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Insect-Foraging in Captive Owl Monkeys *(Aotus nancymaae)*

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Key Words
Faunivory · Insectivory · Primate · Nocturnal · Prey capture · Night monkey

Abstract

Whereas the diets of diurnal primate species vary greatly, almost all nocturnal primate species consume insects. Insect-foraging has been described in nocturnal prosimians but has not been investigated in owl monkeys (*Aotus* spp.). We studied 35 captive owl monkeys *(Aotus nancymaae)* in order to describe their foraging behavior and to determine if there were any age or sex differences in their ability to capture insect prey. Because owl monkeys cooperate in parental care and in food-sharing, we expected social interactions involving insect prey. We found that owl monkeys most often snatched flying insects from the air and immobilized crawling insects against a substrate using their hands. Immatures and adult female owl monkeys attempted to capture prey significantly more often than did adult males; however, there was no difference in the proportion of attempts that resulted in capture. Social interactions involving prey appeared similar to those with provisioned food, but possessors of prey resisted begging attempts more so than did possessors of other food. Owl monkeys attempted to capture prey often (mean = 9.5 ± 5.8 attempts/h), and we speculate that the protein and lipid content of captured prey is important for meeting the metabolic demands for growth and reproduction.

Introduction

The extent that primates rely on insects varies greatly across primate species, from the slender loris and tarsiers that feed mainly on live prey (*Loris lydekkerianus* [Nekaris, 2005]; *Tarsius* [MacKinnon and MacKinnon, 1980; Gursky, 2007]) to leaf

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monkeys and howler monkeys that rely almost exclusively on plant matter (*Trachypithecus johnii* [Oates et al., 1980]; *Alouatta palliata* [Chapman, 1988]). Although a wide variety of diurnal and almost all nocturnal species devote at least some of their time to insect-foraging, relatively little research has focused on the behaviors associated with insect capture. Besides the descriptions of chimpanzees using tools to extract termites [Suzuki, 1966; Sanz et al., 2004], the only other detailed studies of insect-foraging in diurnal anthropoids are those on patas monkeys *(Erythrocebus patas)* [Isbell and Young, 2007], squirrel monkeys *(Saimiri sciureus)* [Hopf and Ploog, 1991; Stone, 2006], capuchins *(Cebus capucinus)* [Chapman, 1988; Hall and Fedigan, 1997; Melin et al., 2008] and tamarins *(Saguinus fuscicollis*, *S. mystax)* [Peres, 1992]. For example, Peres [1992] describes moustached tamarins *(S. mystax)* as active foliage gleaners that use rapid foraging maneuvers aimed at prey on foliage, whereas the saddleback tamarins *(S. fuscicollis)* use manipulative foraging directed at blind microhabitats (e.g. tree bark, leaf litter, woody crevices). On the other hand, only brief reports exist regarding insect-foraging in spider monkeys *(Ateles belzebuth)* [Link, 2003] and bearded sakis *(Chiropotes satanas)* [Frazao, 1991; Veiga and Ferrari, 2006].

The foraging habits of nocturnal primates have been described for spectral tarsiers [MacKinnon and MacKinnon, 1980], slender loris [Nekaris and Rasmussen, 2003; Nekaris, 2005], aye-ayes *(Daubentonia madagascariensis)* [Erickson, 1994], fat-tailed dwarf lemurs *(Cheirogaleus medius)* [Fietz and Ganzhorn, 1999] and mouse lemurs (*Microcebus rufus* [Atsalis, 1999] and *M. murinus* [Siemers et al., 2007]). Aye-ayes use their specialized feeding appendage in percussive foraging to locate and extract insects inside branches [Erickson et al., 1998]. Results from an experimental study of food detection in gray mouse lemurs *(M. murinus)* suggest that visual motion cues and prey-generated acoustic cues are used during insect-foraging [Siemers et al., 2007].

Owl monkeys are nocturnal, generalist omnivores that consume fruits, leaves, flowers, insects and small vertebrate prey [Wright, 1985; Fernandez-Duque, 2007]. Although there have been estimates of the proportion of their diet devoted to insect-foraging from observations and analyses of feces [Wright, 1985], no systematic study has examined their insect-foraging behavior. Because owl monkeys are small arboreal nocturnal primates, observing their insect-foraging behavior in the wild and obtaining quantitative data regarding their arthropod prey would be challenging and had proven impossible so far [Fernandez-Duque, 2007].

