South American Primates

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South American Primates

Comparative Perspectives in the Study of Behavior, Ecology, and Conservation

Springer

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PAG dedicates this volume to Chrissie, Sara, Jenni, Sylvia, and to the memory of my father, Seymour Garber.

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Part I
Introduction

Chapter 1
Advancing the Study of South American Primates

Paul A. Garber and Alejandro Estrada

1.1 Introduction

Given the recent publication of several texts offering a comprehensive review of the behavior and ecology of each genus or major taxonomic group of New World primates (Campbell et al. 2007: Barnett et al. in press, Ford et al. in press), our goals in developing this volume are (1) to test and evaluate recent theories of sexual selection, population genetics, socioecology, predation risk, ontogeny and life history, reproductive endocrinology, foraging strategies, cognition and problem-solving, and conservation biology based on data derived from studies of South American primates, (2) to produce a resource of important scholarly information and intellectual encouragement for the expanding set of South American scientists with interests in primatology, tropical ecology, evolutionary biology, and conservation (more than half of the contributors to this volume are from Latin America), and (3) to encourage researchers focusing on similar or related theoretical issues in other animal taxa including avians, chiropterans, rodents, carnivores, and in particular, Old World primates to expand their use of the published literature on South American primates to inform their studies. For example, based on a review of 60 randomly selected research articles published between 2005 and 2007 in 15 issues of the *American Journal of Primatology* (Table 1.1), only 8.9% of the citations in studies of prosimians, 7.5% of the citations in studies of Old World monkeys, and less than 4% of the citations in studies of apes refer to the relevant literature on New World primates. Although, it is possible that this could be explained by the fact that publications on New World primates are under-represented in the literature, this is not the case. Of the total number of taxonomically-oriented research articles published in these 15 journal issues, 34% were on New World monkeys, 19.3% on prosimians, 20.4% on Old World monkeys, and 26.1% on apes. In addition, given that two forthcoming volumes on South American primates focus exclusively on the callitrichids (Ford et al.) and Pitheciines (Barnett et al.) a major challenge of this volume is to highlight

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Table 1.1 Citation Bias in a Select Sample of Recent Articles Published on Primate Behavior and Ecology

	Prosimian	NW monkey	OW monkey	Ape	Human	Other	Total references
Prosimian							
% references	**58.9**	6.7	7.6	1.2	0.4	25.0	670
% species references[1]	**78.6**	8.9	10.1	1.6	0.6		
NW Monkey							
% references	1.0	**42.5**	14.0	5.5	7.0	29.8	636
% species references[1]	1.4	**60.5**	20.0	7.9	10.0		
OW Monkey							
% references	1.3	5.5	**49.3**	6.3	10.8	26.6	680
% species references[1]	1.8	7.5	**67.2**	8.6	14.8		
Ape							
% references	0.8	2.5	7.5	**52.3**	11.8	25.0	630
% species references[1]	1.0	3.3	10.0	**69.7**	15.7		

[1]References listed under Other are omitted from the calculation. These include articles focused on nonprimate taxa and theoretical issues in which data from a broad range of taxa (primate and nonprimate) are included.
[2]Issues of the American Journal of Primatology used in this analysis are: 2005 volume 65 no. 1, 2, and 3, volume 66 no. 1 and 2, volume 67 no. 1 and 3; 2006 volume 68 no. 2, 7, 9, 10, and 12; 2007 volume 69 no. 3, 4, and 5.
[3]34% of all research articles published in these issues of AJP were on New World monkeys, 19.3% were on prosimians, 20.4% were on Old World monkeys, and 26.1% were on apes.

recent theoretical advances in the study of South American primates and encourage primatologists, biologists, ecologists, and conservationists to use insights gained from studies of a broad range of platyrrhine species in their own research.

1.1.1 South American Primates

As an island continent separated from Africa, North America, Central America, and Asia for most of the past 100 million years, South America has witnessed the evolution of several distinct indigenous animal and plant communities, including the platyrrhini or New World monkeys. The earliest fossil evidence of platyrrhines on the continent (*Branisella-boliviana*) dates to the Deseadan (late Oligocene) of Bolivia, approximately 26 mya (Rosenberger et al. this volume; Fleagle and Tejedor, 2002). Based on biogeography, comparative anatomy, and molecular evidence, however, it is likely that primates first reached South America some 10 million years earlier (Poux et al. 2006), possibly the outcome of a rafting event across the South Atlantic from Africa or a rafting event through the Caribbean Sea from North America (de Oliveira et al. this volume).

