Infant Mortality in Black-and-Gold Howlers (Alouatta caraya) Living in a Flooded Forest in Northeastern Argentina

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Abstract Ecological and social factors have a significant effect on infant survivorship in nonhuman primates. We present 6293 group-months of infant birth and mortality data for 29 groups of *Alouatta caraya* inhabiting a flooded forest in northeastern Argentina, collected over 1.5–8 yr depending on the group. We tested whether infant mortality was a response to the effects of flooding on food availability and whether male takeovers resulted in greater opportunities for infanticide. During our study, 43 of 113 infants died at a mean age of 5 mo. In 24 cases the cause of death was unknown. In the remaining 19 cases infant deaths were attributed to periods of intense flooding ($N=8$), replacement of the breeding male ($N=8$), problems associated with birth ($N=2$), and injuries during an intergroup encounter ($N=1$). Flooding reduced the availability of mature leaves, which appeared to play an important role in the ability of mothers to nurse their offspring. Male replacements occurred in four social groups that contained only one fully adult male. Infant mortality was significantly higher in groups that experienced male replacement compared to groups without male replacement. These results indicate that infant mortality in *Alouatta caraya* is affected by several factors—natural disasters, maternal condition and food availability, infanticide after male replacement, and possibly disease and predation—each of which needs to be evaluated to understand the history and demography of this primate population.

Keywords *Alouatta caraya* · Flooding · Infanticide · Male replacement · Social strategies

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Introduction

Ecological and demographic changes in the size and composition of primate social groups occur over a range of temporal scales and have both immediate and persistent effects on individual and group behavior (Strier 2007). Long-term demographic studies provide insights into how ecological conditions, population dynamics, and reproductive characteristics affect primate life history traits and individual responses to changes in the social environment (Altmann 1998; Cheney *et al.* 2004; Ramirez Llorens *et al.* 2008).

As in other vertebrates, infancy in nonhuman primates is assumed to be a period of great risk and high mortality (Charnov 1993; Cheney *et al.* 2004; Froehlich *et al.* 1981). Infant mortality in wild populations of nonhuman primates may result from a decrease in the seasonal availability of foods required by the infant's mother, leading to a decrease in milk production (Roberts *et al.* 1985); a decrease in food availability caused by natural disturbances such as cyclones, droughts, and floods (Cheney *et al.* 2004; Dittus 1988; Gould *et al.* 1999; Pavelka *et al.* 2007; Tecot 2010); immature development of the infant's immune system resulting in an increased susceptibility to diseases or parasite loads (Brain and Bohrman 1992; Holzmann *et al.* 2010; Kalema-Zikusoka *et al.* 2002; Kuntz 1982); elevated levels of predation risk (Boinski 1987; Isbell *et al.* 2009; Miller and Treves 2011; Nishida *et al.* 1985; Oversluijs Vasques and Heymann 2001; Sampaio and Ferrari 2005); conditions promoting opportunities for infanticide (Cords and Fuller 2010; Crockett 2003; Fedigan 2003; Sherrow and Amsler 2007; Swedell and Tesfaye 2003; Valderrama *et al.* 1990; Van Belle *et al.* 2010; Watts *et al.* 2002; Zunino *et al.* 1986); maternal age or inability of inexperienced mothers to care for their offspring (Cheney *et al.* 2004; Clarke and Glander 1984); changes in female dominance resulting in increased infant kidnapping (Isbell *et al.* 2009; Shopland and Altmann 1987); and random accidental events such as falls (Nakamichi *et al.* 1996; Serio-Silva and Rodriguez-Luna 1994).

Infant mortality in the genus *Alouatta* is reported to be 21–35 % (Table I). Across several howler populations, infanticide associated with changes or replacement of the breeding male, resulting either from a takeover or a change in male dominance hierarchy, is the most easily identified cause of infant mortality (Crockett 2003; Crockett and Janson 2000; Knopff *et al.* 2004; Van Belle *et al.* 2010), although other factors such as natural disturbances (Pavelka *et al.* 2007), susceptibility to disease (Holzmann *et al.* 2010), and predation (Boinski 1987; Miller and Treves 2011) may be more difficult to document. A total of 70 cases of infant disappearance associated with infanticide have been reported in five species of howlers: *Alouatta caraya*, *A. guariba*, *A. palliate*, *A. pigra*, *A. seniculus* (Crockett 2003; Knopff *et al.* 2004; Van Belle *et al.* 2010). Leland *et al.* (1984) suggested that infanticide as a consequence of male replacement is more likely to occur in unimale–multifemale groups than in multimale–multifemale groups because groups with only a single adult male are more vulnerable to attack and takeover. Similarly, Treves (2001) proposed that howler groups characterized by higher proportion of adult and subadult males, relative to adult and subadult females, experienced greater reproductive success because groups with several males provide enhanced protection against invasion by extragoup males.

We here present data collected over an 8-yr period on infant mortality in a population of wild black-and-gold howlers (*Alouatta caraya*) living in a flooded

Table I Infant mortality in different species of *Alouatta*

Species	No. of groups	Infant mortality (%)	Study site	Study period	Reference
A. caraya	11	35	Area de Rio Riachuelo, Argentina	January 1982–November 1984 (monthly or bimonthly census)	Rumiz 1990
A. caraya	15	30.4	Area de Rio Riachuelo, Argentina	September 1987–May 1990 (monthly census)	Zunino 1989
A. palliata	1	34	La Pacifica, Costa Rica	August 1970–August 1981 (discontinuous census)	Clarke and Glander 1984
A. palliata	12-34	30	Santa Rosa, Costa Rica	1985–1992 (annual census)	Fedigan *et al.* 1998
A. palliata mexicana	1	33.3	Las Tuxtlas, Mexico	February 1996–August 2003 (monthly census)	Arroyo-Rodriguez 2008
A. seniculus	43	21.2	Hato Masaguaral, Venezuela	June 1976–February 1981 (monthly census)	Crockett and Rudran 1987b

