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BRIEF REPORT

Natal Emigration by Both Sexes in the La Pacifica Population of Mantled Howlers: When Do Some Stay?

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We have reported previously that all male and female mantled howlers emigrate from natal groups at Hacienda La Pacifica, Costa Rica. In the years since that report, a small number of juveniles have stayed in the natal group without experiencing a solitary phase. Here, we present a post hoc analysis on juvenile emigration in six groups of howlers under observation for varying amounts of time between 1972 and 2005. Our records revealed 139 juveniles for whom emigration status was certain, and 125 of these did emigrate. There was a significant association between presence of mother and emigration: juveniles without mothers were more likely to remain in their natal group ($\chi^2_1 = 53.1$, $P < .0001$). The mean age of emigration for all juveniles ($n = 125$) was 2.47 years (SD = 0.9, range = 1.5–6.5). There was no difference in age of emigration by adult male composition (one-male, multi-male, both), but juveniles of unknown sex emigrated younger than either known males or females ($F_{2,116} = 4.4$, $P < .02$). For emigrating juveniles of known sex ($n = 99$), both males and females without mothers left at a later age than those with mothers ($F_{1,95} = 6.5$, $P < .02$). Although philopatry or delayed emigration occurs in a few motherless animals, most males and females do emigrate from their natal groups at ages consistent with those reported for other species of howlers. Am. J. Primatol. 70:195–200, 2008. © 2007 Wiley-Liss, Inc.

Key words: male and female emigration; juveniles; absence of mother; *Alouatta palliata*

INTRODUCTION

Natal emigration, or leaving the group in which one was born, commonly occurs in one sex or the other in nonhuman primates. In cercopithecine monkeys, males normally disperse while females are philopatric [Isbell & VanVuren, 1996; Moore, 1992], whereas female dispersal is typical of gorillas and some colobines [Harcourt et al., 1976; Marsh, 1979]. New World monkeys exhibit a variety of patterns with male philopatry in Atelins [Rosenberger & Strier, 1989; Strier, 2000], repeated transfers of adult males in female philopatric capuchin monkeys [Jack & Fedigan, 2004] and dispersal by both sexes in several species of howlers [*Alouatta palliata*: Clarke & Glander, 1984; Glander, 1980, 1992; *Alouatta seniculus*: Crockett & Pope, 1993; Izawa and Lozano, 1991; *Alouatta caraya*: Calegaro-Marques & Bicca-Marques, 1996; Rumiz, 1990; *Alouatta fusca*: Mendes, 1989; *Alouatta pigra*: Brockett et al., 2000; Horwich et al., 2000]. In red howlers, female philopatry can occur if there is ''room'' (i.e. three or fewer adult females) for a daughter to remain in her natal group [Crockett & Pope, 1993]. Although we have evidence that some natal males return to their natal group after a solitary period and takeover the group in the same manner as any invading male, we had also noticed that a handful of animals remained in their natal groups without experiencing a solitary phase. Here, we present a post hoc analysis of juvenile emigration patterns and adult group composition.

METHODS

Study Site

La Pacifica is a working cattle ranch/rice farm/tilapia farm in the dry tropical forest zone of Guanacaste Province, Costa Rica [Holdridge, 1967]. There are three rivers that border the farm, and both

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dry deciduous forest and riverine forest exist. The farm was deforested in a conservative manner for cattle ranching in the 1950s [W. Hagnauer, personal communication] with strips of forest maintained for windbreaks between pastures, and forests left in hilly rocky areas deemed unsuitable for grazing. The farm was irrigated through a low-maintenance, low-impact system based on gravity, pulling water from the river on the north side of the farm [for complete description, see Glander, 1992]. In 1986 the farm was sold and irrigation patterns changed. In 1991 a large section was deforested for a major government irrigation canal, and in 1998 a major shift in land use occurred as pastures were converted to wet rice agriculture or tilapia tanks. Although some forest areas have been disturbed, most remain, and new, usable habitat has regrown along the canals [Clarke et al., 2002a,b].

