

Children of divorce: effects of adult replacements on previous offspring in Argentinean owl monkeys

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Abstract According to the Evolutionary Theory of the Family, the replacement of one pair-member by an intruder may have profound consequences for the existing offspring. Step-parents are expected to provide less care towards unrelated immatures than to genetic offspring, unless caring also serves as a mating strategy. Furthermore, because an intruder will be a potential mate for opposite-sexed offspring, relationships between offspring and same-sex parents are predicted to deteriorate. To test these predictions, we studied an Azara's owl monkey (*Aotus azarai*) population in Argentina exhibiting serial monogamy and biparental care. Since 1997, we have collected demographic data from ca. 25 groups and inter-individual distance data from ca. 150 marked individuals. First, we compared survival and dispersal age of immatures in groups with and without replacements to investigate whether parental care serves as a mating strategy. Second, we compared sex-specific age at dispersal for groups with replacement of opposite-sex parents, same-sex parents, or in stable groups in order to test whether relationships between offspring and same-sex parents deteriorated after the replacement of the other parent. Survival and dispersal ages were not negatively associated with replacements, suggesting that male care might serve, at least partly, as a mating strategy. The time lag between a replacement and the subsequent dispersal of

female offspring was greater if the intruder was a male, while the offspring and same-sex parents were less often nearest neighbors after replacements than before. Our results suggest that family disruption through the replacement of a parent is not associated with decreased offspring survival or early dispersion of juveniles, but deteriorates parent-offspring relationships.

Keywords *Aotus azarai* · Dispersal · Evolutionary theory of the family · Night monkeys · Parent-offspring conflict · Survival

Introduction

The break-up of a pair when both partners are alive and when at least one partner subsequently breeds, or attempts to breed, with a new mate is often termed “divorce” in the avian literature (Choudhury 1995). The definition includes both the voluntary leaving of one partner or its expulsion by the former mate or by an intruder. In this context, and keeping with Emlen's definition (1995), the term “family” refers to small groups consisting of an adult pair and one or more younger individuals. In such “family” living species, divorce and the subsequent replacement of one of the members by a new adult may have profound consequences on the offspring of the original pair (Emlen 1995, 1997). Divorce may result in infanticide (Hrdy 1974; Sommer 2000; Fedigan 2003). But even if infants are not directly killed, the replacement of one pair-mate will generally alter the genetic structure of a family and the social dynamics within the group will differ from those of “intact” families (Emlen 1997). For example, in cooperatively breeding acorn woodpeckers (*Melanerpes formicivorus*), dominance interactions between the remaining

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parent and same-sex offspring seemed to prevent breeding of the subordinates (Hannon et al. 1985). Likewise, in philopatric female woodland (pine) voles (*Microtus pinetorum*), mothers tugged at their daughters more frequently after male replacements, possibly a behavioral form of reproductive suppression (Brant et al. 1998).

In an attempt to formulate an evolutionary theory of the family, Emlen (1995, 1997) made several predictions with respect to social dynamics after the disruption of families. He predicted that the intruder might be particularly tolerant of opposite-sexed offspring because they may represent additional and/or future mating partners. On the other hand, the remaining partner should, for the same reason, be less tolerant of its same-sex offspring, leading to mother–daughter and father–son conflict (Emlen 1997). Sometimes the conflict may lead to dispersal of sons or daughters at a younger age than in undisturbed families as observed in Seychelles warblers (*Acrocephalus sechellensis*) where subordinates disperse earlier after the replacement of a parent (Eikenaar et al. 2007). Other times, sons and daughters may delay dispersal if the step-parent prevents the parent from expelling the offspring, thus offering additional mating opportunities to the new individual. This is the case in the stripe-backed wren (*Campylorhynchus nuchalis*), where step-sons remain in their groups more seasons than subordinate males whose mother is still present (Piper and Slater 1993). Thus, if the replacement is opening mating opportunities for the offspring and the intruder, we expect the offspring to disperse at an older age or after a longer time after the replacement. Alternatively or additionally, the replacement could increase the conflict between the parent and the same-sex offspring.

Species with male parental care pose additional complexities to formulating testable predictions. Under Emlen's theoretical framework, a non-related intruding male is not expected to provide care to infants present in the family before his intrusion (Emlen 1995). For example, acorn woodpeckers that had been removed temporarily during egg laying (i.e., having a reduced probability of fertilizing the eggs) often destroyed nests or subsequently showed reduced feeding behavior, whereas the ones that had been removed during the incubation period did not destroy nests and fed the chicks (Koenig 1990). However, an intruding male may not reduce the amount of help provided if by offering substantial infant care he can benefit in at least one of three different ways: (1) enhancing the survival or fitness of his own genetic offspring or highly related individuals (Wuensch 1985; Moreno et al. 1999; Gubernick and Teferi 2000; Charpentier et al. 2008; Kingma et al. 2010), (2) alleviating the reproductive burden of the female to an extent that she may be able to produce infants of better condition or at a higher rate (Stallcup and Woolfenden 1978; Austad and Rabenold 1986; Price 1992a; Kingma et

al. 2010), or (3) increasing mating success (Keddy Hector et al. 1989; Price 1990; Smuts and Gubernick 1992; Härdling and Kaitala 2004; but see Tardif and Bales 1997). In the last two situations, males should provide care to infants regardless of the likelihood that they have sired them. If care, however, is directed solely at own offspring, both male and female intruders should have a negative impact on infant survival. In those circumstances, younger dispersal ages are also expected because intruding adults should be less tolerant of potential food competitors, regardless of the sex of the young.

Divorce, with its subsequent effects on families, has been studied intensively in birds (Choudhury 1995; McNamara and Forslund 1996; Allison et al. 2005; Jeschke and Kokko 2008; Valcu and Kempenaers 2008), but rarely in mammals, with the notable exception of humans (Anderson et al. 1999a, b; Daly and Wilson 1999; Marlowe 1999; Alvergne et al. 2008). The difference may be attributed to the fact that about 90% of birds are socially monogamous (Lack 1968, cited in Choudhury 1995), whereas only few mammals show this social organization (Hendrichs 1978; Clutton-Brock 1989).

