



## The floater's dilemma: use of space by wild solitary Azara's owl monkeys, *Aotus azarae*, in relation to group ranges



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### ARTICLE INFO

#### Article history:

Received 11 November 2016

Initial acceptance 11 January 2017

Final acceptance 9 February 2017

MS. number: 16-00986

#### Keywords:

core area  
dispersal  
floater  
home range use  
intruder  
night monkey  
spatial avoidance  
temporal avoidance  
utilization distribution overlap index

The fate and behaviour of animals that leave their natal group ('floaters') is usually poorly understood, which can limit the understanding of a species' population dynamics. Attempted immigrations can have serious negative effects on residents who therefore may forcibly reject intruders. Consequently, floaters face a dilemma: they need to leave their natal range to find a breeding territory while trying to avoid potentially lethal rejections from established groups. To examine the hypothesis that floating Azara's owl monkeys avoid established groups temporally, we compared time-matched locations of floaters and groups with randomly selected distances. To examine the hypothesis that floaters avoid established groups spatially, we compared the utilization distribution overlap indices (UDOIs) for core areas of floaters and groups with randomly expected UDOIs. Based on average home range sizes and areas of overlap between floaters, we estimated the floater density in the study area to be 0.2–0.5 per group. The temporal avoidance hypothesis was not supported, since time-matched distances were smaller than distances of random locations, and not larger as predicted under this hypothesis. The spatial avoidance hypothesis, in contrast, was supported, with smaller UDOIs for core ranges than predicted. In conclusion, solitary owl monkeys seem to solve the floater's dilemma by trying to stay in relatively close proximity to groups while still avoiding their core ranges. Floaters thus maximize the number of groups with which they have contact, while being able to leave a group's territory quickly if detected by residents. While no marked sex differences in patterns were detected, there was a strong stochastic element to the number of floaters of a particular sex, thus resulting in a locally uneven operational sex ratio. This, in turn, can have important consequences for various aspects of the population dynamics.

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The social and ranging behaviour of group members has been well studied for many pair-living or group-living species (Laver & Kelly, 2008). However, understanding the fate and behaviour of subadults or recently matured individuals that leave their natal group continues to be a challenge, even when the topic has started to receive more attention lately (Fernandez-Duque & Huck, 2013; Penteriani & Delgado, 2012; Penteriani, Ferrer, & Delgado, 2011). Sexually mature, solitary, nonterritorial individuals that may become breeding residents if a suitable territory or mate becomes available are commonly called 'floaters' (Penteriani et al., 2011; Smith, 1978). Since floaters are likely to affect the local operational sex ratio (OSR; Fernandez-Duque & Huck, 2013; Penteriani

et al., 2011), which in turn can influence the evolution of mating and parental care strategies (Kokko & Jennions, 2008), the lack of knowledge about this part of a population may seriously hamper our understanding of a species' population dynamics or the evolution of certain traits such as male care.

From a group's perspective, attempted immigrations, or 'intrusions' by floaters, can have negative effects on residents by disrupting pregnancies (Bruce, 1960), lowering recruitment or proportion of juveniles (Lin, Hayes, & Solomon, 2004; Wolff & Schaubert, 1996), changing the sex ratio (Lin et al., 2004), increasing resource competition leading to the need for larger territories (Norton, Arcese, & Ewald, 1982), or even causing the death of residents (Fernandez-Duque & Huck, 2013; Newton, 1979, page 154). Likely due to the negative impact that floaters can have on residents, floaters are often rejected by established groups, which try to keep them off or expel them from their territories (e.g. Busch, Wingfield, & Moore, 2004). Floaters, therefore, often

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attempt to avoid detection in order to avoid attacks by residents. For example, among eagle owls, *Bubo bubo*, floaters use less visible perches than territory holders (Campioni, Delgado, & Penteriani, 2010). Apart from attacks by resident groups, floaters often face additional risks, possibly due to their solitary roaming and inexperience (Bonte et al., 2012; Bélichon, Clobert, & Massot, 1996). For instance, ruffed grouse, *Bonasa umbellus*, face a considerably higher predation risk when moving through unfamiliar areas (Yoder, Marschall, & Swanson, 2004) and juvenile American martens, *Martes americana*, have an increased mortality risk the further they disperse (Johnson, Fryxell, Thompson, & Baker, 2009). Thus, for many species, living in a group provides net benefits compared to staying solitary (Pulliam & Caraco, 1984). For example, mortality of dispersing male baboons (*Papio cynocephalus*) was three-fold to 10-fold higher than for group-living males (Alberts & Altmann, 1995). Remaining in the natal group, however, might not be a viable option, if this might increase the risk of inbreeding depression, as has been suggested, for example, for baboons (Alberts & Altmann, 1995). In long-lived pair-living species the risk of inbreeding would be much higher if offspring did not disperse. It follows that floaters face a dilemma: they need to leave their natal range to find possible breeding opportunities elsewhere, and to enjoy the safety of living in a group, but they also should try to avoid potentially violent rejections from established groups.

How commonly residents and floaters are in conflict depends on a multitude of factors including resource richness and distribution, habitat saturation and the number of floaters per resident (Enquist & Leimar, 1987; Kokko, López-Sepulcre, & Morrell, 2006; Port & Johnstone, 2013). The influence of these factors, in turn, will depend on various aspects of social organisation. For example, in long-lived pair-living species with permanent, contiguous or overlapping home ranges (i.e. with no unoccupied habitat patches), where potential tenure length is longer than average age at first breeding, offspring of both sexes must necessarily disperse at some point in order to avoid inbreeding, thus becoming floaters. These floaters will then often have to assess suitable territories, as well as the reproductive status and competitive abilities of residents, in order to minimize the costs of encountering potentially more competitive (for example stronger) territory owners (Doerr & Doerr, 2005). Subadult and young adult Azara's owl monkeys face exactly this dilemma.

