2005

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Published in *International Journal of Primatology* 26:5 (October 2005), pp. 1039–1051;
doi: 10.1007/s10764-005-6457-1.

Submitted December 10, 2003; revised April 12, 2004; accepted May 4, 2004.

Terrestrial Behavior of *Ateles* spp.

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Abstract

Spider monkeys (*Ateles* spp.) are well known for their highly arboreal lifestyle, spending much of their time in the highest levels of the canopy and rarely venturing to the ground. To investigate terrestriality by *Ateles* and to illuminate the conditions under which spider monkeys venture to the ground, we analyzed *ad libitum* data from 5 study sites, covering 2 species and 5 subspecies. Three of the sites are in Central/North America: Barro Colorado Island (BCI), Panama (*Ateles geoffroyi panamensis*), Santa Rosa National Park, Costa Rica (*A. g. frontatus*), and Punta Laguna, Mexico (*A. g. yucatanensis*). The 2 remaining sites are in South America: Cocha Cashu Biological Station, Perú (*A. belzebuth chamek*) and Yasuni National Park, Ecuador (*A. b. belzebuth*). Terrestrialism by *Ateles* at all sites is rare; however, it is more restricted at the 2 South American sites. In South America, ground use only occurred in the contexts of eating soil or rotten wood and visiting salt licks. In contrast at the 3 sites with *Ateles geoffroyi* it rarely occurred in a feeding context, but instead more frequently while drinking from streams during the dry season, by adult females escaping attack by adult males, and as part of a chase

game. In addition, on BCI adult males were on the ground before attacking adult females. We discuss potential explanations, e.g., climate, species differences, predation pressure, for the differences between the Central/North and South American observations.

Keywords: Terrestrial behavior, predation, spider monkeys, *Ateles*.

INTRODUCTION

Although many Old World monkey species are largely terrestrial, New World monkeys are almost all exclusively arboreal (Napier and Napier, 1985). Spider monkeys (*Ateles* spp.) are not only almost exclusively arboreal, but they spend most of their time in, and are highly adapted for, the upper canopy (van Roosemalen, 1985; Youlatos, 2002). Unlike *Ateles*, capuchins (*Cebus* spp.) and squirrel monkeys (*Saimiri* spp.) often spend time on the ground foraging for insects and small vertebrates (Fleagle, 1999). *Cebus* and *Saimiri* are generalized quadrupeds (Freese and Oppenheimer, 1981; Boinski, 1989) allowing for the utilization of multiple habitat levels. Spider monkeys however have shoulder joint modifications and elongated forelimbs making terrestrial quadrupedism more difficult. In fact, when spider monkeys venture to the ground, they often walk bipedally.

Spider monkeys are one of the largest of the New World monkeys, with an average body mass of 7–8.5 kg (Coehlo et al., 1976; Karesh et al., 1998) and are ripe fruit specialists (Klein and Klein, 1977; van Roosemalen, 1985; Symington, 1987; Chapman, 1988; Russo et al., 2005). Patches of fruit sufficient to support such large monkeys are found mostly in the main canopy of a tropical forest (Symington, 1987). Spider monkeys rarely visit lower canopy levels and venture to the ground even less frequently (van Roosemalen, 1985; Youlatos, 2002). The ground and lower canopy levels are poor locations to find ripe fruit. More importantly, the ground can be a dangerous place because of the variety of animals that may prey on spider monkeys. Reports of ground use by spider monkeys and by other neotropical primates have emphasized the predation risks that the monkeys face there (Heymann and Hartmann, 1991; DiFiore, 2002; Miller, 2002). Predators include Felidae—jaguars, pumas and ocelots—venomous and constricting snakes, crocodilians, raptors, e.g., harpy eagles, and humans. While many of them are also capable of preying on spider monkeys in trees, the monkeys appear to perceive the ground as being more dangerous, perhaps because, their morphology precludes them from locomoting efficiently there.

Given the seemingly high levels of predation risk to the monkeys and likely poor returns of food, it is not surprising that ground use by spider monkeys is rarely observed. The question then becomes what factors influence a spider monkey's decision to come to the ground? If a real or perceived threat of predation is the main factor limiting ground use, then monkeys should only come to the ground when the risk is outweighed by the benefits, for example to drink water when it is not available in the canopy or to consume an important food or mineral source (Di Fiore, 2002).

We examined data from multiple sites where *Ateles* spp. have been studied to determine the conditions under which they venture to the ground and the approximate rate of ground use.