forest in northeastern Argentina. The study site, Isla Brasilera, is an island characterized by continuous forest located near the confluence of the Paraná and Paraguay Rivers. Isla Brasilera experiences annual flooding of variable intensity and duration (Neiff 1990). During intense flooding of the Paraná River, water covers much of the islands, resulting in a significant decrease in the availability of leaves, flowers, and fruits in the forest canopy (Aceñolaza *et al*. 2010). Previous studies of this howler population indicate that mulitmale–multifemale groups (44.4 %) are common, neighboring groups overlap in home range area by up to 75 %, and intergroup encounters, although frequent (1–2 per day), rarely involve physical aggression (Kowalewski 2007; Kowalewski and Zunino 2004; Kowalewski and Garber 2010). To examine questions concerning factors affecting infant mortality in this howler population we tested the following hypotheses and predictions: 1) If infant mortality is a response to the effects of flooding on food availability (Cheney *et al*. 2004; Dittus 1988; Gould *et al*. 1999), then we expect higher infant mortality in this population during or immediately after periods of intense flooding. 2) If male takeovers result in greater opportunities for infanticide (Janson and van Schaik 2000; Leland *et al*. 1984; Treves 2001), then we expect increased rates of infant mortality to occur in the context of male replacements and to be more common in unimale–multifemale or age-graded male–multifemale groups compared to multimale–multifemale groups.

Materials and Methods

Study Site

We studied a population of *Alouatta caraya* inhabiting Isla Brasilera, Argentina (27°18′S, 58°38′W). The island covers an area of 292 ha and is located near the

confluence of the Paraná and Paraguay Rivers. The climate at this site is subtropical, with a mean annual temperature of 21.6 °C and a mean annual rainfall of 1200 mm (Servicio Meteorológico Nacional de Argentina). The area experiences at least one flooding event annually. Flooding events vary in intensity and duration, lasting from a few days to several months (Neiff 1990). In unusual years, the island may be flooded year round (Franceschi and Lewis 1979). Major floods occurred during 1982–1983, when water covered the island for an entire year, and 1997–1998, when water remained for up to 6 mo. According to studies conducted before and immediately after the flooding of 1997–1998, water levels did not alter plant species richness or the floristic composition of the forest (Kowalewski and Zunino 2004). During our study period (April 2003–November 2010) we recorded four flooding events on Isla Brasilera (January–February 2004, September 2005, January–May 2007, and November 2009–June 2010). During the floods of January–February 2004 and September 2005 we were able to continue observing the howlers because the maximum water level in the lowest parts of the island reached a height of only 0.70 m. During January–May 2007 and November 2009–June 2010, flooding was extreme and the water level rose to a height of *ca*. 2 m across the highest parts of the island, but did not cover the tops of the trees in the lowest parts of the island. During the 2009–2010 flooding period it was impossible to reach the study site for 8 mo. In general, the forest of Isla Brasilera provides howlers with an abundant and stable year-round supply of leaves and fruits and supports a mean population density of 3.25 individuals/ha (Kowalewski and Zunino 2004). The howler population of the island is not a closed system; there are migrations between the island and the mainland because howlers cross the river, mainly during flooding events. The island does not have permanent human settlements. Potential predators of immature howlers at this site include the crab-eating fox (*Cerdocyon thous*), jaguarondis (*Herpailurus yaguarondi*), yellow anaconda (*Eunectes notaeus*), and domestic dogs. Howlers are potentially exposed to these predators when they descend to the ground to feed and to drink water present in lagoons. A more complete description of the site can be found elsewhere (Kowalewski 2007; Kowalewski and Garber 2010; Kowalewski and Zunino 2004).

Focal Subjects

On Isla Brasilera, howlers live in multimale–multifemale (44.4 %), unimale–multifemale (37 %), and age-graded male–multifemale groups (18.6 %) (Kowalewski and Zunino 2004). Multimale–multifemale groups contain two or more fully adult males, whereas age-graded male groups have one adult male and one or more subadult and juvenile males. Female *Alouatta caraya* are polyandrous and resident females mate with all resident males of their groups as well as with extragroup males (Kowalewski 2007). At this site, births occur throughout the year (Kowalewski and Zunino 2004) and gestation lasts from 180 to 194 d (Kowalewski and Garber 2010). In a nearby study site, the mean interbirth interval (IBI), in cases in which infants survive to the first year of life, is 16±3.73 mo (Rumiz 1990). Infants are fully weaned between 7 and 12 mo of age (Kowalewski and Zunino 2004; Pavé, unpublished data). Female *Alouatta caraya* may resume nonfertile copulations once their dependent infant is *ca*. 2–3 mo of age (Pavé *pers*. *obs*.).

Demographic Data

We censused two groups (E and M) monthly from April 2003 to December 2004 and from September 2005 to September 2006. In addition, we censused 29 groups of *Alouatta caraya* monthly from October 2006 to July 2008, with the exception of February–March 2007, when an extraordinary flood prevented us from visiting the study site (Table II). During each census we recorded the age and sex of adults, subadults, juveniles, and infants as well as changes in group membership (births, disappearances, deaths or emigrations, and immigrations). We recognized the groups by their location and composition, and identified individual howlers by age, sex, and natural and/or artificial markings (color anklets, ear tags, and ear cuts). We assigned age categories following Rumiz (1990) based on genital development, estimated body size, and coloration. We defined the infant period from birth to 1 yr of age (Rumiz 1990). When an immature <24 mo of age disappeared, we assumed it had died. We based this assessment on the fact that over >10 yr of study we have never observed an individual of <2 yr of age leave or enter a group.

We also selected four social groups for intense behavioral observations and followed these groups for periods of between 14 and 37 mo between 2003 and 2010 (Table II).