Currently, there are 19 genera, 7 subfamilies, and 199 recognized species and subspecies of New World monkeys (Rylands et al. this volume), making platyrrhines one of the most taxonomically, behaviorally, and anatomically diverse primate radiations. Modern South American primates vary in adult body size by a factor of over 100, with the smallest species, the pygmy marmoset (*Cebuella pygmaea*) weighing 120 gm and the largest species, the muriqui (*Brachyteles arachnoides*) and the gray woolly monkey (*Lagothrix cana*) weighing 10–12 kg (Di Fiore and Campbell, 2007). South American primates are characterized by a number of different foraging strategies, patterns of habitat utilization, and anatomical adaptations of their dental, masticatory, digestive, sensory, and locomotor systems (*see* chapter by Norconk et al.) that enable them to efficiently exploit food types such as insects, small vertebrates, immature and mature leaves, hard unripe fruits and soft ripe fruits, nuts, seeds, exudates, fungi, and floral nectar. *Aotus*, the night monkey is the only taxon of higher primate that includes both nocturnal and cathemeral species (Fernandez Duque, 2007). Monkeys of the genus *Cebus* are reported to cooperatively hunt and share vertebrate prey (Rose, 1997) and to frequently break open difficult to obtain foods, by pounding them against hard substrates (Rose, 1997; Panger, 1998). A capuchin species, *Cebus libidinosus*, has been documented using large stones as tools in the wild to open hard palm fruits (Fragaszy et al. 2004a).

1.1.2 South American Primate Mating and Social Systems

South American primates are also characterized by extreme diversity in reproductive biology, mating strategies, and social systems. There are species of the genus *Aotus* and *Callicebus* that live in small pair-bonded social units (Fernandez Duque, 2007); species of the genera *Saguinus*, *Callithrix*, *Leontopithecus*, *Cebuella*, and *Mico* that produce twin infants, exhibit a polyandrous-polygynous mating system with cooperative care of infants and reproductive suppression of subordinate females (Garber, 1997; Digby et al. 2007; Heymann, 2000; Zeigler and Strier this volume); species of the genus *Saimiri* that live in sex-segregated social groups of 25–60 individuals in which males attain a "fatted stage" and increase body mass by 20% during a short breeding season (Boinski, 1999; Stone, 2006; Izar et al. this volume); species of the genus *Alouatta* that are found in either small one male-multifemale groups or small multimale-multifemale groups (Kowalewski, 2007; Di Fiore and Campbell, 2007); species of the genera *Lagothrix*, *Chiropotes*, *Cacajao*, *Brachyteles* that live in large multimale-male multifemale groups or communities from over 20–100 individuals (Ayres, 1989; Barnett et al. 2005; Defler, 2001; Jack, 2007; Strier, 1997) , and species of the genus *Ateles* that live in fission-fusion communities in which adult males patrol the borders of their range in an attempt to maintain access to a set of adult females (Di Fiore and Campbell, 2007). In addition, adult male to adult female sex ratios in established groups of many species of South American primates more closely approaches 1:1 than is generally found in Old World monkeys and apes, in which adult sex ratios are highly biased toward females (Jack and Fedigan, 2006). The presence of a roughly equal number of adult males and females in established social groups, coupled with the fact that in several species of New World primates the number of female breeding positions appears to be limited, is likely to have an important effect on sexual selection, sexual coercion, reproductive strategies, infanticide risk, and the opportunity for co-operative mate defense by resident males (Garber and Kowalewski, in press).

Compared with Old World monkeys, many species of South American primates exhibit bisexual dispersal and weak social bonds among adult females (Strier, 2000, 2004). An important result of bisexual dispersal is that social groups often are composed of several unrelated adults of both sexes. Although it is generally argued that kinship is the primary basis for dyadic affiliative and cooperative behaviors in primates (Silk, 2007), theories of reciprocity, biological markets, byproduct mutual, and partner competence all outline the mutual advantages that both related and unrelated individuals obtain through coordinated, tolerant, and cooperative interactions and as members of a functioning and cohesive social unit. (Dugatkin, 1997; Barrett and Henzi, 2006; Chapais, 2006; Sussman and Garber, 2007). This may help to explain observations of strong adult male-male tolerance and social bonds that characterize many platyrrhine lineages (Strier, 2000; Di Fiore and Campbell, 2007). In the case of muriquis, for example, data collected by Strier (2000: 73) highlight "the benefits that larger groups of male kin may gain in competition with other groups of related males over access to females. . ." (Strier, 2000: 73), whereas in the case of *Alouatta*, *Chiropotes*, *Saguinus*, and *Callithrix* both related and unrelated resident males may co-operate in ways that enable each to receive social, dietary, and reproductive benefits (Wang and Milton, 2003; Digby et al. 2007; Garber and Kowalewski, in press; Kowalewski, 2007; Kowalewski and Garber, submitted).

