

Size, Site Fidelity, and Overlap of Home Ranges and Core Areas in the Socially Monogamous Owl Monkey (*Aotus azarae*) of Northern Argentina

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Abstract In addition to environmental factors, social variables such as group size may play an important role in explaining primate ranging patterns. In this study we investigated range sizes, site fidelity, and range overlaps of owl monkeys (*Aotus azarae*) in Northern Argentina. We calculated the size of home range and core areas for 18 groups in our study area. For the six most intensively studied groups we tested whether precipitation as a crude proxy for food availability or group size had an influence on range size, assessed the degree of site fidelity by quantifying overlaps of annual ranges and core areas, and calculated the amount of range overlap between neighboring groups for each year. We used the kernel density estimation method to calculate home ranges as 90% kernel and core areas as 50% kernel. Home range size (mean \pm SD) was 6.2 ha (\pm 1.8) and core area size 1.9 (\pm 0.6). Rainfall and group size were not statistically significant predictors of range sizes. Site fidelity was high, with a range overlap of 82% (\pm 11) between consecutive years. Neighboring groups overlapped over 48% (\pm 15) of the outer parts of their group ranges and 11% (\pm 15) of their core areas. We found no evidence that larger groups occupy larger areas than smaller groups, suggesting that food availability might be above a critical threshold for owl monkeys so that larger groups do not need to extend their foraging areas to meet their energy requirements. Our findings indicate that ranges remain stable over several years as groups visit the same locations of fruit trees within their range. We showed that owl monkeys exhibit a considerable degree of range overlap. However, we suggest that this range overlap might be spatial rather than temporal, which maximizes access to

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clumped feeding resources in overlapping areas that are used at distinct times, while excluding other males from access to females in exclusively used areas.

Keywords *Aotus azarae* · Core area · Home range · Kernel density estimation · Site fidelity · Social monogamy · Territoriality

Introduction

Space use is an important aspect of primate behavior that is often described using the concepts of home range and core area. The home range is defined as “that area traversed by the individual in its normal activities of food gathering, mating, and caring for young” (Burt 1943, p. 351), whereas the core area delineates areas more intensively visited within the overall home range (Boitani and Fuller 2000). Different factors influence space use among primates. Ranging is, for instance, directly linked to metabolic expenditure and body size (Clutton-Brock and Harvey 1981; Dobson *et al.* 2010; Lehman *et al.* 2007; Milton and May 1976). In addition, the availability of different resources has also been shown to influence individual spatial behavior. Although the location of water or sleeping sites may affect the use of space (Zhou *et al.* 2011), the diet and quality and distribution of food sources are usually considered the most important resources influencing patterns of ranging (Buzzard 2006). Generally, folivorous primates have smaller ranges as they exploit ubiquitous food resources, whereas frugivorous and insectivorous primates have comparatively larger ranges and longer daily travel distances to exploit unpredictable or patchily distributed resources (Clutton-Brock and Harvey 1977b). When preferred food sources become scarce, primates exhibit dietary responses by increasing the amount of fallback foods in their diet and by reducing their daily traveled distances (Brockman and van Schaik 2005; Fernandez-Duque *et al.* 2013; Zhang 1995), which is subsequently reflected in changes in range size.

In many primate species, home range size is also related to group size, in line with the prediction that groups will expand their range when the number of individuals in a group increases if scramble competition is present (Clutton-Brock and Harvey 1981; Isbell *et al.* 1998; Watts 1998). Thus, larger groups have been observed to expand their ranges when food is limited, to compensate for increasing competition with other group members (Clutton-Brock and Harvey 1977a; Dias and Strier 2003; Teichroeb and Sicotte 2009). This has, for example, been documented in vervets (*Cercopithecus aethiops*: Isbell *et al.* 1998), mountain gorillas (*Gorilla gorilla beringei*: Watts 1998), chimpanzees (*Pan troglodytes*: Herbinger *et al.* 2001), black-and-gold howlers (*Alouatta caraya*: Agostini *et al.* 2010), and tufted capuchins (*Cebus apella nigratus*: Di Bitetti 2001). However, in some primate taxa there seems to be no relationship, such as in the blue-eyed black lemur (*Eulemur flavifrons*: Sylviane *et al.* 2011) and Thomas’s langur (*Presbytis thomasi*: Steenbeek and van Schaik 2001).

Other factors that affect range use in group-living primates are the needs to defend mating partners, offspring, or food resources from neighboring groups (Fashing 2001; Garber *et al.* 1993; Lazaro-Perea 2001). Territorial behavior is expected to evolve when resources are both limited and defendable (Mitani and Rodman 1979). Defendability depends on the size of the overall range, the length of its boundary, detection distance,

and the ability of individual groups or subgroups to patrol the borders of a territory (Lowen and Dunbar 1994). Territorial behaviors in primates, such as vocalizations (Cowlshaw 1992), boundary controls (Mitani and Watts 2005), and aggressive encounters with neighboring groups (Wilson *et al.* 2001), are well documented, yet few studies have analyzed the spatial components of territoriality (Markham *et al.* 2012; Williams *et al.* 2002). Despite intergroup competition due to limiting factors, numerous species, including some territorial ones, show overlapping zones between the home ranges of neighboring groups (Biebouw 2009; Sylviane *et al.* 2011). These overlapping zones are generally underused (Wrangham *et al.* 2007).

