diet principally of fruits, mature and immature leaves, and flowers (Milton, 1980, 1984; Estrada, 1984). Milton (1980) has referred to mantled howlers as behavioral folivores. Black howlers, studied in Belize and more recently in Mexico, are reported to have a similar diet (Silver *et al.*, 1988; Barrueta, 2003; Pavelka and Knopff, 2004; Rivera and Calme, this volume). In contrast, white-faced capuchins exploit a broader-based diet composed of soft fruits, hard fruits, palm nuts, shoots, flowers, leaves, vertebrates, invertebrates, eggs, and insect larvae (Fragaszy *et al.*, 2004). Hard fruits and seeds are often opened or broken by being pounded against a hard substrate (Panger, 1998). The exploitation of embedded resources, enhanced manipulative abilities, and large brain size has been associated with the evolution of complex cognitive skills in capuchins (Fragaszy *et al.*, 2004).

Given these distinctions in diet and life history traits, *Cebus* and *Alouatta* appear to have evolved very different adaptive solutions to ecological problems associated with exploiting a wide range of forest types. These may offer advantages in persisting in highly fragmented landscapes. *Alouatta* may survive in small forest patches by adopting an energy-minimizing foraging pattern (small day range, small home range, and extended periods of rest) associated with the consumption and fermentation of leaves during fruit-limited periods of the year (Milton, 1980), and by expanding the spectrum of plant species used as sources of food (Estrada *et al.*, 1999; García del Valle *et al.*, 2001; Gonzáles-Picazo *et al.*, 2001; Bicca-Marques, 2003; Fuentes *et al.*, 2003). *Cebus* may survive in highly fragmented landscapes by exploiting an extremely broad-based diet including hard-to-locate resources, and by traveling on the ground between forest patches or by using man-made landscapes as stepping-stones or corridors (DeGamma-Blanchet and Fedigan, this volume; Estrada *et al.*, this volume). However, when in proximity to human settlements, capuchins are sometimes considered pests because they raid agricultural crops and gardens (Estrada *et al.*, this volume). Under similar circumstances, howler monkeys may be able to co-exist in a more commensurate relationship with humans (Estrada *et al.*, this volume).

USE OF NEW TECHNOLOGIES AND THEORETICAL MODELS TO STUDY MESOAMERICAN PRIMATES

A second goal of papers in this volume was to use traditional and new technologies and analytical tools to investigate current problems in primate behavioral ecology and conservation. A major question in conservation management is the relationship between the health status and persistence of primate populations living in fragmented landscapes. One measure of persistence and sustainability is censusing the size, composition, age structure, and density of primate groups in forests that vary in size, ratio of edge to interior, and degree and type of disturbances. Several papers in the volume present these important data. In addition, levels of stress hormones such as cortisol obtained from fecal samples and information on parasite loads represent equally important indicators of population health and viability (Stoner and Gonzlez Di Pierro, this volume). Primates can maintain heavy parasite loads that compromise their immune system and reproductive fitness in the absence of outwardly visible indicators of poor health (Gillespie *et al.*, 2004). Information on parasite inventories and measures of parasite incidence or load in primate populations in continuous forests can provide the needed baseline information against which we can compare populations of the same species existing in fragmented landscapes. The study by Stoner and González Di Pierro on *A. pigra* in this volume is a good case in point, stressing the need for more studies on the parasite ecology of Mesoamerican primates.

Recent advances in reproductive endocrinology allow field researchers to non-invasively obtain information on ovarian function, mating during non-fertile periods, reproductive suppression, and female mate choice in primates by measuring steroid hormone levels in feces (Carnegie *et al.*, this volume). Previously, such studies were restricted to captive primates housed in controlled settings. Non-conceptive matings have been reported in several species of capuchins and tamarins (Manson *et al.*, 1997; Carnegie *et al.*, this volume; Garber, 1997). In the case of capuchins, non-conceptive matings have been suggested to reflect a reproductive strategy used by females to discourage infanticide (Fedigan, 2003). In tamarins, non-conceptive mating has been suggested to reinforce a socio-sexual bond between group males and the breeding female to insure male care-giving behavior (Garber, 1997).