1.1.3 South American Primate Conservation

Finally, as in other parts of the world, in South America high rates of human population growth associated with anthropogenic disturbance resulting from deforestation for timber, agriculture, and cattle ranching and increased susceptibility to new vectors of disease in changing landscapes exert a strong negative impact on the sustainability of nonhuman primate populations (Estrada, this volume; Kowalewski and Gillespie, this volume). However, although humans have been a fundamental part of the primate ecological community in Africa and Asia for several million years, it has been only in the past 10,000–20,000 years that populations of humans entered South America and encountered nonhuman primates as an important source of dietary protein. In this regard, the impact of humans as predators of South American primates is relatively recent and its evolutionary effect on the behavior, ecology, and group size of platyrrhines remains unclear (*see* chapters by de Thoisy et al. and Ferrari, this volume). What is clear, is that overhunting by native and nonnative communities, deforestation, and rapid increases in human population growth have resulted in a serious decline in the biomass and survivorship of many primate populations leading to recent local extinction, especially in the case of several ateline species, as well as changes in patterns and processes of seed disperal, pollination, and forest regeneration (de Thoisy et al. this volume; Estrada, this volume; Vulinec and Lambert, this volume; Peres and Palacios, 2007). In this regard, South American primates offer important behavioral and ecological models for addressing contemporary theoretical issues in evolutionary biology, community ecology, and conservation.

1.2 Organization of the Volume

This volume on South American Primates is divided into three main areas of inquiry. Part I: Taxonomy, Distribution, Evolution, and Historical biogeography of South American primates, Part II: Recent Theoretical Advances in Primate Behavior, Ecology, and Biology, and Part III: Conservation and Management of South American Primates. We end the volume with a concluding chapter that focuses on research priorities and conservation imperatives.

1.2.1 Part I: Taxonomy, Distribution, Evolution, and Historical Biogeography of South American Primates

Following the Introduction to the volume, Chapter 2 by Rylands and Mittermeier focuses on issues of platyrrhine taxonomy, acknowledging the substantial efforts and contributions of the late Phillip Hershkovitz to this endeavor. The chapter includes a brief historical discussion of New World primate classification, and then outlines recent revisions to platyrrhine taxonomy adopting a Phylogenetic Species Concept (PSC). PSC integrates morphological, geographical, genetic, and chromosomal lines of evidence to assign species distinctions. These authors caution that although current taxonomic evaluations will undoubtedly change in the future, "a neatly explained taxonomy with a well-drawn map unfortunately tends to inspire complacency." Both species' definitions and geographic distributions are hypotheses that require continuous testing; evaluating the quality and quantity of information upon which they are based.

In Chapter 3, Oliveira et al. examine recent tectonic, biogeographical, geological and paleocurrent information to re-evaluate the question of how and when New World primates first arrived in South America. Given the current fossil evidence, there remain two plausible scenarios for the origin of South American primates. The presence of basal anthropoids in Asia (Eosimiids) that date to 45 mya (Beard, 2002), offer the possibility that an early population of Asian anthropoids migrated into North America and later via a water route dispersed into South America. It also is possible that such a population migrated first to Africa and then via a water dispersal route from Africa to South America. Alternatively, there is fossil evidence of pre-platyrrhine anthropoids in Africa (Parapithecids) dated at approximately 37 mya (Fleagle, 1999) offering the possibility that a population of endemic early African anthropoids may have migrated across the South Atlantic to South America.

Oliveria et al. explore three dispersal models for an African origin of platyrrhines. These are (1) a continuous land bridge connection between Africa and South

America, (2) island hopping, or (3) dispersal on floating islands which are large buoyant masses of soil, roots, shrubs, and entangled trees that have eroded from a terrace of land. Based on ocean paleocurrents, tectonic movements, and seafloor subsidence movements, Oliveria et al. reconstruct a paleodistance of 1000 km between West Africa and eastern-Brazil at 40–50 mya, and argue that the most plausible scenario is that ancestral platyrrhines crossed the transatlantic on large floating islands at the time. Ultimately additional fossil evidence is required to test competing theories of an African or a North American origin for platyrrhines.