Azara's owl monkeys inhabit the subtropical gallery forests of the Gran Chaco region in Northern Argentina, Paraguay and Bolivia (Fernandez-Duque, 2011). In a population in Argentina, owl monkeys are pair-living and genetically monogamous (Huck, Fernandez-Duque, Babb, & Schurr, 2014) and show possibly one of the highest levels of male care reported for any mammal (Huck & Fernandez-Duque, 2012; Rotundo, Fernandez-Duque, & Dixon, 2005). Pairs and their offspring live in defended home ranges of 4–10 ha that remain quite stable over time; groups spend as much as 50% of their time in a relatively smaller (1–2 ha) core area (Wartmann, Juárez, & Fernandez-Duque, 2014). Group home ranges are contiguous and overlapping, leaving no 'free' areas that could be available for floaters (Wartmann et al., 2014). Young owl monkeys leave their natal home range and become floaters when they are between 3 and 4 years old (Fernandez-Duque, 2009; Huck, Rotundo, & Fernandez-Duque, 2011). Floaters become residents by filling vacant breeding positions if a resident of the same sex has died, or they try to forcefully evict residents, which can lead to serious wounds or even death of residents and probably also intruders (Fernandez-Duque & Huck, 2013). Expelled residents may become floaters again, but only rarely are these 'mature floaters' able to regain another breeding position (Fernandez-Duque & Huck, 2013). The oldest male lived at least 20 years (born 1995) and might still be alive; the oldest known female lived at least 16 years (Owl Monkey Database, 2017). Life expectancies of males and females that reached 2 years of age were

estimated to be 6.6 and 6.7 years (Larson, Colchero, Jones, Williams, & Fernandez-Duque, 2016).

Given the fierce defence of home ranges by groups, the associated risks to floaters and the importance of knowing floater numbers to estimate the OSRs, our study had a two-fold aim. We wanted to estimate the floater population, and we wanted to examine a set of hypotheses that explain how owl monkey floaters may avoid groups. Since group ranges are contiguous and overlapping, absolute avoidance is not possible for a floater. We therefore wanted to evaluate whether floaters avoid more highly used parts of groups' home ranges ('spatial avoidance hypothesis'), whether they use specific areas at different times than the groups ('temporal avoidance hypothesis'), or whether they use a combination of both avoidance strategies. If groups are avoided temporally, we predicted that distances between floaters and groups at any specific time ('time-matched distances') would be larger than random distances. If groups are avoided spatially, we predicted that core areas of floater and group ranges would overlap less than expected based on random home range usage. If the core ranges of floaters lie mainly outside the core areas of groups, floaters might still have a large overall overlap with groups while avoiding the groups' centres of activity. Alternatively, if floaters are attracted to groups, time-matched distances would be expected to be shorter than random distances, and overlap of floater and group core areas would be expected to be greater than based on random home range usage.

## METHODS

### Study Area and Population

We conducted the study in the Reserva Mirikiná within the Estancia Guaycolec, a cattle ranch 25 km from the city of Formosa in the Argentinean Gran Chaco of South America (58°11' W, 25°58' S; Fig. 1a). The local owl monkey population has been regularly studied since 1997 (Fernandez-Duque & Bravo, 1997). The study area is covered by a grid of transects spaced at 100 m in North–South and East–West direction. All intersections, as well as half-way and quarter-way points, are marked and georeferenced (Fig. 1b).

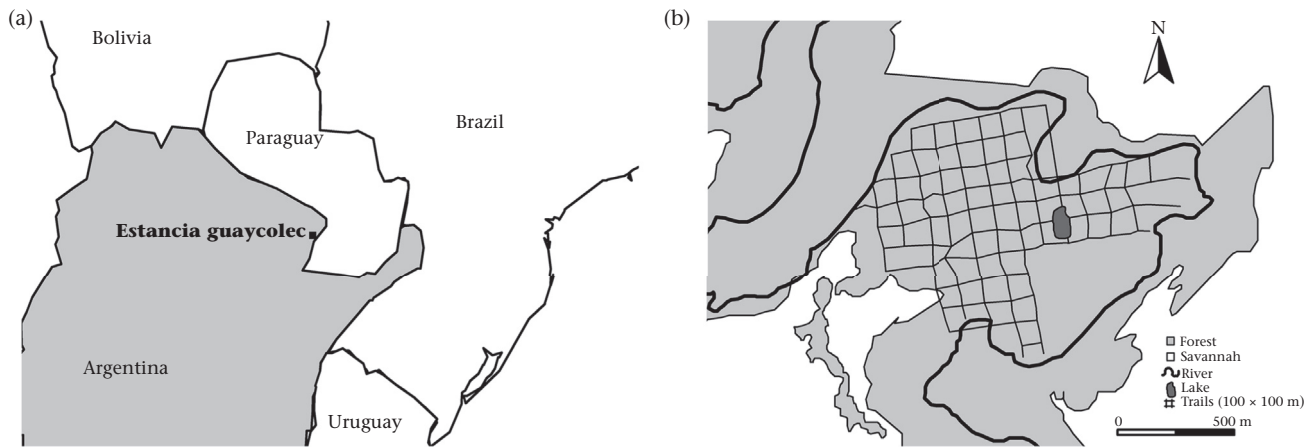
The Azara's owl monkeys inhabiting the gallery forest at the study site are, in contrast to other species of the genus, not strictly nocturnal, but cathemeral (sensu Tattersall, 1987). Cathemeral individuals are active during both night and day (Fernandez-Duque, 2003; Wright, 1989), thus offering a unique opportunity for collecting demographic and behavioural data during daylight hours.