The New World owl monkeys (*Aotus* spp.) are among the few socially monogamous mammal species (Fernandez-Duque 2011a) with a variety of behavioral and life-history traits that makes them ideal for evaluating the evolutionary theory of the family. Owl monkeys are essentially sexually monomorphic, with only slight dimorphism of canine height and width (Aquino and Encarnación 1986; Fernandez-Duque 2011b; Huck et al. 2011). While there is virtually never more than one reproductive male and female in a group, divorce as defined here has been consistently observed in a population of Azara's owl monkey (*Aotus azarai*) in the Argentinean Chaco (Fernandez-Duque et al. 2008; Fernandez-Duque 2011a; Fernandez-Duque and Huck unpublished data). In owl monkeys, the social system of serial monogamy is combined with intensive bi-parental care, but no participation of siblings in infant care (Wright 1984; Welker and Schäfer-Witt 1986; Rotundo et al. 2005; Fernandez-Duque et al. 2009; Fernandez-Duque 2011a). From the second week of life, an infant is almost exclusively carried by the adult male who also plays and provides solid food more than the mother (Welker and Schäfer-Witt 1986; Wolovich et al. 2007; Huck and Fernandez-Duque 2011). Anecdotal evidence also suggests that a mother cannot compensate for the loss of a male caretaker during early infant development, such that an infant would not be able to survive without male help (Jantschke et al. 1998; Huck and Fernandez-Duque 2011). Preliminary genetic analyses suggest that males present in a group when the infant was conceived are the sires of the young (Babb, Fernandez-Duque et al., unpublished data), and infanticide has never been observed. Sub-adults and young adults disperse between

2.2 and 4.9 years of age, with no marked differences between the sexes (Fernandez-Duque 2009).

The occurrence of adult replacements in our owl monkey population allows us to generate a variety of predictions concerning the adults involved in the divorce, and the effect of the divorce on the offspring present in the group. In this study, we test those predictions that are related to the survival and dispersal of non-adults, and to the relationship between same-sex parent–offspring pairs (Table 1). Some other predictions formulated within the framework of the Evolutionary Theory of the Family are either *a priori* not relevant for owl monkeys (e.g., predictions concerning cooperative breeding) or cannot be tested with our data set yet.

Methods

Area of study and population

The owl monkey subspecies *Aotus a. azarai* inhabits the gallery forests of the Río Paraguay and its tributaries in the Argentinean provinces of Formosa and Chaco (Brown and Zunino 1994). The area of study is located in the Guaycolec Ranch, 25 km from the city of Formosa in the Argentinean Gran Chaco of South America (58°11 W, 25°58 S) and has been regularly and intensively studied since 1997 (e.g., Fernandez-Duque et al. 2001, 2010; Fernandez-Duque and Rotundo 2003; Rotundo et al. 2005; Fernandez-Duque 2009). This owl monkey species is, in contrast to other species of the genus, not strictly nocturnal, but cathemeral (Wright 1989; Erkert and Cramer 2006; Fernandez-Duque 2011a), thus

offering a unique opportunity for collecting demographic as well as behavioral data during daylight hours.

Animals have been captured regularly since 2000 (Fernandez-Duque and Rotundo 2003) and fitted with radio or bead collars for individual identification and easier location of groups (for details on capture procedures see Fernandez-Duque and Rotundo 2003; for an evaluation of effects of capture on animal welfare and on population structure see Juárez et al. 2011). Various types of samples have been regularly collected for genetic analyses (Babb et al. 2010, 2011a, b) which additionally aided identification if animals lost collars.

Demographic and behavioral data collection

Approximately 20–25 groups have been monitored since 1997. It was not possible to contact all groups regularly (i.e., at least monthly), but data for groups monitored less frequently than monthly are not included in the analyses. A smaller set of 10 groups was contacted more regularly, normally every week or every second week. During birth seasons (October–December), we intensified demographic monitoring. At each contact with a group, we recorded group size, age structure, births, and disappearances. Animals were classified as adult (>48 months), sub-adult (>24–48 months), juvenile (>6–24 months), or infant (0–6 months) based on size, visible sub-caudal gland secretions, and behavioral patterns (Huck et al. 2011). Owl monkeys cannot be sexed by an observer watching them from the ground but sex was known for all marked individuals. Due to the intense monitoring, we were able to establish the dates of important demographic events (e.g., births, replacements, dispersal) usually within a range of a few weeks; birthdates were generally determined with more

Table 1 Hypotheses and predictions tested in this study

	Hypothesis	Alternative ^a hypothesis
Function of paternal care		
H1	1.1 Adults care only for own offspring	1.2 Care functions (also) as a (male) courtship strategy
Prediction (survival):	1.1.a Reduced infant survival after replacements	1.2.a No difference in infant survival
Prediction (dispersal):	1.1.b Earlier dispersal of sub-adults	1.2.b No difference in sub-adults' age at dispersal
Sex-specific effects of replacements		
H2	2.1 Replacements open opportunity for (sub-adult) offspring	2.2 Mate competition leads to increased conflict between parent and same-sex offspring
Prediction (dispersal):	2.1.c Later dispersal/longer time lag until dispersal after divorce if the intruder is of the opposite sex	2.2.c Earlier dispersal/shorter time lag until dispersal after divorce, if the intruder is of opposite sex (or subsequent expulsion of same-sex parent)
Prediction (behavior):	–	2.2.d Increase of tension between same-sex parent–offspring pairs → Same-sex parent–offspring pairs are less often nearest neighbors after a replacement than before

Predictions with the same final letter are contrasting predictions from alternative hypotheses