Most of the analyses mentioned above have focused on relatively short periods of a few seasons or years. Few studies of primate ranging behavior cover temporal scales that allow the detection of long-term characteristics of ranging behavior, such as range shifts or site fidelity. Those that have include for instance, long-term studies of a population of ring-tailed lemurs (*Lemur catta*), which found that troops remained site-faithful during three decades (Jolly and Pride 1999; Mertl-Millhollen 2000). Another study, which documented high site fidelity of gray-cheeked mangabeys (*Lophocebus albigena*) during a decade, found that range shifts were linked to dispersal of individuals or group fission (Janmaat *et al.* 2009). Possible reasons for site fidelity are the benefits derived from knowing the location of important resources such as sleeping sites, feeding trees, or efficient travel routes. Consequently, movement into unknown areas may be associated with increased costs, as, e.g., in vervets (*Cercopithecus aethiops*: Isbell *et al.* 1990). Moreover, most studies of home ranges in primates have not taken into account differential space use or have not quantified the size of overlapping zones. Those that have mainly focused on examining the conditions under which overlapping ranges may be more likely, costly, or adaptive (Mitani and Rodman 1979; Nievergelt *et al.* 1998; Wrangham *et al.* 2007), rather than empirically analyzing the use patterns of these shared space in comparison with more exclusively used areas (Benadi *et al.* 2008; Wartmann *et al.* 2010). To investigate the degree of range overlap is especially relevant for understanding the evolution of primate social systems (Lukas and Clutton-Brock 2013). The mate-guarding hypothesis for the evolution of social monogamy in mammals predicts that when females occupy small, discrete ranges, males are unable to defend several females from other mating partners, and may form a pair with one female whom they guard from other male competitors (Komers and Brotherton 1997). Under this hypothesis, it is proposed that nonoverlapping territories may be a prerequisite for social monogamy to evolve.

In this study we chose a socially monogamous primate, the Azara's owl monkey (*Aotus azarae azarae*) of the Argentinean Chaco, to describe long-term home range sizes and to study social factors influencing ranging behavior. Owl monkeys (*Aotus* spp.) are distributed over a wide geographic area that extends from Panamá to the South American Chaco (Fernandez-Duque 2011a). These small arboreal primates live in groups that generally consist of an adult reproductive pair, one infant, and one or two juveniles and subadults (Fernandez-Duque 2011a; Wright 1994). Owl monkeys are socially monogamous (Fernandez-Duque 2011b), with males showing intense care of infants (Fernandez-Duque *et al.* 2009; Huck and Fernandez-Duque 2013). Natal dispersal of both males and females usually occurs when individuals are *ca.* 3 yr old (Fernandez-Duque *et al.* 2009). Like other owl monkey species, Azara's owl monkeys are primarily frugivorous (Fernandez-Duque 2011b). Unlike all other owl monkey

species, which are strictly nocturnal, Azara's owl monkeys are cathemeral (Tattersall 2006), being active as much during the day as during the night (Erkert *et al.* 2012; Fernandez-Duque *et al.* 2010).

Across their continental distribution, all species have relatively small home ranges that vary between 4 and 10 ha (Fernandez-Duque 2011b). Owl monkeys, including *Aotus azarae*, have been observed to show forms of territorial behavior during inter-group encounters, varying from ritualized displays and vocalizations with no physical contact to chases and fights that may include violent physical contact between members of different groups (Wright 1978, *pers. obs. of the authors*). Despite these territorial behaviors, owl monkey groups have been sometimes observed to use the same areas, suggesting overlapping ranges. However, there has been some debate on the extent of overlap between neighboring ranges: whether they overlap extensively (Wright 1978) or only slightly (Fernandez-Duque 2011b).

We present here the results of a 10-yr study that examined the home ranges of 18 groups of owl monkeys in Formosa, Argentina. For six of the groups we also evaluated whether there was a relationship between annual range size, precipitation as a crude proxy for food availability and group size, how much the outer range portion of their ranges and the areas of more intense use within the range (core areas) changed across years, and which parts of these ranges overlapped with neighboring groups. For our study we made the following predictions: First, we expected to find a difference in ranging between relatively large groups (five or six individuals) and smaller ones that may be a response to scramble competition, and we expected annual range sizes to remain stable as long as group size remains unchanged. We tested these predictions by assessing the relationship between group sizes and ranging patterns and evaluated whether larger groups overlapped with neighboring groups more than smaller ones. Second, we assumed that for primarily frugivorous primates, knowledge of the location of fruit trees and time of fruiting is essential to exploit patchily distributed resources. Because we had observed that groups frequently revisit feeding trees within their range, we thus predicted that ranges would remain relatively stable over several years. We tested this prediction by quantifying site fidelity as the degree of overlap between annual ranges. Finally, under the mate-guarding hypothesis (Komers and Brotherton 1997) we expect nonoverlapping territories that are actively defended. To test this prediction we quantified the degree of range overlap to evaluate whether owl monkey ranging patterns provide support for the mate-guarding hypothesis. We predicted that range overlap would be <21%, the reported mean for 26 socially monogamous primate species (Lukas and Clutton-Brock 2013). We expected groups with larger annual ranges and core areas to have higher overlapping areas, because of the constraints to defend larger ranges.

Methods

Study Area and Population

The study area is located in the cattle ranch Estancia Guaycolec (S 25.9735/W 58.1913), *ca.* 25 km north of the city of Formosa in Northern Argentina (Fig. 1).

The ranch includes a mosaic of grasslands and savannas, semideciduous gallery forest along the banks of the Pilagá river (Placci 1995), and isolated patches of forests immersed in the savanna matrix. The owl monkey groups inhabit both the gallery forest

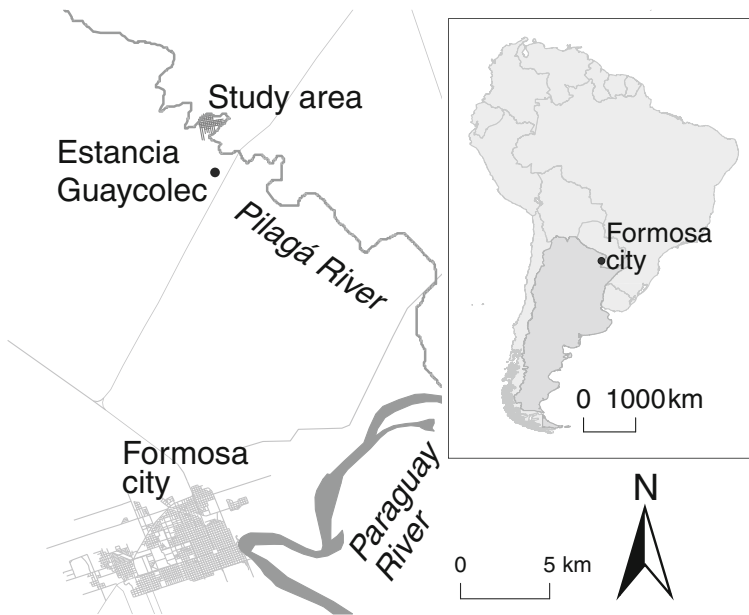


Fig. 1 Location of the study area in Estancia Guaycolec ranch in Formosa Province, Argentina.

