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RESEARCH ARTICLES

Density and Population Structure of Owl Monkeys (*Aotus azarai*) in the Argentinean Chaco

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Owl monkeys are small monogamous primates ranging over a wide area extending from Panamá to the Chaco region of northern Argentina. The Chaco, an alluvial plain covering over one million km^2 of Argentina, Bolivia, Brazil, and Paraguay, consists of a mosaic of grasslands, savannas, xeric thorn forests, and gallery forests. The region shows significant seasonal variation in climate, rainfall, and food availability. The goal of this study was to determine the density, size, and structure of a population of *Aotus azarai* in the seasonal gallery forests of the eastern Argentinean Chaco. Reported population density, as well as group size and composition are based on data collected from 11 groups contacted on approximately 900 occasions, and observed for over 2,000 hours during a three-year period. Group and individual densities were 16 groups/km^2 and 64 individuals/km^2, respectively. Approximately half of the groups (n = 5) were small groups which had three individuals most of the time and never more than four, whereas the remaining groups were large groups composed of four or five individuals, and sometimes even six or seven individuals. This is the first study of *A. azarai* based on monitoring of a relatively large number of distinct groups. Our data suggest that owl monkeys in the seasonal subtropical forests of Formosa live at a density as high as those reported for owl monkey populations observed in tropical forests. The data also show that the social groups in the owl monkey population are of comparable size and composition to those characteristic of populations in the tropics. Am. J. Primatol. 53:99–108, 2001.

Key words: demography; density; owl monkeys; Argentina; *Aotus*; seasonality

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INTRODUCTION

Owl monkeys (*Aotus spp*.) are small arboreal primates living in groups generally consisting of an adult heterosexual pair, one infant, and one or two juveniles [Wright, 1994]. The taxonomy of the genus remains a matter of debate, with the number of recognized species varying between nine and five [Ford, 1994]. The different species cover a wide range extending from Panamá to the Argentinean Chaco. The Chaco is an alluvial plain covering over one million km^2 of Argentina, Bolivia, Brazil, and Paraguay [Redford et al., 1990]; and consists of a mosaic of grasslands, savannas, xeric thorn forests, and gallery forests. In the eastern Argentinean Chaco, owl monkeys (*A. azarai*) are found in the gallery forests and patches of dry forests scattered in the matrix of savannas characteristic of the area [Stallings, 1989; Wright, 1985; Zunino et al., 1985].

The eastern Argentinean Chaco is characterized by significant fluctuations in temperature and rainfall. During 1998–1999, mean winter temperatures were 11° lower (May–August, 16°C) than mean summer temperatures (December–March, 27°C (Fernandez-Duque, unpublished data)). Maximum (42°C) and minimum temperatures (0°C) were also extreme, and persisted for several days. Annual and seasonal rainfall also varies in the Chaco. Relatively dry years (range: 1090–1350 mm, n = 8 yr) alternated with relatively wet years between 1977 and 1999 (1800–2100 mm, n = 8 (Estancia Guaycolec's rainfall records)). Although rainfall is not strictly seasonal (9 mo exceeded 100 mm, 1977–1999), monthly averages tended to be lower during June–August (60 mm/mo) than they were during the fall (April: 240 mm/mo) or spring (November: 211 mm/mo).

The smaller forest cover offered by a relatively less diverse gallery forest [Placci, 1995], as well as the marked rainfall fluctuations, can help explain primate diversity in the Chaco [Kay et al, 1997; Peres & Janson, 1999]. It has been suggested that a decrease in the structural complexity of the forest and the corresponding decrease in the number of available niches may be associated with fewer species coexisting in sympatry [Ganzhorn, 1999]. Descriptions of the primate communities in the Chaco are in general agreement with this model. In the more humid and diverse Chaco of North Paraguay, the primate community includes four species, whereas only two species are found in the drier areas of the region [Stallings, 1989; Wright, 1985]. In the Argentinean Chaco, only two primate species live in sympatry: black howler monkeys (*Alouatta caraya* [Brown & Zunino, 1994] and owl monkeys (*A. azarai* [Arditi & Placci, 1990; Fernandez-Duque & Bravo, 1997; Rathbun & Gache, 1980]).