In this study, we aimed to describe insect-foraging behavior in a captive group of owl monkeys housed in outdoor enclosures in a naturally forested area. We systematically observed a large number of owl monkeys to estimate their frequency of attempts to capture insect prey, to describe their capture techniques and to determine if there are any age and/or sex differences in their ability to capture arthropod prey. We also report all social interactions between owl monkeys involving captured prey. Given that prey items are less abundant and require more effort to obtain than the provisioned food items, monkeys may be more motivated to beg for captured insects than for other food items. Because of the general cooperative nature of owl monkeys (with males carrying and grooming infants [Wright, 1984] and males and females sharing food with their mates and young [Wolovich et al., 2006, 2008]), we expected that there would be a large number of food interactions involving insects.

Methods

Study Site and Subjects

We observed 35 captive owl monkeys *(Aotus nancymaae)* from May to September 2006 at the DuMond Conservancy for Primates and Tropical Forests (Miami, Fla., USA). The subjects were housed in 14 different social groups. Each group of owl monkeys (an adult male-female pair with or without offspring) was housed outdoors in a frame wire cylindrical enclosure (2.4 m diameter × 2.4 m height, or 3.0 m diameter × 3.0 m height) located in a natural hardwood hammock area exposed to natural fluctuations in photoperiod, rainfall and temperature. The enclosures contained wooden nestboxes, perches and flexible poles that allowed natural locomotion. The enclosures are permanently fixed into natural substrate so that local vegetation can grow in or on them. All monkeys were fed a fruit mix, Mazuri® Primate High Fiber Sticks, Lab Diet® Monkey Diet, and Lab Diet® New World Primate Diet every evening. The monkeys also had access to naturally occurring flying and crawling arthropods and small vertebrates, as well as any natural vegetation growing inside the enclosure or just outside of the enclosure within their arms' reach.

Owl monkeys were considered adult if they were ≥3.5 years old and immature if they were <3.5 years old. Immatures included infants that may still have been nursing or carried by an adult, but were able to eat solid foods. There were a total of 12 immature monkeys and 23 adults observed for this study.

Behavioral Observations

We observed the monkeys in the evenings between 19.00 and 22.00 h. Informal observations carried out on 10 nights between dusk and dawn confirmed that the greatest abundance of insects occurred during these hours. We observed the owl monkeys after they had access to provisioned food because they are routinely fed at dusk. Each observation period consisted of a single observer sitting outside the enclosure of one group of owl monkeys with a flashlight (the lens covered with red cellophane to minimize disturbance to the monkeys [Ogden, 1994]) and a checksheet to record data. The observer used focal-animal sampling to score all occurrences of foraging behavior for 10 min.

Each attempt to catch a prey item was scored. An 'attempt' was defined as the monkey moving directly toward a potential prey item with a fixed gaze and clasping a hand into the air or onto a substrate or directly biting an insect on a substrate. For each attempt to catch prey, the following variables were scored: method of attempt (reaching with hand and clenching, clamping hand against a substrate or pressing mouth against a substrate); the surface that the prey item was on (air, wire mesh or a solid substrate such as a pole or perch); the result of each attempt (whether or not the monkey moved its jaw immediately after the attempt), and when possible, the type and size of the prey. The approximate size of the prey was scored on an ordinal scale from 1 to 3: 1 (small) is ≤5 mm, 2 (medium) is >5 mm but ≤3.0 cm, 3 (large) is >3.0 cm.

We also noted any potential food-sharing events by scoring all occurrences of social interactions between owl monkeys with the captured prey items. Such interaction occurred any time one individual held a prey item in its hand or mouth and was within an arm's length of another monkey. For each social interaction we noted the identities of the possessor (the individual with food in its hand or mouth during the interaction), the potential recipient (the individual with no food), whether or not the potential recipient begged, whether or not the possessor resisted a begging attempt and whether or not the prey item was transferred [as defined in Wolovich et al., 2006]. A 'beg' consisted of the potential recipient moving its hand or open mouth toward the food item and a 'resist' was scored if the possessor of the food item subsequently moved the food item away from the potential recipient (e.g. including turning its head, moving its hand, moving its body). A transfer was defined as the movement of a food item from the hand or mouth of the possessor to the hand or mouth of the potential recipient.