and the isolated patches (Juárez *et al.* 2012). Within the gallery forest, a system of transects that runs east to west and north to south, spaced every 100 m, covers an area of *ca.* 300 ha. Transects are marked every 50 m with fluorescent plastic flagging and aluminum tags. We georeferenced these points with GPS to allow easy and reliable recording of location data of marked transect points. Placci (1995) and van der Heide *et al.* (2012) thoroughly characterized the structure, composition, and phenology of the gallery forest. The owl monkey groups inhabiting the 300-ha area are habituated to researchers, as Fernandez-Duque *et al.* (2001) have been monitoring them since 1997.

We considered 16 neighboring groups and 2 peripheral ones in the vicinity of the study area for the analyses of long-term home range and core area size. There are no other non-study groups in the area occupied by the 18 groups we studied. Six neighboring groups (C0, Cola Corta, D100, D500, E500, E350) that have been more intensively studied since 1997 contributed most of the spatial data for the analyses of annual ranging patterns. The number of groups in the area did not change during the study. More detailed analyses of demographic and life-history data for the study population can be found elsewhere (Fernandez-Duque 2009; Huck and Fernandez-Duque 2012; Huck *et al.* 2011; Juárez 2012).

Long-Term Home Ranges and Core Areas

We calculated long-term home ranges for all 18 groups using data from 1998–2008. We contacted groups in the population at least once a month. Given the cathemeral habits of the species (Fernandez-Duque *et al.* 2010), we contacted the groups during active periods that take place early in the morning (05:00–09:30 h) and late in the afternoon (16:00–21:30 h). When we contacted a group, we observed it for a minimum of 15 min and collected data on group composition. A more detailed description of demographic

data collection is presented elsewhere (Fernandez-Duque 2009). We also recorded the group's location in relation to the georeferenced transect system. Later, we estimated the latitude/longitude coordinates for the recorded location with a spreadsheet formula using the distance, angle, and the GPS position from the tagged and georeferenced transect point. We tested this method of ranging data collection by comparing locations for points collected with compass and with a GPS device (Garmin Oregon™ 200, Garmin International Inc., Olathe, KS) and found that the method using georeferenced transect points provided an accuracy of *ca.* 10 m per location, which is acceptable for the questions being explored in our study.

For long-term home range calculations, 8177 locations were available from the 18 studied groups (Table I). The number of locations varied among years, months, and groups. We obtained a mean (\pm SD) of 145 (\pm 24) locations per year. The least sampled year was 1998 at the beginning of the study period (167 locations), and the most sampled one was 2008 (1596 locations). We obtained a mean of 42 (\pm 26) locations per group per year.

Throughout the study period, April was the least (467 locations) and October the most sampled month (925 locations), and we obtained a mean of 38 (\pm 7) locations per group per month. A500 was the least sampled group and D500 the most. To reduce the

Table I Yearly sample sizes of recorded locations for 18 focal groups of owl monkeys (*Aotus azarae*) in Estancia Guaycolec ranch, Formosa Province, Argentina, 1998–2008

Group	Year											Total per group
	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	
A500	0	0	0	0	6	4	4	2	4	10	24	54
A900	0	1	10	6	6	10	37	16	2	4	6	98
B69	16	64	52	46	82	66	39	18	10	16	10	419
C0	39	84	45	58	84	79	102	85	16	42	157	791
CC	27	89	56	47	154	89	117	59	11	44	166	859
Colman	0	0	0	17	146	88	109	59	10	18	98	545
D100	23	71	46	83	34	78	83	85	22	48	179	752
D1200	5	19	19	50	102	46	62	10	6	7	12	338
D500	29	61	60	149	180	104	95	67	31	31	171	978
D800	1	46	70	40	26	28	110	35	12	16	84	468
E350	0	0	0	0	0	103	95	116	39	46	218	617
E500	22	41	44	87	155	51	70	53	16	42	237	818
F700	0	0	5	1	62	57	49	22	12	8	50	266
F1200	5	18	26	15	63	96	80	61	12	16	86	478
G1300	0	0	0	0	42	74	67	59	18	4	26	290
IJ500	0	13	7	5	9	50	26	4	2	6	21	143
L100	0	0	0	0	2	12	18	35	16	6	37	126
Veronica	0	0	0	0	2	48	19	42	4	8	14	137
Total per year	167	507	440	604	1155	1083	1182	828	243	372	1596	8177

potential influence of different sampling intensities across groups and time, and to reduce the amount of autocorrelation present in data sets with high sample sizes (Swihart and Slade 1985), we chose a random subset of 800 locations for groups with >800 locations as an optimal balance between reducing amounts of autocorrelation while retaining as much biologically meaningful information as possible. For subsampling we used Hawth's analysis tools (Beyer 2004) in ArcGIS 9.1 (ESRI Inc., Redlands, CA). In total we retained 7400 locations for analysis.