METHODS

We examined data from 5 sites where spider monkeys have been studied for ≥ 1 yr. Due to the rarity of observing spider monkeys on the ground, all the data were collected *ad libitum* (Altmann, 1974). Background information on the 5 study sites is in Table 1. We excluded accidental ground use such as when a monkey falls from a tree, and counted instances of terrestrial behavior equally regardless how many individuals were involved because in some cases it was difficult to determine the exact number of subjects. We present data as a rate of ground use per hour of contact. Due to the opportunistic nature in which the data were collected, statistical analyses to test for significant differences in rates of terrestrial behavior between the different sites are not appropriate.

RESULTS

Of the 5 study sites, Santa Rosa in Costa Rica showed both the highest and lowest rates of total terrestrial behavior per hour of contact (Figure 1a). Excluding the low rate in the most recent study there, which may be due to a lack of habituation, *Ateles geoffroyi* appears to use the ground more than the South American species does. We further partitioned terrestrial behavior at all sites into the categories in Table 2 (Figure 1). Data concerning males commencing an attack from the ground are only available for BCI, where it occurred at a rate of 0.0035 instances per hour of contact. It occurred recently at Punta Laguna, but the data were not available for this analysis. Whereas *Ateles geoffroyi* appear to use the ground for all categories, though rarely for feeding, their South American counterparts were only on the ground to feed.

Table 1. Study Site Information

Study site	Researcher	Species	Average rainfall	Forest classification	Dates of study	Hours of contact
Barro Colorado Island, Panama	CJC	*Ateles geoffroyi panamensis*	2,600 mm	Tropical Moist	October 1997 –December 1998 (Continuous)	ca. 1,200
Santa Rosa National Park, Costa Rica	CAC, KM, FA	*A. g. frontatus*	1,600 mm	Tropical Dry	July 1983 — Aug 1989 (Periodic) May 2000–June 2002 (Continuous)	ca. 1,200 783
Punta Laguna, Mexico	GRF, LV	*A. g. yucatanensis*	1,500 mm	Tropical Semi-moist	January 1997 –December 1999 (Continuous)	1,896 (2 study groups)
Cocha Cashu, Peru	SER	*A. belzebuth chamek*	2,080 mm	Tropical Moist	Oct 1999–Dec 2001 (Periodic)	ca. 500
Yasuni National Park, Ecuador	SS	*A. b. belzebuth*	3,200 mm	Tropical Moist	February 1999 –June 2000 (Continuous)	1,316