The use of non-invasive techniques to monitor steroid hormonal levels in wild primates will play an increasingly important role in assessing fertility and reproductive seasonality in primates inhabiting environments differentially altered by human modification. For example, Van Belle and Estrada (this volume) report that the mean population density of *A. pigra* was significantly higher in forest fragments than in extensive forests, suggesting crowding and possibly populations living above sustainability thresholds in these forest fragments. However, what remains to be determined is whether population density is a reliable measure of population health and habitat quality (as often assumed), or whether forest fragments contain "refuge" populations in which individuals are characterized by lower fertility, greater parasite loads, and experience higher levels of stress.

The ongoing work at Monkey River, Belize, integrates the investigation of fecal parasites and stress hormones in determining primate densities (see Pavelka and Chapman, this volume). In the future, the implantation of biotelemetry devices in wild primates will also contribute to this endeavor. For example, Susan Williams (pers. comm.) is conducting pioneering field research using biotelemetry to determine the range of mechanical demands placed on the masticatory system of mantled howler monkeys when naturally exploiting resources in a Costa Rican forest. Collaborative studies designed to collect complementary data on behavior, diet, habitat utilization, demography, reproductive endocrinology, population persistence, and population health are needed for effective management of primates and the ecosystems they inhabit.

The use of non-invasive techniques to extract nuclear and mitochondrial DNA from the roots of shed or collected hair, and epithelial cells expelled in feces now allow field primatologists, in conjunction with geneticists, to conduct studies of genetic variation, gene flow, and paternity in wild primates. DNA profiles derived from microsatellite markers facilitate the identification of individuals, their contribution to the gene pool of the population, an assessment of mate choice (see Jack and Fedigan, this volume, for an example with *Cebus*), dispersal patterns and kinship, and genetic variation and genetic distances in primate populations (see García del Valle, 2004 for an example with populations of *A. pigra*). In adopting these analytical techniques, Mesoamerican primate research is beginning to achieve an ever increasing level of precision in addressing questions linking observed behavioral patterns and social networks with individual reproductive success, as well as a greater understanding of how the demographic and genetic features of individual populations vary in response to alternative ecological conditions (e.g. continuous versus fragmented forests).

Mesoamerican primate research also has taken a leading role in using experimental field approaches to examine questions concerning cognition, decision-making, and sensory adaptations in non-human primates (Garber and Brown, this volume; Garber, 2000; Garber and Brown, 2004). Experimental field studies build on the strengths of laboratory and traditional field investigations by presenting wild primates with social and ecological problems analogous to those they naturally encounter, but under systematic and controlled conditions. By varying temporal, spatial, and quantity information available to a forager, the researcher can test hypotheses concerning the degree to which certain cues are more salient than others in the decision-making process, as well as evidence of age- or sex-based differences in cognitive ability (Bicca-Marques and Garber, 2005).

As indicated earlier, Mesoamerican primates are characterized by significant differences in developmental trajectories. Papers by Bezanson (this volume) and MacKinnon (this volume) offer critical frameworks for examining the ontogeny of diet, foraging, and locomotor behavior in howlers and capuchins. There is evidence that, in some primate species, neuromuscular development associated with locomotor skills may have become dissociated from neuromuscular development required for fine motor control, extractive foraging, prey manipulation, or object manipulation. In the case of tamarin monkeys, individuals reach locomotor independence by 3 months of age, but are still provisioned with insects by adult caretakers at 9 months of age (Garber and Leigh, 1997). In other primate species, locomotor skills and fine manipulative skills appear to develop early and at approximately the same stage of development (i.e. *S. oerstedii*; Boinski and Fragaszy, 1989). In this regard, studies of primate locomotion, diet, and cognition should be placed within the context of primate life history strategies and evaluated in terms of patterns of somatic and neural growth and development, age-related survivorship, and the requirements of efficiently exploiting particular resources and forest habitats (Garber, in press).

