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Behavior, Ecology, and Demography of *Aotus vociferans* in Yasuní National Park, Ecuador

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Abstract Given its broad geographical distribution, *Aotus* is a productive genus for comparative studies that evaluate how different ecological factors influence the morphology, behavior, ecology, and demography of closely related species. During 18 mo we collected demographic, ranging, and activity data from owl monkeys (*Aotus vociferans*) in Yasuní National Park in eastern Ecuador. To collect demographic data, we monitored the trail system several times per week searching for groups. To characterize patterns of activity, we recorded the time when the subjects began and ended their nocturnal activity, and we collected data on range use and daily path length during 12 full-moon and 12 new-moon night follows of 1 radiocollared group. They ranged in size between 3 and 5 individuals (n=4 groups). All groups were strictly nocturnal, beginning their activity between 1800 and 1900 h and finishing it between 0500 and 0600 h. The territory size of the radiocollared group was 6.3 ha. On average, the subjects traveled 645 m per night (±286 m) and ranged farther during full-moon than new-moon nights. The owl monkeys used a small number of preferred daytime sleeping trees. Our data conform well with previous studies of other tropical owl monkeys from Colombia and Perú. A comparison of tropical owl monkeys with more temperate *Aotus azarai* from the

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Argentinean Gran Chaco reveals that grouping patterns, day range length, and territory size are relatively conserved across the genus despite dramatic differences in body size and activity pattern.

Keywords activity · monogamy · nocturnal · ranging · territoriality

Introduction

Among neotropical primates, relatively few taxa occupy a geographic range as broad as that of owl monkeys (*Aotus*), which are distributed from the Isthmus of Panamá to the Chaco region of northern Argentina (Defler 2004; Defler and Bueno 2003; Fernandez-Duque 2007; Rylands *et al.* 2000, 2006; Wright 1981). Across the area, the various forms of *Aotus* occupy habitat types that range from evergreen rain forests to semideciduous dry forests. They likewise show dramatic variation in chromosome number (2n=46–54, Defler *et al.* 2001; Galbreath 1983; Hershkovitz 1983; Ma *et al.* 1985; Pieczarka *et al.* 1993; Torres *et al.* 1998), body mass (800–1350 g; Aquino and Encarnación 1986a, b; Fernandez-Duque 2007; Smith and Jungers 1997), and activity pattern. Most species are strictly nocturnal, whereas at least one is cathemeral, with activity taking place during the day and at night (Erkert and Grober 1986; Fernandez-Duque 2003; Fernandez-Duque and Erkert 2006; Wright 1989). However, regardless of the differences, researchers consistently described owl monkeys as living in small, territorial, socially monogamous groups wherein males provide substantial offspring care (Aquino and Encarnación 1994; Fernandez-Duque 2007; Kinzey 1997; Moynihan 1964; Robinson *et al.* 1987; Wright 1981, 1994).

Given the broad geographical range where owl monkeys live, the genus is a rich resource for comparing how different ecological factors may influence the morphology, behavior, ecology, and demography of closely related species. To develop a comparative framework, adequate information is available on the behavioral biology of *Aotus azarai* (Arditi 1992; Fernandez-Duque 2003; Fernandez-Duque and Erkert 2006; Fernandez-Duque and Huntington 2002; Fernandez-Duque *et al.* 2001, 2002; Rotundo *et al.* 2005; Wolovich *et al.* 2007). *Aotus azarai* is the only cathemeral species of *Aotus* and lives at the southern portion of the distribution of *Aotus* in the Chaco region of Argentina and Paraguay (Fernandez-Duque 2003; Fernandez-Duque and Erkert, 2006; Wright 1989). By contrast, researchers know much less about the behavioral biology and ecological strategies of owl monkeys from tropical regions. The seminal work of Wright (Wright 1978, 1984, 1985,1986, 1994) and a few additional brief studies (Aquino and Encarnación 1986a, b; Bicca-Marques and Garber 2004; García and Braza 1987, 1993, 1995; Puertas *et al.* 1992) provide all of the data that are currently available on the strictly nocturnal and tropical species of *Aotus*. As part of a comparative study of social monogamy and paternal care in monogamous platyrrhines (Di Fiore and Fernandez-Duque 2007; Di Fiore *et al.* 2006, 2007; Fernandez-Duque *et al.* 2007; Hurst *et al.* 2005; Schwindt *et al.* 2004; Veiga *et al.* 2006), we conducted an 18-mo pilot study of the behavioral ecology of Ecuadorian owl monkeys (*Aotus vociferans*) in the rain forests of Yasuní National Park.