In this study we use demographic data collected during three years to describe the density, size, and structure of a population of owl monkeys in the seasonal gallery forests of the Pilagá River in the eastern Argentinean Chaco. Our data contribute to an understanding of the possible effects of latitude, rainfall, extreme temperatures, forest diversity, and coexisting species on the demography of one of the most widespread primate genera in the neotropics [Peres & Janson, 1999].

METHODS

Study Area

The area includes a mosaic of grasslands, savannas, and dry and gallery forests. The semideciduous gallery forest, which represents 8.5% of the total area of the ranch [Placci, 1995], is found along the banks of the Riacho Pilagá.

Seventy ha of forest were mapped to facilitate the location of the different groups

of monkeys. Fourteen km of transects, running east–west and north–south, and spaced every 100 m, were established within the 70 ha. Transects were measured and marked every 50 m with fluorescent plastic flagging and aluminum tags.

Study Population

We studied *Aotus azarai*, one of the five primate species that ranges south of the Amazon River [Ford, 1994]. The subspecies *A. a. azarai* is found in the Argentinean provinces of Formosa and Chaco [Brown & Zunino, 1994]. The study population is located on a 25,000-ha private cattle ranch (Estancia Guaycolec, 58°13′ W, 25° 54′S).

As opposed to other species of owl monkeys in lower latitudes that are strictly nocturnal [Wright, 1989], mirikinás are active during the day as well as during the night [Arditi, 1992; Fernandez-Duque & Bravo, 1997; Sloan & Fernandez-Duque, 1999; Wright, 1985]. The cathemeral owl monkeys [Tattersall, 1987] of the Argentinean Chaco provide a unique opportunity for obtaining accurate descriptions of population structure during daylight in an otherwise nocturnal genus.

Population Density and Size

We report population size and density from data collected during a three-year period (June 1997–May 2000), during most of which (25 mo) we were living in the forest. When we were not living in the forest, one of us monitored the population at least once every other month.

Our estimates of population density and population size are computed from data on 11 neighboring groups. We contacted these groups on approximately 900 occasions and spent more than 2,000 hours observing them as part of ongoing studies on cathemerality [Sloan & Fernandez-Duque, 1999] and infant survival and development (Rotundo et al., unpublished results). The data reported here were collected during daylight encounters with the groups.

Group Size

We report group size for all groups contacted on at least four different occasions (n = 17 groups). Eleven groups (Table I) are part of a long-term study and have been monitored since 1997, whereas the remaining six groups were part of a preliminary study (n = 4) [Fernandez-Duque & Bravo, 1997] or observed ad libitum near the area of study (n = 2). Group sizes of the study groups are reported for all months when they were contacted (Table I). Additional information on group size is reported from six additional groups contacted ad libitum during our work in the area and during a preliminary study of the population [Fernandez-Duque & Bravo, 1997].

To estimate group size, whenever we contacted a group we spent a minimum of 15 minutes counting all visible individuals. Still, on most occasions we would remain with the group for several hours while collecting behavioral data for other ongoing studies. Differences in group counts could result from differences in visibility at different times of the day and night, to interobserver differences in the ability to find all individuals, or to certain animals (usually juveniles) spending time apart from the group. Thus, since it is more likely that group size was sometimes underestimated than overestimated, the group size reported for each month is the maximum recorded group size for that period.

