

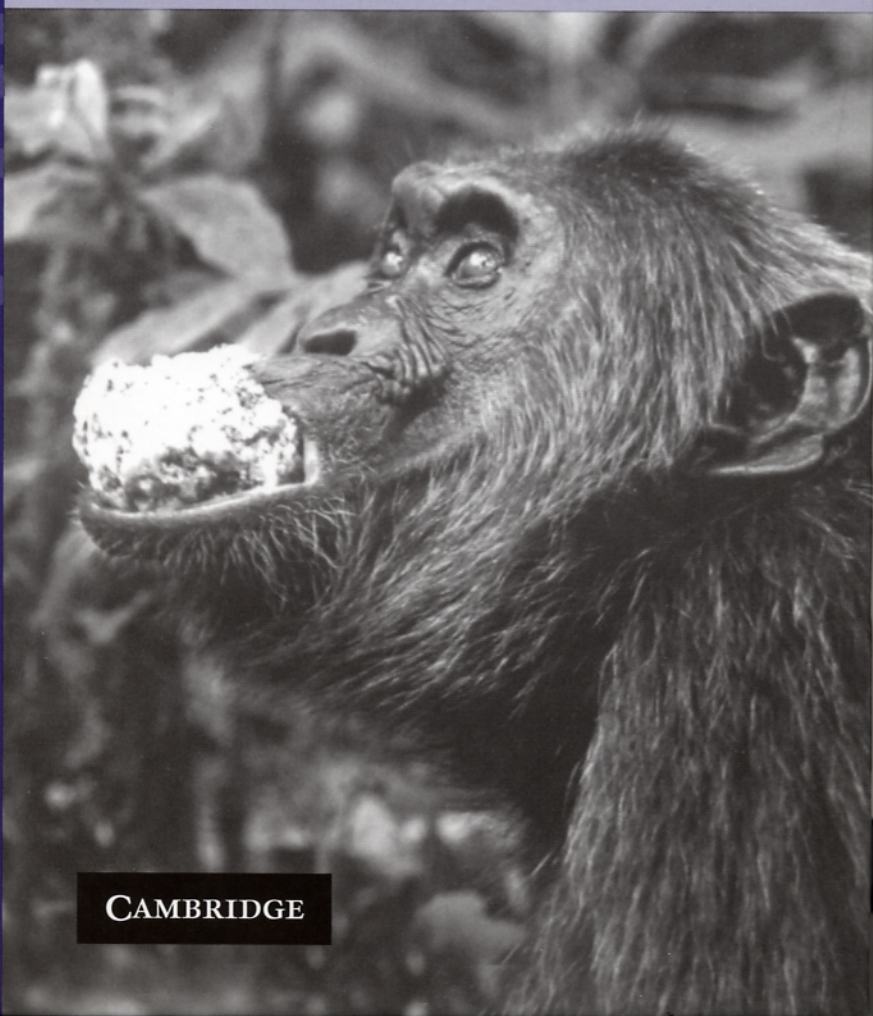
PRIMATES

Feeding Ecology in Apes and Other Primates

Ecological, Physiological and
Behavioural Aspects

Edited by

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CAMBRIDGE

Part III

Analyzing nutritional ecology:

Picking up the pace: nutritional ecology as an essential research tool in primatology

Introduction

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The initial trajectory of primate field studies

The first successful systematic field study of wild primates was carried out by C. Ray Carpenter on Barro Colorado Island (BCI), Panama in the early 1930s. Carpenter, who was jointly sponsored by the National Research Council's Committee for Research in Problems of Sex and Robert M. Yerkes's Department of Psychobiology at Yale, spent some 9 months in total on BCI observing the behavior of wild howler monkeys, and produced a detailed monograph of unusually high quality (Carpenter, 1934). With no precedents to guide his research, he viewed his study as an opportunity "to collect data to answer hundreds of questions . . . on all possible characteristics of . . . a primate living in an undisturbed habitat" (Carpenter, 1965, p. 255). Though Carpenter collected considerable information on the howler diet, at that time there was no comparative framework within which to place it, and his background, training, and interests lay more with behavioral data that could perhaps assist in interpreting results of laboratory research on primates and illuminate aspects of human behavior.

Primate field studies then fell into abeyance for the next 20 or so years, but finally began to pick up speed again in the late 1950s. In 1965, the first collection of papers derived largely from primate field studies, Irvén DeVore's *Primate Behavior*, was published. This collection, as its title implies, is filled with descriptions of primate behavior – patterns of social organization, dominance hierarchies, communication calls, mating behaviors, and the like. Diet gets hardly a nod. In fact, the final chapter of the collection, *The Implications of Primate Field Research* written by Washburn & Hamburg (1965) does not even mention the word *diet* until the Conclusion, and here it simply appears as part of a long list of topics warranting investigation.