Methods

Study Site and Subjects

We conducted our study at the Tiputini Biodiversity Station (76° 08′ W, 0° 38′ S) in the Yasuní National Park and Biosphere Reserve in eastern Ecuador; where Di Fiore and colleagues have studied the primate community since 1994 (Di Fiore 2003a, b; Di Fiore and Fleischer 2005; Di Fiore and Rodman 2001). The site on the left bank of the Río Tiputini covers *ca.* 650 ha of primary tropical rain forest that can be accessed by an extensive trail system. Rainfall in the region typically totals >3000 mm/yr (Di Fiore and Rodman 2001).

On January 15, 2005 we located for the first time a group of 5 owl monkeys sleeping inside a tree cavity. Over the next 2 wk, we attempted to follow and to capture a member of the group. On the night of January 25, 2005, we anesthetized 1 individual from the group via remote injection with ketamine HCl using a tranquilizer dart (Pneu-Dart, Inc.) fired from a CO_2-powered rifle (DanInject, ApS, model JM). We removed him (a juvenile male) from the group for *ca.* 80 min, during which time we collected a range of morphometric data and fitted him with a radiocollar (MD-80, Telonics, Inc.). When capturing him, we followed procedures that we used to capture owl monkeys (*Aotus azarai*), titi monkeys (*Callicebus discolor*), saki monkeys (*Pithecia aequatorialis*), woolly monkeys (*Lagothrix lagotricha*), spider monkeys (*Ateles belzebuth*), capuchins (*Cebus albifrons*), and squirrel monkeys (*Saimiri sciureus*: Di Fiore and Fernandez-Duque, unpub. data; Di Fiore and Schwindt 2004; Fernandez-Duque and Rotundo 2003; Schwindt *et al.* 2004).

Data Collection

We collected ranging and activity data from the radiocollared group in 2 ways. First, we used radiotelemetry to locate the radiocollared group in or near a sleeping tree at dawn or dusk *ca.* once per week. To characterize patterns of activity, we recorded when individuals in the radiocollared group and other groups with known sleeping sites became active at dusk and when they went back to the sleeping tree. Second, between April 2005 and January 2006, we collected systematic ranging data during 32 nocturnal follows of the radiocollared group. We discarded 2 incomplete follows that started at midnight, 3 incomplete follows that lasted until midnight, 2 follows of limited quality given long times without contacting the group, and 1 follow conducted when the moon was neither full nor new, but waning (42% of moon surface illuminated). Thus, we based our analyses on 24 follows that always started when the subjects left the sleeping tree at dusk and lasted until they returned to a sleeping tree the next morning.

To evaluate the effects of moonlight on ranging behavior, we conducted 12 of the full-night follows during nights when the percentage of the illuminated moon surface ranged between 71 and 100% (full-moon follows) and the other 12 when the percentage ranged between 0 and 26% (new-moon follows). We obtained the fraction of the moon illuminated, as well as the times of sunrise, sunset, and astronomical twilight, from the U.S. Naval Observatory Web site (http://aa.usno.

navy.mil/data/). During follows, we recorded the position of the group relative to previously mapped trails and reference points 3 times/h and entered them into a desktop GIS for spatial analysis.

In addition, between January 2005 and July 2006, we monitored the trail system at dawn and dusk several times per week, searching for additional groups of owl monkeys. Nocturnal owl monkeys are most easily located as they exit their sleeping holes at dusk or when they return to their sleeping sites before dawn (Aquino and Encarnación 1986a, b; García and Braza, 1987; Wright, 1978). We collected data from uncollared groups *ad libitum*, as we encountered them. Whenever we sighted a group, we recorded a precise location by measuring the distance from the contacted individuals to a previously mapped point in the trail system. Finally, we also tagged, mapped, and measured trees where owl monkeys slept during daylight hours.

Results

Demography

Our demographic data confirm that nocturnal, tropical owl monkeys live in relatively small groups. We made contact with groups of owl monkeys other than the radiocollared group on 30 occasions. They ranged in size from 3 to 5 individuals. Based on the locations of the contacts and the numbers of individuals, it was reasonable to assume that they represented at minimum 3 different groups. We were not able to collect information on age and sex structure from the groups given the poor light conditions and the absence of conspicuous sexual dimorphism.