^aNote that these hypotheses are not mutually exclusive, but they generate different predictions

precision (see below). When the range of estimates for any date was within ± 30 days, we used the average date between the two known dates most closely around that event. For example, the average date between the last time a sub-adult was observed in its natal group and the first time it was missing or found ranging solitarily was considered the dispersal date. In our analyses, where the order of magnitude for ages is measured in months, an error of a couple of weeks will not influence the results. We therefore considered a range of ± 30 days an acceptable error (average error of 36 uncensored cases ± 10 days). However, for several individuals the time lag between the last time the animal was seen in its group and the first time it was missing was larger than ± 30 days ($N=5$, average error ± 50 days) or they were at the time of data analysis still residing in their natal group ($N=4$). In these cases, the data were considered censored and the “last time seen” was used as the date for which the age was calculated. During birth seasons, we intensified monitoring, and the birth date estimation was further improved using infant development information (Rotundo et al. 2005). When a group was not contacted during the birth season, we assigned a birth date of October 1st to infants later encountered in that group given that never has a birth been recorded before October 1st (Fernandez-Duque 2002). On average, birth date estimates are precise to ± 9 days (treating unknown birth dates as having a range of 45 days).

Starting in August 2002, we collected behavioral data from 16 groups during 20-min focal samples using pen and paper (2002–2007) or later hand-held palm recorders (2007–present), following a protocol being used for four different monogamous primates in Ecuador and Argentina (<http://www.sas.upenn.edu/~eduardof/Protocols%20English/Protocols%20Main%20Menu.htm>). We observed the monkeys during daylight, with most observation hours taking place at dusk and dawn when the individuals are most active (Fernandez-Duque and Erkert 2006; Fernandez-Duque et al. 2010). During focal data collection, we noted every 2 min the basic behavioral state (rest, foraging, moving, social, and other or out of view) of the focal animal, and between these instantaneous sampling points we recorded continuously all occurrences of a set of additional behaviors of interest (infant care behavior, approaches, leaves, follows, agonistic and socio-positive interactions, grooming). Additionally, five times during each 20-min focal sample, we scanned all visible individuals and recorded their distance to the focal animal. Important but infrequent events, like fights between members of the groups, were recorded *ad libitum*. Field assistants were intensely trained and the first (ca. 30) focal samples of each new observer were not included for analyses until inter-observer reliability was $>85\%$. A total of 3,851 focal samples were recorded on 100 individuals between 2002 and 2010; no behavioral data were collected in 2006 and 2007. We analyzed here only focal samples of juveniles of known sex and their

same-sex parent in groups where a replacement had taken place (see section “Behavior (prediction 2.2d)”).

Data analyses

All analyses were conducted using program R vs. 2.13.0 (R Development Core Team 2008). Statistical significance was accepted when $\alpha \leq 0.05$.

Group type

For analyses, we classified groups always in reference to a particular individual. For example, a given group could be classified as stable for an infant born in 2003 and as female replacement for the younger sibling born in 2004. We defined individuals as coming from stable groups when both adults were present during the entire time the individual lived in the group. If either the adult female or adult male died, disappeared, or was evicted from a group while an offspring was still in its natal group, this individual was classified as coming from a female-replacement or male-replacement group, respectively. We did not use data from groups if we were unable to unequivocally identify either of the adults because they had not been marked nor had natural markers. If one adult was not identified, and the other one was replaced, the group was considered a male or female-replacement group, depending on the sex of the replaced adult. However, we considered only those groups as stable when both adults had been identified and were present the whole time.

Survival (predictions 1.1a vs. 1.2a; see Table 1)

In order to compare the survival of young animals after replacements, we had to rely on disappearances that can be due either to death or to dispersal. Dispersal is very unlikely to occur and be successful before 24 months of age (Fernandez-Duque 2009; Huck et al. 2011). None of the successful dispersers in our study population left its natal group before an age of 27 months (median age 44 months, Huck et al. 2011). This suggests that weaned juveniles are still dependent on living with adults in a group, hence we considered disappearances of infants (0–6 months) or juveniles (>6 –24 months) as deaths.

To examine the potential influence of replacements that took place when the offspring was younger than 24 months old on the quality of caretaking, we compared the number of infants or juveniles that died before they reached 2 years of age in stable groups with those in groups with male or female replacements using a *G* test (with William’s correction for small sample sizes). A similar analysis only for infants up to 6 months was not possible due to the small number of replacements in groups with offspring that

young. We did not include cases in which both parents had been replaced ($N=2$) because it would not be possible to separate the effects on the infant of the replacement of the mother from those induced by the replacement of the father. We also compared the survival of individuals who were infants when the male was replaced ($N=4$; including a case where the male was replaced 1.7 months before the birth of the infant) with infants from stable groups ($N=44$) using Fisher's exact test. The case of replacement before birth was included because an infanticidal male would be expected to discriminate also against infants born very shortly after group takeover.

Dispersal (prediction 1.1b vs. 1.2b; see Table 1)

We considered only sub-adults for the dispersal analysis since the youngest age of a known dispersal was at an age of ca. 27 months (Fernandez-Duque 2009), and we never witnessed any solitary floaters younger than this (Huck et al. 2011). In the following paragraphs, we refer to "dispersal", even when an unknown proportion of these "dispersals" may in fact be deaths. We did not include cases where both parents had been replaced because of low sample size ($N=5$). If more than one male or one female had been replaced, we considered only the first replacement (three groups, seven offspring).

To determine age-related probability of dispersal and average age at dispersal for stable groups ($N=26$ individuals), groups with male ($N=15$) and with female replacement ($N=17$), we employed the statistical survival analysis approach (Crawley 2007) that considers censored data. We first determined which "survival" distribution best described the age-specific probability of dispersal. Of the nine models with different hazard functions (extreme, logistic, Gaussian, Weibull, exponential, Rayleigh, log-Gaussian, log-normal, log-logistic, t), we chose the one minimizing the error deviance. This was the log-Gaussian function. The difference among models was not always significant when comparing them in an ANOVA (following suggestions in Crawley 2007), with the biggest difference in the error deviance being compared to the logistic function (deviance=108.2, $p \ll 0.001$), and no difference between the log-Gaussian and the log-normal function (deviance=0, $p=1.0$). Different models led to qualitatively similar conclusions, showing that the choice of hazard function did not influence our results.