Finally, the expanded use of Geographic Information Systems (GIS) and remotely sensed (RS) satellite data represent critical conservation and research tools for identifying vegetation types and for documenting changes in vegetation cover at various landscape scales over time. Such landscape changes can be caused by natural events (e.g. hurricanes and fires) or by human activity (e.g. mining, oil exploration, timber extraction, among others). In our volume, the chapter by Alexander *et al.* on the impact of Hurricane Iris on the habitat of a population of black howler monkeys in coastal Belize serves as a case study of how GIS can be applied to evaluate habitat change and its effect on primate populations.

Continued work linking satellite imagery, forest cover, vegetation types, habitat fragmentation, climate, topography, human land-use patterns, and relationships between areas of human population centers, ecotourism, and primate survivorship is needed. Progress in this direction is being made through the unfolding of the Mesoamerican Biological Corridor Project (see next section of this chapter), where remote sensing is being used to map the current system of natural protected areas in each Mesoamerican country and to project, in intermediate areas, the vegetation corridors that could be protected and/or established to enhance long-term species viability. Moreover, such information coupled with sorely needed surveys of primate population in many localities can update our "maps" regarding the current distribution of species and their populations in Mesoamerica (see Serio-Silva *et al.*, this volume). Thus the combination of layered data sets containing information on primate population distribution, land-use patterns, human settlements, geological and climatological features, and vegetation types can provide the diagnostics required to identify "hot spots" of conservation or risk for individual primate populations, or species in particular countries, or geographic localities in the region.

KEY ISSUES IN MESOAMERICAN PRIMATE CONSERVATION

Chapters in this volume have identified major issues and priorities for the conservation of Mesoamerican primates. We summarize these below.

Negative Impact of Land-Use Patterns Upon the Persistence of Tropical Rain Forest Vegetation and Primate Populations in the Region

Currently, only 30% of the original forest cover remains in Mesoamerica. Deforestation continues to fragment forested landscapes and this constitutes an important pressure upon extant primate populations. Countries such as Belize, Honduras, Nicaragua, and Guatemala contain the largest extensions of forest vegetation in their territories, but are also countries with the highest deforestation rates (Estrada *et al.*, Chapter 1). We continue to lack systematic and updated information regarding the current distribution of primate species and populations for these countries. Belize, Honduras, Nicaragua, and Guatemala represent a priority in primate conservation research.

Positive Impact of Some Agricultural Practices Upon the Persistence of Primate Populations

There is a general perception that agricultural activities are the principal threat to biodiversity in the tropics and a major cause of local extinctions, including primates. Such a binary view perceives conservation as a conflict between agriculture and tropical rain forests. The investigations of primates in agro-ecosystems reported in this book for landscapes in Mexico, Guatemala, and Costa Rica and by others elsewhere (Estrada and Coates-Estrada, 1996; McCann *et al.*, 2003; Harvey *et al.*, 2004), suggest that there is an alternative view that needs to be considered. Using a landscape perspective allows one to focus on the interactions among forests, agro-ecosystems, and the needs of the human population as important components in the conservation equation. The concurrent cultivation in some Mesoamerican localities of shaded and unshaded arboreal crops has resulted in fragmented landscapes that, in some cases, seem to contribute to the persistence of primate populations. These situations merit further investigation, as they open the possibility of enhancing the conservation of primates in human-modified landscapes. The landscape view also requires that attention be placed on investigating ways in which local subsistence economies can be diversified, involving the participation of multidisciplinary research teams. It also stresses the need to document the economic and ecological benefits for people of maintaining land-use patterns in which heterogeneous landscapes containing arboreal crops may play an important role in the persistence of primate populations and species.

Expanding Human Population

Environmental pressures on native vegetation in the region also come from an expanding human population. Mesoamerica is characterized by a high growth rate of 3% per year, and an expected doubling of current population from 45 to 84 million people in the next 25–35 years. This, combined with extreme poverty in the majority of the population, exerts direct pressure on land-use and the quality of life of the human inhabitants. Primate conservation research must consider the needs of rural people and indigenous populations in developing viable and individual conservation plans for the various regions of Mesoamerica. This needs to be integrated into educational outreach programs to stress the fact that the primate fauna is an integral part of the cultural and natural patrimony of the people of this region.