Data Collection and Data Analyses

We recorded the monthly distribution of births and mortality of infants for 29 groups, by dividing the number of infants that were born or died each month by the number of adult females present in the groups observed that month. We used circular statistics (Zar 1999) in Oriana ver. 4.01 (Kovach 2012) to test for monthly peaks in infant births and infant mortality. We examined the degree to which infant mortality varied with the social structure of the group at the time of infant death/disappearance for October 2006 to July 2008, when we censused all the groups monthly. We calculated the rate of infant mortality as the number of infants that disappeared in 1 mo divided by the number of infants present the previous month. Because we normally recorded and analyzed infant mortality rate on a monthly basis but were unable to census howler groups during February and March 2007 owing to intense flooding on the island, we assigned half of the infant disappearances recorded in our census at the

Table II Type and duration of the studies howler groups on Isla Brasilera

Number of groups	Period	Study type
2 (Groups G and X)	April 2003–December 2004 (5 d/ mo/group); September 2005–September 2006 (5 d/mo/group)	Behavioral study
2 (Groups E and M)	April 2003–December 2004; September 2005–September 2006	Monthly census
29[a]	October 2006–July 2008	Monthly or bimonthly census
4 (Groups G, E, M, and X)	September 2008–October 2009 (1 d/mo/group)	Behavioral study
3 (Groups E, G, M)	August–November 2010 (1 d/mo/group)	Behavioral study

[a] Groups G, E, M, and X are included in these 29 groups.

beginning of April 2007 to February and half to March. To determine whether infant mortality during the flooding of 2007 was affected by food availability, we estimated mean monthly production of phenophases (mature leaves, new leaves, shoots, flowers, and fruits) from October 2006 to May 2008, following Kowalewski and Zunino (2004). We monitored monthly 10 trees each, from 14 different species, for presence and abundance of phenophases. We subdivided each crown into four parts, and ranked the abundance of each phenophase on a scale of 0 to 4, wherein 0 is the absence of a specific phenophase and 4 is when the crown was 100 % in the phenophase. We averaged the phenological values of the individuals of each species to obtain a Phenological Index for Species (PISp) for each date and phenophase. We calculated an index showing the relative abundance of each phenophase for each month = PISp × BASp, where BASp is basal area of species *i*. We used circular statistics to determine the mean month of the peak in food availability. We also examined whether the monthly availability of phenophases correlated with changes in infant mortality from October 2006 to May 2008.

We considered an infanticide event to have occurred when we directly observed an attack that led to an infant's death. We considered a suspected infanticide to have occurred when an infant disappeared during the first 2 mo after a new male entered the group and replaced the central male (Crockett 2003; Fedigan 2003; Izawa and Lozano 1991). We lack genetic data for most individuals in our study groups and were unable to determine the paternity of infants that died. We scored a male replacement when a new male entered an established group and challenged and expelled one or all of the resident adult males. We also included one case in which a nonresident adult male entered a group containing two subadult males and three adult females and became the central male (group G, case 5 in Appendix) as a male replacement. We calculated the rate of adult male replacement as the number of male replacements divided by the length of the study period (in months) for each group (Jason and van Schaik 2000). We compared infant mortality rates in groups with male replacements (groups E, G, PN, and X) across periods with and without male replacement following Fedigan (2003). For this analysis we compared the 3-mo period corresponding to the month of male replacement and the subsequent 2-mo period after male replacement with a comparable 3-mo period (during the same months of the year) without male replacement, to control for other sources of mortality that might be affected by season. We used χ^2 tests, Mann–Whitney U tests, and Spearman ranked order correlations. We considered $P \leq 0.05$ as the criterion for significance for all statistical tests.

All data collection adhered to the legal requirements of Argentina (IACUC protocol no. 06207) and the Dirección de Fauna y Areas Naturales Protegidas de la Provincia del Chaco, Argentina.

Results

Infant Births and Mortality

Between April 2003 and November 2010, the total number of infants born into our 29 study groups was 113. The distribution of births across the year differed from

random, with a birth peak in August (winter; Rayleigh test: births: $Z=16.365$; $P<0.001$). Of 113 births, 43 (38 %) infants died during their first 12 mo of life. The mean age at death was 5.03 mo (SD=2.98; range=1–12 mo; $N=43$). Thirty infants (69.8 %) died or disappeared within 6 mo of their day of birth. We could assign the month of disappearance for 42 infants. Infants disappeared throughout the year with the exception of August. The distribution of deaths differed from a random distribution across the year with a peak in September (spring; Rayleigh test: deaths: $Z=10.651$; $P<0.001$).

Of the 29 groups studied during the census period, 12 were unimale–multifemale (with 1–3 adult females), 4 were age-graded male–multifemale groups (with 1 adult male, 1–2 subadult males, and 3–5 adult females), 10 were multimale–multifemale (with 2–4 adult males, 0–3 subadult males, and 2–4 adult females), and 3 groups changed from multimale–multifemale to unimale–multifemale. In one of these three last groups, the central male died after falling from a tree, and one or two adult males emigrated or disappeared in the other two groups. During the census period, 86 infants were born and 32 (37.2 %) died/disappeared. Overall infant mortality was 43.2 % (19 of 44 infants died) in unimale–multifemale and age-graded male–multifemale groups and 25 % (8/32) in multimale–multifemale groups. In groups that changed from multimale–multifemale to unimale–multifemale, infant mortality was 50 % (5 of 10 infants) but none of these infants died during the period in which group composition changed. Infant mortality did not differ between unimale–multifemale plus age-graded male–multifemale and multimale–multifemale groups ($U=74.50$; $N_{1,2}=16, 10$; $P=0.77$).

Factors Associated with Infant Mortality

We were able to determine the probable cause of mortality for 19 (44 %) infants that died between April 2003 and November 2010. During this period, eight infants (18.6 %) disappeared during February–March 2007. This corresponded with a period of intense flooding that occurred from January and May of that year. Only one of these deaths was associated with male replacement: An infant of unknown sex and 1–2 mo old disappeared after a suspected male replacement. An additional eight infants (18.6 %) died during the first 2 mo after a male replacement. Two infants (4.7 %) of the same multiparous female died during the first 24 h of life (one in September 2004 and the other in October 2009); in neither case was this associated with male replacement. We examined the body of one of these infants and it was of normal size for a newborn howler (Coppo and Resoagli 1978). Finally, one infant (2.1 %) died as the result of an intergroup encounter after being attacked by an adult male from a neighboring group. We give details of observed and suspected cases of infanticide in the Appendix. We did not witness or suspect any predation events during the study period and we considered predation as an unlikely cause of infant mortality in this population.