Sex-specific dispersal (prediction 2.1c vs. 2.2c; see Table 1)

We compared the mean age at dispersal of nine females and eight males in groups where a replacement of either the same-sex or the opposite-sex parent had taken place

(with no restriction to when the replacement took place relative to the offspring's age) using Mann–Whitney U tests. For females, we also compared the time lag between the replacement of either the mother or putative father and the time of dispersal. For males, this analysis was not possible due to low sample sizes ($N=3$ and $N=2$ for female and male replacements, respectively). We used only females that had already left their groups (i.e., we did not include censored data), and we excluded a case of a sub-adult female and male that had died in their groups.

Behavior (prediction 2.2d)

For groups in which a replacement took place and the intruder was of the opposite sex of an offspring, we compared interactions of same-sex parent and offspring during two periods: (1) 10 months before the replacement and (2) the period between replacement and dispersal of the offspring or the last 10 months before the dispersal if the period between replacement and dispersal was longer than this. For comparison, we also analyzed the data for stable groups in the 10 months before dispersal. We chose 10 months, the average time lag between replacements and dispersal, to have a sufficiently large number of focal samples for each period while minimizing the inclusions of periods when interactions may not have been influenced by a possible future dispersal. We used data on inter-individual distances and identity of the nearest neighbor as an indicator for the quality of the relationship; the small number of events of grooming and other socio-positive and agonistic interactions prevented quantitative analyses of these variables. We calculated for each focal sample the proportion of sampling points that the offspring and same-sex parent were nearest neighbors, "close" (body contact to 1 m) or "far" (>5 m), and then calculated an average per individual. We only used data from individuals for which we had at least five focal samples.

We compared, using Mann–Whitney U tests, the median proportion of "times" (i.e., sampling points) that a same-sex parent was nearest neighbor before the replacement of the opposite-sex parent with the proportion of times it was nearest neighbor after the replacement and before the dispersal of the offspring. We used a non-parametric test because data were not normally distributed, even after transformation of the data. Similar analyses were conducted for the proportion of times of "close" and "far" distances between offspring and same-sex parent. Matched-pair comparisons were not possible because we did not have sufficient data during both periods for all individuals. Sample sizes were not adequate for analyzing female and male offspring separately.

Case study: “Enrique”

Sub-adults often undertake short (a few hours to a few days) excursions out of their natal groups’ territory before dispersing (Fernandez-Duque 2009). We report here on the only observed case of a dispersing sub-adult returning to the group after 3 months of ranging solitarily. Around the timing of his natal dispersal, but while still in the group, his mother was replaced. When he returned, he lived in his natal group again for three more months before he was evicted by his putative father. We used the date of his “first” dispersal to calculate his age at dispersal. For the behavioral analysis, we used data of the relationship between him and his father before the first dispersal (and the replacement of his mother) and compared them to data gathered after he returned and until his final dispersal.

Results

Survival (predictions 1.1a vs. 1.2a; Table 1)

There was no marked effect of replacements on the survival of infants and juveniles. Regardless of whether they lived in stable groups, or had experienced a male or female replacement, roughly half of all infants or juveniles disappeared from their natal groups (G test, $G_{\text{corrected}}=0.92$, $df=2$, $p=0.63$; Fig. 1). There was no strong evidence either that infants were more likely to die when the male was replaced before the infant was 6 months old than in stable groups. After male replacements, one infant died at 4 months and one at 23 months of age, while one infant survived at least

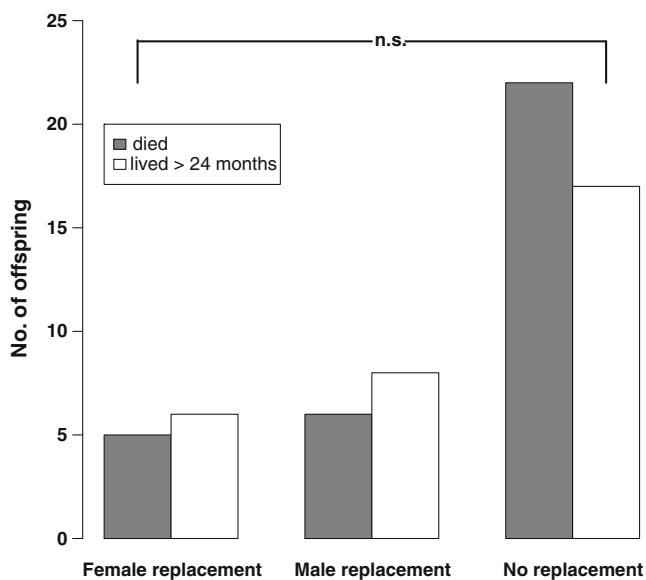


Fig. 1 Number of infants or juveniles that died or disappeared before the age of 24 months, or that survived at least until that age in stable groups and in groups with male or female replacement

44 months (male replacement before birth). The fourth case involved a female replacement when the infant was only 1 month old and resulted in the death of the infant. After very early female replacement, one infant died (see above) and one infant whose mother was replaced when it was 4.4 months old survived for 16 more months. In stable groups, nine infants and 23 juveniles died, whereas 20 individuals survived to an age older than 24 months (Fisher extension test, $p=0.84$).

Dispersal (prediction 1.1b vs. 1.2b; see Table 1)

The stability of the group was not related to the probability of dispersal. The proportion of individuals remaining in their natal group with increasing age did not differ between animals from stable groups (mean age at dispersal $\bar{d}=37.5$ months, $n=26$ individuals), groups with female replacement ($\bar{d}=40.5$ months, $n=17$), or groups with male replacement ($\bar{d}=35.3$ months, $n=15$; survival analysis with censored data, using log-Gaussian hazard distribution, $\chi^2=2.3$, $df=2$, $p=0.32$; Fig. 2).