Three observers collected data throughout the study. Interobserver reliability was assessed at weekly intervals at the beginning of the study. A reliability score of at least 90% between each dyad of observers was achieved before we used the data [Martin and Bateson, 1986].

Statistical Analyses

All statistical tests were completed using Systat version 11.0. The number of attempts per hour, the proportion of attempts that resulted in capture, and the number of captures per hour were calculated for each individual. Wilcoxon's matched-pairs signed-ranks tests were used to compare the number of attempts per hour and the proportion of attempts that resulted in capture between the different prey size classes, the two possible locations of the prey, and for the two different types of capture techniques (reaching and clenching the hand or clamping on substrate). Kruskal-Wallis tests were used to determine if each of these variables varied significantly among the three age/sex classes (adult male, adult female and immatures). If there was significant variation, Mann-Whitney U tests were used to determine which age/sex classes differed from one another. Using 1-sample t tests, we compared the proportion of begs that resulted in transfer and the proportion of begs that were resisted to previously reported values for non-prey items [reported in Wolovich et al., 2006]. All statistical procedures followed Sokal and Rohlf [1995].

Results

We observed the monkeys during a total 161 ten-minute observation periods (26.8 h). Each monkey was observed at least twice (mean = 4.4 ± 1 observation periods, n = 35 monkeys). Monkeys caught prey by grabbing them from the air or by clamping them against a substrate. The monkeys moved throughout their cages, fixing their gaze on potential prey (at times hanging by their feet) and leapt quickly in their direction (sometimes greater than 1 m). They used either one or both hands or even their mouth to secure a prey item. We could not reliably detect any distinct vocalizations emitted from the monkeys while they were engaged in these behaviors.

The subjects frequently attempted to capture arthropods (mean = 9.5 ± 5.8 attempts/h, n = 35 monkeys) but less than half of those attempts resulted in capture (mean = 0.4 ± 0.2 captures/attempt, n = 34 monkeys); therefore, the mean rate of capture per monkey was 3.5 ± 2.8 arthropods/h (n = 34 monkeys). Flying and crawling insects (Blattaria, Coleoptera, Diptera and Lepidoptera) as well as spiders (Arachnida) and millipedes (Diploda) were consumed. Beetles and moths were the most frequently captured prey items (34 and 32%, respectively, of all identified captures), followed by flies (16%), millipedes (10%), cockroaches (5%) and spiders (3%). There was one attempt to capture an unidentified tree frog (Amphibia); however, the monkey was deterred after the frog emitted a liquid.

Capture Technique and Prey Size

Owl monkeys used their hands to attempt to capture prey items (mean = 6.4 ± 4.2 attempts/h) significantly more often than they used their mouths directly (mean = 0.77 ± 0.96 attempts/h; $Z = -4.9$, n = 34, $p < 0.001$). The proportion of attempts that resulted in capture when monkeys used their hands (mean = 0.35 ± 0.22) does not differ from those when monkeys used their mouths (mean = 0.44 ± 0.45; $Z = 0.776$, n = 16, $p = 0.438$). When the monkeys used their mouths, there was no evidence that their free upper lip was facilitating prey capture.

Owl monkeys attempted to capture prey items that were flying as well as those that were stationary or moving on a substrate. There is no difference in the proportion of attempts that resulted in capture of flying prey (mean = 0.31 ± 0.39) with that of prey that was on a substrate (mean = 0.38 ± 0.24; $Z = 0.96$, n = 23, $p = 0.338$).

We observed the owl monkeys attempt to capture small and medium-sized prey items most often. Only 6 of the 35 owl monkeys were observed to attempt to capture

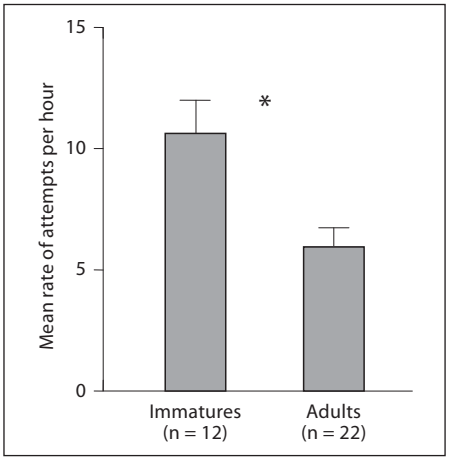

Fig. 1. The mean rate of attempts per hour for immature and adult owl monkeys. One adult monkey was never observed to attempt to capture an arthropod prey resulting in a reduction in sample size. Error bars represent standard errors. * $p < 0.05$.

a large prey item. When comparing owl monkeys that attempted to capture both small and medium-sized prey, we found that they did not differ in the proportion of attempts that resulted in capture for small prey (mean = 0.67 ± 0.34) and for medium-sized prey (mean = 0.59 ± 0.38; Z = –0.357, n = 9, p = 0.721).