Impact of Natural Events on Primate Distribution and Density

Specific localities of Mesoamerica are regularly or occasionally affected by hurricanes, volcanic activity, earthquakes, torrential rains, flooding, and other natural events which are likely to have an important ecological impact on primate habitats, primate population dynamics (including human primates), and population viability. In conjunction with anthropogenic disturbance, these events may contribute significantly to habitat loss and fragmentation, and forest degradation, with direct impacts on primate population health and survivorship. Understanding the impact of these natural events remains an important issue in Mesoamerican primate conservation.

Economic Incentives for the Conservation of Primate Populations

Economic incentives can play an important role in primate conservation. These incentives relate to specific patterns of land-use that currently exist in several regions and landscapes across Mesoamerica. In Mexico, Belize, Guatemala, Honduras, and El Salvador the government protects forested areas that harbor Maya archeological remains. There also exist ecological reserves dedicated to research and/or ecotourism in every Mesoamerican country. Excellent examples of these are the Los Tuxtlas field station in Mexico, Barro Colorado Island in Panama, and La Selva field station in Costa Rica. Recently, there have been several attempts to preserve forest habitats and generate revenue by developing educational field courses for university students and biological field stations to promote primate research in northeastern Costa Rica (e.g. La Suerte Biological Field Station), Isla de Ometepe, Nicaragua (Ometepe Biological Field Station), and Bocas del Toro, Panama (ITEC).

Conservation Initiatives by Mesoamerican Countries

In spite of poverty, overcrowding, and underdevelopment, the countries of Mesoamerica have expressed great concern over the need to conserve their biodiversity. Between 1993 and 1994, all Mesoamerican countries ratified the international convention on biological diversity, which led to the consolidation of existing protected areas and the creation of new, naturally protected areas in each country. There currently exists a total of 420 protected areas, encompassing about 15 million ha, or about 20% of the area of Mesoamerica. Mesoamerican countries have gone one step further with the interest of protecting their biodiversity, while at the same time improving the quality of life for their rural populations. The result of such action is the Mesoamerican Biological Corridor (MBC) project, a unique program in Latin America linking conservation efforts by several governments. Each nation has proposed a system of corridors that will connect the existing system of naturally protected areas. This will serve to avoid habitat fragmentation and isolation, enhance the viability of species and populations, and promote sustainable use of the land and forest remnants in intermediate areas. The MBC project completed a 5-year-long diagnostic phase in 2004, and will proceed to a phase of consolidating agreements (paralleled by field projects) among Mesoamerican countries, with the general goal of "improving the connectivity of ecosystems, the sustainable use of the land and the services generated for the region's development" (CBM, 2004). The MBC project has the potential to enhance the persistence of primate species and populations and their habitats throughout the region. However, mapping the location and state of conservation of such species and populations within this framework is still a task to be accomplished.

Contribution by Primatologists to Conservation

Primatologists have been investigating primate species and populations in the region since the 1930s and thus have a critical role to play in Mesoamerica. Their contribution over the last 70 years has focused mainly on providing documentation of the natural history, ecology, behavior, and evolutionary history of Mesoamerican primates. This has resulted in a large body of scientific and technical literature on the primates of the region. In spite of these efforts, however, we still lack sufficient and current information on several species. For example, the absence of individual chapters in this volume dedicated to species such as *A. zonalis*, *S. geoffroyi*, and *S. oerstedii* are a clear indication that much work needs to be done. Studies of these primates are a research priority, as no systematic and detailed field studies have been published on any of these species since the 1980s.

While primatologists have contributed detailed longitudinal information on primate life-history traits that further our understanding of primate biology, ecology, and behavior, and on the plasticity of responses primates show to various environmental conditions, success in translating these efforts and information into conservation initiatives has been more limited. In this regard, we call upon primate researchers in Mesoamerica to focus on the empirical, conceptual, and theoretical tools needed to develop explicit conservation recommendations for individual primate populations, individual primate species, and threatened habitats.