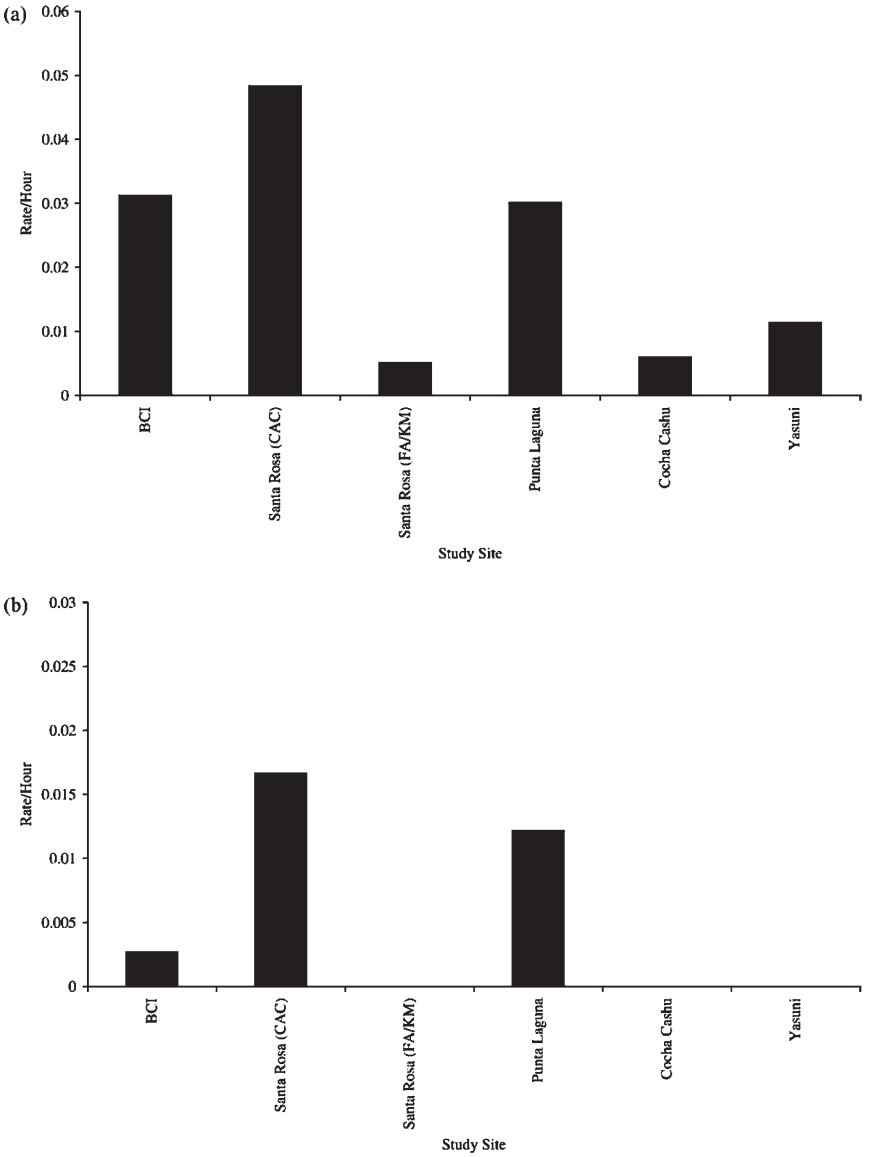

Figure 1. Comparisons of terrestrial behavior by spider monkeys at 5 different study sites; **a.** Rate of overall terrestrial behavior; **b.** Rate of drinking water from terrestrial sources; **c.** Rate of feeding on soil, rotten wood or using clay licks; **d.** Rate of using ground to traverse gaps in the forest cover; **e.** Rate of ground use by females escaping attacks by adult males; **f.** Rate of ground use during the chase game.

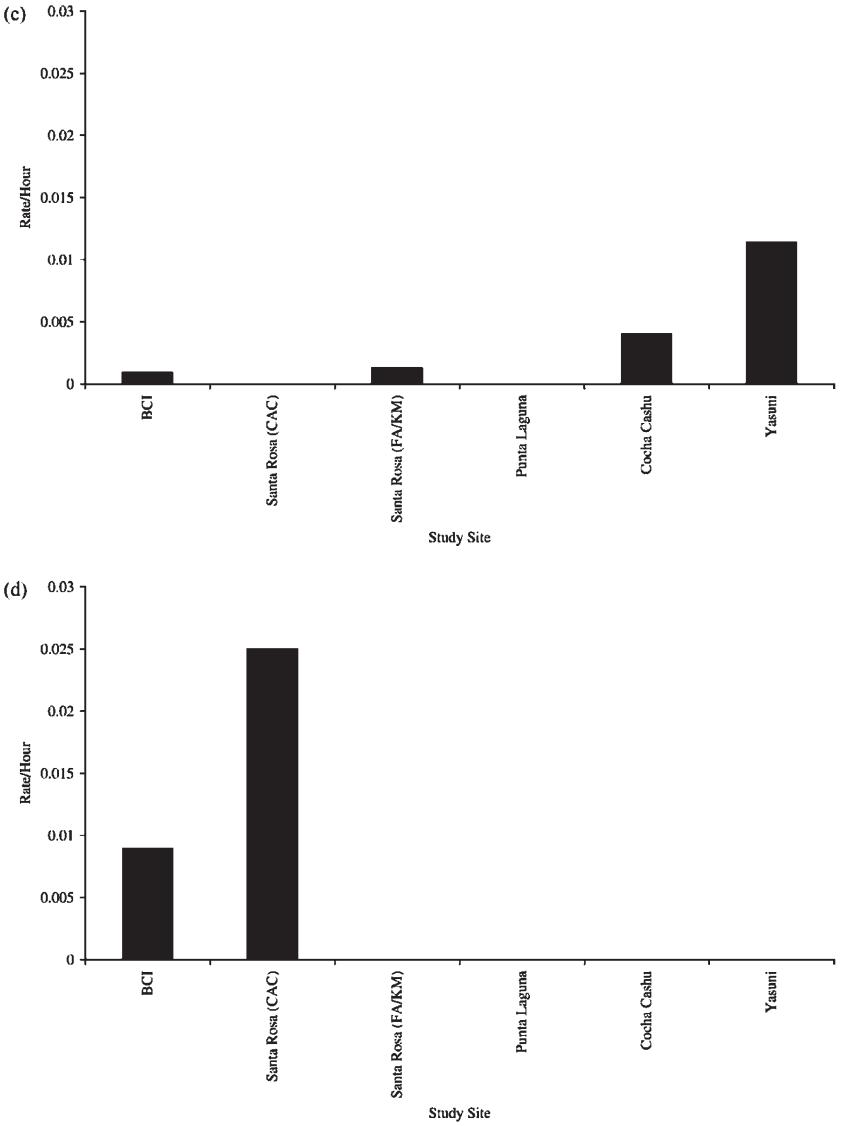

Figure 1. Continued.