Between February 16, 2005 and July 14, 2006 we contacted the radiocollared group on 109 d (monthly median number of days contacted: 6, range: 1–12). When first contacted, the radiocollared group had 5 individuals. Between January and March 2006, *ca.* 1 yr after we radiocollared the juvenile male, 2 juveniles that were both smaller than the collared individual disappeared from the group. The group continued to have 3 individuals until February 16, 2006 when we last contacted the radiocollared juvenile male in the group.

Activity Patterns

The individuals in the radiocollared group concentrated their activities entirely during the dark portion of the 24-h cycle. On the 25 occasions that we followed them as they left a sleeping tree, the onset of activity at dusk took place between 1820 and 1840 h (n=15 contacts), 1800 and 1820 h (n=5 contacts), 1840 and 1900 h (n=3 contacts), and 1900 and 1920 h (n=2 contacts). In other words, they always became active after sunset (1751 h–1822 h), but before the end of astronomical twilight (1902 h–1933 h). They always returned to an area around a sleeping tree in the morning between 0500 h and 0600 h just before sunrise (0545 h–0616 h), but after the onset of astronomical twilight (0434 h–0505 h), and they were always inside the sleeping tree before 0600 h. Further evidence for the strictly nocturnal pattern of

activity of tropical *Aotus vociferans* comes from the data collected *ad libitum* on additional groups. We always detected the groups either while resting inside of their sleeping holes during daylight hours or when beginning to become active at dusk.

Ranging and Use of Space

The territory size of the radiocollared group was 6.3 ha, estimated as a minimum convex polygon from 834 fixes recorded across all contact days (Fig. 1). On average, they traveled 645 m (±286 m) per night (range: 150 m–1358 m). Nocturnal travel distance was influenced by moonlight, averaging 795 m (±273 m, $n=12$ follows) during full-moon follows and only 495 m (±216 m, $n=12$ follows) during new-moon follows (Mann-Whitney U test, 2-tailed, $U=31$, $z=-2.367$, $p=0.018$).

Sleep Trees

We identified the sleeping tree used by the radiocollared group on 81 d of 109 contact days, either by finding the monkeys during the night and following them until they settled into a tree at dawn or locating them via telemetry in the afternoon or early evening before they left the tree. For the remaining days, we were unable to identify confidently in which trees the subjects slept, either because we left them before dawn or because we began our follows after the group had exited its sleep tree.

Radiocollared owl monkeys used only 5 sleep trees over the course of the study (Fig. 1). Two trees (1 and 2, Fig. 1), used on 41 and 22 occasions, respectively, accounted for 78% of the instances in which we could confidently identify a sleep tree. The individuals tended to use a particular tree repeatedly for several days before changing to another. They returned to the same tree in 29 of 39 cases (74%) in which we could confidently identify the tree used on 2 successive days. We also recorded an additional, nonradiocollared group, monitored less regularly, using a single tree on ≥19 different occasions.

Sleep trees the radiocollared group used tended to be relatively large, with a minimum diameter-at-breast height (DBH) of 72 cm. Nonetheless, before the start of data collection, the focal group regularly slept in a much smaller dead palm tree of 15-cm diameter and other groups of owl monkeys also used small-diameter palms as sleeping sites. The sleep trees were not particularly dense with vines, nor were the hole openings covered by vine tangles.

Discussion

Aotus vociferans in eastern Ecuador live in relatively small social groups of ≤5 individuals. They range over their territories only during the night and they do so more when the moon is full than when it is new. Our findings agree with the only other studies of *Aotus vociferans* in Perú (Aquino and Encarnación 1988, 1994), and with reports on other nocturnal tropical *Aotus* species (Aquino and Encarnación 1986a, b; Aquino *et al.* 1990; Bicca-Marques and Garber 2004; Erkert 1999;