To estimate the size of the home ranges, we used the kernel density estimation (Worton 1989), currently the prevalent method in wildlife biology to calculate home ranges (Laver and Kelly 2008). The kernel density estimation (KDE) provides a probabilistic measure of how animals use space and allowed us to distinguish between areas of different intensities of use (Home and Garton 2006), which, e.g., is not possible with the minimum convex polygon method (Wartmann *et al.* 2010). We used the fixed kernel density estimation method as implemented in the home range tools extension HRT (Rodgers *et al.* 2007) in ArcGIS with a raster resolution size of 150 m. This raster resolution provided adequate results given the size of the home ranges we were calculating, without being too computationally intensive. One of the limitations of the kernel method is that it is sensitive to the choice of the smoothing parameter, or bandwidth (Gitzen *et al.* 2006). Various methods are available to select the smoothing parameter objectively (Kernohan *et al.* 2001). We used biased-cross validation for smoothing parameter selection because, compared to other smoothing parameter selection methods, such as least-squares cross validation, it is stable at large sample sizes (Hemson *et al.* 2005; Wartmann *et al.* 2010). The mean (\pm SD) of all smoothing parameters calculated for home range estimates was 0.38 (\pm 0.06, $N = 18$). We report home ranges based on 90% volume contours of kernel probability density surface, as the 95% curve is less accurate (Börger *et al.* 2006). As most home range studies employing KDE calculated core areas based on 50% volume contours (Laver and Kelly 2008), including primate ranging studies (Williams *et al.* 2002), we employed the same measurement. To assess the accuracy of the fixed kernel density estimation, we visually compared the spatial distribution of the original locations with the home range as estimated by the model. All kernel estimates fitted the distribution of the original locations well, except for one group (Colman). This group lives in an isolated, narrow island of forest surrounded by grassland outside the main area of study. Because of the relatively narrow and linear shape of this island of forest, the estimation established the home range boundary outside the area where the group actually ranges. Thus, for this group, we manually adapted the smoothing parameter to $h = 0.1$ to produce a more conservative home range estimate. All results are presented as means with standard deviation (\pm SD).

Variation in Annual Ranges, Core Areas, and Group Size

To analyze ranging patterns at smaller temporal scales of years, we calculated annual ranges and core areas for the six intensively studied groups. We used the same kernel density estimation method to calculate annual ranges as described for the long-term home ranges in the preceding text. The number of recorded locations varied among groups and years. Thus, for the calculation of each annual range, we chose a random

subset of 100 locations if the total number exceeded 100 locations. When we had less than 35 locations available for a certain group and year, we did not estimate a range for that year. To ensure that the number of locations did not have an influence on range estimates, we used Spearman's correlation in PASW 18 (SPSS Inc., IBM Corporation, New York, NY) to evaluate the relationship between the total number of locations used to calculate a range and the resulting range size for both annual ranges and core areas. The relationship was weak and not statistically significant for annual ranges (Spearman's $\rho = 0.091$, $P = 0.512$, $N = 54$) or for core areas (Spearman's $\rho = 0.126$, $P = 0.363$, $N = 54$). The mean (\pm SD) of smoothing parameters used to estimate annual ranges and core areas was $0.47 (\pm 0.04)$, $N = 54$ smoothing parameters). We used one-way ANOVA to test whether there were statistically significant differences among groups in annual ranges, core areas, and group size. We tested the relationship between annual range and core area sizes and changes in group size with Spearman's correlation tests using data on group size for January–February of each year. We chose group size in January–February because it is a time when demographic events that change group size are less likely; births are concentrated in October–December (Fernandez-Duque 2002), dispersals in August–December (Fernandez-Duque 2009) and replacements of adults in April–June (Huck and Fernandez-Duque 2012). We used general linear mixed models to determine if the dependent variables “annual range” and “core area” were related to rainfall and group size (fixed effects), including group identity as a random factor.

Site Fidelity

To assess the degree of site fidelity, we analyzed the extent of areas that owl monkeys used repeatedly over time. We tested for site fidelity for annual ranges, as well as for core areas, by calculating the intersection of kernel contours for consecutive years in ArcGIS. To test for possible long-term range shifts, we calculated the amount of range overlap between the annual range in 1999 for each group with the annual range of the same group in 2008, e.g., overlap of range in 1999 with range in 2008 for the group Cola Corta, and repeated this calculation for core areas.

Overlaps of Annual Ranges and Core Areas Between Neighboring Groups

To quantify the degree of range overlap between owl monkey groups we calculated the extent of each group annual range that overlapped with the ranges of neighboring focal groups. We calculated range overlap only between focal groups, and not between focal and nonfocal groups, although there is also some additional overlap with those. Using both annual ranges as outer range boundaries, as well as delineations of core areas, we were able to also consider internal space use patterns. We calculated overlaps for the annual range and for the core area as the size of the polygons formed by the intersection of the respective kernel contours in ArcGIS. The sample sizes reported correspond to the number of pairs of years that were compared. We tested whether larger groups overlapped more with neighboring groups more than smaller ones by assessing whether there was a relationship between the size of annual ranges and core areas and the size of overlapping areas using Spearman's correlation.

Results

Long-Term Home Ranges and Core Areas

The mean home range size was 6.2 ha (± 1.8 ha, $N = 18$) between 1998 and 2008. The largest home range was three times as large as the smallest one (Veronica: 10.9 ha vs. D500: 3.6 ha; Fig. 2, Table II). The mean core area size was 1.9 ha (± 0.6 , $N = 18$) and the range was relatively smaller (1.0–2.6 ha; Table II).

Variation in Annual Ranges, Core Areas, and Group Size

The mean annual range was 6.0 ha (± 2.2 ha, $N = 6$ groups) and groups differed markedly in the size of their annual ranges (one-way ANOVA: $df = 5$, $F = 18.8$, $P < 0.001$; Table III, Fig. 3). For example, D500 with a mean annual range size of 3.8 ha (± 0.4 ha, $N = 10$ yr) consistently occupied less than half the range of D100 (8.4 ha ± 1.9 , $N = 8$) or Cola Corta (8.2 ha ± 1.6 , $N = 9$). The mean core area was 1.9 ha (± 0.7 , $N = 6$ groups), and groups also differed markedly in the size of those (one-way ANOVA: $F = 17.74$, $df = 5$, $P < 0.001$).

There was no significant within-group variation in the size of the annual ranges across years (Table III, one-way ANOVA: $F = 0.738$, $df = 10$, $P = 0.685$).