Age Class and Sex Differences

Overall, there was significant variation among age/sex classes in the rate of attempts to capture arthropods (H = 15.5, d.f. = 2, $p < 0.001$) and the rate of capture (H = 6.4, d.f. = 2, p = 0.042). The proportion of attempts that resulted in capture, however, did not significantly vary among age/sex classes (H = 0.3, d.f. = 2, p = 0.849). Immatures attempted to capture arthropods more frequently (mean = 13.4 ± 5 attempts/h, n = 12) than did adult males (mean = 5.1 ± 3.5 attempts/h, n = 14; U = 15.0, $p < 0.001$; fig. 1), but with similar frequency as adult females (mean = 11.1 ± 5.4 attempts/h, n = 9; U = 41.5, p = 0.369). When comparing adult females and males, we found that females attempted to capture arthropods significantly more often than did males (U = 108.5, p = 0.004; fig. 2).

Immatures captured arthropods more frequently (mean = 4.9 ± 3.4 captures/h, n = 12) than did adult males (mean = 2.0 ± 1.6 captures/h, n = 14; U = 35.5, p = 0.020) but with similar frequency as adult females (mean = 3.9 ± 2.7 captures/h, n = 9; U = 43.0, p = 0.431). Adult females also captured arthropods more frequently than did adult males (U = 93.5, $p < 0.050$).

Food-Sharing of Prey Items

Owl monkeys engaged in social interactions involving prey items in all of the social groups (mean = 1.8 ± 1.0 interactions/h, n = 14 groups). We observed begging for a prey item in 11 of the 14 social groups (mean = 1.5 ± 0.8 begs/h). A substantial proportion of these begs resulted in the transfer of the prey item to another monkey (mean = 0.42 ± 0.4). The proportion of begs that were met with resistance by the possessors (mean = 0.59 ± 0.36) is significantly greater than that previously described for non-prey items (median = 0.14 [Wolovich et al., 2006]; t = 4.16, p = 0.002).

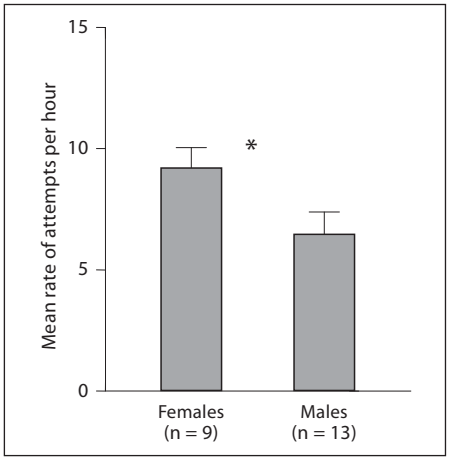

Fig. 2. The mean rate of attempts per hour for adult female and male owl monkeys. Error bars represent standard errors. * $p < 0.05$.

The proportion of begs that resulted in transfer, however, does not differ from that previously described for non-prey dietary items (median = 0.54 [Wolovich et al., 2006]; $t = -1.07$, $p = 0.305$).

Discussion

These captive monkeys attempted to capture arthropod prey approximately once every 6 min. This finding corroborates previous suggestions that captive owl monkeys spend a significant amount of their time insect-foraging [Tapanes et al., 2007]. In this study, we observed one attempt to capture a frog. Although there were no successful vertebrate prey captures during this study, owl monkeys at the DuMond Conservancy regularly capture lizards *(Anolis carolinensis*, *A. sagrei)* during the day and geckos *(Hemidactylus turcicus)* at night [pers. obs.]. These prey items are usually clamped against a substrate and then eaten head first. On one occasion, an adult female owl monkey captured and ate a small bird that had flown into her enclosure. We did not observe the method of capture, but C.K.W. observed the female ingesting the entire bird (species unknown) including its feathers and bones.