Finally, it is important to point out that despite seven decades of field research in Mesoamerica by primatologists, many of the countries in the region continue to lack trained primate specialists. Mexico is the only Mesoamerican country that maintains a small contingent of professionally trained primatologists, a possible reason for the rapid increase in field data and publications on primate species and populations in that country over the last two decades (Estrada and Mandujano, 2003). Most Mesoamerican countries lack primate scientists native to the region, and therefore experience great difficulty in sustaining long-term conservation initiatives and research. Countries such as Nicaragua, Honduras, and El Salvador are still in the earliest stages of collecting basic information on the presence, location, and viability of their primate populations. And, as forests continue to be cut and non-human primates continue to be captured as pets or hunted for food, we face greater and greater challenges in developing an effective plan of conservation for the Mesoamerican region. However, political stability, revenues generated through ecotourism, and a generation of young Mesoamerican scientists offer hope that effective changes to conservation policy and increases in financial resources devoted to conservation efforts become national priorities.

It is the hope of the editors and the contributors to this volume that we have identified critical, new, and important issues in primate research and conservation, allowing the reader to achieve a greater level of understanding, and integration of Mesoamerican primate taxonomy, biogeographic history, behavior, ecology, and conservation. We emphasize that the human population of Mesoamerica has for several thousand years, and continues to this day, to be an important component of the tropical ecosystems and must be considered when developing conservation strategies to insure the persistence of primate species and populations. The impact of humans on the native ecosystems is likely to be more pervasive and harmful today than in the distant past. Therefore, primatologists must pay special attention to the social, economic, and political forces at play in the region. This includes consideration of the need for sustainable land-use patterns and equity for the human population. Human and non-human primates have coexisted in Mesoamerica for thousands of years. We are hopeful that the Mesoamerican landscape can sustain the needs of human primates and the needs of non-human primates in an equitable way. In our view, it is imperative that we perceive primate research, not only as a way to enhance scientific knowledge, but also as means to insure the conservation of the natural and cultural patrimony of the nations in this biologically important region of the world.

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REFERENCES

Barrueta, T. 2003, Reconocimiento demográfico y dieta de *Alouatta pigra* en un fragmento de selva en El Tormento, Campeche, México. MSc Thesis, El Colegio de la Frontera Sur, México, p. 49.

Bicca-Marques, J. C. 2003, How do howler monkeys cope with habitat fragmentation? in: L. K. Marsh, ed., *Primates in Fragments: Ecology and Conservation*, Kluwer Academic/Plenum Publishers, New York, pp. 283–303.

Bicca-Marques, J. C. and Garber, P. A. 2005, Use of social and ecological information in tamarin foraging decisions. *Int. J.Primatol.* 26:

Boinski, S. 1986, *The Ecology of Squirrel Monkeys in Costa Rica*. PhD Thesis, University of Texas, Austin.

Boinski, S. 1987a, Birth synchrony in squirrel monkeys (*Saimiri oerstedii*). *Behav. Ecol.Sociobio.* 21:283–310.

Boinski, S. 1987b, Mating patterns in squirrel monkeys (*Saimiri oerstedii*). *Behav. Ecol.Sociobiol.* 21:13–21.

Boinski, S. 1987c, Habitat use by squirrel monkeys (Saimiri oerstedi) in Costa Rica. *Folia Primatol.* 49:151–167.

Boinski, S. 1992, Olfactory communication among Costa Rican squirrel monkeys: A field study. *Folia Primatol.* 59:127–136.

Boinski, S. 1994, Affiliation patterns among male Costa Rican squirrel monkeys. *Behaviour* 130:191–209.

Boinski, S. and Fragaszy, D. M. 1989, The ontogeny of foraging in squirrel monkeys, *Saimiri oerstedii. Anim.Behav.* 37:415–428.

Cant, J. H. G. 1986, Locomotion and feeding postures of spider and howling monkeys: Field study and evolutionary interpretation. *Folia Primatol.* 46:1–14.

Carpenter, C. R. 1934, A field study of the behavior and social relations of howling monkeys. *Comp.Psychol.Monogr.* 10, 48:1–168.

CBM. 2004, Resumen corredor biologico Mesoamericano-CBM programa estrategico regional. Draft. CBM, CCAD and SICA, 6 October, 2004, Managua, Nicaragua.