### Ethical Note

Animals have been captured regularly since 2000 (Fernandez-Duque & Rotundo, 2003) and fitted with radiocollars or bead collars for individual identification and easier location of groups (for details on capture procedures, see Fernandez-Duque & Rotundo, 2003; for an evaluation of the potential effects of capture on animal welfare and on population structure, see Juárez, Rotundo, Berg, & Fernández-Duque, 2011). The study conformed to Argentinean and U.S. laws, and was approved by the National Wildlife Directorate in Argentina and by the animal research committees of the Zoological Society of San Diego (2000–2005), the University of Pennsylvania (2006–2011) and Yale University (2012–2016). All animal procedures followed the guidelines for the treatment of animals for teaching and research recommended by ASAB/ABS (2014).

### Data Collection

Systematic collection of ranging data started in 2001 and is ongoing. Every time we encounter a group or single individual, we



**Figure 1.** (a) Location of the Estancia Guaycolec within Argentina (black rectangle). (b) Main study area of the Reserva Mirikiná within the Estancia.

record the positions when encountered and when left or lost relative to the georeferenced grid system using a compass and estimating the distance to the animal(s). All observers are trained in accurately estimating distances using their own step length prior to data collection. Additionally, during longer group follows, we record locations every 20 min. Owl monkey groups are quite cohesive, commonly feeding or resting in the same tree, and adults are rarely more than 10 m apart. A 'group location' is therefore appropriate for the analyses presented here. For these analyses, we considered consecutive ranging data in the same location (e.g. during a resting period) to be one single data point to minimize autocorrelation.

We used for the analyses presented here ranging data collected from 24 floaters between June 2001 and January 2016 (Table 1). The range for the number of locations available was 23–96 (median = 42, mean = 46) for floaters and 25–973 (median = 93, mean = 165) for groups. We considered groups to be neighbours of a floater when both the 99% minimum convex polygons (MCPs) and the 95% kernels (see below) of their ranges overlapped. The ranging data of neighbouring groups were used only if they had been collected within 3 months of a specific floater's location data points. This consideration ensured that possible slight changes in the groups' ranges would not affect the analysis, since owl monkeys in this population usually have stable ranges over many years (Wartmann et al., 2014).

We knew the natal, previous or future group of 20 floaters from the long-term demographic records of the Owl Monkey Project Database (Table 1). We define the natal group as the one into which an animal was born, the future group as the one into which an animal immigrated following natal (or secondary) dispersal, and the previous group as the group from which a formerly residential adult had been expelled. We classified all other groups as 'different', including those for which we lacked information on the origin or destiny of the floater (Table 1).

We performed the statistical analyses using R (version 3.2.2) and packages 'adehabitatHR', 'nlme' and 'MuMIn' (Barton, 2016; Calenge, 2006; Pinheiro, Bates, DebRoy, Sarkar, & R Core Team, 2015; R Core Team, 2015), using a probability threshold of 0.05 for type I errors. We calculated 2.5–97.5% confidence intervals (CI) for all effect sizes as a more informative approach than conducting post hoc power analyses (Colegrave & Ruxton, 2003).

#### Estimate of Floater Population

We estimated the number of floaters in the study area using the mean (or median) area of 95% kernels of floaters' home ranges and

the mean (or median) proportion of overlap of the ranges of two floaters that had at least partially overlapping ranges in a specific time period (see below, Formula 1). We defined the study area as the 99% minimum convex polygon (MCP) around all locations for the study groups (for details on the calculation of home ranges, see *Spatial Avoidance Hypothesis*).

$$\frac{\text{Study area}}{\text{Mean home range size}} \times (1 + \text{mean proportional overlap}) \quad (1)$$

This approach essentially calculates how many 'average' home ranges fit into a certain area without overlap, and then accounts for overlap by adding additional ranges according to the proportional overlap of ranges. We also checked how well this formula would calculate the known number of groups in the same area, which indicated a good performance (see Results for details). Since one of the floaters ('Sepia') had an unusually large home range of 201 ha based on only 23 locations, we calculated means both including and excluding her data.

#### Temporal Avoidance Hypothesis

To evaluate the hypothesis that floaters avoid groups temporally, we analysed the distances between floaters and groups. Floaters and neighbouring groups were sometimes followed simultaneously by different observers. We considered each floater–group 'dyad' that was observed simultaneously, with locations collected less than 20 min apart (median = 2 min, mean = 4.7 min), to be time-matched. We first calculated Euclidean distances between time-matched locations and then computed the mean for each dyad.

We conducted two different analyses using two slightly different data sets: a restricted one to test whether time-matched distances were larger than expected, and an extended one to analyse the possible associations between the sex of the floater and the group type. When using the restricted data set, we only used mean distances estimated from at least 13 data points, since a preliminary analysis of the sample number against the cumulative mean suggested that at this point a stable mean was reached. This resulted in a set of 23 data points from seven floaters and their respective neighbouring groups (range 3–7, mean = 5; Table 1).

We calculated random distances between a floater and its neighbouring groups by randomly selecting any of a floater's and a group's locations, regardless of whether we had observed the two at the same time or not, and calculating the distances between