Mean group size was 3.6 individuals (± 1.0 , $N = 6$ groups; Table IV). Differences in size among groups were pronounced and statistically significant (Table IV; one-way ANOVA: $F = 2.8$, $df = 5$, $P = 0.026$). Cola Corta was consistently the largest group (4.2 ± 0.8 , $N = 10$ yr), whereas D100 was the smallest one (2.9 ± 0.6 , $N = 10$).

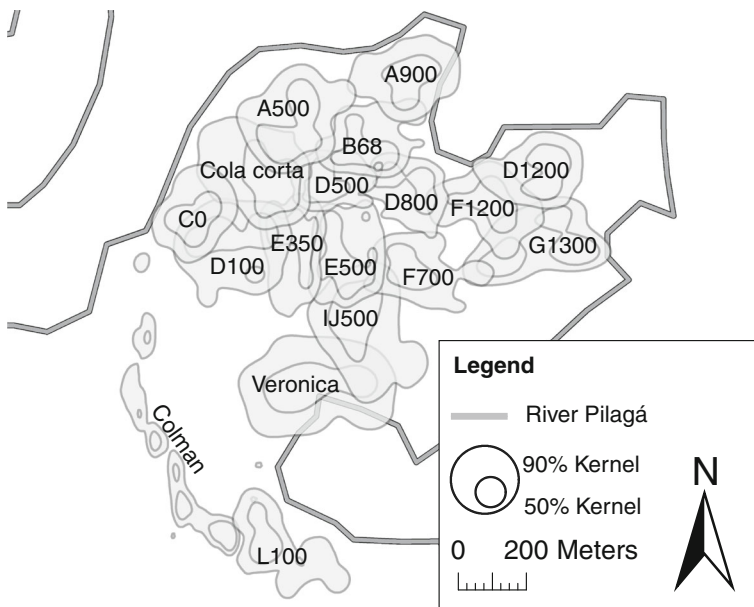


Fig. 2 Owl monkey home ranges and core areas of the 18 focal groups in Estancia Guaycolec ranch in Formosa Province, Argentina, 1998–2008.

Table II Home ranges and core areas of 18 focal groups of owl monkeys (*Aotus azarae*) in Estancia Guaycolec ranch, Formosa Province, Argentina, 1998–2008

Group	Home range (ha)	Core area (ha)
A500	7.2	2.6
A900	5.8	1.7
B68	5.2	1.6
C0	5.1	1.6
Cola corta	8.2	2.6
Colman	4.4	1.0
D100	8.0	2.5
D1200	5.1	1.6
D500	3.6	1.2
D800	4.3	1.3
E350	5.3	1.8
E500	5.8	2.3
F700	5.2	1.4
F1200	5.7	1.7
G1300	7.3	2.7
IJ500	9.1	2.6
L100	5.4	1.2
Veronica	10.9	3.2
Mean	6.2	1.9
SD	1.9	0.7

Neither annual range nor core area size was significantly related to group size (Table V).

Table III Annual ranges (ha) for six focal groups of *Aotus azarae* in Estancia Guaycolec ranch, Formosa Province, Argentina, 1998–2008

Year	C0	Cola Corta	D100	D500	E350	E500	Mean annual range (ha)	SD
1998	3.5	—	—	—	—	—	3.5	0.0
1999	5.0	7.3	8.0	3.5	7.7	7.4	6.5	1.8
2000	3.1	6.7	8.1	3.3	5.2	8.3	5.8	2.3
2001	3.3	12.1	12.2	4.0	—	6.5	7.6	4.3
2002	7.2	7.6	—	4.3	—	5.2	6.1	1.6
2003	5.7	7.1	8.4	3.8	4.5	4.9	5.7	1.7
2004	5.5	8.1	9.9	4.5	5.5	6.6	6.7	2.0
2005	4.0	7.9	7.3	4.2	6.3	5.6	5.9	1.6
2006	—	—	—	3.4	4.7	—	4.1	0.9
2007	3.1	8.5	6.7	3.6	3.5	5.4	5.1	2.1
2008	4.2	8.9	6.6	3.6	5.7	6.0	5.8	1.9
Mean	4.5	8.2	8.4	3.8	5.4	6.2	6.0	
SD	1.4	1.6	1.9	0.4	1.3	1.1	2.2	

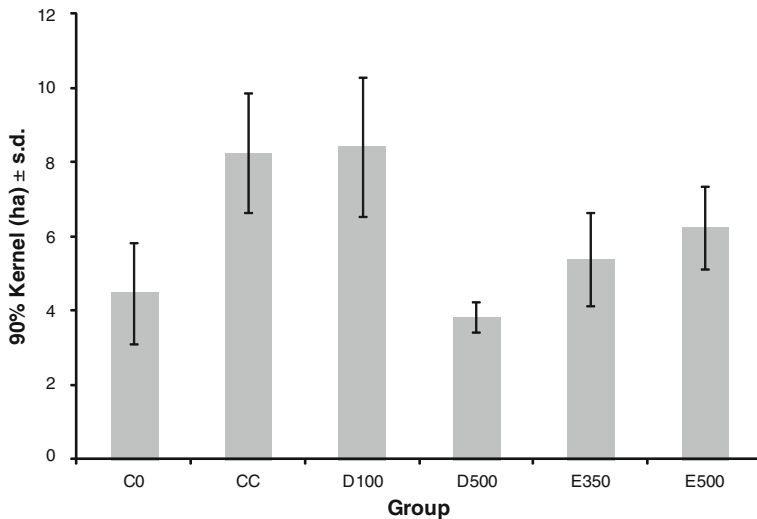


Fig. 3 Owl monkey group annual ranges, core areas, and overlaps for the six focal groups in Estancia Guaycolec ranch in Formosa Province, Argentina. Data for 2004 are displayed as an example.