The mean monthly infant mortality rate between October 2006 and July 2008 was 0.04 (SD=0.04; range=0–0.14; $N=20$). The highest infant mortality rates were 0.14 in February 2008, 0.1 in March 2007, and 0.09 in February 2007 (Fig. 1). Three infants disappeared after male replacements in February 2008, and eight infants disappeared during a period of intense flooding in February–March 2007.
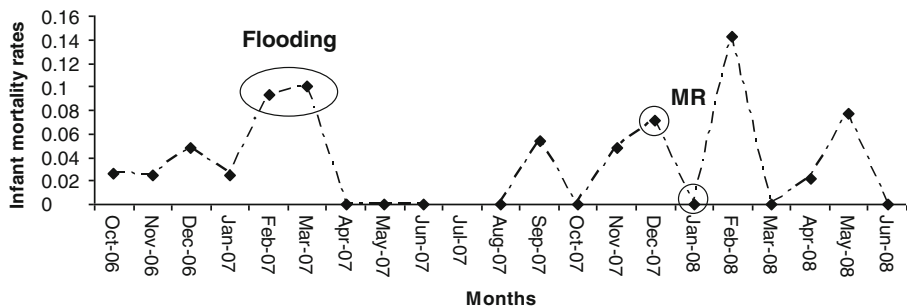
Fig. 1 Infant mortality rates to *Alouatta caraya* during the census period October 2006–July 2008. MR = male replacement.

Infant Mortality and Flooding

No infants disappeared in our four focal study groups during the floods of January–February 2004 and September 2005. During the flooding in January–May 2007 much of the island was under water, with the highest water levels during February–March, when eight infants disappeared. No adult females disappeared during this period. No infants died in April or May 2007. The next infant death after the flood was not until September 2007. The eight infants disappeared at a mean age of 4.3 mo (SD=2.71; range=1–8). Of these, five (62.5 %) were 1–4 mo, five (62.5 %) disappeared from four multimale–multifemale groups, and three (37.5 %) disappeared from three unimale–multifemale groups.
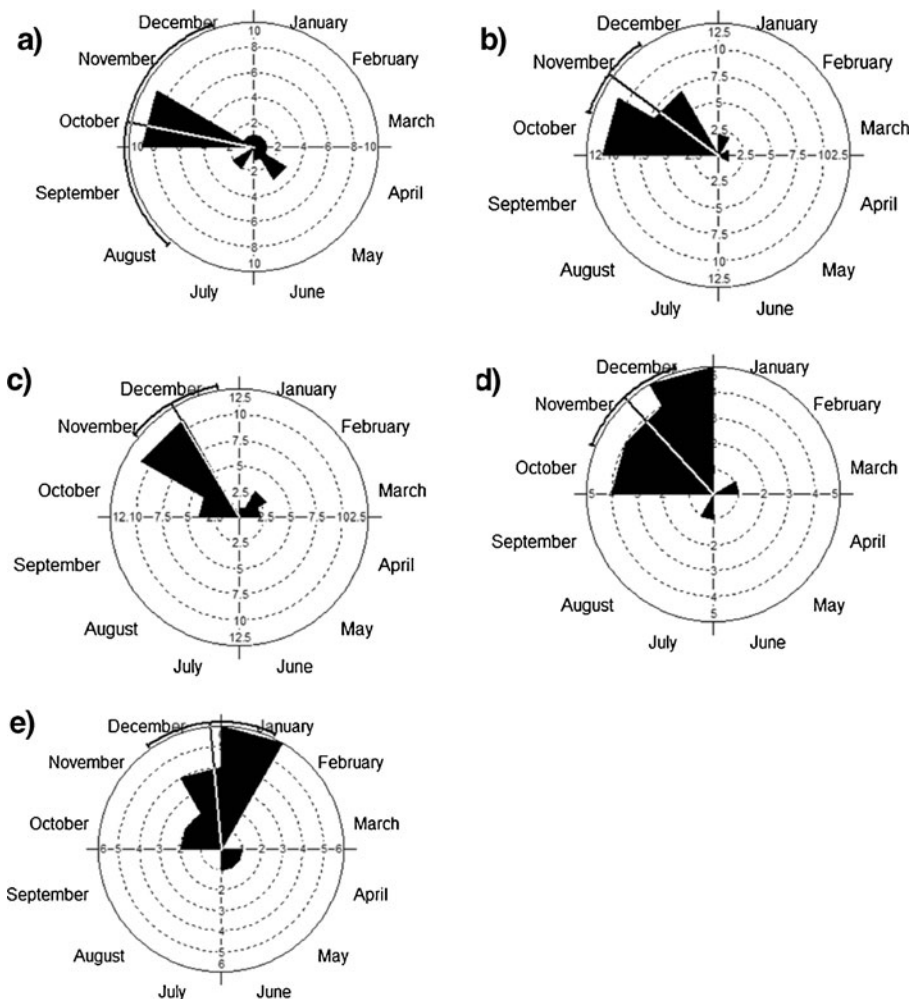
New leaf, shoot, flower, and fruit availability was extremely low during the period of intense flooding, compared to the availability of mature leaves (Fig. 2). Moreover, the availability of mature leaves decreased from January to August 2007 and the availability of this food resource in April 2007 was 33 % lower than that recorded for April 2008.