The next published collection, *Primates: Studies in Adaptation and Variability*, stemmed from a symposium on primate social behavior with the

emphasis on data from primate field studies. This collection, edited by P. Jay, was published in 1968. The topic of diet is little in evidence. It is rather amazing to read long papers on the behavior of particular primate species in the wild that discuss group size and composition, home range size, activity patterns and so on but hardly mention, much less discuss, diet. Hall's (1968) paper on the behavior and ecology of wild patas monkeys does devote almost four pages to dietary information – but this, in an 88-page paper, is not a great deal. One striking exception to the general non-ecological approach in the Jay volume, however, is provided by Gartlan & Brain (1968) in their paper comparing ecology and social variability in free-ranging vervet (*Cercopithecus aethiops*) and blue monkeys (*Cercopithecus mitis*). This paper is modern in its approach and repeatedly stresses that primate behavior needs to be integrated with ecology, not examined in isolation: "Social behavior can be seen to be a function of the interaction of the population with the environment . . . Social behavior is deeply rooted in the evolutionary history of the species; it does not exist in a vacuum, but is the means by which species are adapted to the efficient exploitation of particular niches in just the same way as the evolution of physical structures permits this." (Gartlan & Brain, 1968, p. 282, p. 290). Another pioneer in this area, was Hans Kummer, whose 1971 book *Primate Societies* examined "group techniques of ecological adaptation" for free-ranging hamadryas baboons.

After this point, as the number of primate field studies rapidly increases and training begins to broaden in scope, interest in ecology, and particularly dietary ecology, picks up dramatically. By 1986, with the publication of another book titled *Primate Societies*, this one a collection of papers edited by Smuts *et al.*, there is no longer any doubt about the importance of ecological influences on primate social organization and social behavior and, in particular, the importance of diet (e.g., see papers in *Primate Societies* by Oates, 1986; Silk, 1986; Waser, 1986; Wrangham, 1986). No field primatologist today would likely try and examine a behavioral question without obtaining a solid understanding of the diet and food distribution patterns of the species under study.

Since its inception, the ultimate goal of field primatology has repeatedly been stated to be to understand the array of factors giving rise to the wide diversity of primate social systems. However, getting off initially on a heavily behaviorally based research footing, one that largely ignored the role of ecological factors in shaping primate social organization and social behavior, seems to have impeded rather than assisted attainment of this stated goal. Indeed, even today it would seem that full appreciation of the overwhelming influence of diet on almost all aspects of any primate's behavior, morphology, and physiology has yet to be fully realized. We were all taught that behavior

is the cutting edge of evolution. But it still seems difficult for some to appreciate that the key force driving behavioral change generally relates to dietary pressures. In fact, as is probably now realized by almost everyone, either overtly or at some unconscious level, social and organizational features largely derive, either directly or indirectly, from the food choices and dietary energetics of the primate species under consideration, and for this reason can only be properly understood in integration with them. Two examples may help to clarify this point.

Ateles

According to Jerison's data (1973), the encephalization quotient (EQ – an estimate of cortical complexity) of spider monkeys (*Ateles* spp.) is unusually high. (I am aware that there are more recent sets of calculations that estimate relative brain size, comparative neocortex size, and so on for primates, but Jerison's EQ serves the purpose.) Regardless of the method employed, all seem in general agreement that among monkeys, spider monkeys are notably "brainy." A popular explanation for their considerable cerebral development might be that their large brain or neocortex relates to large group size and concomitant complex social behavior (Byrne & Whiten, 1988; Dunbar, 1992; Barton, 1996). Spider monkeys, however, do not live in particularly large social groups. Average group size for spider monkeys is around 26.6 ± 11.1 individuals ($n = 11$ groups; see Appendix for references used in calculation). And, as noted by Symington, in their "group size and sociometric sex ratio, spider monkeys appear to lie somewhere near the middle of the range reported for multimale groups of cercopithecine primates" (Symington, 1988, p. 60). Furthermore, due to their unusually strong focus on ripe fruits in the diet, spider monkeys generally are found foraging in small sub-groups of three or four individuals or even alone (fission-fusion pattern) as only in this way, apparently, are they able to obtain sufficient ripe fruits each day without incurring unacceptable travel costs (Milton & May, 1976; Chapman, 1990) or intragroup food competition (McFarland, 1986; Wrangham, 1986; Symington, 1988).