In Chapter 4, Rosenberger and colleagues integrate issues of phylogeny, geology, paleontology, paleoclimate and paleoecology in developing a new perspective on platyrrhine evolution. Although it has been argued that the radiation of extant platyrrhines is principally Amazonian in origin, with several modern lineages traced to ancestral forms that inhabited forested regions of Amazonia 12–16 mya (Hartwig, 2007), these authors identify four different regions in South America (the Amazonian, Atlantic, Patagonia, Caribbean) where individual primate taxa appear to have first evolved. For example, lineages such as *Alouatta*, *Cebus*, *Aotus*, and *Callicebus* may have originated outside of Amazonia in drier and more marginal forested habitats analogous to present day semi-arid savanna, cerrado and caatinga vegetation. These genera today are characterized by an extremely widespread geographic distribution ranging from southern Argentina (*Aotus, Cebus,* and *Alouatta*) and Paraguay (*Callicebus* and *Aotus*), through the Amazon Basin, Colombia, the Guianan shield, and into Panama (*Aotus, Cebus*, and *Alouatta*, but not *Callicebus*) (Fernandez Duque, 2007; Cortes-Ortiz et al. 2003; Fragaszy et al. 2004b). The distribution of *Cebus* extends west to Honduras and the distribution of *Alouatta* continues across Mesoamerica into Mexico (Rylands et al. 2006). These authors present evidence that during much of the past 15 million years, Amazonia was severely flooded and part of a giant riverbed or lake. They argue that in response to this ecological condition, several platyrrhine lineages evolved positional adaptations such as a prehensile tail, claw-like nails, and trunk-to-trunk leaping in order to exploit subcanopy resources.

1.2.2 Part II: Recent Theoretical Advances in Primate Behavior, Ecology, and Biology

This Part of the volume begins with Chapter 5, a paper by Blomquist et al. on primate life history evolution. Recent studies of platyrrhine life histories offer a critical perspective from which to examine questions of ontogeny, maternal investment, brain growth, and developmental trajectories (Garber and Leigh, 1997; Leigh and Blomquist, 2007). For example, among both New and Old World primates there are species characterized by extensive prenatal brain growth and delayed postnatal somatic growth, as well as species that reach adult body mass relatively early in development but fail to reach adult brain size until late in development (Garber and Leigh, 1997; Leigh and Blomquist, 2007). Perhaps more importantly, it has become clear that classifying species as having either a "fast" or "slow" life history fails to account for tradeoffs in the timing and duration of growth of energetically expensive tissues (Leigh and Blomquist, 2007) and disassociations in the ontogeny and development of individual traits. Relative to body mass, platyrrhine lineages such as *Cebus*, *Ateles, Brachyteles*, *Lagothrix*, and *Saimiri* exhibit a delay in certain life history traits such as late age at first reproduction, long interbirth interval, and extended period of gestation that are analogous to those reported for apes and humans. Some of these species, however are characterized by accelerated locomotor development and the attainment of adult-like foraging skills (Bezanson, 2006; Stone, 2006). As indicated by Blomquist et al. (pp. 124) "This dissociation of developing structures is a core concept for understanding how ontogeny can be molded into adaptive patterns, and contrasts remarkably with traditional 'fast vs. slow' models for mammalian life history evolution in which development is entirely absent or is the vacant space between neonatal and adult endpoints." In addition, these authors argue that demographic modeling of life history traits in Old and New World primates has the potential to identify those variables with the greatest effects on population growth rates, and thus, also has considerable relevance for determining effective policies of conservation and management.

In Chapter 6, Strier and Mendes outline the unique insights that long-term field studies make to our understanding of primate demography, group structure, and for testing theories of fitness and natural selection. The first extended field study of a primate in the wild was conducted on mantled howling monkeys (*Alouatta palliata*) in Panama and published by Clarence Raymond Carpenter in 1934. In the mid-to-late 1950s and early 1960s field studies of Old World monkeys and apes began in earnest, resulting in several species now studied continuously or nearly continuously for over 40 years. Although historically, long-term studies of New World primates have lagged behind their Old World counterparts, Strier and Mendes point out that using the criteria of "the number of primate generations" a study spans, we have reached a point at which detailed long-term data exist for species of the genera *Saguinus*, *Leontopithecus*, *Brachyteles*, *Alouatta*, and *Cebus.* These data enable researchers to address critical questions concerning long-term relationships between individual reproductive success, age at dispersal, dominance, social affiliations, and survivorship, as well as how individuals, groups, and species respond behaviorally to proximate changes in predator pressure, group size and composition, and food availability. In addition, long-term studies of primate groups offer an important framework for modeling the ability of local populations to recover from natural environmental perturbations such as drought, disease, and hurricanes, as well as anthropogenic change such as deforestation (Strier and Mendes this volume; Estrada this volume; Kowalewski and Gillespie, this volume; Pavelka and Chapman, 2006).