**Table 1**  
Number of locations (*N*) and data collection periods for floaters and their neighbouring groups

	Sex	Natal/previous group	Future group	No. of neighbouring groups	<i>N</i> (floater)	<i>N</i> (neighbouring groups)	Time period	No. of groups with ≥13 (5) time-matched data points	Used in analysis
<b>Floaters with ≥13 time-matched locations</b>									
Cansada	F	CC	NA	3	57	42–416	06 Apr 2011–24 May 2012	2	S, T1, T2
Celeste	F	D100/CO <sup>a</sup>	NA	3	36	88–421	19 Jun 2012–16 Jan 2014	1	S, T1, T2
Discoteca	F	D500	NA	6	78	300–522	04 Aug 2014–19 Jan 2016	4 (6)	S, T1, T2
Dixi	F	D500	NA	7	80	50–93	14 Oct 2013–20 Aug 2015	5 (7)	S, T1, T2
Dulcinea	F	D500	NA	5	96	61–420	10 Dec 2010–23 Dec 2011	3 (4)	S, T1, T2
Emma	F	E500	NA	4	75	367–458	13 Aug 2007–21 Jan 2009	4	S, T1, T2
Evaristo	M	E350	NA	7	55	91–458	13 Aug 2007–21 Jan 2009	4 (6)	S, T1, T2
<b>Floaters with ≥3 time-matched locations</b>									
Conchita	F	CC	NA	13	45	39–157	01 Jul 2002–25 Dec 2003	(1)	S, T2
Dardo	M	D1200	F1200	8	29	30–94	16 Apr 2002–21 Jan 2003	(2)	S, T2
Diosa	F	D500	D800	3	25	35–119	24 Mar 2005–16 Jun 2006	(3)	S, T2
Diuresis	F	D500	G1300	7	42	31–223	15 May 2004–13 Feb 2006	(3)	S, T2
Elino	M	E500	D500	9	56	32–159	11 Jul 2002–11 Feb 2004	(2)	S, T2
Enrique	M	E500	NA	7	25	35–288	28 Dec 2009–25 Mar 2011	(2)	S, T2
Esperanza	F	(E500 <sup>b</sup> )	NA	3	37	49–90	21 Jun 2001–19 Feb 2002	(1)	S, T2
Fabian	M	NA	E500	5	55	43–147	21 Jun 2001–14 Aug 2002	(3)	S, T2
Galaxia	F	(G1300 <sup>b</sup> )	NA	4	42	42–72	15 Apr 2002–17 May 2003	(1)	S, T2
Garza	F	(G1300 <sup>b</sup> )	NA	2	44	42–52	25 Jul 2005–01 Feb 2007	(1)	S, T2
Sepia	F	NA	NA	5	23	56–160	02 Jan 2003–22 Oct 2004	(1)	S, T2
Sotreta	M	(D100 <sup>c</sup> )	Corredor	7	59	58–184	12 Dec 2002–22 Oct 2004	(2)	S, T2
<b>Floaters without time-matched locations, only included in home range overlap analysis</b>									
Gaviota	F	(G1300 <sup>b</sup> )	NA	6	34	37–99	13 Jul 2003–16 Sep 2004	0	S
Mabela	F	(B68 <sup>b</sup> )	NA	1	38	53	17 Jul 2002–08 Aug 2003	0	S
Salada	F	NA	NA	3	25	33–82	19 Oct 2003–20 Oct 2004	0	S
Simon	M	NA	NA	4	24	55–105	31 Dec 2004–15 Jun 2006	0	S
Sirena	F	NA	NA	6	34	54–134	10 Sep 2003–30 Sep 2004	0	S
<b>Sum</b>				129				23 (52)	

For each floater's neighbouring groups the minimum and maximum number of locations are given. The natal group is the one into which an animal was born, the previous group is the group from which a formerly residential adult had been expelled, and the future group is the one into which an animal immigrated. The number of time-matched data points indicates the number of neighbouring groups for which the mean time-matched distances could be calculated based on at least 13 or at least three time-matched locations. The analyses on home range overlap include data for all floaters. The last column indicates whether the data for this floater were used in the spatial analysis (S), the temporal analysis with fewer dyads but more locations (T1) or the temporal analysis with extended data with more dyads based on fewer locations (T2).

<sup>a</sup> Celeste had immigrated as a juvenile together with her father from D100 (which dissolved) into CO, so this group could be regarded as her 'natal' group.

<sup>b</sup> Previous group.

<sup>c</sup> Sotreta was one of the few recorded cases of secondary dispersal. Marked as a solitary, he first immigrated into group D100, was expelled half a year later by an intruder and after another half year of ranging solitarily he immigrated into group Corredor.

those locations. We then calculated for each dyad the mean of 10 000 random distances (see [Supplementary Material for annotated coding in R](#)). We built a general linear mixed model to compare the means of time-matched distances and random distances between floaters and groups, with mean distances as the dependent variable, and distance type (i.e. whether it was time-matched or random) as the independent variable. We considered floater and group identity as random variables, with 'group' nested within 'floater'.

To evaluate the extent to which distances to groups were related to the sex of the floater or the group type (i.e. natal, future, previous or different), we conducted a linear mixed model using an extended data set. This data set included all floater–group dyads for which a mean based on at least three distances was available, resulting in a data set of 52 data points from 19 floaters and their respective neighbouring groups (Table 1). In the analysis of the extended data set we only used actual distances as the dependent variable, and as independent variables, we used the sex of the floater and group type, with 'group' nested within 'floater' as random variable.

We checked assumptions of the models by plotting the fitted values against the standardized residuals, and the residuals against the standard normal distribution for each individual separately (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). We considered the heterogeneity of variance of the residuals by using different variance structures for each floater, since this resulted in a lower corrected Akaike information criterion (AICc = 511.6 versus 512.7) for the model without differing variance structures. For the extended data set for the effects of sex and group type on time-matched

distances, the residuals conformed to the assumptions of normality and homogeneity of variance.