Chapman, C. A. 1987, Flexibility in diets of three species of Costa Rican primates. *Folia Primatol.* 49:90–105.

Chapman, C. A. 1988a, Patterns of foraging and ranging use by three species of neotropical primates. *Primates* 29:177–194.

Chapman, C. A. 1988b, Patterns of foraging and range use by three species of Neotropical primates. *Primates* 29:177–194.

Chapman, C. A. and Peres, C. A. 2001, Primate conservation in the new millennium: The role of scientists. *Evol.Anthropol.* 10:16–33.

Coelho, A. M. Jr., Coelho, L., Bramblett, C., Bramblett, S., and Quick, L. 1976, Ecology, population characteristics, and sympatric associations in primates: A socioenergenetic analysis of howler and spider monkeys in Tikal, Guatemala. *Yearbk.Phys.Anthropol.* 20:96–135.

Dawson, G. A. 1975, Behavioral ecology of the Panamanian tamarins, *Saguinus oedipus* (Callitrichidae, Primates). PhD Thesis, East Lansing, Michigan State University, Michigan.

Duarte, A. and Estrada, A. 2003, Primates as pets in Mexico City: An assessment of species involved, source of origin and general aspects of treatment. *Am.J.Primatol.* 61:53–60.

Emmons, L. 1990, *Neotropical Rainforest Mammals.A Field Guide.* The University of Chicago Press, Chicago.

Estrada, A. 1984, Resource use by howler monkeys (*Alouatta palliata*) in the rainforest of Los Tuxtlas, Veracruz, Mexico. *Int.J.Primatol.* 5:105–131.

Estrada, A. and Coates-Estrada, R. 1993, Aspects of ecological impact on howling monkeys (*Alouatta palliata*) on their habitat: A review, in: A. Estrada, E. Rodriquez Luna, R. Lopez-Wilchis, and R. Coates-Estrada, eds., Avances en: Estudios Primatologicos en Mexico I. Asociacion Mexicana de Primatologia, A.C. y Patronatto Pro-Universidad Veracruzana, A.C. Xalapa, Veracruz, Mexico, pp. 87–117.

Estrada, A. and Coates-Estrada, R. 1996, Tropical rain forest fragmentation and wild populations of primates at Los Tuxtlas. *Int.J.Primatol.* 15:759–783.

Estrada, A., Juan Solano, S., Ortíz Martínez, T., and Coates-Estrada, R. 1999, Feeding and general activity patterns of a howler monkey (*Alouatta palliata*) troop living in a forest fragment at Los Tuxtlas, Mexico. *Am. J. Primatol.* 48:167–183.

Estrada, A. and Mandujano, S. 2003, Investigaciones con *Alouatta* y *Ateles* en Mexico. *Neotrop.Primates* 11(3):147–156.

Fedigan, L. 2003, Impact of male takeovers on infant deaths, births and conceptions in *Cebus capucinus* at Santa Rosa, Costa Rica. *Int.J.Primatol.* 24:723–741.

Fedigan, L. M. and Rose, L. M. 1995, Interbirth interval variation in three sympatric species of neotropical monkeys. *Am.J.Primatol.* 37:9–24.

Ford, S. and Davis, L. 1992, Systematics and body size: Implications for feeding adaptations in New World monkeys. *Am.J.Phys.Anthropol.* 88:415–468.

Fragaszy, D. M., Visalberghi, E., and Fedigan, L. M. 2004, *The Complete Capuchin: The Biology of the Genus Cebus.* Cambridge University Press, Cambridge.

Fuentes, E., Estrada, A., Franco, B., Magaña, M., Decena, Y., Muñoz, D., and García, Y. 2003, Reporte preliminar sobre el uso de recursos alimenticios por una tropa de monos aulladores, *Alouatta palliata*, en El Parque La Venta, Tabasco, México. *Neotrop.Primates* 11:24–29.

Garber, P. A. 1980, Locomotor behavior and feeding ecology of the Panamanian tamarin (*Saguinus oedipus geoffroyi*, Callitrichidae, Primates). *Int.J.Primatol.* 1:185–201.