DISCUSSION

Data from the 5 sites indicate that the spider monkeys rarely venture to the ground. Patterns of terrestrial behavior are not consistent across sites; there are differences in the frequency of ground use and the cir-

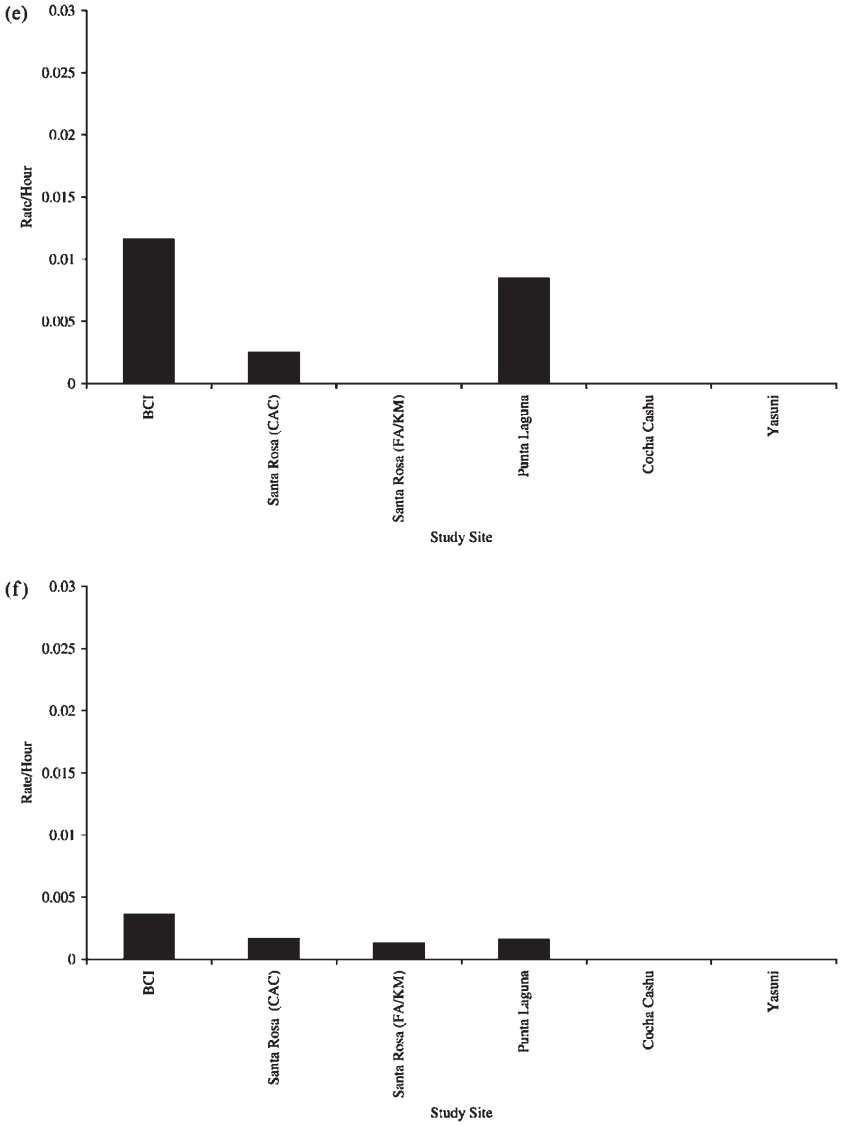

Figure 1. Continued.

cumstances under which monkeys visited the ground. Spider monkeys at Punta Laguna and the 2 Central American sites not only used the ground more frequently than their South American counterparts, but also their ground use occurred in a greater variety of circumstances. The South