Sex-specific dispersal (prediction 2.1c vs. 2.2c; see Table 1)

For males, the median age at dispersal was younger after the replacement of the mother than after the replacement of the putative father, still the difference was not statistically significant (Mann–Whitney U test, $W_{6,3}=12$, $p=0.55$; Table 2). On the other hand, females’ age at dispersal was not related to whether the mother or putative father had been replaced

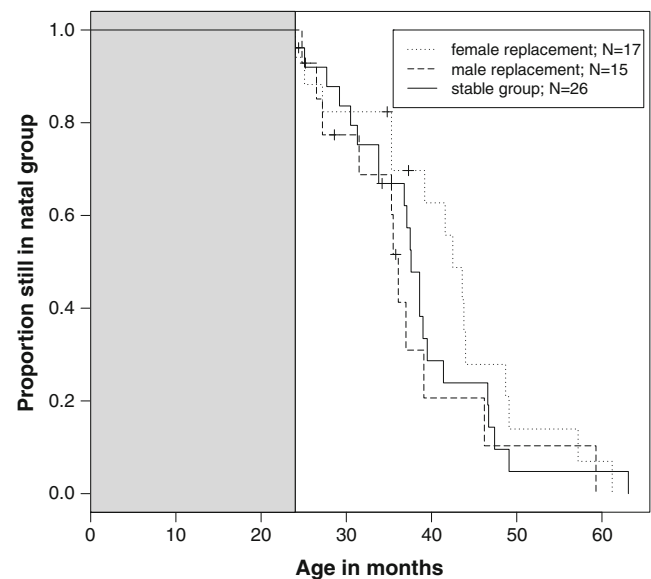


Fig. 2 Proportion of offspring that are present in their natal group with increasing age for groups with male (striped line) or female (dotted line) replacement and without replacement (solid line). The light gray shaded area signifies that only individuals that reached at least 24 months were considered

Table 2 Median sex-specific age (months) at dispersal (upper and lower quartile; sample size) depending on the whether there was a replacement or not, and on the sex of the intruding adult

Sex infant \ sex intruder	Female	Male	Stable group
Female	43.6 (37.3–46.3; 7)	<i>40.8 (35.4–49.4; 4)</i>	37.1 (35.5–38.1; 7)
Male	<i>42.7 (29.2–47.8; 6)</i>	31.5 (29.4–33.8; 3)	40.0 (36.0–46.9; 8)

The cells with italicized values show the ages when the intruder was of the opposite sex of the young

($W_{7,4}=13.5$, $p=1.0$, Table 2). However, female offspring clearly dispersed sooner after the replacement of the mother (i.e., had a shorter “time lag” between replacement and dispersal) than when a step-father entered the group [median time lag for female replacement (lower and upper quartile)—2.5 (2.2–3.4), $N=6$; male replacement—10.9 (9.7–16.8), $N=4$; $W=24$, $p=0.009$; Fig. 3].

“Enrique”

Enrique left his natal group at the relatively old age of 51.5 months. The day before he left, his mother was missing from the group, and the next time the group was encountered a new adult was in the group. Unlike other dispersing individuals, Enrique returned to his natal group approximately 3 months later. Short excursions of several hours or even a few days of sub-adults have been witnessed before,

but never excursions lasting several months. Enrique stayed with his putative father, step-mother, and younger sibling for another 3 months upon returning. On two successive days at the end of this period, he was observed copulating with his step-mother. On the second occasion, his putative father behaved very aggressively (biting) towards him after the copulation, chasing him even to the ground and wounding him, and later also defecating and urinating on him, while Enrique did not defend himself. That same afternoon, Enrique left the group and ranged again as a floater in the study area for 7 months before he was found dead. Enrique and the putative father were relatively often nearest neighbors before the first natal dispersal, as well as after Enrique returned to the group. Apart from the final days in his group, we never witnessed any particular aggression between them.

Behavior (prediction 2.2d; see Table 1)

Offspring were less frequently the nearest neighbor of their same-sex parent after the intrusion of a new adult than before the replacement (median=13% vs. 39%; Mann–Whitney U test— $W_{4,6}=1$, $p=0.025$, Fig. 4). Offspring were also less frequently the nearest neighbor of their same-sex parent after intrusion than offspring in stable groups before dispersal, although this difference was only significant after excluding the outlying data point “Enrique” (13% vs. 28%; including “Enrique”— $W_{4,6}=4$, $p=0.11$; excluding “Enrique”— $W_{4,5}=0$, $p=0.019$; Fig. 4). There is no difference between the relationship of same-sex parents with their pre-dispersing offspring from stable groups compared to immatures before a replacement took place ($W_{4,4}=14$, $p=0.11$; Fig. 4).

After replacements by opposite-sex adults, offspring were less often very close to their same-sex parent than before the replacement (17.6% vs. 29.5%; Mann–Whitney U test— $W_{8,6}=4$, $p=0.008$), but there was no difference for offspring in stable groups (17.6% vs. 18.9%; $W_{8,5}=16$, $p=1.0$), or between stable groups and groups before replacement ($W_{5,6}=20.5$, $p=0.09$; Fig. 5a). The proportion of time when offspring were far away (more than 5 m) from their same-sex parent did not differ between offspring in stable groups or in opposite-sex replacement groups before or after replacement (35.3%, 18.8%, and 26.8%, respectively; “before” vs. “after”— $W_{6,8}=32.5$, $p=0.30$;