Based on an assessment of food availability over the course of 16 mo, food resources exploited by howlers exhibited a nonrandom temporal distribution, except
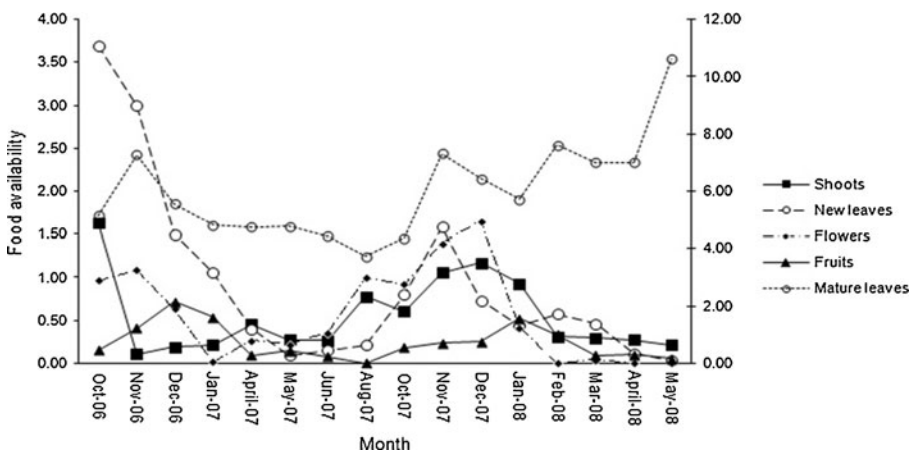
Fig. 2 Mean monthly food availability on Isla Brasilera between October 2006 and May 2008. The right *y*-axis corresponds to mature leaf availability and the left *y*-axis corresponds to the availability of other resources (shoots, new leaves, flowers, and fruits).

for shoots (Rayleigh test: mature leaves $Z=3.642$, $P<0.001$; new leaves $Z=12.414$, $P<0.001$; flowers $Z=7.965$, $P<0.001$; fruits $Z=5.664$, $P=0.002$). The production of mature leaves was greatest in November. The production of shoots, new leaves, and flowers was greatest from August through December (especially the month of November to new leaves and flowers). The production of fruits increased in November–December and reached a peak in December (Fig. 3). The production of new leaves remained low during the flooding, but overall there was no difference in new leaf availability between January–April 2007 (flooding) and January–April 2008. There was an increase in the availability of shoots from January to April 2007 (Fig. 2). There was a positive relationship between the monthly availability of mature leaves and the number of infants present each month ($N=16$; $r=0.61$; $P=0.012$). There was no relationship between the number of infants present each month

Fig. 3 Circular plots showing the distribution and the mean in the peak of shoots (**a**), new leaves (**b**), mature leaves (**c**), flowers (**d**), and fruits (**e**) on Isla Brasilera between October 2006 and May 2008.

and the availability of new leaves ($N=16$; $r=0.98$; $P=0.62$), shoots ($N=16$; $r=0.95$; $P=0.42$), flowers ($N=16$; $r=0.95$; $P=0.39$), and fruits ($N=16$; $r=0.99$; $P=0.85$).

Male Replacements and Infant Disappearances

During our 8-yr study period we monitored 29 howler groups, with a total of 6293 group-months, and observed four male replacements that occurred in four groups. Two groups were unimale–multifemale, each with two or three adult females (cases 1 and 2 in Appendix) and two groups were age-graded male–multifemale groups, each with three adult females (cases 3 and 5 in Appendix). We observed no infant disappearances associated with a male replacement in multimale–multifemale groups. The mean rate of adult male replacement was 0.02 replacements/month (SD=0.02; range=0.01–0.05; $N=4$) or about one per group every four years (Table III).

During these four male replacements, there were nine infants present in the groups and all of them disappeared. Of these, one infant of 11 mo disappeared 3 mo after the male replacement, and therefore we assigned its death to unknown causes. Seven of the remaining eight infants were born before the new adult male entering the group. The mean age of infants at the time they disappeared was 4.6 mo (SD=1.98; range=3–9 mo; $N=8$). Four infants (50 %) were <4 mo of age and none of the infants were fully weaned at the time of their disappearance (Table III). Of these eight infants, four were males, three were females, and one was of unknown sex. Given that we monitored the four groups only once or twice per month, we could not determine whether infant disappearances occurred immediately after the takeover or after several weeks. In addition, there was evidence of injury to an adult female whose infant disappeared after a male replacement in one group (the female was missing a patch of hair on her back; case 5 in Appendix).

The infant mortality rate during the 3-mo period with male replacement (0.875) was significantly higher than the rate (0.083) during the 3-mo period without male replacement ($\chi^2=65.43$; df=1; $P<0.001$). Given that extragroup males were not marked, we were able to identify the origin of the invader male in only one group (X). He was the central male of a neighboring group (Fig. 3). In the groups we studied more intensely (E, G, and X), the replacement male who was suspected of committing infanticide remained in the group for >1 yr.

The IBI after male replacement for three females whose infants disappeared at 3, 5, and 9 mo of age was 15.67 mo (SD=0.58; range=15–16 mo; $N=3$ females and IBIs). For the period without male replacement the IBI of females whose infants disappeared before reaching their first year of life (mean age=4 mo; range= 1–7 mo; $N=5$ infants) was 11.2 months (SD=2.86; range=9–16 mo; $N=5$ females, 5 IBIs). The IBI of females whose infants survived their first year of life was 14.07 mo (SD=1.87; range=11–17 mo; $N=10$ females, 15 IBIs). The IBI for females whose infants died during their first year of life (with and without male replacement) did not differ from the IBI of females whose infants survived their first year of life ($U=37$; $N_{1,2}=8$, 15; $P=0.14$). Although the sample size for IBI after male replacement is small, they represent more than half of the recorded infanticide cases (three of four).

Table III Summary of cases of disappearance or death of infant *Alouatta caraya* related to male replacement or attack on Isla Brasilera

Case no. and group	Date of MR/attack	Initial structure of group	Current structure of group	MRR	No. of adult females before MR	No. infant dead[a]	Sex and age of infants	Time between MR and dead of infants	Subsequent IBI of mothers
1: PN	December 2007	Unimale	Unimale	0.05	3	2	M: 5 mo	<1 mo	N/A
							M: 5 mo	2 mo	N/A
2: E	January 2008	Unimale	Age-graded male	0.01	3	2	F: 5 mo	1 mo	16 mo
							F: 9 mo	1 mo	16 mo
3: X	January 2008	Age-graded	Unimale	0.01	3	1 of 2 (?: 3 mo)	?: 3 mo	2 mo	15 mo
							M: 11 mo	3 mo	–
4: G/X	November 2008– January 2009	2 unimale	2 unimale	–	2 (Grit.) 2 (Xen.)	1 of 2 (M: 10 mo)	M: 20 days	–	–
							M: 10 mo		
5: G	August 2010	Age-graded male	Age-graded male	0.01	3	3	M: 3.5 mo	2 mo	N/A
							M: 3.5 mo	1.5 mo	N/A
							F: 3 mo	1 mo	N/A

M = male; F = female; MR = male replacement; MRR = male replacement rate. N/A = not available.