In a paper published in 2000, I noted (as had McFarland, 1986; Wrangham, 1986; Chapman *et al.*, 1995; and others) that the dietary focus of spider monkeys appeared related to their fission-fusion foraging behavior – a foraging pattern suited to their extreme ripe fruit diet but one requiring each adult individual to possess its own data bank of information regarding the types, locations, and travel routes to a wide array of edible fruit sources (see also Milton, 1982, 1988). I hypothesized that because of this dietary focus

Howler monkey nutritional ecology

In the mid-to-late 1970s, Barro Colorado Island was a popular crossroad for visiting tropical scientists from a wide range of disciplines. Students or post-docs such as myself, working on BCI during this period received broad exposure to a wealth of new ideas and were often able to form research collaborations. By then, I had already compiled data on the dietary behavior of BCI howlers (Milton, 1978, 1980). This material provided the foundation for expansion into the area of howler monkey nutritional ecology. As it might be useful for students to see a range of topics that can be addressed for a single primate species, here is a list of those we examined: (1) basal metabolism of howler monkeys (Milton *et al.*, 1979); (2) free-ranging metabolism of howler monkeys (Nagy & Milton, 1979a); (3) estimates of nutrient intake in howler monkeys (Nagy & Milton, 1979b); (4) quality and anti-quality components of howler foods (Milton, 1979); (5) efficiency of protein and fiber digestion in howlers (Milton *et al.*, 1980); (6) gut passage rates and fermentation returns of howlers eating natural items of diet (Milton, 1981a; Milton & McBee, 1983; Milton, 1998; Milton & Demment, unpubl. data); (7) nitrogen to protein conversion factors for wild plant parts (Milton & Dintzis, 1981); (8) pectin estimates for wild plant parts (Milton, 1991); and (9) vitamin C content of wild plant parts (Milton & Jenness, 1987). I also carried out work on attributes of the nutritional ecology of black-handed spider monkey (*Ateles geoffroyi*), a species sympatric with howler monkeys on BCI (Milton, 1981b). This work explored the question of whether internal features (gut morphology and/or physiology) might set limits to niche breadth for these similar-sized plant-eating monkeys, facilitating their coexistence. This leads me to address the question of just how plastic primate species are in terms of food choice in the natural environment (and indeed, in terms of their social organization and social behaviors).

How plastic are the diets (and social behaviors) of wild primates?

Dietary quality is a much used (and abused) term in the primate literature. The term relates (I believe) to the amount of digestible material relative to the amount of indigestible or unavailable material present in any food item – it is the animal's potential net from eating that item. Though quality in the most general sense relates to the nutritional value of the food to the animal, it can have a more specific sense when placed in the context of animal requirements and availability in the environment. So protein may be more important to a growing animal than to a mature one. Dietary quality therefore is not a

constant but a moving target and differs from species to species and even from individual to individual. It depends on many variables – the metabolic body size of the consumer, its sex and age, its digestive physiology, the nutrient mix consumed at any given time and so on. Just like the sweepingly broad (and therefore largely useless) terms *omnivore*, *folivore* or *frugivore* (see Danish *et al.*, Chapter 18, this volume), the term *dietary quality* needs to be understood as something that must be determined for each primate species.

Analysis of the quality and anti-quality components of the wild plant foods a given primate selects, its net from eating them, and the factors underlying its pattern of food selection continue to be only superficially explored for most primate species. Lacking information on factors that may set limits to dietary breadth for a particular species and constrain its range of food choices in the natural environment, many primatologists may overestimate the plasticity of wild primates – viewing them as capable of altering their behavior, including their dietary behavior, to fit almost any environmental circumstance. There is no doubt that primates, with their large brain-to-body ratios and fairly generalized morphology, exhibit considerable plasticity on many different levels and many primate species seem equally at home in a variety of different habitats. However, all primates appear to show species-specific dietary patterns. If we look at primate species, particularly when sympatric – we see that they choose different foods, or eat the same foods but at different stages of maturation, or consume different proportions of a few or many of the same foods while all living together in the same forest and even using many of the same arboreal pathways and food trees. Yet if we bring these same sympatric species into captivity, we often find that many can do equally well on the same diet – often, for monogastric primates, a diet composed of manufactured primate chow and water, although each species or, within species, each sex or age class may consume different quantities of chow, depending on body size and other considerations. This fact suggests, perhaps, that many primate species in the wild have sufficient dietary flexibility to subsist on one another's diets.