To describe changes in group size, we calculated the percentage of the total

TABLE I. Monthly Group Size and Number of times Each Group Was Contacted Between June 1997 and May 2000

	1997							1998											1999											2000						
Group name	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	# mo	# cont.
B68 size	4	5	5	5	4			4	4			4		4	4		4	4	4	4	5	5	5	5	5	5			4	5	5	5	5	5		26	84
# contacts	2	4	7	5	1			1	1			1		2	2		3	3	2	4	3	4	4	6	1	1			4	4	4	10	2	2		0		
CAMP size				4									4			5				4	4	4		4	4	4			5	3	3	3	3	3		1	16	30
# contacts				1									2			1				1	1	1		1	2	3			4	1	3	4	3	1		1		
CC size	4	4	4	4		5		4	4				4	4	4		5	5	5	5	5	5	5	5	5	5	5			4	5	5	5	4	3		5	28	117
# contacts	1	7	4	2		1		2	1				1	2	5		6	6	2	8	6	11	2	4	4	5	6			6	5	2	7	6	4		1		
CO size	6	6	6	6	6	6		7	5				5	5	5	5	5	5	4	4	4	4	4	4	4	4	4	4	5	5	5	5	5	5		5	31	122
# contacts	1	1	11	4	2	1		2	1				1	3	3	4	9	5	4	7	3	5	5	3	7	3	12	1	4	3	5	3	6	2		1		
D100 size		4	3	3		3		3	3			3		3	3	3	3	3	3	3	3	3	3	3	3	3	3			4	4	4	4	4	4		2	28	113
# contacts		3	5	2		1		1	1			5		2	2	2	2	7	3	8	7	4	8	9	7	2	3			8	3	3	5	6	2		2		
D1200 size	5	5	5	5	5			4				4	4				5										5			6	6	6	6	5			4	16	32
# contacts	2	1	3	2	1			1				2	1				1										3			4	4	1	3	1			1		
D500 size	3	3	3	3	3			4						3	3	3	4	4	4	4	3	3	3	3	3	3	3			4	4	4	4	4	4		4	27	119
# contacts	6	13	5	4	1			1						4	5	3	6	7	5	6	5	2	1	2	1	5	3			4	6	6	6	9	2		1		
D800 size		3		3								3									3	3		3	3	3			3	4	4	4	4	4		4	15	69
# contacts		3		5								1									1	1		2	2	1			5	8	7	12	10	10		1		
E500 size	4	4	4	4				4	4			4	4	4	4	4	4	4	4	4	4	4	4		4	4	4			4	5	5	5	5	5		5	28	86
# contacts	2	1	2	2				1	1			3	1	2	1	1	4	4	2	5	4	5	1		2	3	2			6	5	5	8	11	1		1		
F1200 size								3						3			3			3	4				4		4			4	4	3	3	3	3		3	14	26
# contacts								1						3			2			1	2				1		5			2	1	2	2	2	1		1		
INTR. size	4	4	4	4	3			4				4		3	3	4		3	3	3	3		3	3	3		3	3	3	3	3	3	3	3	3		3	26	74
# contacts	5	2	2	1	1			1				1		1	1	1		1	3	4	5		1	6	4		1	1	5	6	7	6	4	3		1		

mo, total number of months contacted; # cont, total number of times each group was contacted.

number of months that each group had three, four, five, or six individuals. We consider it more informative to report that a group had three individuals during 84% of the months observed (26 mo) and four individuals the rest of the time (5 mo) instead of reporting that it had an average group size of 3.2 individuals.

On approximately 100 occasions we contacted individuals that seemed to be solitary when found. These presumed solitary animals were not systematically observed or studied. Thus, we do not report in this study the data collected ad libitum from them.

Group Composition

We describe the age structure of the population towards the end of the study (March 2000), when our ability to estimate age based on relative size, as well as on our knowledge of each group's history, had improved. During data collection in the forest, animals were assigned to one of the following age categories based on their relative size: adult, juvenile, or infant. In many cases, this resulted in groups being reported as having two, three, or even four adult-size individuals.