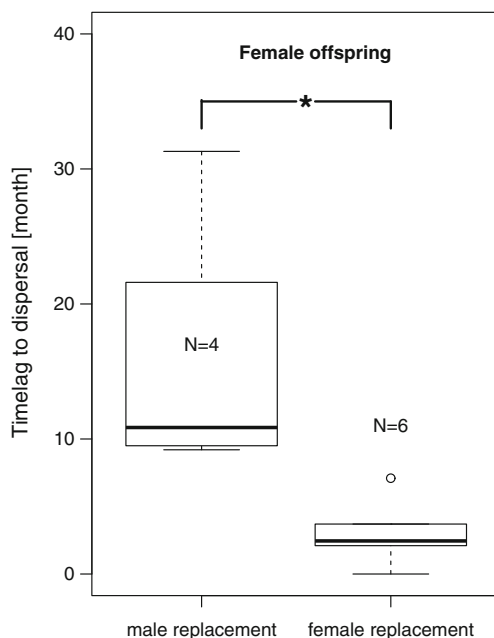


Fig. 3 Time between the replacement of the mother or the putative father and the subsequent dispersal of young female owl monkeys. Box plots show the median and inter-quartile range, while whiskers show the range except for outliers that are more than 1.5 times the inter-quartile range away from the median. Asterisk (*) denotes significant difference (see text for details)

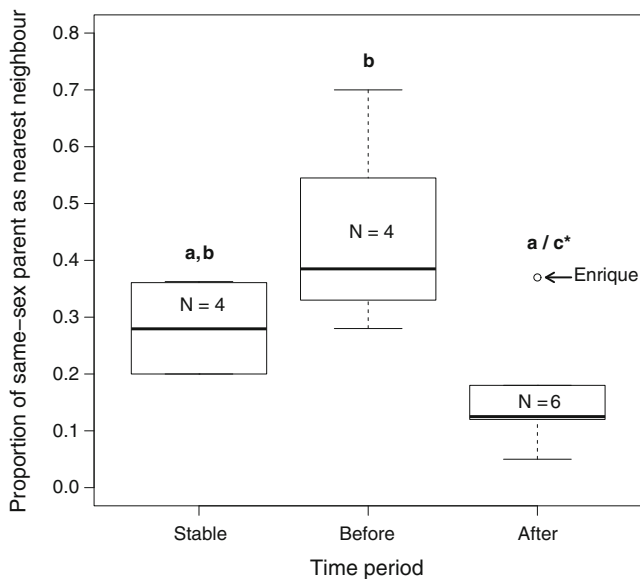
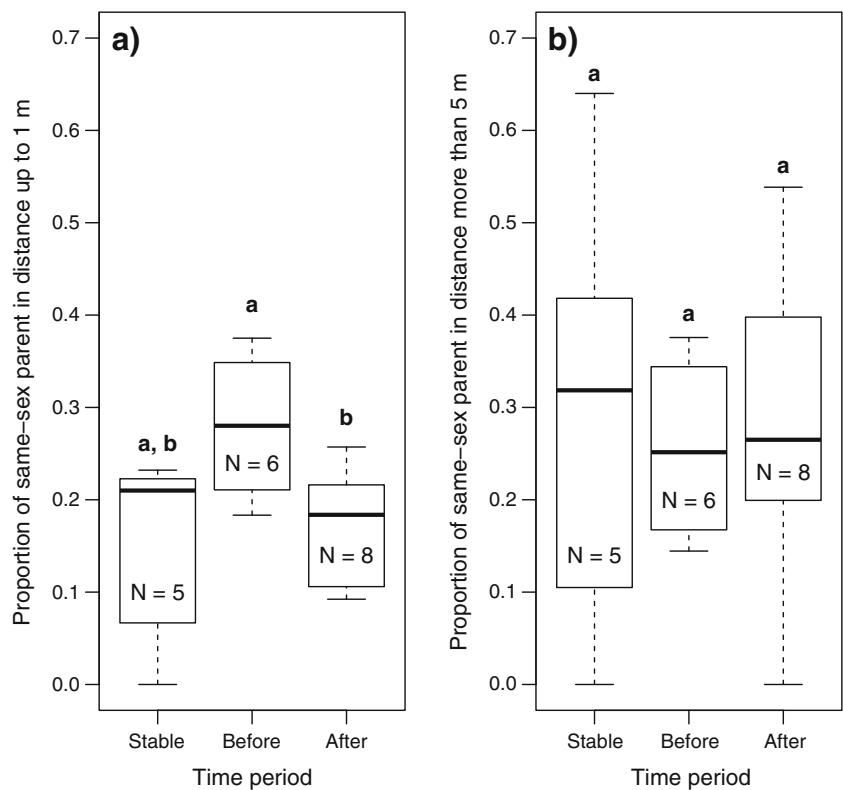


Fig. 4 Proportion of instantaneous scans when the offspring and the same-sex parent were nearest neighbors in stable groups, 10.3 months before the replacement, and the time period after the replacement until the dispersal or disappearance of the offspring. Different letters above the boxes signify statistical differences. Box plots show the median and inter-quartile range, while whiskers show the range except for outliers that are more than 1.5 times the inter-quartile range away from the median. a/c* the difference is only significant if excluding the outlying data point “Enrique” (see text for details)

“stable” vs. “after”— $W_{5,8}=13.5, p=0.73$; “stable” vs. “before”— $W_{5,6}=6.5, p=0.30$; Fig. 5b).