Chapter 7 by Izar et al. examines issues of sexual selection, mate choice, male coercion, female promiscuity, male reproductive tenure, and female avoidance strategies in understanding primate reproductive behavior. Using data on capuchins and squirrel monkeys, these authors test a series of hypotheses concerning the set of conditions under which females exercise mate choice associated with a preference for particular male qualities and the set of conditions under which female mating behavior reflects behavioral tactics designed to reduce infanticide risk. In examining patterns of sexual conflict, these authors argue that in species in which males provide females minimal direct benefits of infant care and protection, resource defense, or territorial defense (*Saimiri sciureus*), male-male breeding competition rather than female mate choice is a primary driver of mating behavior. In the case of two capuchin species (*Cebus nigritus* and *Cebus capucinus*), patterns of female mating were found not to closely reflect differences in the level of infanticide risk. Although female mating patterns in each species were found to include paternity concentration and paternity confusion, in *Cebus capucinus* resident males were tolerant of each other and females mated promiscuously whereas in *Cebus nigritus*, male social interactions were more despotic and females mated principally with the alpha male. Overall, this study supports the contention that intersexual conflict plays an important role in the primate mating strategies.

In Chapter 8, Ziegler, Strier, and Van Belle focus on recent advances using non-invasive techniques to measure endocrine profiles in wild and captive primate populations to examine the effect of ecological and social factors on male and female fertility. Unlike many mammals, mating behavior in anthropoid primates "is not restricted to the periovulatory period" (Zeigler et al. this volume pp. 204). Females in many primate species mate during all phases of their reproductive cycle (ovulation, pregnancy, and lactation). This creates a wider opportunity for female mate choice and a reduction in male mating competition if females (a) preferentially mate with a particular male or males when they are most fertile, (b) reinforce a sociosexual bond with individual male group members by mating throughout the year, or (c) mate promiscuously such that males collectively defend resident females from males in neighboring groups (Garber and Kowalewski, in press). Zeigler et al. present endocrine data on in several New World primate species outlining a set of conditions under which conception is most likely to occur, identify species differences in the occurrence and duration of nonconceptive ovulatory cycles, and discuss factors that may affect the cessation of ovulatory cycling in adult females. These authors (pp. 205) stress the importance of female nutrition, steroid hormone production, and the social environment in understanding "the factors that regulate the onset of ovarian cycling and conception, and environmental influences on reproductive patterns."

In Chapter 9, Di Fiore provides a comprehensive review of analytical techniques using molecular genetic data to address questions of kinship and within-group social behavior in primates. He identifies two critical factors, dispersal patterns (solitary, paired, or the common migration of individuals from one group or population into a second group or population; sex-biased dispersal, bisexual dispersal) and individual reproductive tactics (partner fidelity, promiscuity, sexual coercion, or rank related effects on reproductive success) as primary determinants of genetic relatedness among individuals in the same group and among individuals in neighboring groups. Di Fiore argues that (pp. 212) "Given the widespread acceptance of kinship as a key explanatory principle underlying and structuring much of primate social lives, it is imperative that future primate studies pay more attention to exploring the link between relatedness and individual behavior using molecular data." To this end, genetic information enables researchers to examine the success of individual male and female reproductive strategies by distinguishing between the mating group (i.e., the set of individuals that engage in sexual behavior during both fertile and non-fertile periods) and the breeding group (i.e., the set of individuals that successfully contribute genes to the next generation), as well as determine the degree to which kinship, familiarity, and/or partner competency offer more robust explanations of affiliative and agonistic social interactions among group members. Di Fiore also presents data based on an ongoing study of woolly monkey and spider monkey populations in Ecuador. Using genetic information extracted from tissue and fecal samples he found that for woolly monkeys, both males and females commonly dispersed from their natal groups, that adult males residing in the same group or local population are not more closely related to each other than are females, and that some males and some females were found to reside in groups with closely related same-sex kin. In the case of spider monkeys, however, the genetic evidence indicates that in one study population males are philopatric, dispersal is strongly female-biased, and groups were composed of closely-related males, whereas in a second population (this volume, pp. 240) "many adult females seemed to reside with likely close kin and the mean degree of relatedness among both adult males and females was close to zero." The presence of both related and unrelated same-sex individuals co-residing in the same groups offers an important opportunity to more directly examine the effects of kinship, partner competency, and familiarity on primate social interactions.