Table 2. Ground use categories

Category	Description
Drinking	Animals would descend to the ground to drink water from a puddle, trough, or stream.
Feeding	Animals would descend to the ground to consume food/mineral sources not available in the forest canopy. Such food sources included soil, rotten wood, and nutrient sources found in salt licks.
Crossing gaps	When faced with navigating a large gap in the forest cover, monkeys would descend to the ground in order to move from one feeding patch to another. At one site (Santa Rosa) this also included dispersal across a major highway.
Females escaping attack	During aggressive encounters between adult males and adult females, females were chased to the ground in obvious distress.
Males attacking	At one site (BCI) males would approach females silently on the ground before commencing an attack.
Chase game	Animals used the ground in an obvious play context. The animals would leap onto the ground from small trees and then run to another tree that they would climb up briefly before repeating the behavior. At different sites the activity involved either juveniles only (Punta Laguna), adult males or juveniles (Santa Rosa), or all group members including female with young (BCI).

American spider monkeys came down to the ground to feed only. In contrast, feeding was the least common reason for ground use by *Ateles geoffroyi*.

There are many possible reasons for the difference in terrestrial behavior between the South America spider monkeys and their northern counterparts. The first is phylogenetic i.e., spider monkeys in the 2 regions are different species. Given the similarities in behavioral ecology between the different spider monkey species, e.g., fission-fusion social system, vocalizations, diet and male-female relationships, this seems to be an unlikely explanation.

The higher rate of drinking from the ground for *Ateles geoffroyi* is almost certainly related to climatic differences. Strong seasonality in climate can lead to dry seasons where little to no rain falls for months. Normal sources of drinking water dry up and the monkeys are forced to search for water in less desirable locations. Rainfall seasonality at the 2 South American sites is less extreme than at the more northerly sites (Terborg, 1983; Di Fiore and Rodman, 2001) and the monkeys are likely to be able to locate arboreal water sources year round. Klein (1972, p. 487) reported that Colombian spider monkeys never came down to the ground to drink, as there were always arboreal water sources available.

It is unclear why descending to the ground to feed on rotten wood or soil or from a salt lick occured more frequently at the 2 South America sites; however, geophagy by Neotropical primates generally is confined to South American sites (Heyman and Hartmann, 1991; Izawa, 1993; Müller et al., 1997; Setz et al., 1999; De Souza et al., 2002). Explanations for Neotropical primate geophagy typically revolve around nutrient supplementation (Heyman and Hartmann, 1991; Izawa, 1993; Müller et al., 1997; Setz et al., 1999) or detoxifying secondary compounds consumed during times of heavy leaf consumption (De Souza et al., 2002). Izawa (1993) reported similar rates of geophagy by *Ateles belzebuth* in Colombia. Analysis of the soil and water from salados (salt licks) at Izawa's (1993) site showed that the soils were nutrient rich, but there was no consistent composition of in the nutrients. Salado water was 3 times higher in sodium than other water (Izawa, 1993). Dew (2005) suggested that phosphorous in the soils consumed by the monkeys may be an important factor. There is no reason why geophagy by different species, at different locations, or even at different times should have one explanation; however, the apparent lack of soil-eating by Neotropical primates in the more seasonal forests of Central America and Mexico is interesting. Geographically based differences in plant communities and soil types may mean that the South American spider monkeys have additional nutrient requirements. Alternatively, leaves in seasonal and aseasonal forests are dissimilar in chemical composition (nitrogen:fiber ratios) due to their different life spans (Leigh, 1999, pp. 162-163). The possibility that leaf-eating by primates in aseasonal but not seasonal forests leads to geophagy as a means to detoxify secondary compounds warrants further investigation also.

Crossing between discontinuous forest fragments occurred at BCI and Santa Rosa. It occurred also at Punta Laguna (Ramos Fernández and Vick, unpubl. data). Its absence at the 2 South American sites is almost certainly due to the more continuous forest there.

A potential explanation for the overall lower rates of ground use by South American spider monkeys relates to the predator communities at the 2 sites. In general the predator communities are more intact at these sites. While large felids are present at the 3 northern sites, their population densities are likely or known to be significantly lower than at the more remote and intact forests of Yasuni and Cocha Cashu (Glanz, 1982; Emmons and Feer, 1990; Wright et al., 1994). Anecdotal evidence suggests that much of the decision making about ground use relates to a perceived or real threat of predation by ground dwelling predators. Spider monkeys on the ground appear very nervous, continually scanning the environment and often taking long periods of time before finally descending. On BCI, where large felids are only intermittently observed on the island (Wright et al., 1994), the monkeys scanned ≤ 20 min before

coming to the ground to drink. At Yasuni, where large felids are more common (DiFiore pers. comm.), the monkeys scanned the environment for ≤ 2 h before coming down to a salt lick. Woolly monkeys (*Lagothrix lagotricha*) at Yasuni are also more vigilant than expectant when close to the ground, which has been interpreted to be a behavioral response to increased risk of predation there (Di Fiore, 2002).