Fig. 5 Proportion of instantaneous sampling points when the offspring and the same-sex parent were in a distance **a** up to 1 m or **b** more than 5 m, in stable groups and in groups with opposite-sex replacement 10.3 months before the replacement, and the time period after the replacement until the dispersal or disappearance of the offspring. Box plots show the median and inter-quartile range, while whiskers show the range. Different letters above boxes signify statistical differences



Discussion

Effect of replacements on infant survival and age of dispersal

Adult owl monkeys did not mistreat unrelated infants or juveniles when they entered a new group, in sharp contrast to many other species (hanuman langurs *Semnopithecus entellus*, Sommer 1994; lions *Panthera leo*, Packer 2000; brown bears *Ursus arctos*, Fernández-Gil et al. 2010). The lack of effect of replacements on immatures is also in contrast to recent findings for leaf monkeys (*Trachypithecus leucocephalus*) where females wean offspring abruptly after male take-overs since these often lead to infanticide (Zhao et al. 2011). Our finding is supported by data showing that the probability of survival until sub-adulthood was roughly 50%, regardless of whether the group was stable or the mother or putative father had been replaced. It should be noticed, however, that only on eight occasions the observed replacements took place while the offspring was still an infant. Although it is possible that a negative effect of a male replacement might only manifest itself when there are young infants in the groups, anecdotal evidence does not support this objection. On one occasion, we observed an intruding male contributing to infant care, carrying, and interacting socially with the infant in much the same way as any putative father regularly does (Fernandez-Duque et al. 2008). Furthermore, even those infants that died after male replacements survived usually several months. It

could be argued that male replacement does not affect infant survival because the mother or older siblings compensate, and that the intruder does in fact not participate in the rearing of a step-child. However, this is not likely since our data suggest that step-fathers care for infants in a very similar way as fathers do (Fernandez-Duque et al. 2008) and that a single mother was not able to fully compensate the mate's carrying effort (Huck and Fernandez-Duque 2011).

The intense infant care male owl monkeys are famous for is most conspicuous, and probably most costly, during infancy. While juveniles are still more closely associated with the putative father than the mother, the costs of providing paternal care at this stage are probably low once the immature is moving independently. Hence, historically, there might have been little selective pressure against infant care behavior in males. Infanticide, for example, would not offer the selective benefits it may have in other species (Hrdy 1974; Sommer 1994; Packer 2000; Fernández-Gil et al. 2010) because the necessary conditions are not met: female owl monkeys in the Argentinean Chaco do not resume cycling after the loss of an infant, but have to wait for the next breeding season 1 year later and, if infants survive, females can still have offspring every year. Replacements did not hasten the dispersal of immatures either, which usually occurred between three and a half and 4 years of age both in stable and in replacement groups (see also Fernandez-Duque 2009). Similarly, in white-faced capuchins (*Cebus capucinus*), natal dispersal by males is not triggered by replacements of adult males (Jack and Fedigan 2004). In contrast, in some birds like the Seychelles warbler (*Acrocephalus sechellensis*) or some primates like the purple-faced langurs (*Trachypithecus vetulus vetulus*, formerly *Presbytis senex senex*) or grey langurs (*Semnopithecus entellus*), the intrusion of new adult males can lead to the peripheralization and subsequent dispersal of sub-adult group members (Rudran 1973; Boggess 1980; Eikenaar et al. 2007).

Together, these results argue against the hypothesis that male infant care behavior in owl monkeys serves solely the purpose of promoting the fitness and welfare of own offspring. While it is possible that owl monkeys are simply not able to recognize kin and that the observed step-parental care is misdirected and maladaptive behavior, we doubt this apparently simple explanation on two grounds. Firstly, about half of all offspring (51.5%, 38 out of 75) lived at some point before dispersal with at least one step-parent, and for juveniles the percentage is still quite high (37%, 19 out of 52). It seems a very high proportion of “misdirected” care to be evolutionary stable. Secondly, animals do not need sophisticated mechanisms to discriminate kin, but relatively simple rules of thumb like “treat any infant that has been born at least 5 months after you entered the group as kin, and all other infants as non-kin” are sufficient for adaptively

kin-directed behavior to evolve (reviews in Tang-Martinez 2001; Rendall 2004; Aktipis and Fernandez-Duque 2011). Other monkeys, like hanuman langurs, clearly treat infants differently depending on whether they have been resident at the time of conception or not (Hrdy 1974; Sommer 1994). A relatively simple mechanism of treating familiar animals differently is consistently found in primates (reviewed in Rendall 2004). Thus, we think the results rather suggest that male care might, additionally to direct benefits for genetically related offspring, be employed as a mating strategy. In a theoretical model tested on the golden egg bug *Phyllomorpha laciniata*, Härdling and Kaitala (2004) showed that caring for others' offspring can be a stable strategy for males, if a caring male does not lose, but rather gains mating opportunities. Among olive baboons as well, Smuts and Gubernick (1992) showed that males who carry and share food with infants unlikely to be their offspring gain increased sexual access to the infants' mothers. The evidence for male care serving a mating strategy in callitrichid monkeys is more disputed. While Price (1990) found some evidence that male cotton-top tamarins (*Saguinus oedipus*) were more often copulating with females while carrying infants than when not, these results were not repeated by Tardif and Bales (1997) for either cotton-top tamarins (*S. oedipus*) or common marmosets (*Callithrix jacchus*). Although a more conclusive test of whether female mate choice is influenced by the quality of paternal care is necessary, the data required are not yet available nor will they be easy to collect during observational field work. Additional support for the mating-strategy hypothesis would be obtained from showing that step-parents maintain between them similar proximity than genetic parents. Unfortunately, a sufficient number of sex-specific step-parent–offspring pairs are not yet available.

Infant care as a mating strategy is, however, not the only possible explanation for step-parental behavior. A non-mutually exclusive benefit of male care is to relieve the female of her burden such that she will be in a better condition for the next breeding attempt (Stallcup and Woolfenden 1978; Austad and Rabenold 1986; Price 1992a, b; Sánchez et al. 1999; Achenbach and Snowdon 2002; Morcillo et al. 2003; Kingma et al. 2010). Energetic costs are extremely difficult to measure in the wild, and no data on energy expenditure during lactation and carrying are available for owl monkeys. The important point made by our data, though, is that care is not exclusively directed to genetically related immatures.