But in the natural environment, primates do not have unlimited access to nutritionally fortified, highly digestible monkey chow. In the wild, each primate species has an array of different factors – environmental, behavioral (including social behaviors), morphological and physiological – that appear to constrain it to a particular dietary niche. As has been remarked, the most profitable way to approach an understanding of any animal species may be to view it as a type of “natural experiment,” predicated on securing some portion of the always finite dietary resources available on the planet at any one time. The natural experiment we refer to as *Alouatta* or *Ateles* is a *food-acquisition*

design worked out over eons of selection. Certainly some degree of dietary plasticity should be possible for any primate species. Some primates, such as savanna baboons (*Papio* spp.), are dietary generalists showing considerable dietary plasticity. But even though they may eat hundreds of different items, they still must take in items of high enough quality to sustain themselves. Just as spider monkeys, wherever studied behave socially and organizationally like spider monkeys (Milton, 1993), I would maintain they must eat like spider monkeys too. One can provide a set of tentative hypotheses as to why a spider monkey cannot eat like a howler monkey (food passage rates, dentition, etc.) or a capuchin monkey (different body size, dentition, lack of manual dexterity, etc.). The question of why a spider monkey cannot eat like a woolly monkey is more difficult to answer but a partial focus on different fruit chemistries (perhaps relating to different digestive or physiological traits) and the deliberate use of animal prey by woolly monkeys are suggested possibilities (Di Fiore, 2004; Dew, 2005). Overall, I continue to view the dietary (and social) plasticity attributed to wild primates as likely over-rated, or to say it another way, at times no more or perhaps even less plastic than the dietary behavior of a number of other non-primate species under similar circumstances. We need to remember that most animals require the same basic set of nutrients. Any readily available nutritious and digestible food source in the natural environment surely can be utilized by a wide array of opportunistic consumers if they can perceive it as potential food.

Analyzing nutritional ecology

The five contributions presented here provide a good cross-section of papers indicating the scope and promise of this area of research. Two of the papers (Chapters 15 and 16) discuss methodologies for estimating dietary intake and food composition for wild primates, two others (Chapters 17 and 18) are "case studies" which explore energy or protein questions for particular primate species, while the final paper (Chapter 19) examines data on the sensory modalities involved in primate food selection.

In Chapter 15, Ortmann *et al.* provide a critical review of methods for estimating the quality and composition of plant foods in wild primate diets, including several newer methods. This compendium will be useful for those contemplating research questions involving some type of dietary analysis and needing orientation in terms of potential methodologies. Of particular value are the authors' detailed comments on the collection and preservation of wild plant foods. The methodologies presented in Chapter 15 are from various sources but many derive directly from livestock studies and grass

and herb analysis. As most primates are small- to moderate-sized arboreal animals, some of these analytical techniques, techniques derived largely for forages consumed by large-bodied terrestrial ruminants, may need re-thinking and modification before being applied to the foods and physiologies of monogastric (or polygastric) primates consuming tropical tree parts.

In the final portion of their paper, Ortmann *et al.* discuss some potentially promising new analytical methods for dietary analysis. The analysis of different plant parts and accurate determination of the fate of their chemical constituents in the digestive tract of any animal is a difficult process, fraught with potential errors. Many decades of thoughtful research have gone into the development, refinement and calibration of the analytical methods currently in wide use today and it is likely that newer methods will require time and further study to become as well understood and reliable in terms of results produced.

Chapter 16, by Mayes, examines the applicability of novel marker methods for estimating dietary intake and nutritive value in primate field studies. As Mayes notes, "the quality of data relating to the nutrition of wild primates is generally rather poor." To assist in improving this situation, he discusses several new and relatively straightforward analytical techniques for estimating the composition and digestibility of plant-based diets in the natural environment. Most attention is focused on the use of long-chain fatty acids of plant wax, particularly n-alkanes (also discussed in Chapter 15). Individual n-alkanes in plant wax differ widely from species to species and these different patterns can be used to determine diet or plant mixture composition. To perform this determination, however, one needs food as well as fecal samples. This method has now been demonstrated to work well for herbivores eating diets composed of only a few plant species. Reliability may decline, however, with increasing dietary heterogeneity, though Mayes offers several suggestions for addressing this problem. The cuticular wax of insects and other invertebrates likewise contains saturated branch-chain hydrocarbons which differ significantly between taxonomic groups and have the potential to serve as markers. Mayes also offers possible techniques for fecal identification of ingested honeys or clays.