Capture Technique and Prey Size

Owl monkeys used their hands most often to capture prey items that were relatively small and required slight manipulation of their fingertips. The size of the prey captured (usually ≤ 3 cm) is similar to that reported for tarsiers (mean = 1.9 cm [Gursky, 2007]), suggesting that *Aotus* is catching smaller insects relative to its body size than *Tarsius*. Their slender long fingers with enlarged apical pads appear similar to those of *Saimiri* [Hill, 1960], a small-bodied insectivorous New World primate. These anatomical features that offer *Saimiri* the fine dexterity necessary to handle moving prey [Hamrick, 1998] would also make *Aotus* well equipped for insect prey capture. In fact, in comparison to *Saimiri*, *Aotus* has longer third metacarpals, proximate phalanxes and intermediate phalanxes and a greater phalangeal index (length

of manual digits relative to palm length) [Kirk et al., 2008]. The availability of larger insects (>3 cm) was likely limited by the size of the holes in the wire mesh screen of their enclosures (2.54 × 2.54 cm). Therefore, it is reasonable to assume that wild owl monkeys include more of these larger-bodied insects in their diet.

Owl monkeys can be described as active foragers that glean insects from substrates and grab them in mid-flight. This type of foraging differs from the 'foliage-scrape' method of biting or licking prey directly off foliage used commonly by squirrel monkeys [Boinski and Fragaszy, 1989; Stone, 2006]. Our observations confirm Wright's description [1985] that *Aotus* does not simply sit and scan for prey, but actively moves along branches grabbing insects from the air or from a substrate. While foraging, owl monkeys appear quite agile as they may hang by their feet or leap more than 1 m while snatching a flying insect.

Age Class and Sex Differences

Immature and adult female monkeys captured prey items more frequently than adult males did. This finding reflects a difference either in their abilities to detect prey or in their motivation to attempt to capture prey. Unlike other New World primates, both male and female owl monkeys are monochromatic and color-blind [Jacobs et al., 1996]. Therefore, it is not likely that females have a potential advantage over males in locating food (as is possible in heterozygous trichromatic vs. homozygous dichromatic individuals [Osorio and Vorobyev, 1996; Melin et al., 2008]). Rather, it seems likely that immatures and adult females are more motivated to consume prey items. This motivation is unlikely to result from differences in consumption of provisioned food because previous studies indicate that males and females consume equal amounts of these food items (measured by number of pieces removed from dish) [Wolovich, 2006].

The higher rate of attempts to capture prey may, instead, be a result of the greater metabolic demands of growing juveniles and reproductive females. Captive owl monkeys do not ordinarily conceive until approximately 3.5 years of age [Gozalo and Montoya, 1990]. Females are pregnant and/or lactating for up to 9 months a year [Wright, 1979]. Because these reproductive states are metabolically demanding, females might be expected to increase their dietary intake and/or to minimize their activity levels [Thompson, 1992]. Insects are a good source of protein and lipids [Adedunta, 2005; Lambert, 2007; Teffo et al., 2007], so females that require additional nutrition when they are pregnant or lactating [Oftedal, 1991] would benefit by capturing more insect prey. Indeed, immature and pregnant/lactating female primates often increase their intake of leaves and/or insects [Lambert, 2007]. For example, adult female and immature (both male and female) Japanese monkeys *(Macaca fuscata yakui)* spend more time consuming insects than adult males [Agetsuma, 2001]. Insect-foraging as a means to cope with the metabolic demands for growth and reproduction may be a common behavioral strategy across primate species.

Food-Sharing of Prey Items

As with provisioned food items, the owl monkeys interacted socially with other cage mates over the captured prey. Our findings did not support our prediction that a greater proportion of the prey items would be transferred than their provisioned food. Instead, owl monkeys resisted begging attempts for prey items more

often than they did for provisioned items. It seems that the possessors' motivation to retain the prey is greater than that for food that is offered regularly. The energetic cost expended in obtaining the prey or the cost of relinquishing the calories afforded by the prey may be too great for the possessor to incur if the prey was to be ultimately transferred to another individual. The benefits of these transfers, however, are likely to change with other factors (such as the need of a growing infant or lactating female).

Conclusion

This study represents the first formal investigation of insect-foraging in nocturnal owl monkeys. Our findings support previous suggestions that owl monkeys frequently adjust their gaze and leap quickly in attempting to capture insects. We discovered that they use their long and dexterous fingers to grasp flying prey or to clamp crawling prey against a substrate. Owl monkeys do not share insects more so than their provisioned food, but further investigation into their social interactions involving prey items would shed light on their role in mate provisioning and parental investment. These data provide the essential details of owl monkey foraging behavior that could be necessary for future investigation into how insect-foraging relates to other behavior patterns in this highly cooperative primate.