Sex-specific effects of replacements on dispersal

According to the Evolutionary Theory of the Family (EFT, Emlen 1995, 1997), the replacement of an opposite-sex

parent can generate mating opportunities for sub-adult and young adults, but can also increase competition for the new adult as mating partner. If new mating opportunities had a strong influence on age at dispersal, we should see delayed dispersal of individuals whose opposite-sex parent had been replaced. This pattern is, for example, observed in stripe-backed wrens (*Campylorhynchus nuchalis*) where subordinate males were less likely to disperse if their mother had been replaced by another female (Piper and Slater 1993). We did not find such an effect in our population. However, due to the small sample size, it was not possible to consider other influences that might have affected the results. For example, the age at replacement is likely to play a significant role. Group size is also likely to influence dispersal decisions of sub-adults, but we have no reason to believe that the different group types (stable, female or male replacement) are biased in any particular way with respect to group size, so that we do not believe that could have influenced our results much. More suggestive, and according to the prediction, is the result that the time lag between the replacement and the dispersal event is much longer for young females after the entering of a new male than after the immigration of a step-mother.

Overall, our results offer weak support for the prediction that opposite-sex step-parents offer mating opportunities for offspring from the intruder's predecessor. The repeated copulations between "Enrique" and his step-mother provide additional support to this conclusion. It should be kept in mind, however, that the virtual absence of single-parent groups (with the notable exception reported above, see also Huck and Fernandez-Duque 2011) does not allow to tear apart effects on the dispersal behavior of sub-adults due to the absence of the parent and those due to the presence of a step-parent.

Sex-specific effects of replacements on relationships

The predictions of the EFT with respect to the relationship between same-sex parents and their offspring after the intrusion of a new adult were better supported by our data. If spatial association is indeed an indicator of the quality of the relationship between offspring and same-sex parent, then the relationship deteriorated after the intrusion of a new opposite-sex adult. Same-sex parents were more frequently the nearest neighbor before the replacement than after, and were also more often at a close distance. However, these results are not yet conclusive evidence since it could be partly explained by increasing distances between parents and offspring with increasing age. Yet immatures and their same-sex parent were also more often nearest neighbors in stable groups than in groups after the replacement of the other adult. The effect size (15%) is rather large even if the difference failed to reach statistical significance; moreover,

the statistical non-significance is due to a single outlier of a young male ("Enrique", Fig. 3) who was relatively often nearest neighbor to his putative father. Still, the distances, even between nearest neighbors, seem to increase with age since there was no difference in the frequency of close contact between same-sex parent–offspring pairs in stable groups and after the replacement of the other adult. Offspring and their same-sex parents were also not more often far away from each other, but since owl monkey groups are very cohesive and any two individuals rarely more than 5–10 m apart, the measure "far" probably does not reflect relationships between individuals as well as who is the nearest neighbor.

The interactions between Enrique and his putative father illustrate that parent–offspring conflict over a potential mate after the replacement of the opposite-sex parent occurs in owl monkeys. Furthermore, the conflict can even take the form of very aggressive interactions that in captivity are known to have led to the death of one of the individuals (H. Erkert, personal communication). Nonetheless, platyrrhines are generally rather peaceful (Fernandez-Duque 2011a) when compared to Old World monkeys, and it has been noted before that levels of agonistic interactions are too infrequent to allow quantitative analyses in other New World primates (Caine 1993; Huck et al. 2004). In primates, proximity measures have been regularly used to assess the quality of social relationships (e.g., Cords 1997; Silk et al. 2006), and it has been shown that inter-individual distances increase with increasing rates of aggression in a variety of species in other taxonomic groups (e.g., hens *Gallus gallus*, Kent 1992). Thus, our assumption that inter-individual distances reflect the quality of a relationship is reasonable and our results indicate that, as predicted by the Evolutionary Theory of the Family (Emlen 1995), relationships between offspring and the same-sex parent tend to deteriorate after a replacement.

Conclusions

Theoretically, new opportunities for mating or increased mating competition can be expected after the replacement of an opposite-sex parent. In the case of owl monkeys, both possibilities are at least partly supported by our data. Overall, however, the balance seems to be shifted towards benefiting the remaining parent more than the offspring: while the female offspring apparently stay longer in their natal group in the presence of an opposite-sex step-parent, this will probably rarely enable them to form a long-lasting mating relationship with the step-parent. As the example of Enrique shows, even if tolerated as long as no matings are attempted, this tolerance might quickly give way if a copulation is attempted. Despite the clearly aggressive expulsion

of Enrique, the usual lack of visible aggression between parents and offspring does not allow us to speculate on whether intra-sexual aggression of parents towards their same-sex offspring is a general proximate mechanism to maintain social monogamy in owl monkeys, as it has been suggested for gibbons (see also review by Tilson 1981; Brockelmann et al. 1998).

Clear distinctions are further complicated because the relationship between parents and offspring are not only dependent on potential competition for mates but also on various other factors. For example, there may be an optimal group size that is a compromise between food competition and anti-predator benefits (van Schaik 1983; Majolo et al. 2008). In relatively small groups, parents might be more tolerant towards their same-sex offspring after replacements than in large groups, thus potentially masking the effect of mate competition. Furthermore, the outcome of parent–offspring conflict for potential mates also depends on the dominance relationships between parent–offspring on the one hand, and remaining adult and intruder on the other. Owl monkeys being a sexually monomorphic species (Aquino and Encarnación 1986; Fernandez-Duque 2011b; Huck et al. 2011), the differing interests between the remaining parent and the intruder might not be as easily detected as in more dimorphic species, leading to more ambiguous results.

Summarizing, young owl monkeys do not seem to suffer from the replacement of either parent, lending some support to the notion that male care does partly serve as a mating strategy in the species. Intriguingly, immatures occasionally even live (and survive to sub-adulthood) with two step-parents, but our data did not allow to explore this any further. The results on sex-specific effects on age at dispersal and on the relationships to the same-sex parent are less straight-forward but still suggest that replacements can lead to mate competition between parents and their same-sex offspring, as predicted by the Evolutionary Theory of the Family.

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