The use of baits labelled with even-chain alkanes or other marker compounds is suggested as a possible technique for monitoring food intake and gut passage rates in free-ranging primates. It likely would not be difficult to get most fruit-eating primates to ingest an alkane-labeled bait as they often show instant affinity for bananas. This thoughtful paper provides a number of interesting new ideas and techniques for primatologists to consider and begin to test in field situations.

In Chapter 17, Conklin-Brittain *et al.* use findings from nutritional ecology to address the question of whether the energetic intake of wild orangutans shows higher variance than that of wild chimpanzees. In their examination, they use data from an array of sources – actual food items and dietary intakes for both species, analysis of the quality and anti-quality components of wild plant foods, fermentation efficiency data derived from captive chimpanzees and so on. For each ape species, energy calculations for each food item are estimated and then total energy intake per month for a 9-month period is obtained by summing the products of the grams of each food consumed for that month and the metabolizable energy content per gram per food. The authors are careful in their assumptions and even though they are working with a variety of different data sets, they appear to have done an excellent first approximation of estimating energy intake for the two apes. Their paper well illustrates how one can take various components and bring them to bear on a specific and important question. Others interested in similar diet-based questions would do well to carefully study the methodologies used in this paper. Conklin-Brittain *et al.* also provide a useful glossary to guide the reader through the various terms employed in their text.

To address a question raised by Conklin-Brittain *et al.* in their text, in digestion trials with captive chimpanzees, M. Demment and K. Milton used wheat bran with a mean particle size of 726 μm as the fiber source (Milton & Demment, 1988). Wheat bran fiber derives from a grass and for this reason likely differs in many attributes relative to the fiber constituents of the woody tree and vine parts eaten by wild primates. This could affect estimates presented in Chapter 17. Judith Caton's research on gut passage rates in captive orangutans (Caton *et al.* 1999) may be of interest to readers wishing to know more about the digestive kinetics of apes.

Danish *et al.* (Chapter 18) examine sugar concentrations in the diets of sympatric redbellied monkeys and red colobus monkeys. Redbells are monogastrics and red colobus are polygastrics. The authors find a surprisingly high sugar content in some foliage eaten by both species and note that, at times, there is considerable sugary fruit in the diet of red colobus. Ultimately the authors make several important and original points and raise some valuable questions. The analytical data they present suggest that primatologists may be misled by blindly accepting as fact, certain broad generalizations regarding dietary limitations for "colobines" as "folivores" or "frugivores." If, for example, a colobine has an unusually rich source of dietary nitrogen available to it in leaves or other food sources, at such times, it may be able to tolerate a higher sugar content in the diet from fruits.

As Danish *et al.* stress, until more work is done on the digestive physiology of particular primate species, factors facilitating congeneric sympatry in many

colobine and cercopithecine species may remain unclear. In future studies, we need to bear in mind, that colobines are not necessarily analogous to small ungulates. Many small ungulates possess primitive rumens and are able to pass some food (e.g., sugary fruits) directly into the acid portion of the stomach, bypassing the fermentation chamber (Demment & Van Soest 1985). The question of the presence of an esophageal shunt in colobines remains unresolved (Milton 1998).

The final paper, Chapter 19, by Dominy *et al.* discusses cognitive processes used by primates to mediate fruit selection in the natural environment. This question of what cues primates use to select edible fruits is a little explored area in primate nutritional ecology and one deserving more attention. In their comparative examination, the authors draw on data from two sites, Pasoh Forest Reserve, Peninsular Malaysia and Kibale National Park, Uganda.

For readers interested in expanding their knowledge in this area, the elegant experimental studies of M. Laska and his associates (e.g., Laska & Seibt 2002a, 2002b) may be of utility. These studies reveal the considerable olfactory sensitivity of some primate species, both Old and New World, to specific aliphatic esters and alcohols involved in the fruit ripening process. These aromatic compounds may alert primates to the maturation state of wild fruit crops and as such could be useful cues mediating fruit selection.

Before, as Dominy *et al.* suggest, we get into study of the integration of different sensory modalities in the central nervous system of primates, perhaps more work is needed on the question of what, besides "texture" and fruit sugars, is actually serving to cue or signal wild primate species as to what is or what is not an appropriate item of diet. Hopefully, increasing interest in this important topic will lead to further experimental work in this area of nutritional ecology.