#### *Spatial Avoidance Hypothesis*

To evaluate the hypothesis that floaters avoid the core ranges of neighbouring groups, we calculated 50% ('core area'; [Blundell, Maier, & Debevec, 2001](#)), 85% and 95% fixed kernel ranges for all floaters and their neighbouring groups ([Seaman & Powell, 1996](#)). We determined the bandwidths (*h*) separately for each floater or group using the ad hoc method for the 95% kernel ([Schuler, Schroeder, Jenks, & Kie, 2014](#)); that is to say the smallest *h* that still resulted in a continuous isopleth without any holes, unless the 95% kernel using the href method ([Worton, 1989](#)) already resulted in a discontinuous kernel. In such cases, we used the smallest *h* that had the same number of discrete areas within the range as when using the href. This approach avoided oversmoothed kernels and thus overestimation of home range sizes. We then used the ad hoc bandwidth for the core areas. We calculated the standard kernels for the core area and the 95% range and also the 85% range, because we wanted to evaluate whether floaters avoided larger areas than just the core range. If floater and group ranges overlap at all, but there is a clear avoidance of 50% or even 85% ranges, this would indicate that floaters use mainly the border zones (i.e. beyond the vertices of the 50% or 85% ranges) of groups.

As a measure of overlap, we used the utilization distribution overlap index (UDOI; [Fieberg & Kochanny, 2004](#)). The index takes the actual utilization distribution of animals into account, in



contrast to, for example, simple measures such as the percentage overlap that only consider the spatial area covered. The UDOI is zero if two ranges do not overlap, and one if two uniformly distributed ranges completely overlap; the index can also exceed one if ranges have a high degree of overlap but are not uniformly distributed (Fieberg & Kochanny, 2004).

The 'true' UDOIs were then compared to UDOIs based on randomized home ranges. To create these random ranges we first created the 99% MCP of both the floater's and the group's ranges. We used the 99% and not the 100% MCPs to exclude outliers. Within each 99% MCP we created as many random locations as there were for the original data set for this floater or group. From these random locations, 50%, 85% and 95% kernels were calculated using the same bandwidth as for the true 95% range. The procedure was repeated 1000 times. We first calculated the UDOIs for the random floater and the random group ranges for each of the 1000 random sample pairs ('random UDOIs'), then calculated the mean random UDOI for each floater–group dyad. This resulted in a data set of 24 floaters with 1–13 (median = 5, mean = 5.4) neighbouring groups (total = 128 data points; Table 1).

It was not possible to use for this analysis the same statistical approach employed for the distance analysis, since the linear mixed model for the 50% kernel did not comply with the assumptions of homogeneity of variance and normality of the residuals, even after taking different variance structures for floaters and groups into account. Because of zero values it was also not possible to use a gamma distribution for the error structure. We therefore employed a randomization approach. For each floater–group dyad, we calculated the difference between the true and the random UDOI, and computed the sum of these differences. We then randomized the sign of the difference (i.e. whether the true or the random UDOI was smaller). We repeated this 10 000 times, and compared the sum of the true differences to the distribution of randomized differences (see [Supplementary Material for annotated coding in R](#)). We also evaluated how sensitive the analysis was to data from specific individuals for the 50% kernel, by repeating this approach 24 times, each time excluding data for a different floater.

To evaluate how much the overlap for the 50% kernels differed in relationship to the sexes or the group types, we used a linear mixed model with the difference between the true and the mean randomized UDOI as the dependent variable, sex and group type as independent variables and group nested within floater as random factors. The residuals of the fitted model conformed to the assumptions of normality and homogeneity of variance.

## RESULTS

### *Estimate of Floater Population*

There were two to five floaters for every 10 groups (ratio of floaters to breeding pairs = 0.2–0.5) based on the following estimates. The floater mean 95% kernel home range size was 39.8 ha (32.8 ha, when excluding the home range for one individual (*Sepia*) with an exceptionally large range based on only 23 locations). This resulted in an estimate of 3.5 floaters (4.4 excluding *Sepia*) for the 100.6 ha study area. The maximum observed number of overlapping floaters was nine.

The mean 95% kernel home range size for groups was 6.1 ha, and the median overlap between neighbouring groups was 12%. This resulted in an estimate of 18 groups in the 101 ha study area. This estimate corresponds well with the identified 16 study groups and the two 'empty' areas, where groups were likely to be present but not studied (e.g. because they were beyond a river; see [Appendix Fig. A1](#)). Thus, we estimated that there were four to nine floaters for the 18 study groups.

### *Temporal Avoidance Hypothesis*

Our data do not provide support for the temporal avoidance hypothesis. Time-matched distances were 7% shorter, not longer, than random distances (mean = 274 m versus 293 m; linear mixed effects model (lme): estimate (Est) = 14.9, CI = 6.1–23.6;  $t_{22} = 3.5$ ,  $P = 0.002$ ; Fig. 2). Male and female floaters showed little difference in their distances to groups (Fig. 3a, Table 2). On the other hand, the data suggest that the distance between floaters and groups was to some extent related to the floater's relationship to the group. Floaters maintained shorter distances to their natal and previous groups than others (log-likelihood ratio test comparing the models including and excluding group type:  $\chi^2_{5,8} = 37.2$ ,  $P < 0.001$ ; Table 2, Fig. 3b).