In Chapter 10, Ferrari reviews data on predation risk in South American primates in order to better understand the relationship between antipredator strategies and group structure. He presents information on primate body mass, predator type and behavior, primate pelage coloration, patterns of habitat utilization, group size, and antipredator behavior (mobbing, crypticity, alarm calls, branch shaking and object throwing, selection of sleeping sites, limited reuse of sleeping sites). "From both an ecological and an evolutionary viewpoint, predation events are rare and unpredictable." (pp. 267). However, studies of predator nests and feces indicate that primates are preyed upon by raptors and mammals at a considerably higher rate than observed by primate field researchers. Smaller bodied species appear to be more vulnerable than larger bodied species to raptors and possibly snakes, whereas felids may be the most frequent predator of larger bodied playtrrhines. Ferrari also suggests that predation rates on primates appear to be higher in fragmented and edge habitats, and more common near or on the ground. This has important implications for conservation and the size and design (relative area of the center to edge) of reserves. Finally, intragroup cooperative behavior associated with vigilance, mobbing, alarm calling, and chasing potential predators is argued to be an important factor in reducing predation risk in primates.

In Chapter 11, Norconk et al. examine the challenges that primate foragers face in obtaining, dentally processing, and digesting plant tissues that vary in their mechanical properties. These authors integrate three critical areas of investigation, namely dental and masticatory morphology, the toughness of food items, and the nutrient quality (metabolizable energy) of foods ingested. In a comparison of 16 New World primate genera, Norconk and colleagues present evidence of a size related decrease in the bite force produced at M1 and the incisors. This relationship was especially pronounced in callitrichines and may be related to gouging into tree trunks during exudate feeding (Vinyard and Ryan, 2006), and opening large, tough legume pods with their anterior dentition (Tornow et al. 2006). Hard-object feeders such as *Cebus*, *Pithecia*, *Chiropotes*, and *Cacajao* were found to produce the greatest mechanical advantage with their incisors, canines, and M1. This may be required to process difficult to open foods such as unripe fruits, nuts, and seeds. Leaf-eating platyrrhines (*Brachyteles* and *Alouatta*) produced considerably lower bite force with their anterior dentition. These authors also found that although platyrrhines tend to exhibit a generalized digestive tract, in many cases smaller-bodied taxa are characterized by longer gut retention times than closely related larger bodied forms.

Finally, an examination of the nutritional composition of 128 plant species indicates that (pp. 301) "seeds are more energy dense than are fruit, flowers or leaves. . ..." "fungi were equivalent to fruit pulp in terms of crude protein. . ..." "flowers are moderately high in fiber too (*as are whole fruit with pulp and seeds chewed together*), and their protein content is as high as leaves." In integrating data on metabolizable energy intake, masticatory anatomy, and dietary toughness in South American primates these authors identify several distinct evolutionary trajectories that vary across body mass and dietary pattern. For example, on average both *Callithrix* (chewing bark to obtain plant exudates) and *Alouatta* (chewing leaves) consume the toughest foods, but neither taxa exhibit the most robust jaws. However, *Cebus* consumes both less tough and extremely tough foods. In this regard, critical function or the use of fallback foods during times of resource scarcity may offer important insight into a species' ecomorphology and dietary adaptations.

In Chapter 12, Vulinec and Lambert examine and compare the predictive value of neutral models and niche models for understanding tree species assemblages, richness, species abundance, and community ecology, using the example of primates as seed dispersers and seed predators. Several authors have argued that primates have played a critical evolutionary role in shaping fruit and seed characteristics of many species of flowering plants (Janson, 1983; Gautier-Hion et al. 1985; Julliot, 1996). These authors have defined a suite of fruit and seed traits (size, shape, phenology, pulp weight, color, number of seeds) or "syndrome" that represent primate dispersed fruits. Vulinec and Lambert challenge this assumption and present data on primate densities, tree species distributions, and the fate of seeds secondarily dispersed by dung beetles in a forest community in the State of Amazonas, Brazil. They argue (pp. 323) high variance in factors such as the diversity and biomass of frugivores in an area, the manner in which primates treat seeds (swallow whole, drop under the parent tree, consume), the time of day or night seeds are voided, the conditions of the site at which the seed is deposited, the fruiting patterns of nearby trees, and the behavior of secondary dispersers and predators (fungal pathogens, rodents, ants, dung beetles) "can swamp directional selection pressure and effectively neutralize competitive interactions and resulting species assemblages." Thus, rather than the efforts of a single species or taxon, it is the combined effects of fruit and seed handling by primary dispersers, seed predators, secondary dispersers, and post-secondary dispersal seed and seedling fate that act to determine patterns of forest regeneration and tree species characteristics (Garber and Lambert, 1998). Vulinec and Lambert conclude that with increasing deforestation reducing mammalian and avian communities in the tropics, effective policies of rainforest conservation will need to determine the effects of stochasticity or neutrality on plant and animal species assemblages.