Appendix

1. Average size for spider monkey groups is around 26.6 ± 11.1 individuals per group ($n = 11$ groups). Sources of data on group sizes include: 15, Ahumada, 1989; 21, Nunes, 1995; 27 & 20, Klein, 1972; 37 & 40, Symington, 1988; 42, Chapman, 1990; 16 & 41, Ramos-Fernandez & Ayala-Orozco, 2003; 18, van Roosmalen, 1985; 16, Suarez, 2003).
2. Here I provide some estimates for community size for common chimpanzees. Community size for two communities of common chimpanzees at Gombe in the 1970s was reported to be 37 and 19, respectively (Wrangham, 1977). More recently, community size for three communities at Gombe was estimated at 25, 40–45 and 60–80,

respectively (Greengrass, 2000). The largest Gombe community crashed and may now number less than 20 individuals (Greengrass, 2000). A community of common chimpanzees at Bossou, Guinea was reported to contain 20 individuals (Shimada, 2000); a community at Kahuzi, Democratic Republic of Congo was estimated at 23 individuals (Basabose, 2005); Clark & Wrangham (1994) report a community of 27 chimpanzees at Kanywara; C. Stanford, pers. comm., 2005, reports a community of 25 at Bwindi; at Mahale in the late 1960s and early 1970s, K-community contained 28 individuals (mean size for years 1967–1973) and M-community 70 (Nishida, 1979); at Ngogo, 144 individuals has been reported for a single community by Watts & Mitani (2001). It is possible that in some instances, human-modified landscapes surrounding forests inhabited by chimpanzees or other factors related to human intervention may affect community size.

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References

- Ahumada, J. A. (1989). Behavior and social structure of free-ranging spider monkeys (*Ateles belzebuth*) in La Macarena. *Field Studies of New World Monkeys, La Macarena, Colombia*, **2**, 7–31.
- Barton, R. A. (1996). Neocortex size and behavioural ecology in primates. *Proceedings of the Royal Society of London, B*, **263**, 173–7.
- Basabose, A. K. (2005). Ranging patterns of chimpanzees in a montane forest of Kahuzi, Democratic Republic of Congo. *International Journal of Primatology*, **26**, 33–54.
- Byrne, R. W. & Whiten, A. (1988). *Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes, and Humans*. Oxford: Oxford University Press.
- Carpenter, C. R. (1934). A field study of the behavior and social relations of howling monkeys. *Comparative Psychology Monographs*, **10**, 1–168.
- (1965). The howlers of Barro Colorado Island. In *Primate Behavior: Field Studies of Monkeys and Apes*, ed. I. DeVore, pp. 250–91. New York, NY: Holt, Rinehart & Winston.

- Caton, J. M., Humen, I. D., Hill, D. M., & Harper, P. (1999). Digesta retention in the gastro-intestinal tract of the orangutan (*Pongo pygmaeus*). *Primates*, **40**, 551–8.
- Chapman, C. A. (1990). Ecological constraints on group size in three species of neotropical primates. *Folia Primatologica*, **55**, 1–9.
- Chapman, C. A., Wrangham, R. W., & Chapman, L. J. (1995). Ecological constraints on group size: an analysis of spider monkey and chimpanzee subgroups. *Behavioral Ecology and Sociobiology*, **36**, 59–70.
- Clark, A. P. & Wrangham, R. W. (1994). Chimpanzee arrival pant-hoots: do they signify food or status? *International Journal of Primatology*, **15**, 185–205.
- Dearing, M. D., Mangione, A. M., & Karasov, W. H. (2000). Diet breadth of mammalian herbivores: nutrient versus detoxification constraints. *Oecologia*, **123**, 397–405.
- Demment, M. W. & Van Soest, P. J. (1985). A nutritional explanation for body-size patterns of ruminant and non-ruminant herbivores. *The American Naturalist*, **125**, 641–72.
- DeVore, I. (1965). *Primate Behavior: Field Studies of Monkeys and Apes*. New York, NY: Holt, Rinehart & Winston.
- Dew, J. L. (2005). Foraging, food choice and food processing by sympatric ripe-fruit specialists: *Lagothrix lagothricha poeppigii* and *Ateles belzebuth belzebuth*. *International Journal of Primatology*, **26**, 1107–35.
- Di Fiore, A. (2004). Diet and feeding ecology of woolly monkeys in a western Amazonian rain forest. *International Journal of Primatology*, **25**, 767–801.
- Dunbar, R. I. M. (1992). Neocortex size as a constraint on group size in primates. *Journal of Human Evolution*, **20**, 469–93.
- Gartlan, K. S. & Brain, K. C. (1968). Ecology and social variability. In *Cercopithecus aethiops* and *C. mitis*. In *Primate Ecology: Studies in Adaptation and Variability*, ed. P. C. Jay, pp. 293–312. New York, NY: Holt, Rinehart & Winston.
- Greengrass, E. (2000). The sudden decline of a community of chimpanzees at Gombe National Park. *Pan Africa News*, **7**.
- Hall, K. R. L. (1968). Behaviour and ecology of the wild patas monkey, *Erythrocebus patas*, in Uganda. In *Primate Ecology: Studies in Adaptation and Variability*, ed. P. C. Jay, pp. 32–120. New York, NY: Holt, Rinehart & Winston.
- Hladik, A. (1978). Phenology of leaf production in rain forests of Gabon: distribution and composition of food for folivores. In *The Ecology of Arboreal Folivores*, ed. G. G. Montgomery, pp. 51–72. Washington, DC: Smithsonian Institution Press.
- Hladik, C. M. (1978). Adaptive strategies of primates in relation to leaf-eating. In *The Ecology of Arboreal Folivores*, ed. G. G. Montgomery, pp. 373–96. Washington, DC: Smithsonian Institution Press.
- Hladik, C. M., Hladik, A., Bousset, J., Valdebouze, P., Veroben, G., & Delort-Laval, J. (1971). Le regime alimentaire des primates de l'île de Barro Colorado (Panama). *Folia Primatologica*, **16**, 85–122.
- Jay, P. C. (1968). *Primates: Studies in Adaptation and Variability*. New York, NY: Holt, Rinehart & Winston.