Neither rainfall nor group size was a strong predictor of the annual range (rainfall, $F = 3.291$, $P = 0.192$; group size, $F = 1.2$, $P = 0.272$) or the core area (rainfall, $F = 0.279$, $P = 0.606$, group size, $F = 0.509$, $P = 0.480$). However, the variable “group” was highly predictive of the annual range ($F = 18.68$, $P < 0.001$) and core area ($F = 4.777$, $P < 0.001$), suggesting that most of the observed variation in range sizes was explained by variation among individual owl monkey groups.

Site Fidelity

Site fidelity in owl monkeys was high; ranges remained fairly stable during almost a decade. We found a mean overlap between outer range boundaries of successive years of 82% (± 11 , $N = 6$ groups; Table VI). The highest mean overlap was 86% and the lowest 78% (Table VI). The highest annual range overlap between two successive years was 98% and the lowest 54%. For core areas, the average overlap between successive

Table IV Group size of six focal groups of owl monkeys (*Aotus azarae*) in Estancia Guaycolec ranch in Formosa Province, Argentina in January of each year, 1998–2008

Group	Year											Mean	SD
	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008		
C0	5	4	5	4	4	2	3	2	2	2	2	3.2	1.3
Cola Corta	—	5	5	4	5	3	3	4	4	4	5	4.2	0.8
D100	—	3	4	3	2	3	2	3	3	3	3	2.9	0.6
D500	—	3	3	4	4	5	6	3	3	4	4	3.9	1.0
E350	—	3	3	3	—	2	3	4	4	4	4	3.3	0.7
E500	—	—	5	5	3	2	3	4	5	5	3	3.9	1.2

Table V Spearman's ρ for the correlation of group size and annual range/core area for six focal groups of owl monkeys (*Aotus azarae*) in Estancia Guaycolec ranch, Formosa Province, Argentina, 1998–2008

Group	Annual range			Core area		
	ρ	P	N	ρ	P	N
C0	-0.25	0.478	10	-0.25	0.490	10
CC	-0.16	0.680	9	-0.61	0.084	9
D100	-0.22	0.604	8	-0.44	0.280	8
D500	0.63	0.049	10	0.39	0.259	10
E350	0.39	0.927	8	-0.20	0.642	8
E500	0.50	0.206	8	0.45	0.263	8

years was 65% (± 15 , $N = 6$ groups, Table VI). The highest mean overlap was 71% and lowest 60% (Table VI). The highest core area overlap between two successive years was 100% and the lowest 34%.

Mean overlap was 77% (± 19 , $N = 6$) between the annual ranges in 1999 and those occupied in 2008. The highest annual range overlap was 99% and the lowest was 62%. The mean overlap of core areas was 47% (± 25 , $N = 6$); the highest was 84% and the lowest 16%.

Overlaps Between Annual Ranges and Core Areas of Neighboring Groups

Groups overlapped considerably in the outer parts of their ranges (Fig. 4). On average, almost half of a focal group's annual range overlapped with neighboring focal groups ($48\% \pm 15$). There was also variation among groups in the range of overlap. The groups that shared, on average, the smallest parts of their range were Cola Corta ($41\% \pm 25$, $N = 8$ yr) and D100 ($43\% \pm 5$, $N = 8$), whereas the largest mean overlaps were observed for C0 ($54\% \pm 15$, $N = 8$) and E350 ($56\% \pm 6$, $N = 5$).

Groups with larger annual ranges overlapped more with neighboring groups than groups with smaller ranges (Spearman's $\rho = 0.63$, $P < 0.001$, $N = 34$). However, we found no evidence that larger groups overlapped more with other groups than smaller ones ($\rho = 0.13$, $P = 0.475$, $N = 34$).

Table VI Mean and standard deviation of core area and annual range overlap (%) for six focal groups of owl monkeys (*Aotus azarae*) in Estancia Guaycolec ranch, Formosa Province, Argentina, 1998–2008

Group	N	Mean core area	SD	Mean annual range	SD
C0	7	62	11	78	15
Cola Corta	7	71	20	84	14
D100	5	72	8	86	8
D500	6	60	14	85	5
E350	3	62	14	85	17
E500	6	64	21	78	7
Total	34	65	15	82	11

N = number of comparisons between successive annual ranges.

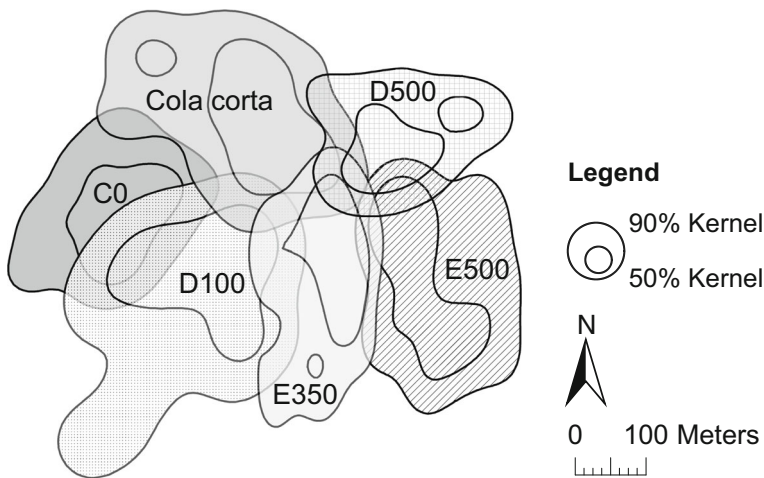


Fig. 4 Owl monkey mean annual ranges for the six focal groups in Estancia Guaycolec ranch in Formosa Province, Argentina, 1998–2008.

The extent of overlap of the core areas was much smaller ($11\% \pm 15$), but the variation among groups was still pronounced. For example, there was almost exclusive use of the core area by Cola Corta ($1\% \pm 1$, $N = 8$ yr) and E500 ($2\% \pm 4$, $N = 5$), whereas C0 and D100 overlapped on average almost a fifth of their core areas with other groups (C0: $17\% \pm 12$, D100: $18\% \pm 23$). We did not find that groups with larger core areas had larger parts of their core areas overlap with neighbors ($\rho = -0.1$, $P = 0.574$, $N = 34$). There was also no relationship between the amount of overlap and group size ($\rho = 0.01$, $P = 0.942$, $N = 34$).