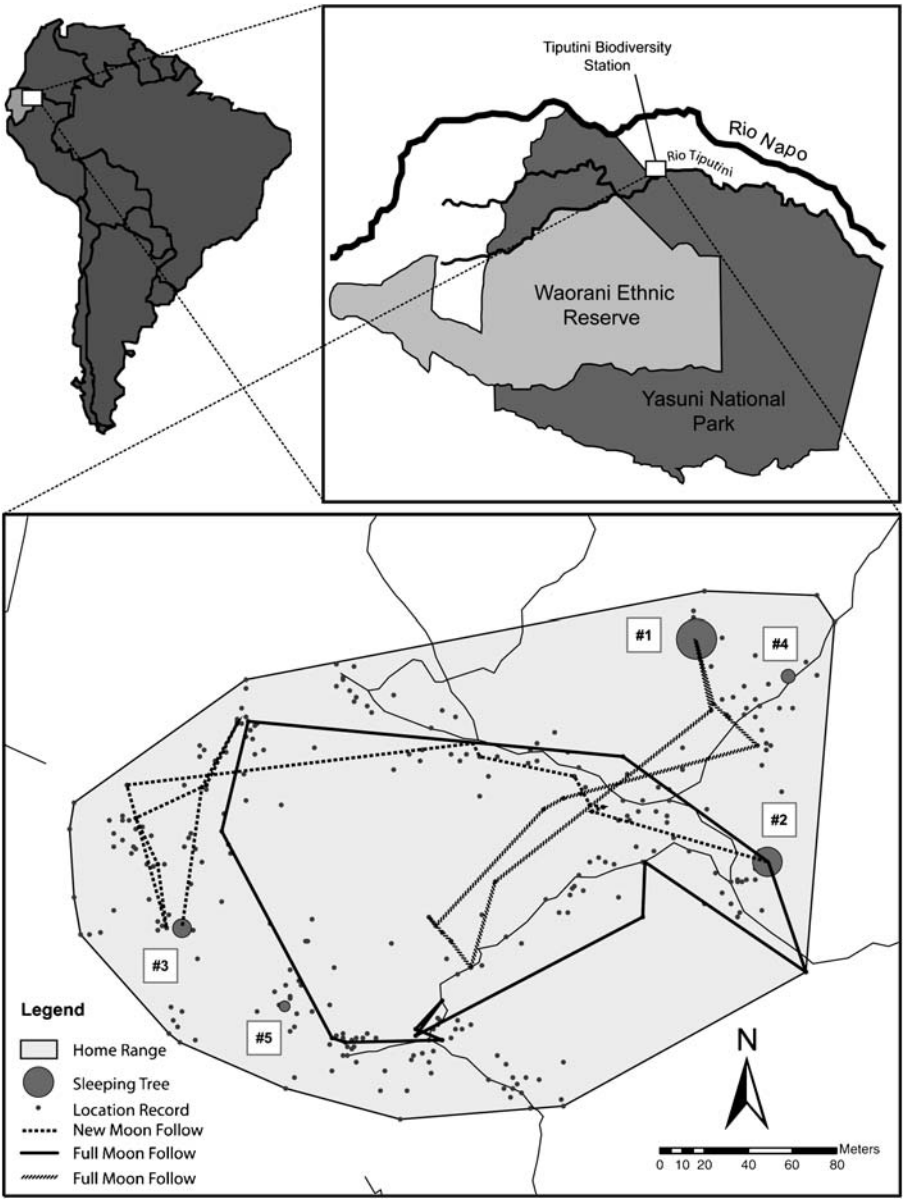

Fig. 1 Location records (n=834) for 1 radiocollared group of owl monkeys (black dots) within their territory (shaded and enclosed by a solid thin line). Five sleep trees the group used over the course of the study (gray circles with associated numbers) are scaled proportional to their relative use. We also indicate 3 representative nocturnal paths, 2 on full-moon nights (solid thick line and hashed line), when the subjects returned to the same sleep tree on 2 consecutive days, and one on a new-moon night (dotted thick line), when they switched sleep trees.

Fernandez-Duque 2007; Kinzey 1997; Moynihan 1964; Wright 1994). In the following paragraphs we discuss our results in the context of what is known about the behavior, demography, and ecology of other populations of tropical *Aotus* spp.,

and we compare them with *Aotus azarai*, a larger, cathemeral species from the extreme southern end of the generic distribution.

Researchers have consistently reported owl monkeys living in small groups of 2 to 6 individuals (Fernandez-Duque 2007; Kinzey 1997; Robinson *et al.* 1987; Wright 1981). Our data on group size in *Aotus vociferans* reinforce the notion. However, though in all *Aotus* species studied, most individuals live in relatively small social groups, recent findings on *Aotus azarai* suggest that a significant percentage of the adults (25%) live, at least temporarily, as solitary individuals floating among territories (Fernandez-Duque *et al.* 2006, 2007). Though there is no report of the existence of a subpopulation of floaters for *Aotus* spp. other than *A. azarai*, we think that this is likely a result of the difficulties of locating solitary individuals in strictly nocturnal species. A combined approach that relies on following radiocollared dispersing individuals and attracting floaters via playback experiments may elucidate this aspect of the social organization of nocturnal owl monkeys.