[a] The number of dead infants corresponds to the total of infants present in each group before the male attack or male replacement with the exception of cases 3 and 4, in which one infant survived in each group.

Intergroup Infant Attack

The only infant attack that we witnessed directly occurred in group G, a unimale–multifemale group (case 4 in Appendix). The infant was attacked on two occasions, once at 8 mo old (observed) and then at 10 mo old (inferred), when it died. The first attack occurred during an intergroup encounter and the attacker was the leader adult male of the neighboring group X. The same male was associated with the deaths of two infants in group X (9 mo earlier) during a successful group takeover. We monitored group G at that time as part of our behavioral study and this infant appeared to be in good health before the first attack. Although we did not witness the second attack, we located and collected the dead infant's body. The head had two holes in the parietal bone of the skull, consistent with an infanticidal attack (Fig. 4).

Discussion

Infant Birth and Mortality

Both infant births and infant mortality were regularly distributed throughout the year, and we found no effect of seasonality on these events. This agrees with a previous study, that also found that births in *Alouatta caraya* on Isla Brasilera occurr year-round, in contrast with a nearby (*ca.* 20 km) but more fragmented and disturbed site
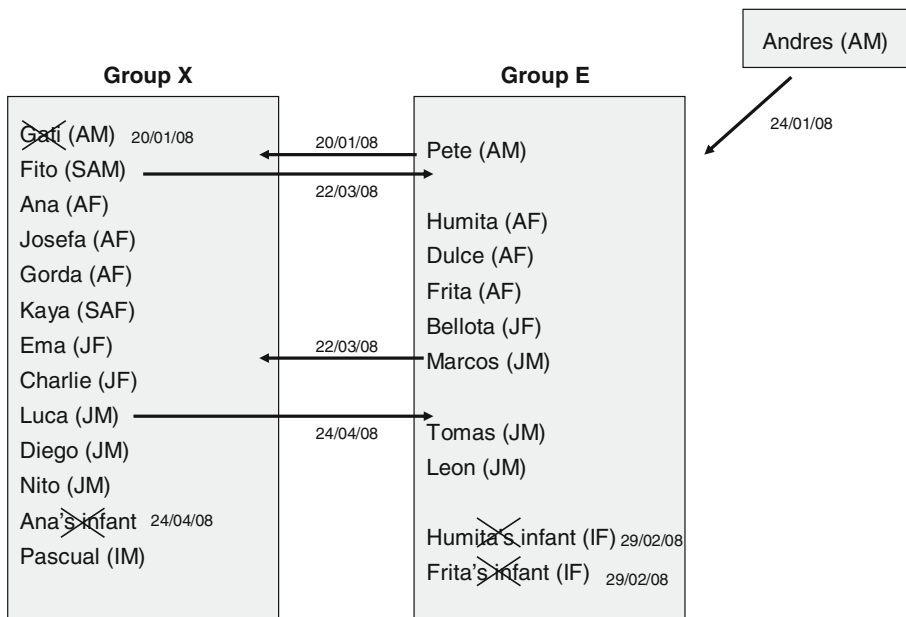
Fig 4 Group composition, infant disappearances, and migrations in two neighboring groups of *Alouatta caraya*, X and E (cases 2 and 3), inhabiting Isla Brasilera, Argentina. Arrows indicate migration between the groups. Crossed out names correspond to individuals that died. AM = adult male; SAM = subadult male; AF = adult female; SAF = subadult female; JM = juvenile male; JF = juvenile female; IM=male infant; IF = female infant.

on the mainland, where the same species exhibit a distinct pattern of seasonal births (from May to August) (Kowalewski and Zunino 2004). The authors of this comparison suggested that year-round births on Isla Brasilera are the result of the absence of major seasonal changes in food availability (new and mature leaves) at this site. During the present study, infants died at a mean age of 5.03 mo old, with *ca.* 70 % of deaths/disappearances occurring between birth and 6 mo of age. This coincides with the period of maximum nursing and the increase in the consumption of solid food (Pavé, unpublished data; Rumiz 1990). Likewise, Crockett and Rudran (1987b) found that infant mortality in *Alouatta seniculus* was higher during the first 4 mo of life (58 %) at Hato Masaguaral in Venezuela. Thus, it is likely that many of the 24 infant deaths/disappearances in our focal population of *Alouatta caraya* that were not directly attributable to flooding or infanticide were the result of inadequate maternal nutrition, inadequate maternal care for dependent offspring, and/or difficulties associated with the transition to independent foraging.

Infant mortality in *Alouatta caraya* on Isla Brasilera was 38 %, which is similar to previous values reported for this species in a nearby population living in a mainland forest, where infant mortality was between 30.4 % and 35 % (Rumiz 1990; Zunino 1996). These rates also are similar to those found in other *Alouatta* species: 21.2 % in *A. seniculus* and 30–34 % in *A. palliata* (Arroyo-Rodriguez 2008; Clarke and Glander 1984; Crockett and Rudran 1987b; Fedigan *et al.* 1998).