Study Subjects

The subjects for this study are animals born into and surviving beyond 1 year of age in six groups of free-ranging mantled howlers (*A. palliata*) living on Hacienda La Pacifica between 1972 and 2005. The youngest natal emigrant known to survive and reproduce left at 14 months of age, an age defined as ‘‘juvenilehood’’ in this species [Clarke, 1990]. Many group animals have been captured and marked for other projects according to established protocols [Glander et al., 1991], and captured immatures are sexed and given unique bleach marks (Seventh Heaven R L’Oreal Paris) in addition to tattoos and/or microchips (AVID Identification Systems, Folsom, LA). Infants and juveniles not captured are aged based on size and activity level [for definitions, see Clarke, 1990], but sex cannot be determined unless they are seen within the first few weeks of life [Clarke et al., 2007]. Individual juveniles could be identified through naturally occurring white patches on tails and palmar surfaces.

Data Collection

This population was initially surveyed in the 1960s [Heltne et al., 1976], and was surveyed as part of a capture-and-mark project between 1974 and 1976 [Scott et al., 1979]. The population was surveyed formally in 1984, 1991, and 1998 [see Clarke et al., 2002b]. Type of data collection and dates (shaded areas indicate years used in analysis) for the six groups are presented in the appendix. Data came from intermittent periods of daily behavioral observations and capture and mark sessions between 1972 and 2005, from population surveys between 1974 and 1998, and group surveys at 6–12-month intervals between 1998 and 2005. The minimal acceptable interval between contacting each individual was 12 months, and most were contacted more frequently.

Analysis

For the years included in this analysis (see shaded area, appendix), 180 animals of the 270 born survived to juvenilehood. Of these 180, four died as juveniles in the group, 13 disappeared at the same time as their mothers (fate unknown), and 24 could not be identified at the time of emigration (i.e. when there was more than one unmarked juvenile of the same size in the same group, it is impossible to tell which one left). There were 139 juveniles with reliable birth and emigration dates and known presence/absence of mother. Each juvenile’s fate was treated as an independent data point with births combined over groups and years. Howlers are nonseasonal breeders, and although birth clusters do occur, multiple juveniles of the same age are the exception, and most were included in the 24 ‘‘unidentifiable’’ animals mentioned above.

Animals that emigrated and those that remained in their natal group were compared for presence or absence of mother using a χ^2 test. Age of emigration for all animals was compared by sex (male, female, unknown) and male group composition (one-male, multi-male, both) using two-way analysis of variance. Age of emigration for all animals of known sex were compared for sex (male, female) and presence or absence of mother using two-way analysis of variance [ABSTAT: Anderson Bell, 1989].

RESULTS

Stay vs. Emigrate

Of the 139 juveniles for whom migration status was certain, 125 emigrated and 14 remained in the natal group, there were 18 animals without mothers in the group (see Table I), and absence of mother associated significantly with juveniles not emigrating ($\chi^2_1 = 53.1$, $P < .0001$). Although absence of mother was unusual, it was not abnormal: six had mothers that died of old age, five had mothers that emigrated after their infants were independent, and seven had mothers that had died (two electrocuted, others found dead with identifying collar). Overall, there were six female juveniles that were philopatric (four without mothers) and eight male juveniles that were philopatric (seven without mothers) (see Table I). Less than 6% of animals born in these groups (14 out of 270) were philopatric.

Age of Emigration

Mean age of emigration for the 125 emigrating animals was 2.47 years, SD = 0.93, and $r = 1.5–6.5$. There were no significant differences in age of emigration by adult male composition, but there was a significant difference by sex ($F_{2,116} = 4.4$, $P < .02$). There were no differences between males and females, but there was a significant difference with animals that remained unsexed at the time of