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References

Adedunta SA (2005). Nutritional and antinutritional characteristics of some insects foraging in Akure Forest Reserve Ondo State, Nigeria. *Journal of Food Toxicology* 3: 563–567.

Agetsuma N (2001). Relation between age-sex classes and dietary selection of wild Japanese monkeys. *Ecological Research* 16: 759–763.

Atsalis S (1999). Diet of the brown mouse lemur *(Microcebus rufus)* in Ranomafana National Park, Madagascar. *International Journal of Primatology* 20: 193–229.

Boinski S, Fragaszy D (1989). The ontogeny of foraging in squirrel monkeys, *Saimiri oerstedi*. *Animal Behaviour* 37: 415–428.

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

Erickson CJ (1994). Tap-scanning and extractive foraging in aye-ayes, *Daubentonia madagascariensis*. *Folia Primatologica* 62: 125–135.

Erickson CJ, Nowicki S, Dollar L, Goehring N (1998). Percussive foraging: stimuli for prey location by aye-ayes *(Daubentonia madagascariensis)*. *International Journal of Primatology* 19: 111–122.

Fernandez-Duque E (2007). Aotinae: social monogamy in the only nocturnal haplorhines. In *Primates in Perspective* (Campbell CJ, Fuentes A, MacKinnon KC, Panger M, Bearder SK, eds.), pp 139–154. New York, Oxford University Press.

Fietz J, Ganzhorn JU (1999). Feeding ecology of the hibernating primate *Cheirogaleus medius*: how does it get so fat? *Oecologia* 121: 157–164.
Frazao E (1991). Insectivory in free-ranging bearded saki *(Chiropotes satanas chiropotes). Primates* 32: 243–245.
Gozalo A, Montoya E (1990). Reproduction of the owl monkey *(Aotus nancymai)* (Primates: Cebidae) in captivity. *American Journal of Primatology* 21: 61–68.
Gursky S (2007). Tarsiiformes. In *Primates in Perspective* (Campbell CJ, Fuentes A, MacKinnon KC, Panger M, Bearder SK, eds.), pp 73–85, New York, Oxford University Press.
Hall CL, Fedigan LM (1997). Spatial benefits afforded by high rank in white-faced capuchins. *Animal Behaviour* 53: 1069–1082.
Hamrick MW (1998). Functional and adaptive significance of primate pads and claws: evidence from New World anthropoids. *American Journal of Physical Anthropology* 106: 113–127.
Hill WCO (1960). *Primates: Comparative Anatomy and Taxonomy,* vol 4: Cebidae, part A. Edinburgh, Edinburgh University Press.
Hopf S, Ploog D (1991). Insect-catching behavior in socially inexperienced infant squirrel monkeys. *Primates* 32: 111–114.
Isbell LA, Young TP (2007). Interspecific and temporal variation of ant species within *Acacia drepanolobium* ant domatia, a staple food of patas monkeys *(Erythrocebus patas)* in Laikipia, Kenya. *American Journal of Primatology* 69: 1387–1398.
Jacobs GH, Neitz M, Neitz J (1996). Mutations in S-cone pigment genes and the absence of colour vision in two species of nocturnal primate. *Proceedings of the Royal Society London B* 263: 705–710.
Kirk CE, Lemelin P, Hamrick MW, Boyer DM, Bloch JI (2008). Intrinsic hand proportions of euarchontans and other mammals: implications for the locomotor behavior of plesiadapiforms. *Journal of Human Evolution* 55: 278–299.
Lambert JE (2007). Primate nutritional ecology: feeding biology and diet at ecological and evolutionary scales. In *Primates in Perspective* (Campbell CJ, Fuentes A, MacKinnon KC, Panger M, Bearder SK, eds.), pp 482–495. New York, Oxford University Press.
Link A (2003). Insect-eating by spider monkeys. *Neotropical Primates* 11: 104–107.
MacKinnon J, MacKinnon K (1980). The behavior of wild spectral tarsiers. *International Journal of Primatology* 1: 361–379.
Martin, P, Bateson P (1986). *Measuring Behavior: An Introductory Guide*. Cambridge, Cambridge University Press.
Melin AD, Fedigan LM, Hiramatsu C, Kawamura S (2008). Polymorphic color vision in white-faced capuchins *(Cebus capucinus):* is there foraging niche divergence among phenotypes? *Behavioral Ecology and Sociobiology* 62: 659–670.
Nekaris KAI (2005). Foraging behaviour of the slender loris: implications for theories of primate origins. *Journal of Human Evolution* 49: 289–300.
Nekaris KAI, Rasmussen DT (2003). Diet and feeding behavior of Mysore slender lorises. *International Journal of Primatology* 24: 22–46.
Oates JF, Waterman PG, Choo GM (1980). Food selection by the south Indian leaf-monkey, *Presbytis johnii*, in relation to leaf chemistry. *Oecologia* 45: 45–56.
Oftedal OT (1991). The nutritional consequences of foraging in primates: the relationship of nutrient intakes to nutrient requirements. *Philosophical Transactions of the Royal Society London B.* 334: 161–170.
Ogden T (1994). Ophthalmologic research in the owl monkeys. In *Aotus: The Owl Monkey* (Baer JF, Weller RE, Kakoma I, eds.), pp 263–286. San Diego, Academic Press.
Osorio D, Vorobyev M (1996). Colour vision as an adaptation to frugivory in primates. *Proceedings of the Royal Society London B.* 263: 593–599.
Peres CA (1992). Prey-capture benefits in a mixed-species group of Amazonian tamarins, *Saguinus fuscicollis* and *S. mystax*. *Behavioral Ecology and Sociobiology* 31: 339–347.
Sanz C, Morgan D, Gulick S (2004). New insights into chimpanzees, tools, and termites from the Congo basin. *American Naturalist* 164: 567–581.
Siemers BM, Goerlitz HR, Robsomanltrandrasana E, Piep M, Ramanamanjato J, Rakotondravony D, Ramilijaona O, Ganzhorn JU (2007). Sensory basis of food detection in wild *Microcebus murinus*. *International Journal of Primatology* 28: 291–304.
Sokal R, Rohlf F (1995). *Biometry,* 3rd ed. New York, Freeman and Company, p 887.
Stone AI (2006). Feeding ontogeny is not linked to delayed maturation in squirrel monkeys *(Saimiri sciureus). Ethology* 112: 105–115.
Suzuki A (1966). On the insect-eating habits among wild chimpanzees living in the savanna woodland of western Tanzania. *Primates* 7: 481–487.
Tapanes E, Wolovich CK, Evans S (2007). Leaping into the night: when owl monkeys awake. *American Journal of Primatology* 69(suppl 1): 57.