Infant Mortality and Flooding Events

Eight cases (18.6 %) of infant mortality were associated with an intense period of flooding between February and March 2007. The mean age of the eight dead infants was 4.3 mo old, corresponding to a period of development when howler infants are still heavily dependent on mother's milk and transitioning to solid food (Clarke 1990; Pavé, unpublished data; Rumiz 1990). Information on the deleterious effects of flooding on nonhuman primate populations is limited. However, a study of baboons (*Papio ursinus griseipes*) living in the Okavango Delta of Botswana found that adult female, juvenile, and infant mortality increased during periods of flooding (Cheney *et al.* 2004). The authors suggested that baboons were more vulnerable to both terrestrial predators and infanticide when they moved between islands of remaining woodland during flooding. There are several studies on the effects of natural disturbances (cyclones, hurricanes, and droughts) on populations of nonhuman primates (Dittus 1988; Dunham *et al.* 2011; Gould *et al.* 1999; Pavelka *et al.* 2007; Tecot 2010). For example, adult female mortality and infant mortality increased 17.7 % and 32 % respectively during a 2-yr drought relative to non-droughts periods on a population of *Lemur catta* living in Southwestern Madagascar (Gould *et al.* 1999). The authors associated these deaths with a decrease in food availability during the drought that affected maternal condition. In our study, although all mothers survived the period of marked reduction in food availability attributed to flooding, 8 of 40 infants did not survive. Of the 32 infants that survived, 18 were <6 mo old. Food shortages at this time may have affected maternal nutrition and a reduction in the quantity and/or quality of their milk (Milligan *et al.* 2008; Roberts *et al.* 1985). This is supported by the fact that the availability of mature leaves decreased by approximately one-third during the 4-mo flooding period. Although other food resources

such as new leaves, shoots, flowers, and fruits did not experience a change in availability during the flooding compared with the same period the following year, these resources were at or near their lowest production levels of the entire year during the flooding event. Finally, there was a strong positive correlation between the availability of mature leaves and the number of infants present in groups each month, and therefore we hypothesize that the decrease in the availability of mature leaves was a major factor contributing to infant deaths.

Other factors that may also have contributed to infant deaths include disease and accidental falling. There is evidence from other howler populations that changes in habitat and ecosystem disturbance increases the rate of parasitic infection (Kowalewski and Gillespie 2009). It also is possible that some infants may have died as a consequence of falls resulting in drowning. We have observed several instances in which infants have fallen to the ground but were retrieved successfully by their mothers. Retrieval may be impossible during flooding. One study on infant *Alouatta palliata* reported one case of infant death as the direct result of falling to the ground (Serio-Silva and Rodriguez-Luna 1994). Overall, intense flooding of the Parana River, similar to natural disasters at other sites, appears to have a critical effect on infant survivorship in *Alouatta caraya* inhabiting Isla Brasilera.

Male Replacements and Infant Disappearances

The second context to which we could attribute the cause of infant deaths or disappearances was during the replacement of a group's central male. Howlers on Isla Brasilera live in multimale–multifemale groups, age-graded male–multifemale groups, and unimale–multifemale groups. Each of these social groupings remains relatively stable over an extended period of time (in many cases for several years) and we found a very similar distribution of social groupings to those reported by Kowalewski and Zunino (2004) for the same howler population. Infant mortality was higher in unimale–multifemale and age-graded male–multifemale groups than in multimale–multifemale groups, and this was directly related to male replacements. Infants present at the time of all takeovers died or disappeared. We observed no cases of replacement of the central male and infanticide in multimale–multifemale groups. Overall, our data support the hypothesis that infant *Alouatta caraya* living in unimale–multifemale or age-graded male–multifemale groups experience a higher risk of infanticide than infants living in multimale–multifemale groups.

In our focal groups, the rate of infant mortality during periods of male replacement was significantly higher than the rate of infant mortality during periods without male replacement. Similar differences were reported for *Cebus capucinus* (Fedigan 2003). These results suggest that groups with a single adult male are more vulnerable to takeover and infanticide, whereas resident males in multimale–multifemale groups act cooperatively in group and mate defense (Kowalewski and Garber 2010; Leland *et al.* 1984). In this regard, tolerance and social bonds among resident males living in multimale–multifemale groups may represent an effective behavioral strategy that serves to decrease takeovers by extragroup males and increase infant survivorship.

The rate of adult male replacement found in our 29 study groups (0.02 replacements/mo) is considerably lower than previous values for the genus *Alouatta* (Janson and van Schaik 2000). Based on a limited sample (except for

Alouatta seniculus), Janson and van Schaik (2000) estimated a male replacement rate of 0.15 in *A. caraya* (4 groups), 0.25 in *A. seniculus* (42 groups), and 0.40 in *A. palliata* (1 group). Our data suggest that male replacement in *Alouatta caraya* at our study site is less common than previously thought. The large number of multimale–multifemale groups, the fact that male *Alouatta caraya* engage collectively in mate and group defense (Kowalewski and Garber 2010), and evidence that resident males remain in a group for a period of 4–6 yr appear to limit opportunities for male takeovers and infanticide in this population (Kowalewski 2007).

The infant disappearances or deaths we observed were generally consistent with the sexual selection hypothesis (Hrdy 1974, 1979). The conditions required to support this hypothesis include a takeover by extragroup males, killing of dependent infants, shortening of the IBI of females, and the new leader male siring the next set of offspring in the group (Hrdy 1974). Based on our observations, each of the four cases involved replacement of the breeding male. In each case, the invader male had not previously been a member of the group he took over. None of the infants who disappeared were fully weaned. However, we do not know whether the invader males sired the new offspring in these groups. In addition, the IBI for females whose infants died during their first year of life (as a result of male replacement or other causes) was not significantly lower than the IBI during periods without male replacement. Our limited data on this latter point suggest that although new leader males may have mated with resident females soon after they took over the group, in our population these initial mating did not result in conception.

Infant mortality associated both with observed or suspected cases of infanticide and male replacement in *Alouatta caraya* on Isla Brasilera (18.6 %) and on nearby mainland sites (25 %) (Zunino *et al*. 1986) is lower than values reported for *Alouatta seniculus*, the howler species in which the majority of cases of infanticide have been reported. Infant mortality due to infanticide in *Alouatta seniculus* at Hato Masaguaral, Venezuela and at La Macarena, Colombia, was 44 % and 53 % respectively (Crockett 2003; Crockett and Rudran 1987a). Thus, infanticide appears to play a more limited role in individual reproductive success in *Alouatta caraya*, especially among multimale–multifemale groups, than in *A. seniculus*.