Individuals are unequivocally of smaller size until they are at least 18 months of age. Since most births (96%, 25 births in 11 groups) occurred between October and November of each year (n = 3 yr, 1997–1999, unpublished data), it was possible to determine in March 2000 that all "infants" were approximately 5–6 months old, whereas all "juveniles" were approximately 17–18 months old. To obtain these estimates we assumed that infants and juveniles do not transfer between groups. This is a reasonable assumption since we have never encountered infants or juveniles wandering alone or missing from groups.

Estimating the age of adult-size individuals requires a greater degree of speculation. Still, we feel compelled to provide estimates, even if speculative, since those individuals represented 65% of the population in March 2000 (32 individuals). Our age estimates are based on the following assumptions: 1) there is only one pair of reproducing adults in each group, and 2) there is no transferring of infants and juveniles between groups. Although animals born in the 1997 birth season could not be distinguished by size from adults in March 2000, we estimate their age at approximately 29–30 months and classify them as "J97." For the most part, these animals have been observed since they were born in 1997.

It was not possible to sex individuals since owl monkeys are sexually monomorphic.

RESULTS

Population Density and Size

The study population was formed by 11 neighboring groups. The number of groups in the area did not change during the study, and total population size ranged between 40 and 45 individuals.

Group density as calculated from 11 groups ranging over approximately 70 ha of forest was 16 groups/km^2. Group density was slightly higher than previous census estimates in the area (range: 8–14 groups/km^2 [Arditi & Placci, 1990; Rathbun & Gache, 1980; Zunino et al., 1985]), or for tropical populations of owl monkeys (*Aotus azarai* (Beni, Bolivia): 14 groups/km^2 [García & Braza, 1989]; *A. nancymai* (Iquitos, Perú): 6–11 groups/km^2; *A. vociferans* (Iquitos, Perú): 2–10 groups/km^2 [Aquino & Encarnación, 1988]; and *A. nigriceps* (Manú National Park, Perú): 10 groups/km^2 [Wright, 1985]).

The number of individuals present in the area (64 individuals/km^2) was almost twice that reported in the past (range: 25–32 individuals/km^2 [Arditi & Placci, 1990; Rathbun & Gache, 1980, Zunino et al. 1985]).

Group Size and Composition

Studied groups ranged in size between three and seven individuals. Approximately half of the groups (n = 5) were "small" groups generally composed of three individuals and never having more than four individuals. The remaining groups (n = 6) were "large" groups composed of four or five individuals, but sometimes having six or even seven individuals (Table II). One of these large groups (Group C0) had six individuals during 1997, including two adults, two juveniles, and two similarly-sized infants. A month after the birth of an infant in 1997, the group lost two adult-size individuals.

Data on group size from the six groups observed ad libitum agree with the pattern observed in the more intensively studied groups. One group had three individuals, three groups had four, and two had five.

Small groups tended to be land-locked, whereas large groups occupied areas near the river. Four of the five small groups ranged over an area of the forest that provided no access to the river bank. The fifth group, although it had access to the river, did so only in a portion of the river without floodable forest. On the other hand, five of the six large groups had territories that included river banks and floodable forest. The difference in size between groups with or without access to the river is statistically significant, as indicated by Mann-Whitney tests done using the minimum (U = 5.5, P = 0.045) or the maximum (U = 19.5, P = 0.039) group size (Table II).

All groups fluctuated in size during the period of study (Table II). Most groups (n = 8) only added or lost one individual, fluctuating between three and four individuals (n = 5 groups), or four and five (n = 3 groups). The remaining two groups varied their size in two (n = 2 group) or even three individuals (n = 1 group). Despite these fluctuations, there was no indication that groups tended to increase or decrease in size over the years, as indicated by a Friedman analysis of variance (X^2 = 2.364, df = 2, P = 0.307).