### *Spatial Avoidance Hypothesis*

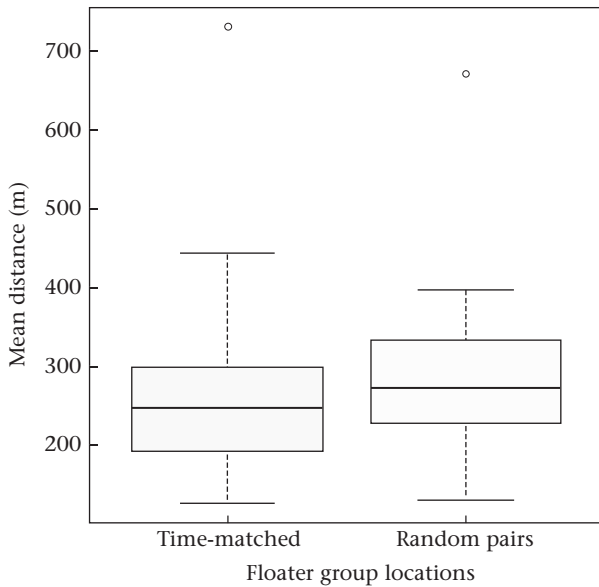
The spatial avoidance hypothesis was supported by our data. True home range overlap was smaller than overlap for randomly created 50% kernel ranges (mean: 0.013 versus 0.020, median: 0.0 versus 0.014; randomization test: mean of true sum of differences = -0.918, mean of randomized sum of differences = 0.266;  $CI_{2.5\%} = -0.520$ ,  $CI_{97.5\%} = 0.513$ ;  $P < 0.001$ ; Fig. 4). This was also true for 85% kernel UDOIs (mean true ranges = 0.067, median = 0.047; mean random ranges = 0.079, median = 0.060; mean of true sum of differences = -1.509, mean of random sum of differences = 0.360;  $CI_{2.5\%} = -1.296$ ,  $CI_{97.5\%} = 1.320$ ;  $P = 0.012$ ; Fig. 4). However, for 95% kernels, true and random overlap did not statistically differ (mean true ranges = 0.108, median = 0.091; mean random ranges = 0.118, median = 0.097; mean of true sum of differences = -1.270, mean of random sum of differences = -0.753;  $CI_{2.5\%} = -1.883$ ,  $CI_{97.5\%} = 1.877$ ;  $P = 0.092$ ; Fig. 4).

Females and males had virtually the same mean difference between true and random 50% UDOIs (lme: Est = 0.002; CI = -0.006–0.002,  $t_{22} = 0.5$ ,  $P = 0.59$ ; Fig. 5a) and the extent of overlap of the floater's and group's range was not strongly related to the type of group (log-likelihood ratio test comparing lme with and without group-type as independent variable:  $\chi^2_{5,8} = 1.0$ ,  $P = 0.80$ ; Table 3; Fig. 5b).

## DISCUSSION

Solitary owl monkeys seem to solve the floater's dilemma by trying to stay in relatively close proximity to groups while still avoiding their core ranges. This implies that floaters mainly move on the edges of groups' home ranges; they move in the area where the ranges of neighbouring groups overlap. This would have two consequences for them. Firstly, floaters maximize the number of groups with which they have contact, and secondly, if they are detected by residents, they can leave their ranges more quickly, thus potentially avoiding serious fights.

Floaters have been reported to move closer than expected to territorial individuals in other taxa (blue grouse, *Dendragapus obscurus*, Jamieson & Zwickel, 1983), and this prospecting behaviour has been linked in various studies to the fitness of floaters (Boulinier, Mariette, Doligez, & Danchin, 2008; Reed, Boulinier, Danchin, & Oring, 1999). Proximity to groups might help floaters gain information about the reproductive or health status of residents, as well as about the habitat quality (Boulinier et al., 2008; Reed et al., 1999). Likewise, proximity may allow a floater to assess group composition, a clue as to whether immigration attempts are likely to be successful. This is the case among Siberian jays, *Perisoreus infaustus*, where the presence of nondispersing juveniles hinders floaters from entering (Griesser, Nystrand, Eggers, & Ekman, 2008). Currently, we do not know whether owl



**Figure 2.** Distances between floaters and neighbouring groups for time-matched and random locations. Box plots show the median and interquartile range, while whiskers show the range except for outliers (circles) that were more than 1.5 times the interquartile range away from the median. Note that the analyses take nonindependence of data points into account, while the box plots weigh all data points equally.

**Table 2**

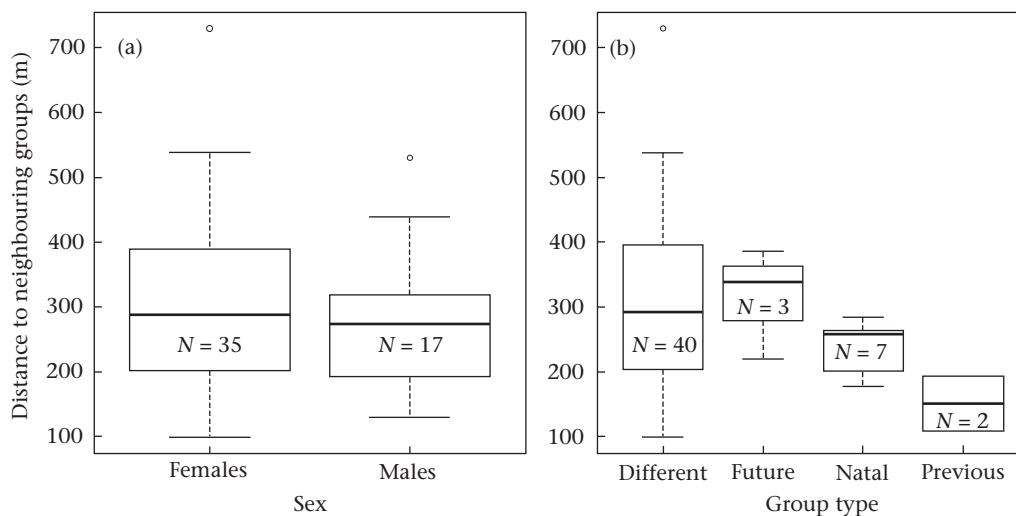
Test statistics for the linear mixed effects model (extended data set) of distance against sex and group type

	Estimate	2.5% CI	97.5% CI	df	t	P
Intercept	325.1	260.9	325.1	30	10.3	<0.001
Sex	-26.6	-138.1	84.9	17	-0.5	0.62
Future group	23.1	-121.2	167.4	30	0.32	0.75
Natal group	-65.6	-156.9	25.7	30	-1.5	0.15
Previous group	-204.9	-392.5	-17.3	30	-2.2	0.033