Intergroup Infant Attack

One infant died as a consequence of male attacks when a resident male (PE) from a neighboring group attack an 8-mo-old infant during an intergroup encounter. Two months later that infant was attacked again and died. This case may support the generalized male aggression hypothesis (Bartlett *et al*. 1993). First, the attack on the infant occurred 9 mo after PE had established himself as the leader male of group X and PE remained in this group at least an additional 2.5 yr after the attack of the infant. Second, physical aggressive interactions by adult males from neighboring groups with overlapping home ranges are rare (Kowalewski 2007). However, PE was involved in a series of intragroup aggressive interactions in which two infants died or disappeared in the 2 mo after his takeover of group X. He was also involved in aggressive interactions with four individuals from another neighboring group (one infant, two juveniles, and one adult female) during the same month that SA was attacked.

Conclusions

We conclude that infant mortality and group demography in *Alouatta caraya* on Isla Brasilera is affected by several factors, two of which are periodic and intense flooding of the Parana River, and the frequency of male replacement. Additional data are needed on the specific events and social contexts associated with infant attacks and the causes of infant mortality in primate populations to understand better the evolutionary consequences of howler mating and social strategies on infant survivorship and reproductive success. Several factors such as natural disasters, infanticide, disease, parasite load, maternal condition, maternal age and experience, and possibly predation are likely to play critical roles in infant survivorship.

Appendix Description of Observed and Suspected Cases of Infanticide in *Alouatta caraya* Living on Isla Brasilera, Argentina

Case 1: Group PN

On December 10, 2007, the composition of group PN was one adult male, three adult females, one subadult female, two juvenile females, and two infants (3 mo, 5 mo). On January 19, 2008, the adult male and the 5-mo-old infant disappeared and a new adult male and a new subadult male were residents of the group. On February 28, one adult female, one juvenile female, and the remaining infant disappeared. We did not record any additional male replacements in group PN during October 2006–June 2008 (Table III).

Case 2: Group E

On January 20, 2008, the composition of group E was one adult male (PE), three adult females, three juvenile males, one juvenile female, and two infants (4 mo, 8 mo). PE was observed in the vicinity of a neighboring group, group X, whose only adult male had disappeared on several occasions. On January 24, we found that a new adult male (AN) had entered group E and PE had transferred into group X. On February 29, the two infants in group E disappeared. On March 22, a juvenile male 2.5–3 yr old (MA) entered group X and a subadult male (FI) of group X transferred into group E. On April 24, a 2-yr-old juvenile male (LU) of group X transferred into group E. This juvenile male was the younger brother of FI. No additional male

replacements occurred in group E from November 2003 to October 2010. PE was the central male from at least April 2003 until January 2008. AN remained in group E from January 2008 until May 2009. He then disappeared and his position was taken by FI, who was now an adult male. In September 2008, the adult female who lost her 9-mo-old infant gave birth a new infant (IBI=16 mo) and the adult female that lost her 5-mo-old infant gave birth in January 2009 (IBI=16 mo) (Table III).

Case 3: Group X

On December 13, 2007, the composition of group X was one adult male (GA), one subadult male (FI), three adult females (GO, JO, and ANA 5 mo pregnant), one subadult female, three juvenile males, two juvenile females, and one 6-mo-old infant. On January 20, 2008, GA disappeared (we found his skeleton with his colored anklet in group X's home range on February 29) and we observed the adult male resident (PE) of a neighboring group, group E, traveling on the periphery of group X. ANA had a newborn infant of *ca*. 5 d old. On February 29, PE was resident in group X and had a fresh wound on his lip. On March 22, FI immigrated into group E and a juvenile male (MA) from group E immigrated into group X. On April 24, the ANA's 3-mo-old infant disappeared. A 10 mo old infant disappeared on May 19, but we did not consider this as a case of infanticide because the infant disappeared 3 mo after the male replacement. GA was the central male from October 2002 until he died (Oklander 2007). PE remained the central male until at least July 2011. ANA gave birth in April 2009 (IBI=15 mo) (Table III). Figure 4 shows demographic changes in groups E and X.

Case 4: Groups G and X

On November 21, 2008, the composition of group G was one adult male (HE), two adult females, three juvenile males, one 8-mo-old infant male (SA), and a 20-d-old infant. The composition of group X remained as it was on May 19, 2008 (see case 3) except that one of the three adult females had died in September 2008. At 08:10 h on November 21, 2008, the neighboring groups G and X engaged in an intergroup encounter with howling. At 08:20 h all of the adults of both groups were resting, with members of the two groups separated by 15 m. SA approached two juveniles in group X that were in an adjacent tree and the three immatures played together. At 08:23 h SA went to the tree where his group was resting and rested 3 m from HE. At 08:27 h SA traveled toward HE and at that moment the adult male of group X (PE) approached SA and bit him in the thigh. The infant fell 7 m and remained in a small tree with his leg bleeding. HE and the two adult females chased PE immediately. At 08:31 h, both groups began howling. At 08:41 h, SA's mother approached and carried him to a nearby tree. The remaining members of the group moved away. SA had a deep wound of *ca*. 3 cm×2 cm in his groin and a second wound in his thigh. By December 17, the infant had completely recovered from his wounds. On January 22, 2009, SA, now 10 mo old, was attacked again. Although this attack was not witnessed, we putatively attributed these injuries to PE. The infant had two new wounds, one in the ventral part of the elbow of his right arm which was swollen and the other on his back. On January 29, we found SA's dead body. Examination of his body revealed two holes in the parietal bone of his skull (Fig. 5).

Fig. 5 Photographs of damage to the parietal bone of the skull of the male infant in group G (case 4).

Case 5: Group G

On August 1, 2010 the composition of group G was one adult male (HE), three adult females, two subadult males, one juvenile male, and three infants (two males of 1.5 mo and 2 mo respectively, and one female of 2 mo). On August 8, we found the remains of HE within the group's home range (the remains included HE's colored ear tag). On August 20, the group had a new adult male. On September 26, 2 infants (one male and one female) disappeared and the mother of one of these infants had hair missing from her back. On October 23, the remaining infant disappeared. HE had been the central male from September 2004 to August 2010. The origin of the new adult male was unknown and he remained in the group until at least July 2011. As of July 2011, none of the three resident females in group G had produced further offspring (Table III).

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