Garber, P. A. 1984a, Use of habitat and positional behavior in a neotropical primate, *Saguinus Oedipus*, in: P. S. Rodman and J. G. H. Cant, eds., *Adaptations for Foraging in Nonhuman Primates*, Columbia University Press, New York, pp. 112–133.

Garber, P. A. 1984b, The proposed nutritional importance of plant exudates in the diet of the Panamanian tamarin, *Saguinus oedipus geoffroyi. Int.J.Primatol.* 5:1–15.

Garber, P. A. 1997, One for all and breeding for one: Cooperation and competition as a tamarin reproductive strategy. *Evol.Anthropol.* 5:135–147.

Garber, P. A. 2000, Evidence for use of spatial, temporal, and social information by primate foragers, in: S. Boinski and P. A. Garber, eds., *On the Move: How and Why Animals Travel in Groups*, University of Chicago Press, Chicago, IL, pp. 261–298.

Garber, P. A. Primate locomotor behavior and ecology, in: S. Bearder, C. J. Campbell, A. Fuentes, K. C. MacKinnon, and M. Panger, eds.,*Primates in Perspective*, Oxford University Press, Oxford, in press.

Garber, P. A. and Brown, E. 2004, Wild capuchins (*Cebus capucinus*) fail to use tools in experimental field study. *Am.J.Primatol.* 62:165–170.

Garber, P. A. and Leigh, S. R. 1997, Ontogenetic variation in small-bodied New World primates: Implications for patterns of reproduction and infant care. *Folia Primatol.* 68:1–22.

García del Valle, Y. 2004, Efecto de la fragmentación en la variación genética de poblaciones de monos aulladores *Alouatta pigra* en la selva Lacandona, Chiapas. México. Master's Thesis, Colegio de la Frontera Sur, San Cristóbal de las Casas, Chiapas.

García del Valle, Y., Muñoz, D., Estrada, A., Franco, B., and Magaña, M. 2001, Uso de plantas como alimento por monos aulladores, *Alouatta palliata*, en el parque Yumká, Tabasco, México. *Neotrop.Primates* 9:112–118.

Gillespie, T. R., Greiner, E. C., and Chapman, C. A. 2004, Gastrointestinal parasites of the guenons of western Uganda. *J.Parasitol.* 90: 1356–1360.

González-Picazo, H., Estrada, A., Coates-Estrada, R., and Ortíz-Martínez, T. 2001, Consistencias y variaciones en el uso de recursos alimentarios utilizados por una tropa de monos aulladores (*Alouatta palliata*) y deterioro del habitat, en Los Tuxtlas, Veracruz, Mexico. *Universidad y Ciencia* 17:27–36.

González-Zamora, A. and Mandujano, S. 2003, Uso de fragmentos por *Ateles geoffroyi* en el sureste de México. *Neotrop.Primates* 11:174–177.

Harvey, C., Tucker, N., and Estrada, A. 2004, Can live fences, isolated trees and windbreaks help conserve biodiversity within fragmented tropical landscapes? in: G. Schroth, G. Fonseca, C. Gascon, H. Vasconcelos, A. M. Izac, and C. Harvey, eds., *Agroforestry and Conservation of Biodiversity in Tropical Landscapes*, Island Press Inc., New York, pp. 261–289.

Hershkovitz, P. 1977, *Living New World Monkeys (Platyrrhini)*, Vol. 1. University of Chicago Press, Chicago.

Hladik, C. M., Hladik, A., Bousset, J., Valdebouze, P., Viroben, G., and Delort-Laval, J. 1971, La regime alimentaire des primates de l'ile de Barro-Colorodo (Panama). Resultats des analyses quantitatives. *Folia Primatol.* 16:85–122.

Janson, C. H. and Boinski, S. 1992, Morphological and behavioral adaptations for foraging in generalist primates: The case of the cebines. *Am.J.Phys.Anthropol.* 88:483–498.

Kinzey, W. G. 1997, *New World Primates. Ecology,Evolution and Behavior.* Aldine Press, New York.

Lambert, J. E. and Garber, P. A. 1998, Ecological and evolutionary implications of primate seed dispersal. *Am.J.Primatol.* 45:9–28.