Curiously, when spider monkeys were involved in a chase game they seemed to be unwary. At BCI, Santa Rosa and Punta Laguna individuals would run on the ground with much less regard for the threat of predation. Indeed, on BCI (July 2003) juveniles engaged in a chasing game on the edge of the lakeshore (often contacting the water), where potential aquatic predators such as crocodiles and caiman are frequent (Campbell, pers. obs.). At BCI and Punta Laguna adults may act as sentries while juveniles are playing. At Punta Laguna adult females appeared to be vigilant while juveniles played on the ground, and they shook branches at the human observer. On BCI juveniles and females with young offspring never engaged in the game unless adult males were nearby. Adult males would refrain from joining the game and appeared to take a sentry role, staying nearby and low in the trees. Juveniles played the same game on the rooftops of the laboratory and dormitory buildings on BCI without the presence of adults.

Further evidence from Santa Rosa supports the notion that ground use by *Ateles* spp. is limited by a perceived threat of predation. In the most recent study terrestriality occurred at a much lower frequency that in the previous study. Indeed, only one instance of playing on the ground occurred in the later study, and it terminated when the field assistant approached the scene. Juvenile spider monkeys played with white-faced capuchins (*Cebus capucinus*), which frequently engage in chase-like games on the ground (M. Panger, K. C. MacKinnon, K. Jack, and M. Baker, pers. comm.). The spider monkeys that KM and FA observed were not fully habituated to human observers. Accordingly, if they perceive humans to be as a threat, then this may explain this difference between ground use during the recent study and the earlier study when they were more fully habituated.

As the monkeys have become more habituated in ongoing studies at Santa Rosa, they have been on the ground during more observations (Aureli, unpubl. data). Klein (1972; p. 488) also suggested that the presence of a human observer probably deterred a group of females and juveniles from coming to the ground on one occasion in his study. Another factor important to the difference in ground use observations between the 2 Santa Rosa studies is that the earlier study was mostly carried out during dry season months, suggesting that the rate of drinking may have been inflated.

In conclusion, while spider monkeys are clearly adapted for a life in the trees, there are occasions when they venture to the ground. Where predator communities are more intact and there is a high risk of predation (or at least a perception of a high risk) spider monkeys do not come down to the ground except in very limited conditions when nutritional returns are high. In contrast, where predator communities are less intact, spider monkeys not only come down to the ground for nutritional reasons, e.g., water, but also to socialize and to traverse gaps in the canopy.

Acknowledgments — Fieldwork on BCI by Campbell was supported by grants from the National Science Foundation (SBR-9711161), the L.S.B. Leakey Foundation, the Department of Anthropology, University of California, Berkeley, and a Short-term Fellowship from the Smithsonian Tropical Research Institute. Campbell also thanks Antigone Thomas and Dr. Thomas A. Wake for help in collecting data pertaining to the project. Fieldwork at Punta Laguna was supported by the Margot Marsh Fund, the Peace College Faculty Development Fund and the National Council for Science and Technology (CONACYT, Mexico). Ramos-Fernández and Vick thank Eulogio and Macedonio Canul for their assistance in the field. The L.S.B. Leakey Foundation supported fieldwork carried out at Santa Rosa by Matthews and Aureli, who also acknowledge the work of Sarah Carnegie, Yvonne Constancio, Sasha Gilmore, Cara Murphy, Kate Nowak, and Hugo Rojas for gathering data. Data from Cocha Cashu were collected during fieldwork supported by the National Science Foundation and grants from the Organization for Tropical Studies and the University of Illinois Dissertation Travel and Clark Research Grants. Russo thanks her field assistants, particularly Jill Roland, for their dedication and help. Suarez thanks the L.S.B. Leakey Foundation, the National Science Foundation and Dr. Peter Rodman for funding fieldwork at Yasuni and Gorky Villa, Nigel Pitmen, Jill Anderson, Jacob Nabe-Nielson, and Robyn Burnham for their help in collecting data. Finally we thank an anonymous reviewer for suggestions and comments that greatly improved the paper.

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