In Chapter 13, da Cunha and Byrne examine a critical set of research questions concerning primate cognition, group movement, spatial cohesion, intentionality, and the function of primate vocalizations (call and answer systems). These authors argue that theory of mind or the ability of a caller to know information possessed by other callers and to manipulate that information is unlikely to offer the most accurate explanation of primate call and answer systems. These authors examine two main hypotheses; the personal-status hypothesis in which "calls are not given with the intent of maintaining contact or informing the whereabouts of the group to the separated animal(s)" but rather reflect "the state of mind of the 'responder' itself," (pp. 346), and the reunion hypothesis which assumes that both caller and responder share the same goal of reuniting or rejoining. Both hypotheses are tested using the paradigm of intentionality. Whereas theory of mind requires 2nd order intentionality, these other hypotheses require either zero order or 1st order intentionally. Authors da Cunha and Byrne use the example of the moo call in black howler monkeys (*Alouatta caraya*), which appears to function for purposes of reuniting individuals, to explore these cognitive hypotheses and to outline a framework to describe the function of contact calls in primates. The scheme has as its first functional level, calls that serve to maintain the cohesiveness of the group. The second functional level involves targeted calls that serve to maintain or attain close proximity with a particular individual. Calls that serve to maintain group cohesion are further divided into those designed to keep contact, regaining lost contact, and coordinating group movement. The scheme proposed by da Cunha and Byrne can be used to examine the specific function of contact calls within and across primate species. These authors suggest that call-and-answer systems in primates are generally consistent with first-order intentionality and the reunion hypothesis.

Part II ends with Chapter 14 by Garber et al. presenting a series of controlled experimental field studies designed to examine the ability of two species of tamarin monkeys (*Saguinus imperator* and *Saguinus fuscicollis*) to integrate ecological information (spatial and temporal predictability of the location of baited feeding sites and expectations concerning the quantity of food available at feeding sites) and social information (identity, tolerance, and dominance status of co-feeders) in foraging decisions. Virtually all primates are social foragers, and therefore individuals are commonly faced with decisions whose effective solutions require the ability to integrate both social and ecological information. Under the conditions of these field experiments, individuals could act as searchers (use ecological information to encounter a feeding site), joiners (co-feed or usurp food patches found by others using social information), or opportunists (more evenly distribute their time and energy budgets to both searching for food and visiting food sites located by conspecifics) and integrate social information and ecological information. Experimental feeding sites varied systematically both in the quantity of the food reward and the monopolizability of the food reward (either 2 or 8 individual platforms contained concealed food rewards). In each species, individuals flexibly switched from searcher, joiner, and opportunist foraging patterns under changing conditions of food availability and distribution. However, species-specific differences in social tolerance influenced the degree to which dominant and subordinate individuals were successful when adopting a joiner strategy or opportunist strategy. At productive feeding sites, differences in individual feeding success were minimal and not influenced by the strategy adopted by individuals in either species. However at small and monopolizable feeding sites, searchers had higher feeding success than joiners or opportunists regardless of rank. The results indicate that primate foragers attend to the behavior of conspecifics and cognitively solve problems of food acquisition by integrating both social information and ecological information in their decision making.

1.2.3 Part III: Conservation and Management of South American Primates

This Part of the volume begins with Chapter 15 by de Thoisy et al. examining factors that impact and regulate subsistence hunting of Amazonian primates by indigenous Amazonian groups. These authors compiled a database of case studies from 41 sites in French Guiana and 70 sites in the lowland Amazon Basin of Brazil. Data on the degree to which primates were hunted (heavily, moderately, or minimally), information on primate harvest rate, group size, level of habitat disturbance, and the duration of hunts (single day or multi-day) are presented. These authors found (pp. 401) "that hunting effort allocated to multi-day expeditions in infrequently hunted areas primarily attempts to maximize yield of preferred (and locally depleted) prey species rather than the overall bag size (or biomass) of all potential prey species . . . thereby diluting their impact on a per area basis." Nevertheless, hunting was found to frequently result in the local extinction of larger bodied primate species such as *Ateles* and *Lagothrix*, significant population declines in *Pithecia*, *Chiropotes*, and *Cebus*, and, on occasion to overhunt but maintain sustainable populations of *Alouatta* and *Cebus*. Changes in hunting pressure due to an increase in the number of indigenous neighboring communities, incursion by nontribal peoples, and logging make urgent the need for the protection of indigenous land-rights and incentives to promote long-term resource sustainability and management.