TABLE I. Natal Dispersal

Group	Birth year	Name	Sex	Mother	Emigration year	Age emigrates
Mother gone, emigrate						
2	1993	Toups	F	Tulip	99–00	6.5
7	1980	Skipper	F	Yellow	83	3.0
7	1991	Linus	M	Lemon	94–95	3.5
18	1992	Venice	F	Volta	94–95	2.5
18	1993	Alberta	F	Amazon	96–97	3.5
19	1987	Topper	M	Topaz	90–91	3.5
19	1992	Onyx	F	Jade	94–95	2.5
Mother gone, philopatric						
1	1996	Calliope	F	Trinka		
2	1992	Orf	M	JQ		
7	1982	Roddy	M	GreenRed		
7	1993	Pelican	F	Purple		
19	1984	Roo	M	Ruby		
19	1989	Jose	M	Jade		
33	1990	Nino	M	Neptune		
33	1993	Schwep	F	Sherry		
33	1993	Julio	M	Lana		
33	1999	Manuel	M	Cindy		
33	2002	Cosima	F	Cindy		
Mother there, emigrate						
All			57 females			$m = 2.6$
			42 males			$m = 2.5$
			26 unknown sex			$m = 2.0$
Mother there, Philopatric						
2	2000	Agate	F	Azalea		
7	1972	Bonnie	F	DogCollar		
7	1971	Able	M	WhiteRed		

dispersal (male: $m = 2.5$, SD 0.9, $r = 1.5$–5.5; female: $m = 2.6$, SD 1.0, $r = 1.5$–6.5; unsexed: $m = 2.0$, SD 0.6, $r = 1.5$–2.5). For animals of known sex ($n = 99$), there was a statistically significant difference in age of emigration if the mothers were present or not ($F_{1,95} = 6.5$, $P < .02$). Animals without mothers in the group that emigrated left at a later age (males = 3.5, SD = 0.0, $r = 3.5$; females = 3.6, SD = 1.7, $r = 2.5$–6.5) than animals with mothers (males = 2.5, SD = 0.9, $r = 1.5$–5.5; females = 2.6, SD = 0.9, 1.5–5.5).

DISCUSSION

We can say with confidence that most juveniles emigrate from their natal groups. Average age of emigration is later than we reported previously for males [Clarke & Glander, 1984], but this more extensive data set indicates that both sexes of mantled howlers emigrate at about the same age as red howlers [Crockett & Rudran, 1987; Crockett & Pope, 1993]. There is variation in age of emigration, but most animals left after 1.5 years, but before 4.0 years, of age. Nonrelated opposite sexed adults chase and harass juvenile/subadults as part of the emigration process, an event closely tied to the appearance of adult genitalia [Clarke & Zucker, 1989; Clarke et al., 2007]. Once howlers emigrate, they experience a solitary phase of up to several years before joining a new group as full adults [Clarke & Glander, 1984, 2004; Glander, 1980]. The younger they emigrate, the longer they are solitary, a variation that could affect an individual's survival and success at joining a new group. Indeed, we have argued previously that juvenile monomorphy is a strategy to prolong natal group membership to reduce the length of the solitary phase [Clarke et al., 2007].

The limited number of animals that were philopatric were significantly more likely to be motherless, and motherless animals were tolerated as group members until a later age. Motherless juveniles do exhibit behavioral profiles that mimic adults [Clarke & Glander, 1981; Clarke et al., 1996], and motherless juveniles behaving like an adult might be less threatening. The three philopatric animals that had mothers in the group had mothers of high, medium, and low rank, suggesting no association with maternal rank.

This is obviously a different situation than in red howlers, although it still could be a case of ''an available place''. In red howlers, the presence of the mother, combined with three or fewer adult females, creates a situation where a female offspring can stay in her natal group [Crockett & Eisenberg, 1987; Crockett & Janson, 2000; Crockett & Pope, 1993]. There still could be ''an available place'' in a mantled howler group, but the dynamics are different than red howlers. A motherless female could take her mother's place, but she risks mating with her father, and the situation is rare as it occurred in $<2\%$ of the animals (4 of 270) born during this time. A motherless male, however, would not only be unrelated to group females, but could also form an alliance with his father: Older males have been observed forming a coalition with an incoming male which is associated with the younger male successfully taking over the group [Clarke, 2005]. The pattern of the philopatric natal male resembles that of the male that returns to take over his natal group, but with the advantage of skipping the solitary phase. Eliminating the solitary phase not only reduces inherent risks for an animal living alone, but it presumably would allow the male to begin mating sooner and share some reproductive success with his resident father, with no risk of incest. As both males and females emigrate, the chances of mating with an unfamiliar relative in a new group might be higher for a motherless male than if it stayed in its natal group of nonrelatives. Philopatry is still an unusual pattern in howlers, but it occurs more frequently in motherless males ($n = 7$) than motherless females ($n = 4$).