In March 2000, one-third of the population consisted of infants and juveniles, whereas the remaining two-thirds were adult-size individuals (Table III). Every group had a reproducing pair, which accounts for 22 of the adult-size indi-

TABLE II. Percentage of Months Contacted With Different Group Size

	Number of individuals in group							
Group name	3	4	5	6	7	Min	Max	Access to river
D100	71	29	0	0	0	3	4	No
D500	56	44	0	0	0	3	4	No
D800	60	40	0	0	0	3	4	Yes
F1200	64	36	0	0	0	3	4	No
INTRUSO	78	22	0	0	0	3	4	No
B68	0	42	58	0	0	4	5	Yes
E500	0	79	21	0	0	4	5	No
CAMP	38	50	13	0	0	3	5	Yes
CC	0	43	57	0	0	4	5	Yes
D1200	0	25	50	25	0	4	6	Yes
CO	0	32	45	19	3	4	7	Yes

TABLE III. Age Structure of the Population in March 2000

	Adult-size individuals				
Group name	I	J	J97	?	A
D100	1			1	2
D500	1	1			2
D800	1	1			2
F1200	1				2
INTRUSO			1		2
E500	1	1	1		2
CAMP	1	1	1		2
CC	1	1		1	2
B68	1	1		1	2
D1200	1	1	1	1	2
CO	1		1	1	2
Total	10	7	5	5	22
%	20	14	10	10	45

I, infant (approx. 5-6 mo. old); J, juvenile (approx. 17-18 mo old); J97, approx 29-30 mo old; ?, age undetermined (see text for details); A, reproducing adults.

viduals observed. Of the remaining 10 adult-size individuals, five were born during the 1997 birth season (approximately 29–30 mo old, "J97").

The age estimates of the remaining five adult-size individuals should be considered with caution, given the cumulating evidence on the existing variability in monogamous social systems [Palombit, 1994; Sommer & Reichard, 2000]. Two of those individuals were probably born during 1996 (approximately 41–42 months old in March 2000). A description of how we estimated the age of one of them will clarify our procedures for estimating age: When Group D100 was first contacted in July 1997, it consisted of three adult-size individuals and an infant whose size indicated that it had been born in the 1996 birth season. By November 1997, one of the adult-sized individuals disappeared, leaving the group with three individuals. The group did not have a recorded birth during 1997 or 1998, but had an infant during the 1999 birth season. In March 2000, the group included the 1999 infant and the three individuals who were present already in July 1997. Therefore, the infant born in 1996 was approximately 44 months old in May 2000. Using similar reasoning, we estimate that another individual was born in 1996 (Group C0), whereas the last three were born in 1996 or earlier (Groups CC, B68, and D1200).

DISCUSSION

This is the first study of owl monkeys (*A. azarai*) focusing on a relatively large number of identified groups and spanning several years. Our data show that owl monkeys in the seasonal subtropical forests of Formosa live at a density as high as that found in tropical forests of Perú and Bolivia. The data also show that the population is formed by social groups of composition comparable to those found in tropical populations. Group size in this population (n = 11) differed from previous estimates (range: 2.3–3.3 individuals, Arditi & Placci, 1990; Rathbun & Gache, 1980; Zunino et al., 1985). Previous reports of smaller groups in this area were based on census data, which tend to underestimate group size. Our own estimate of group size from census data not reported here was smaller than the known mean group size for the population (3.1 vs. 4.0 individuals).

The existence of "small" and "large" groups in our population cannot be readily explained. Groups could become larger as a consequence of higher reproductive rates, lower mortality rates, older age at dispersal, or a combination of these factors. All groups but one had an individual born during the last two years, and we did not notice obvious differences in sudden disappearances of individuals. Still, the length of our study does not justify any speculation regarding differences among groups in life-history traits. Differences in group size could also be explained due to differences in availability of resources among territories or differences in number of reproductive opportunities to dispersing individuals.