Teffo LS, Toms RB, Eloff JN (2007). Preliminary data on the nutritional composition of the edible stinkbug, *Encosternum delegorguei* Spinola, consumed in Limpopo province, South Africa. *South African Journal of Science* 103: 434–436.
Thompson S (1992). Gestation and lactation in small mammals: basal metabolic rate and the limits of energy use. In *Mammalian Energetics* (Tomasi TE, Horton TH, eds.), pp 213–259, Ithaca, Cornell University Press.
Veiga LM, Ferrari SF (2006). Predation of arthropods by southern bearded sakis (*Chiropotes satanas*) in eastern Brazilian Amazonia. *American Journal of Primatology* 68: 209–215.
Wolovich CK (2006). *Food Sharing in Monogamous Owl Monkeys (*Aotus *spp.).* Dissertation, University of Miami, p 153.
Wolovich CK, Evans S, French JA (2008). Dads do not pay for milk but do buy the milk: food sharing and reproduction in owl monkeys (*Aotus* spp.). *Animal Behaviour* 75: 1155–1163.
Wolovich CK, Feged A, Evans S, Green SM (2006). Social patterns of food sharing in owl monkeys. *American Journal of Primatology* 68: 663–674.
Wright PC (1979). Paternal care in primates. *International Journal of Primatology* 11: 89–102.
Wright PC (1984). Biparental care in *Aotus trivirgatus* and *Callicebus moloch*. In *Female Primates: Studies by Women Primatologists* (Small MF, ed.), pp 59–75. New York, Liss.
Wright PC (1985). *The Costs and Benefits of Nocturnality for* Aotus trivirgatus *(The Night Monkey).* Dissertation, City University of New York, p 339 (available from: UMI; AAT 8601707).