Discussion

Inter- and Intraspecific Variation in Owl Monkey Home Ranges

Our study provides some new findings on space use by Azara's owl monkeys of the Argentinean Chaco. Focusing on a large number of identified groups intensively sampled during a decade, our data show that owl monkey groups occupy home ranges that average 6 ha and include a core area that is *ca.* 2 ha. These estimates of home range size are in good agreement with previous estimates of 4–12 ha for the same population (Fernandez-Duque 2011b), for two other populations inhabiting isolated patches of forest in the region (Juárez 2012) and for a different subspecies (*Aotus azarae boliviensis*, 10 ha, $N = 1$ group; García and Braza 1987). Estimates of home range size for other tropical owl monkey species have also reported sizes within this range: Groups of *Aotus nigriceps* occupy 4–17 ha in Manú NP, Peru ($N = 3$ groups, Wright 1994), and *A. vociferans* of 6 ha in Yasuní, Ecuador ($N = 1$; Fernandez-Duque *et al.* 2008a). That all owl monkey species, strictly nocturnal or cathemeral, tropical or subtropical, in continuous or fragmented landscapes, seem to occupy ranges of similar size suggests influences that exceed the merely ecological ones.

Comparing different populations, subspecies and species is a powerful approach to identify ecological factors influencing patterns of use of space. In fact, much of comparative primate socioecology has been developed by comparing data from different species in various habitats to investigate the influence of those habitats on the behavioral ecology of the species under consideration. However, comparative studies are complicated by differences in sampling strategy, sample sizes, and home range models. Most studies quantifying home ranges in *Aotus* spp. have used minimum convex polygon (MCP) methods on a relatively small number of groups sampled during time intervals of several months or few years. MCP methods have the undesirable tendency to underestimate ranges at low sample sizes and to overestimate them at higher sample sizes (Burgman and Fox 2003; Wartmann *et al.* 2010), whereas kernel estimates are much less susceptible to sample size (Kernohan *et al.* 2001; Wartmann *et al.* 2010). To be able to conduct comparative studies in the future, researchers should use standardized methods to estimate ranges and report the model and methods used carefully (Laver and Kelly 2008; Sterling *et al.* 2000). Our results illustrate an impressive range of variation; some home ranges were three times as large as others. This intrapopulation variation exceeds the reported interspecies variation.

Variation in Annual Ranges, Core Areas, and Group Size

We found no significant intragroup variation in mean annual range size. This may explain why we found no intragroup relationship between range size and environmental or social factors such as rainfall or group size. However, it seems likely that food availability might influence owl monkey ranging on smaller temporal and spatial scales than we assessed in this study. For example, future studies should investigate whether ranging patterns vary between the dry and wet seasons.

We found significant intergroup variation in the size of ranges used. Variability in the size of core areas between groups was lower but still pronounced. We predicted that variation in group size would be related to differences in range sizes, with larger groups ranging over bigger areas than smaller ones. However, our data do not support this prediction, as the number of individuals in owl monkey groups was not significantly associated with the size of the annual range or core area. An earlier study (Fernandez-Duque *et al.* 2013) suggested that food availability in core areas is above a critical threshold necessary for owl monkeys; thus larger groups may not need to expand their core area to meet their energy requirements. In other words, it is possible that the outer part of the range may be more important for social behavior than for foraging. In chimpanzees (*Pan troglodytes*), for instance, the size of home ranges reflects the abundance of resources; areas with low abundance and high dispersal of food resources result in larger ranges (Dunbar 1988; Herbinger *et al.* 2001) and those with local high abundance of food resources produce smaller ones (Newton-Fisher 2003).

Due to the varying proportions of floodable, lowland, and transitional forest in the owl monkey study area, habitats differ in the quality and abundance of food resources they offer to the various groups (van der Heide *et al.* 2012). Thus, one would expect to find higher local food abundance in owl monkey groups with smaller ranges. However, despite pronounced differences in the distribution of important tree species and food availability across four owl monkey ranges, there was no evidence that groups with smaller ranges had more food available in their overall range (van der Heide *et al.*

2012). The differences in food availability between the ranges of different groups were more pronounced within outer range boundaries. The core areas were more similar to each other, with important food species such as *Ficus* spp. being similarly abundant (van der Heide *et al.* 2012). The core areas were also comparatively more productive than the overall ranges, and predictably produced food even during the dry seasons when overall food availability in the area markedly decreased (van der Heide *et al.* 2012). During these dry seasons, core areas were similar in fruit production for the different groups, and comparatively more productive than the overall group ranges (Fernandez-Duque *et al.* 2013). The core areas had the smallest differences in food availability among territories, which suggests that it is the quality of those that is the critical factor for owl monkey feeding and foraging. Our findings support this argument, as we found the core areas to be used almost exclusively, whereas the overall ranges overlapped considerably between neighboring groups.

Further, we found that core areas are only one third the size of the annual range, which means that owl monkeys spent on average half of their time in less than half of their range. Such intensive use of only a small part of the overall range is common in primates. Chimpanzees (*Pan troglodytes*) spent 75% of the time in 35% of their range (Boesch and Boesch-Ackermann 2000) and brown howlers (*Alouatta guariba*) spent 50% of their time in only 10% of their range (Agostini *et al.* 2010). Even though the notion of a “core area” has been questioned (Barg *et al.* 2005; Wray *et al.* 1992), our results show that, at least for owl monkeys, they exist as a biologically relevant space.