These occasional ''exceptions to the rule'' are thought provoking because of the association with maternal loss, and it is unfortunate that we do not have the data to undergo rigorous hypothesis testing for effects of competition, both for resources and social status. Despite this limitation, this analysis, based on many years of data in six different social groups, does indicate that natal males and females emigrate at an age similar to those reported for other howler species, and does not alter the overall species-specific pattern of male and female natal dispersal in mantled howlers.

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Appendix

See Table A1.

TABLE A1. Contact History for La Pacifica Howler Groups: Juvenile Emigration Data

Year	Group 1	Group 2	Group 7	Group 18	Group 19	Group 33
1970			Sept DO			
1971						
1972			Aug–Dec DO			
1973			Jan–June DO			
1974			June CT			
1975			Feb, Aug CT			
1976			Jan, Jul CT			
1977			Mar, Nov CT			
1978			May, Nov–Dec DO			
1979			Whole year DO		Nov CT	
1980			Jan–Sept DO		Aug CT	
1981			Mar, Aug CT		Mar, Aug CT	
1982			Mar, Nov CT		Mar, Nov CT	
1983	Sept CM		Apr CT, Sept CM		Sept CM	
1984	July PS	July PS DO	July PS,DO	July PS	July PS, DO	
1985	Aug CM	July DO, Aug CM	July DO, Aug CM			
1986	Aug CM	Aug DO, CM	Mar CT, Aug CM	Aug CM	Mar CT, Aug CM	
1987	July CT, Aug CM	July DO	July CT		Aug CM	
1988		July, Aug DO	Feb, Aug CT		Feb, July CT	
1989	Aug–Dec DO	July CT, CM	Aug–Dec DO		Aug–Dec DO	Aug–Dec DO
1990	All year DO	July–Aug DO, CM	All year DO		All year DO	All year DO
1991	July PS, all yr DO	July PS, DO	July PS, all year DO	July PS	July PS, all year DO	July PS, all year DO
1992	All year DO	July, Aug DO	All year DO	July CM	All year DO	All year DO
1993	Feb CM, Jan–Aug DO	Feb CM, July DO	Feb, CM, Jan–Aug DO	Feb CM, July DO	Feb CM, Jan–Aug DO	Feb CM, Jan–Aug DO
1994	Feb, July CM	June DO	Feb CM, June DO	Feb CM, June DO	Feb, July CM, June CT	Feb, July CM, Jun CT
1995		July–Aug DO	Feb CM, July–Aug DO	July–Aug DO	Feb CM, July–Aug CT	Feb CM
1996	July CM	Jun DO	Jun DO, July CM	Jun DO	Jun CT, July CM	July CM
1997	July DO	Jun–July DO	July DO	June DO	July DO	July DO
1998	Feb, July CM Aug PS	Aug PS, DO	Feb, July CM, Aug PS	Feb CM, Aug PS, DO	Feb, July CM, Aug PS	Feb CM, Aug PS
1999	Feb, July CM	Jun–July DO	Jul CM	Jun CT	Jun CT, July CM	July CM
2000	Jun CT	Mar CM, Jun–July DO	Jun–July DO	Jun CT	Feb, CM, Jun–July DO	Jun CT
2001	Feb CM, Jun–July DO, CM	Feb CM, Jun–July DO	Feb CM, Jun–July DO, CM	Feb CT	Feb CM, Jun–July DO, CM	Feb CM, Jun DO, CM
2002	Apr CT	Apr, Jun CT	Apr CT		Apr, Jun CT	Apr CT
2003	Feb CT, CM	Feb CT, CM	Feb CM		Feb CT, CM	Feb CM
2004	Feb CT, CM, Jul CT	Jul DO	Feb CT, CM		Feb, Jul CT	Feb CT, CM
2005	Mar CM	Mar CM, May DO	Mar CM, May CT		Mar CM, May CT	Mar CM

Shaded areas indicate years used in analysis.
DO, daily observations; CT, group count; PS, population survey; CM, capture/mark.