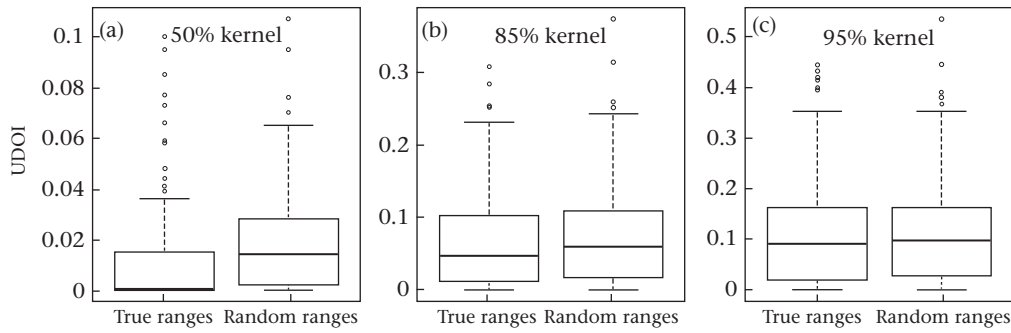
The values for females (sex) and 'different groups' (group type) were taken as the baseline.

monkey floaters assess the habitat quality of potential group home ranges, the physical strength of the (same-sex) adults in groups or other parameters of group composition. The fact that they seek proximity while remaining at a safe distance suggests that they may gain some valuable information. Further suggestive evidence for this possibility can be found from the different distances maintained to various group types. Even when this particular analysis should be treated with caution due to low sample sizes for some group types, it appears that distances to groups depended on how familiar the floater was with the group, the most interesting difference being between future and truly different groups. With the constant presence of prospecting floaters, vacancies are usually filled up quickly in most species. For example, after the death of the breeding female in a group of moustached tamarins, *Saguinus mystax*, a new female tried to enter the group within hours (Löttker, Huck, & Heymann, 2004). This example also exemplifies the often very surreptitious behaviour of floaters: this new female had never been spotted by the researchers before, despite nearly continuous observation of that group during the previous year (Löttker et al., 2004). While it is likely that resident animals themselves have a better knowledge about the presence of conspecifics than human observers, it is still conceivable that there is an asymmetry in the amount of knowledge floaters and groups have about each other. At the same time, there is also an asymmetry in the costs of losing an interaction (the 'asset-protection principle'; Clark, 1994; Harts, Jaatinen, & Kokko, 2016), and certain characteristics, like reproductive success (e.g. the number of chicks produced by resident common loons, *Gavia immer*; Piper et al., 2006) can be linked to intruder pressure from floaters. Thus, because the chances of an evicted resident owl monkey regaining a breeding position are low (Fernandez-Duque & Huck, 2013), residents should be expected to vigorously defend their territories against floaters. By keeping to the outskirts of a group's home range, a floater is therefore minimizing the risks of potentially lethal fights, since it could quickly retreat in another group's home range upon detection.

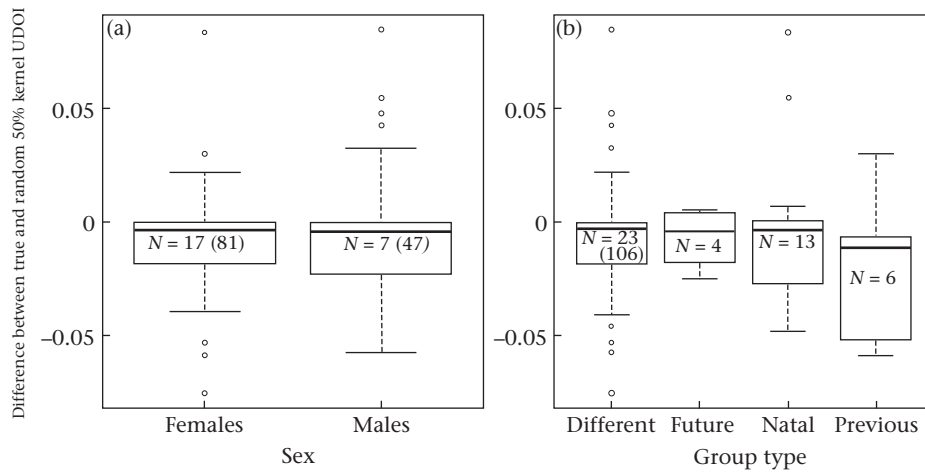
As expected, these observed patterns (closer than expected time-matched distances between floaters and groups, but avoidance of group core areas by floaters) did not differ between male and female owl monkeys. In many other species, dispersal is sex biased and therefore floaters mainly consist of one sex (Lawson Handley & Perrin, 2007; Mabry, Shelley, Davis, Blumstein, & van



**Figure 3.** Distances between floaters and neighbouring groups depending on (a) sex and (b) relationship to group. Box plots show the median and interquartile range, while whiskers show the range except for outliers (circles) that were more than 1.5 times the interquartile range away from the median. Note that the analyses take nonindependence of data points into account, while the box plots weigh all data points equally.



**Figure 4.** Difference in the utilization distribution overlap index (UDOI) for true and randomly created (a) 50%, (b) 85% and (c) 95% kernel home ranges of floaters and their neighbours. Box plots show the median and interquartile range, while whiskers show the range except for outliers (circles) that were more than 1.5 times the interquartile range away from the median. Note that the analyses take nonindependence of data points into account, while the box plots weigh all data points equally.



**Figure 5.** Difference between true and randomized 50% utilization distribution overlap index (UDOI) for (a) females and males and (b) different group types. Sample sizes refer to number of individuals (number of total data points). Box plots show the median and interquartile range, while whiskers show the range except for outliers (circles) that were more than 1.5 times the interquartile range away from the median. Note that the analyses take nonindependence of data points into account, while the box plots weigh all data points equally.