- Jerison, H. J. (1973). *Evolution of the Brain and Intelligence*. New York, NY: Academic Press.
- Klein, L. L. (1972). *The Ecology and Social Behavior of the Spider Monkey*, Ateles belzebuth. Unpublished Ph.D. Thesis, University of California-Berkeley.
- Kummer, H. (1971). *Primate Societies*. Chicago, IL: Aldine.
- Laska, M. & Seibt, A. (2002a). Olfactory sensitivity for aliphatic alcohols in squirrel monkeys and pigtail macaques. *Journal of Experimental Biology*, **205**, 1633–43.
- Laska, M. & Seibt, A. (2002b). Olfactory sensitivity for aliphatic esters in squirrel monkeys and pigtail macaques. *Behavioural Brain Research*, **134**, 165–74.
- McFarland, M. J. (1986). Ecological determinants of fission-fusion sociality in *Ateles* and *Pan*. In *Primate Ecology and Conservation*, ed. J. G. Else & P. C. Lee, pp. 181–90. Cambridge: Cambridge University Press.
- Milton, K. (1978). Behavioral adaptations to leaf-eating by the mantled howler monkey. In *The Ecology of Arboreal Folivores*, ed. G. G. Montgomery, pp. 535–50. Washington, DC: Smithsonian Institution Press.
- (1979). Factors influencing leaf choice by howler monkeys: a test of some hypotheses of food selection by generalist herbivores. *The American Naturalist*, **114**, 362–78.
- (1980). *The Foraging Strategy of Howler Monkeys: A Study in Primate Economics*. New York, NY: Columbia University Press.
- (1981a). Food choice and digestive strategies of two sympatric primate species. *The American Naturalist*, **117**, 476–95.
- (1981b). Diversity of plant foods in tropical forests as a stimulus to mental development in primates. *American Anthropologist*, **83**, 534–48.
- (1982). The role of resource seasonality in density regulation of a wild primate population. In *Ecology of a Tropical Forest*, ed. A. S. Leigh, A. S. Rand, & D. M. Windsor, pp. 273–89. Washington, DC: Smithsonian Institution Press.
- (1988). Foraging behavior and the evolution of primate cognition. In *Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes and Humans*, ed. A. Whiten & R. Byrne, pp. 285–305. Oxford: Oxford University Press.
- (1991). Pectin content of neotropical plant parts. *Biotropica*, **23**, 90–2.
- (1993). Diet and social behavior of a free-ranging spider monkey population: the development of species-typical behaviors in the absence of adults. In *Juvenile Primates: Life History, Development and Behavior*, ed. M. Pereira & L. A. Fairbanks, pp. 173–81. Oxford: Oxford University Press.
- (1998). Physiological ecology of howlers (*Alouatta*): energetic and digestive considerations and comparison with the Colobinae. *International Journal of Primatology*, **19**, 513–48.
- (2000). Quo vadis? Tactics of food search and group movement in primates and other animals. In *On the Move: How and Why Animals Travel in Groups*, ed. S. Boinski & P. Garber, pp. 375–418. Chicago, IL: University of Chicago Press.