Our data show a territorial use of space by the radiocollared group. The individuals in the group ranged over a little more than 6 ha, and we detected no other owl monkey within the range. The territory size of *Aotus vociferans* falls squarely within the ranges of tropical *Aotus nigriceps* (7–14 ha, Wright, 1989, 1994) and *Aotus azarai* inhabiting more seasonal, drier, and less diverse forests of the South American Gran Chaco (4–10 ha, Fernandez-Duque 2007; Wright 1994).

Owl monkeys in Ecuador routinely ranged over their territory during the dark portion of the 24-h cycle. They began their activity soon after sunset and returned to their sleeping sites before sunrise in a manner similar to that of *Aotus nigriceps* in Perú (Wright 1978, 1989). The observed peaks of activity at dawn and dusk indicate that owl monkeys prefer to be active with a luminosity of 0.1–0.5 lux (Erkert and Thiemann-Jager 1983), which corresponds to the brightness of full-moon nights, whereas lower and higher luminosities in the dark portion of the circadian cycle lead to considerably reduced activity (Erkert 1976). Their reduction of activity in complete darkness is further shown by the effects of moonlight on their activity and ranging patterns. Researchers have observed effects of moonlight in several South American *Aotus* spp. in captivity (Erkert 1974, 1976) and in the wild (Aquino and Encarnación 1986a, b; Fernandez-Duque 2003; Fernandez-Duque and Erkert 2006, García and Braza 1993; Wright 1978, 1989).

Owl monkeys in Yasuní used relatively few sleeping trees, like other populations of *Aotus* spp. –*Aotus vociferans* (Puertas *et al.* 1995) and *A. nigriceps* in Perú (Wright 1978, 1989) and *A. azarai boliviensis* in Bolivia (García and Braza 1993) – and other nocturnal primates (Rasoloharijaona *et al.* 2003). The use of specific sleep trees by strictly nocturnal, smaller, and more tropical species of owl monkeys contrasts dramatically with the sleeping habits of Azara's owl monkeys in the Chaco of Argentina and Paraguay, which regularly use numerous arboreal sleep sites (Wright 1989). Owl monkey species not only differ in the number of trees used for sleeping, but also in the way they use them. In all examined populations, tropical owl monkeys sleep inside tree holes (Aquino and Encarnación 1986a, b; Puertas *et al.* 1995; Wright 1989). By contrast, in the South American Chaco, owl monkeys never sleep inside tree holes, but choose instead vine tangles or open branches (Wright 1989).

Differences in predation risk and body mass between tropical and subtropical owl monkey species may be important in accounting for variation in the use of sleeping trees and activity patterns. Wright (1989) hypothesized that high predation pressure and competition for resources with other sympatric primates, 2 important selective forces that may have favored nocturnality in *Aotus nigriceps* in Perú, may be reduced at the southern end of the generic distribution where cathemeral *Aotus* range. Differences in body mass may also help to explain the use of different antipredator strategies by various owl monkey species. The 2 tropical species (*Aotus vociferans* and *A. nancymaii*) for which there are adequate body mass data from free-ranging individuals range between 700 and 800 g (Fernandez-Duque 2007), whereas the average body mass of *A. azarai* in Argentina is 1254 g (Fernandez-Duque 2007). It is thus possible that the small owl monkeys are able to use relatively small sleeping holes where 4 or 5 *Aotus azarai* would not fit.

The comparative method is an extremely powerful tool that has contributed much to our understanding of primate socioecology. We have shown that body mass and activity patterns of owl monkeys are very different across the generic range. However, there appears to be no variation across owl monkey species in group size or territory size. The observation raises several important questions that remain unanswered. First, what are the main determinants of territory size in owl monkeys, and why is it that territory size remains relatively constant among species that differ by as much as 50% in body mass? Is it possible that social factors, more than ecological ones, are key to determine territory size? Second, why do we note no change in ranging patterns or behavior occurring together with changes in body size? Finally, why do small group size and social monogamy seem to be such resilient features of the behavioral biology of the genus?

Answering the questions will require detailed comparative data from closely related *Aotus* spp. in different environments and comparative data on the behavioral biology of *Aotus* and other socially monogamous platyrrhines, e.g., *Callicebus* and *Pithecia* living in the same environments. We are convinced that implementing standardized methodologies across field sites and taxa is a necessary step to develop a robust, comparative framework to examine the evolution and maintenance of monogamy, territoriality, and parental care in socially monogamous primates. To expand the use of our standard protocols to the study of other monogamous populations in the Neotropics and elsewhere, we invite colleagues to evaluate and consider them in their future research (http://www.sas.upenn.edu/~eduardof/Owlmonkeyproject.html).

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