**Table 3**

Test statistics for the linear mixed effects model (extended data set) of difference between true and randomized utilization distribution overlap index (UDOI) of 50% core ranges against sex and group type

	Estimate	2.5% CI	97.5% CI	df	t	P
Intercept	−0.008	−0.014	−0.002	101	−2.8	0.007
Sex	0.001	−0.008	0.010	22	0.2	0.83
Future group	−0.001	−0.024	0.022	101	−0.1	0.94
Natal group	−0.006	−0.007	0.020	101	0.1	0.34
Previous group	−0.010	−0.029	0.009	101	−1.1	0.29

The value for females (sex) and ‘different groups’ (group type) were taken as the baseline.

Vuren, 2013). In pair-living species, however, dispersal is expected to be equally likely for both sexes (Dobson, 1982), which is what actually happens in owl monkeys (Fernandez-Duque, 2009). Nevertheless, similar rates of dispersal can still be associated with sex differences in the average dispersal distance (Huck, Roos, & Heymann, 2007), which could lead to sex-biased mortality amongst floaters if mortality is linked to dispersal distance (Johnson et al., 2009). Yet even if this is not the case, at any point in time and in a given area there will be a stochastic element to the number of floaters of a particular sex, thus resulting in a locally uneven operational sex ratio. This, in turn, can have consequences for various aspects of the population dynamics. For example, the manipulative biasing of the sex ratio towards male fledglings in

male-philopatric great tits, *Parus major*, led to an increase in local breeding densities in the following year (Nicolaus et al., 2012). Generally, density-linked floater pressure is likely to affect breeding success and overall population size, for example through conflicts between residents and floaters (Hunt, 2013).

Therefore, the floater-to-breeder ratio is an important parameter for the assessment of a population’s status (Hunt, 2013; Penteriani et al., 2011). We estimated that there were usually between four and nine floaters in our 100 ha study area, a floater-to-breeding pairs ratio of 0.2–0.5. Since floaters have larger home ranges than groups, several floaters might still overlap with a single group; with small numbers like ours, stochastic events of uneven local adult or operational sex ratios should therefore be fairly common. This in turn means that, in any given group at a given time, either the male or the female might have to face a higher level of competition. Furthermore, the floater–resident ratios and relationships are likely to be in a high state of flux, since floaters usually disappear after a few months, either because they might shift their ranges or because of high mortality amongst them (Fernandez-Duque, 2009).

Much is still to be learned about floaters and the process of dispersal in owl monkeys, as well as in other animals. For example, in order to get a clearer understanding on the impact of floaters on local and wider population dynamics, we need to determine survival rates of floaters, the cues owl monkeys use to gain information from group ranges or group composition, what triggers take-over

attempts, dispersal distances, as well as trade-offs between the number of group ranges monitored by floaters and the likelihood to step into a vacancy (Zack & Stutchbury, 1992). By cautiously staying at the borders of home ranges while seeking comparatively close proximity to the current position of resident groups, floater owl monkeys seem to maximize their likelihood of obtaining a breeding position in the end, but the effect on local population parameters needs further evaluation.

## Acknowledgments

E.F.D. acknowledges financial support from the L.S.B. Leakey Foundation, National Geographic Society and the National Science Foundation of the U.S.A. (NSF-BCS-0621020, 0837921 (REU), 0924352 (REU), 1026991 (REU), 1219368 (RAPID) and 1232349 (2012)). We thank F. Middleton, Manager of Estancia Guaycolec and A. Casaretto (Bellamar Estancias) for the continued support of the Owl Monkey Project and the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET, Argentina). We also thank all field assistants and volunteers that contributed to the ranging data over the years and the Ministerio de la Producción y Ambiente of Formosa Province for allowing the research. M.H. thanks Mark Bulling for many inspiring hours of discussion of statistical procedures. Finally, we gratefully acknowledge the suggestions of two referees and Editor R. Holland that helped improve the manuscript.

## Supplementary Material

Supplementary Material associated with this article is available, in the online version, at <http://dx.doi.org/10.1016/j.anbehav.2017.02.025>.

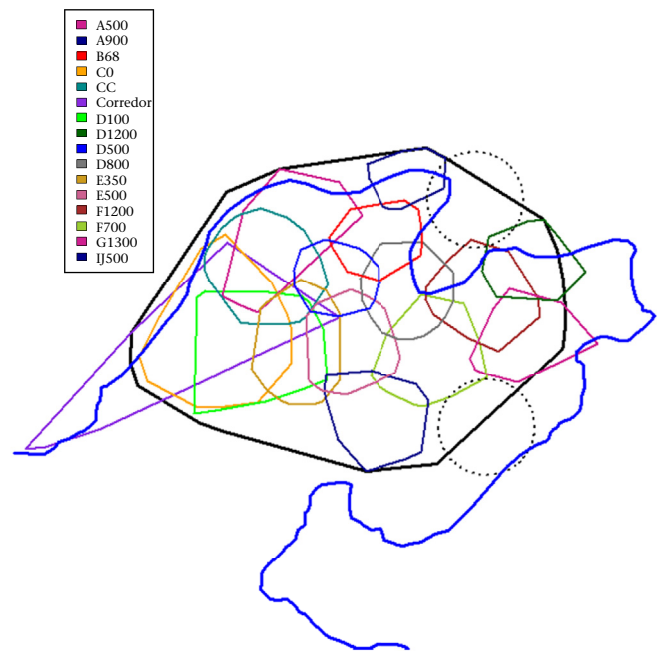
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## APPENDIX



**Figure A1.** Minimum convex polygon (MCP) of the 106 ha study area (thick black line) and 99% MCP group ranges. Circles with dotted lines represent suspected ranges of nonidentified groups, and the thick blue line denotes the river.