Due to varying proportions of floodable, highland, lowland, and transitional forest, it is reasonable to expect territories to differ in the quality and abundance of the food resources they offer. Five out of six groups have territories that include access to the river, whereas four of the five small groups are land-locked. Given that the floodable forest is less seasonal than the other types of forest [Placci, 1995], groups with access to the river may have access to a more continuous resource base than land-locked groups. In turn, a better resource base may allow animals to delay dispersal until the right reproductive opportunity arises. A recent study on territory size, ranging behavior, and forest structure will allow us to evaluate this hypothesis [Sloan & Fernandez-Duque, 1999].

Regarding the number of reproductive opportunities to dispersing animals, it is possible that the geometry of land-locked territories provides dispersing monkeys in those smaller groups greater access to neighboring groups into which they might disperse. This alternative would imply that dispersing animals transfer between groups, as opposed to establishing themselves in a new territory. We have not yet noticed a pair of owl monkeys establishing themselves in a new territory. Still, whether dispersing owl monkeys form new groups or transfer to already established groups (as has been described in gibbons [Brockelman et al., 1998; Palombit, 1994; Treesucon & Raemaekers, 1984] and titi monkeys (*Callicebus moloch*; Bossyut, personal communication)) remains an open question.

The relatively high densities and large groups characteristic of the population are probably the result of environmental factors such as temperature, rainfall, forest productivity, number of competitors, and number of predators. Owl monkeys in this part of their range show behavioral and morphological adaptations that may help them cope with the extreme temperatures of the Chaco. Owl monkeys are cathemeral [Arditi, 1992; Sloan & Fernandez-Duque, 1999; Wright, 1985], showing periods of activity during the night as well as during the day. The diurnal activity of owl monkeys may allow them to compensate for missed foraging opportunities during cold nights. Morphological adaptations may include an increase in body weight; there is some indication that owl monkey species at more southern latitudes (*A. azarai*) can be 10–30% heavier than those living closer to the equator [Smith & Junger, 1997].

The effects of rainfall on population density are apparent from an examination of densities along the existing rainfall gradient in the Chaco. Both in Paraguay [Stallings, 1989] and Argentina [Zunino et al., 1985] the abundance of owl monkeys in drier areas was lower than in wetter areas. The western limit to owl monkey distribution seems to be set by the amount of available rainfall in the area. No owl monkey populations exist at locations getting less than 500 mm/yr [Stallings, 1989], whereas the average 1,600 mm/year of rainfall of the eastern Argentinean Chaco seems to be enough to support existing densities.

The pattern of rainfall is usually highly correlated with the productivity and structure of the forest, at least within the range of rainfall characteristic of the area of study [Proctor, 1984, as cited in Kay et al., 1997]. In the gallery forests of

Formosa, rainfall influences the seasonal character of the forest, including peaks and lows of productivity [Placci, 1995]. The availability of insects and fruits reaches a peak during the warmer summer months and a minimum during the relatively cold winter [Arditi, 1992; Placci, 1995]. During the months when fruit productivity is lower, owl monkeys may switch to other resources like leaves or flowers [Ganzhorn, 1988; Overdorff, 1993; Terborgh, 1983]. Arditi [1992] reported more than 40% of leaves being consumed in the diurnal and crepuscular diet of owl monkeys in Formosa, and Wright [1985] found similar values in Paraguay. A broader diet may enable them to satisfy their energetic needs ranging over smaller areas, leading to a higher density.

Two additional hypotheses can be formulated to explain this population's demography. Owl monkeys may have reached high densities due to the absence of potentially competing primate species. In this part of their range, owl monkeys are sympatric with only one other primate species (*Alouatta caraya*), whereas they can coexist with as many as 11 primate species in some tropical forests [Terborgh, 1983]. Finally, it remains to be examined whether the absence or presence of particular predators could explain the characteristics of the owl monkey population. Although it is a most interesting hypothesis, we are forced to postpone evaluation of this explanation until systematic data are collected on the composition of the local predator community and its foraging habits.

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