- Milton, K. & Demment, M. (1988). Digestive and passage kinetics of chimpanzees fed high and low fiber diets and comparison with human data. *Journal of Nutrition*, **118**, 1–7.
- Milton, K. & Dintzis, F. (1981). Nitrogen-to-protein conversion factors for tropical tree samples. *Biotropica*, **13**, 177–81.
- Milton, K. & Jenness, R. (1987). Ascorbic acid content of neotropical plant parts available to wild monkeys and bats. *Experientia*, **43**, 339–42.
- Milton, K. & May, M. (1976). Body weight, diet and home-range in primates. *Nature*, **259**, 459–62.
- Milton, K. & McBee, R. H. (1983). Structural carbohydrate digestion in a new world primate, *Alouatta palliata* gray. *Comparative Biochemistry and Physiology*, **74**, 29–31.
- Milton, K., Casey, T. M., & Casey, K. K. (1979). The basal metabolism of mantled howler monkeys. *Journal of Mammalogy*, **60**, 373–6.
- Milton, K., Van Soest, P. J., & Robertson, J. (1980). Digestive efficiencies of wild howler monkeys. *Physiological Zoology*, **53**, 402–9.
- Nagy, K. & Milton, K. (1979a). Energy metabolism and food consumption by howler monkeys. *Ecology*, **60**, 475–80.
- (1979b). Aspects of dietary quality, nutrient assimilation and water balance in wild howler monkeys. *Oecologia*, **30**, 249–58.
- Nishida, T. (1979). The social structure of chimpanzees of the Mahale Mountains. In *The Great Apes*, ed. D. A. Hamburg & E. R. McCown, pp. 73–122. Menlo Park: Benjamin/Cummings Publishing Co.
- Nunes, A. (1995). Foraging and ranging patterns in white-bellied spider monkeys. *Folia Primatologica*, **65**, 85–99.
- Oates, J. F. (1986). Food distribution and foraging behavior. In *Primate Societies*, ed. B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, & T. T. Struhsaker, pp. 197–209. Chicago, IL: University of Chicago Press.
- Ramos-Fernandez, G. & Ayala-Orozco, B. (2003). Population size and habitat use of spider monkeys at Punta Laguna, Mexico. In *Primates in Fragments: Ecology and Conservation*, ed. L. K. March, pp. 191–209. New York, NY: Kluwer Academic/Plenum Publishers.
- Shimada, M. K. (2000). A survey of the Nimba Mountains, West Africa from three routes: confirmed new habitat and ant-catching wand use of chimpanzees. *Pan Africa News*, 7.
- Silk, J. B. (1986). Social behavior in an evolutionary perspective. In *Primate Societies*, ed. B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, & T. T. Struhsaker, pp. 318–29. Chicago, IL: University of Chicago Press.
- Smuts, B. B., Cheney, D. L., Seyfarth, R. M., Wrangham, R. W., & Struhsaker, T. T. (1986). *Primate Societies*. Chicago, IL: University of Chicago Press.
- Suarez, S. (2003). *Spatio-temporal Foraging Skills of White-bellied Spider Monkeys (Ateles belzebuth belzebuth) in the Yasuni National Park, Ecuador*. Unpublished Ph.D. thesis, State University of New York-Stony Brook.
- Symington, M. (1988). Demography, ranging patterns and activity budgets of black spider monkeys (*Ateles paniscus chamek*) in the Manu National Park, Peru. *American Journal of Primatology*, **15**, 45–67.

- Van Roosmalen, M. G. M. (1985). Habitat preferences, diet, feeding strategy and social organization of the black spider monkey (*Ateles paniscus paniscus* Linnaeus 1758) in Surinam. *Acta Amazonica*, **15**, 1–238.
- Waser, P. M. (1986). Interactions among primate species. In *Primate Societies*, ed. B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, & T. T. Struhsaker, pp. 210–26. Chicago, IL: University of Chicago Press.
- Washburn, S. L. & Hamburg, D. A. (1965). The implications of primate research. In *Primate Behavior*, ed. I DeVore, pp. 607–22. New York, NY: Holt, Rinehart & Winston.
- Watts, D. P. & Mitani, J. C. (2001). Boundary patrols and intergroup encounters in wild chimpanzees. *Behaviour*, **138**, 299–327.
- Wrangham, R. W. (1977). Feeding behaviour of chimpanzees in Gombe National Park, Tanzania. In *Primate Ecology*, ed. T. H. Clutton-Brock, pp. 504–38. London: Academic Press.
- (1986). Evolution of social structure. In *Primate Societies*, ed. B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, & T. T. Struhsaker, pp. 282–96. Chicago, IL: University of Chicago Press.