Site Fidelity

Owl monkeys made stable use of their ranges from one year to the next, and for almost a decade. Generally, in any given year, groups occupied as much as 80% of the overall range they had occupied the previous year. This finding provides some support for the prediction that owl monkey ranges remain stable over several years, as groups keep visiting the same locations of fruit trees within their range. However, our method to determine site fidelity did not include the direction of range shifts (Janmaat *et al.* 2009) or the number of years in which certain areas were used (Ramos-Fernandez *et al.* 2013), which we propose as methods for future and more detailed analyses. The high site fidelity observed for owl monkeys also fits well with overall abundance of food species reported for the area (van der Heide *et al.* 2012), rendering range switches unnecessary in the absence of pronounced social or ecological pressures. These results contribute to a small set of studies on site fidelity by primates conducted over periods of many years. Ring-tailed lemurs (*Lemur catta*) were found to occupy similar ranges even across generations (Jolly and Pride 1999; Mertil-Millhollen 2000), and gray-cheeked mangabeys (*Lophocebus albigena*), which, like owl monkeys, are highly frugivorous, also showed pronounced site fidelity with an overlap of >60% over 10 yr (Janmaat *et al.* 2009).

Naturally, site fidelity largely depends on the time scale at which it is analyzed. Even species considered site-faithful at relatively long temporal scales may exhibit seasonal movement patterns within their overall home range (Janmaat *et al.* 2009). Frugivorous primates often adapt their ranging behavior to local fruiting patterns; Sumatran orang-utans, for example, follow peaks in fruit production along altitudinal bands within their overall range (Buij *et al.* 2002). To analyze seasonal movement patterns in frugivorous

owl monkeys, movement analyses at finer temporal granularities, such as during dry or wet seasons, will be needed in the future; ideally those studies should be performed together with accurate estimates of actual food availability in these seasonal ranges (Fernandez-Duque *et al.* 2013).

Range Overlaps, Monogamy, and Mate Guarding

Following the mate-guarding hypothesis (Komers and Brotherton 1997), we predicted that for socially monogamous owl monkeys, groups would occupy nonoverlapping territories. Our results do not provide direct support for the hypothesis because we found that on average half of their outer range overlapped with neighboring groups. Comparing range overlaps for owl monkeys with other monogamous species, we observed higher average overlap in our study (48%) than the 21% reported mean overlap for 26 socially monogamous primates (Lukas and Clutton-Brock 2013). In contrast to spatial overlap in the outer range parts, owl monkey groups occupied almost exclusive core areas that only overlapped minimally (10%) with other groups. In contrast with the high overlap areas towards the outer range, the existence of such exclusively used spaces provides support for the mate-guarding hypothesis. The high overlap of annual ranges and low overlap in core areas indicates that owl monkey groups use the inner parts of the home range more exclusively, while overlap occurs in the outer areas of the range. In those outer areas resident owl monkeys may thus have potential access to more than one mating partner. Such potential access to mating partners also exists for other socially monogamous and pair-living species (Dobson *et al.* 2010; Fietz *et al.* 2000; Palombit 1994). However, no extra-pair matings have been documented in owl monkeys (Babb *et al.* 2011; Fernandez-Duque *et al.* 2008b).

The high overlaps in less used areas is in accordance with the findings that overlap zones in primate ranges tend to be underused (Wrangham *et al.* 2007). The core areas are thus where groups maintain almost exclusive access to resources such as food, sleeping sites, and mates by excluding competition from other groups. In other words, it seems that for owl monkeys one can think of the core area as a territory. Ongoing examinations of the spatial distribution of territorial behavior, feeding, and sleeping trees will allow us to test the potential function of the core area (Corley *et al.* 2014; Savagian *et al.* 2014).

In the future it will be important to extend our analyses to consider in more depth the temporal dimension of range use. Our analyses were almost exclusively on spatial overlap, but much will be gained from detailed examinations of temporal overlap. We have observed that different groups visit the same feeding trees that are located in overlapping areas. However, they mostly visited during them during different times, although we documented few instances when groups coincided in the same observation. These observations suggest that the overlap of these group ranges is mostly spatial, and not temporal. Owl monkey groups may attempt to maximize access to clumped high-quality feeding resources such as fig trees, while minimizing the possibility of inter-group encounters that could lead to competition with same-sex individuals.

It is also possible that overlapping areas are important for dispersing individuals. When individuals move into new areas, they lack knowledge of important resources such as location of food and shelter. Dispersing red howlers (*Alouatta seniculus*), for instance, had a poorer diet than resident ones (Pope 1989 in Isbell and van Vuren 1996). In this context, overlapping areas between group ranges may provide dispersing

individuals with the possibility to explore new social opportunities while, at least for some time, staying in a familiar area. In owl monkeys, all individuals of both sexes disperse, when they are *ca.* 3 yr of age. The cost of dispersal is apparently high, given that it is the life stage when most animals die or disappear (Fernandez-Duque 2009). During dispersal some individuals were observed to linger in areas close to range boundaries (Fernandez-Duque 2009), which would indicate a gradual dispersal process away from the natal range. However, more detailed analyses are needed of movement paths of dispersing individuals with respect to group ranges to make inferences about the spatial aspects of the dispersal process in owl monkeys.

In conclusion, we have shown that owl monkey occupy home ranges of 6 ha and core areas of 2 ha. The variability was high both within and between groups, but neither rainfall as an environmental variable nor group size as a social variable was a statistically significant predictor of this variation. Because we found no evidence that larger groups occupy larger areas than smaller groups, this indicates that food availability might be above a critical threshold for owl monkeys so that larger groups do not need to extend their foraging areas to meet their energy requirements. These results notwithstanding, we speculate that environmental and social factors might still have an influence, but that this influence occurs at temporal and spatial scales that we were unable to detect with our methods. Future studies could analyze these effects on ranging during smaller time periods, for instance, during wet and dry seasons. We found that owl monkeys occupy ranges that stay stable over several years, which supports the prediction that in the absence of severe social or ecological pressure, owl monkey groups keep visiting the same locations of fruit trees within their range. We found considerable overlap between neighboring groups and showed that this overlap occurs in the outer, less frequently used parts of their ranges. However, the overlap is more spatial than temporal, which maximizes access to clumped feeding resources in overlapping areas that are used at distinct times, while excluding other males from access to females in exclusively used areas.

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