In Chapter 16, Pinto et al. synthesize data on the differential impact of anthropogenic change on the density and distribution of individual primate species inhabiting the Atlantic forests of Brazil. This area is characterized by extremely high rates of endemism in both plant and animal communities. The Atlantic forest of Brazil contains a human population of over 130 million people, with less than 8% of the original habitat remaining and distributed as scattered and isolated fragments. Using geographical information systems (GIS) technology and a statistical method (Regression Trees) designed to control for non-linear interactions among environmental predictors of primate population size (forest type, rainfall, elevation, fragment size), these authors found that the five primate species examined differed in response to particular changes in the habitat availability including the characteristics of “hot spots” or areas of high density. This is critical for developing successful conservation and management programs. For example, the population density of *Callicebus* was positively affected by the amount of nearby land devoted to agriculture, whereas in *Alouatta* the impact was negative. The density of capuchin monkeys was found to increase in the vicinity of industrialized cities. The ability of some primate species to survive in landscapes that contain agricultural fields, archaeological sites, or sites of ecotourism (*see* Estrada et al. 2006a, b) offer hope for the development of sustainable practices of land use that maintain both human and nonhuman primates. The results of this study indicate that detailed information on “patterns of land use and social indicators from municipalities where fragments are located” including income and hunting, serve to identify locations that have the potential to support and maintain primate populations (pp. 422).

In Chapter 17, Kowalewski and Gillespie examine the role of parasites (gastrointestinal, blood, and ectoparasites) in community biodiversity, primate heath, and opportunities for cross-transmission in undisturbed versus fragmented habitats. Similar to baboons, macaques, and some colobines, several genera of South American primates (e.g., marmosets, howler monkeys, and capuchins) are able to survive in highly modified environments, including areas adjacent to cattle pasture, gardens, agricultural fields, parks set aside for ecotourism, and urban areas (Bicca-Marques, 2003; Frões, 2006; Sabbatini et al. 2006). Capuchins, for example, are known to raid crops such as bananas, coconuts, and maize (Garber, pers. obser), and in doing so come into contact with humans and domesticated animals. Similarly, howler monkeys represent an important model for the “dynamics of infectious disease transmission among wild primates, humans, and domesticated animals” because of their frequent proximity to human settlements and susceptibility to parasitic, bacterial, and viral diseases found in humans and their livestock (Kowalewski and Gillespie, this volume pp. 434). The threat of disease transmission across humans, domesticated animals, and nonhuman primates remains an extremely serious public health issue throughout the New and Old World tropics, as well as a serious environmental and conservation issue as human populations expand and encroach more and more on areas once only inhabited by nonhuman primates. Kowalweski and Gillespie conclude that (pp. 449) “almost 86% of gastrointestinal parasites, and 100% of blood-borne parasites found in howlers are found in humans. Our results provide a baseline for understanding causative factors for patterns of parasitic infections in wild primate populations and may alert us to iminent threats to primate conservation.”

In Chapter 18, Estrada details the complex and specific set of human (population increase and poverty), economic, sociopolitical, historical, and ecological drivers that impact patterns of land use, biodiversity, and conservation pressures in South America. Integrating data bases obtained from several governmental, United Nations, and Development agencies for 10 South American countries located within and outside of the Amazon Basin, his analysis reveals that increases in human population growth (1.7% per year), poverty (25% of the population of South America live on less than US $2 per day), and conversion of forest to cattle pasture and agricultural fields in response to global markets for meat, biofuels, food production, and timber have resulted in the loss of 37 million ha of forest per year, and significant reductions in biodiversity. Countries with the largest amounts of deforestation are Brazil, Bolivia, Venezuela, and Ecuador. These are countries that harbor a diverse and increasingly threatened primate community. Using a model of exponential decay, Estrada projects the magnitude of forest loss in South America over the next 50–100 years, stresses the responsibility of national governments to make decisions in improving the standard of living of their people, to protect the environment and natural patrimony, to establish and maintain national parks, to restore native habitats, and to expand research on the (pp. 467) "ways indigenous populations manage their forests and primate wildlife, on their traditional ecological knowledge, and on ways to incorporate their interest in conservation plans." The chapter concludes with a list of high priority issues for primate conservation in South America.

The final Chapter 19 of the volume, by Estrada and Garber, recognizes the contributions of early biologists and mamalogists, as well as more recent primate specialists in advancing the development of Primatology in South America. This chapter provides a chronological overview of the richness of published scientific information on South American primates by country and major taxa in order to assess the current state of accumulated knowledge available to scholars and researchers. Finally, the authors identify and detail critical research priorities and conservation imperatives for the study and preservation of South American primates and their habitats, and emphasize the importance of working with indigenous scholars and the local human communities in order to achieve this goal.

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