Manson, J. H., Perry, S., and Parish, A. R. 1997, Nonconceptive sexual behavior in bonobos and capuchins. *Int.J.Primatol.* 18:767–786.

McCann, C., William-Guillen, K., Koontz, F., Roque, A., Martinez, J. C., and Koontz, C. H. 2003, Shade coffee plantations as wildlife refuges for mantled howler monkeys (*Alouatta palliata*) in Nicaragua, in: L. K. Marsh, ed., *Primates in Fragments: Ecology and Conservation*, Kluwer Academic/Plenum Publishers, New York, pp. 321–340.

Milton, K. 1980, *The Foraging Strategy of Howler Monkeys: A Study in Primate Economics.* Columbia University Press, New York.

Milton, K. 1981a, Diversity of plant foods in tropical forests as a stimulus to mental development in primates. *Am.Anthropol.* 83:534–548.

Milton, K. 1981b, Food choice and digestive strategies of two sympatric primate species. *Am.Nat.* 117:476–495.

Milton, K. 1984, The role of food-processing factors in primate food choice, in: P. S. Rodman and J. G. H. Cant, eds., *Adaptations for Foraging in Nonhuman Primates*, Columbia University Press, New York, pp. 249–279.

Morales H. K. 2002, Wild populations of spider monkeys (*Ateles geoffroyi*) in El Salvador, Central America. *Neotrop.Primates* 10:153–154.

Moynihan, M. 1964, Some behavior patterns of platyrrhine monkeys 1. The night monkey (*Aotus trivirgatus*). *Smithson.Misc.Coll.* 146:1–84.

Murcia, C. 1995, Edge effects in fragmented forests: Implications for conservation. *Trends Ecol.Evol.* 10:58–62.

Panger, M. 1998, Object-use in free-ranging white-faced capuchins (*Cebus capucinus*) in Costa Rica. *Am.J.Phys.Anthropol.* 106:311–321.

Pavelka, M. S. M. and Knopff, K. 2004, Diet and activity in *A. pigra* in Southern Belize: Does degree of frugivory influence activity level? *Primates* 45:105–112.

Reid, F. 1997, *A Field Guide to the Mammals of Central America and Southeast Mexico.* Oxford University Press, London.

Restrepo, C., Gomez, N., and Heredia, S. 1999, Anthropogenic edges, treefall gaps, and fruit–frugivore interactions in a neotropical montane forest.*Ecology* 80:668–685.

Rowe, N. 1996, *A Pictorial Guide to the Living Primates.* Pogonias Press, Charlestown, RI.

Silver, S. C., Ostro, L. E. T., Yeager C. P., and Horwich R. 1988, Feeding ecology of the black howler monkey (*Alouatta pigra*) in northern Belize. *Am.J.Primatol.* 45:263–279.

Thorington, R. W. Jr., Muchenhirn, N. A., and Montgomery, G. G. 1976, Movements of a wild night monkey, *Aotus trivirgatus*, in: R. W. Thorington Jr. and P. G. Heltne, eds., *Neotropical Primates*, National Academy of Sciences, Washignton, D.C., pp. 32–34.

Van Roosmalen, M. G. M. and Klein, L. L. 1988, The spider monkeys, genus *Ateles*, in: R. A. Mittermeier, A. B. Rylands, A. F. Coimbra-Filho, and G. A. B. da Fonseca, eds.,*Ecology and Behavior of Neotropical Primates*, Vol. 2, World Wildlife Fund, Washington, D.C., pp. 455–537.

Williams-Linera, G. 1990, Vegetation structure and environmental conditions of forest edges in Panama. *J.Ecol.* 78:356–373.

Wright, P. C. 1981, The night monkeys, genus *Aotus*, in: A. F. Coimbra-Filho and R. A. Mittermeier, eds., *Ecology and Behavior of Neotropical Primates*, Vol. 1, Avademia Brasileira de Ciencias, Rio De Janeiro, pp. 211–240.

Wright, P. C. 1989, The nocturnal primate niche in the New World. *J.Human Evol.* 18:635–658.