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Brief Report

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Male Dispersal among Free-Ranging Red Howler Monkeys *(Alouatta seniculus)* in Venezuela

Key Words
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Migration
Sex ratio

Introduction

In non-human primates, avoidance of mating between relatives is often maintained by dispersal of mature males from natal groups [1, 2], although active avoidance of mother-son incestuous mating within a group has been reported for chimpanzees [3]. In fact, dispersal can enhance the reproductive success of migrating males in two ways, either because the cost of inbreeding depression incurred by staying in the natal groups would exceed that of transferring or because emigration provides access to more oestrous females [4]. Indeed, it has been suggested that the cause for male dispersal is competition for access to females [5, 6]. However, in red howlers *(Alouatta seniculus)* and mantled howlers *(A. palliata)*, both sexes are reported to disperse routinely [7–9]. This paper describes the male dispersal pattern in free-ranging red howler monkeys of Venezuela.

Methods

The red howlers described here inhabit the savanna woodlands at Hato Masaguaral in Guarico State of Venezuela. The howlers of Hato Masaguaral have been under long-term study since 1976 [7, 8, 10–14]. 36 red howler groups, including 10 groups from which male dispersal occurred, were studied between April 1989 and October 1991. Among these 10 groups, 5 were censused on a weekly basis to record demographic data. The remaining 5 groups were monitored for 5 consecutive days (for 12-hour periods) on a monthly basis to record social interaction data [13, 14], using the all-occurrences and scan sampling methods [15]. All the animals mentioned here were identifiable by their ear tags, and their life histories were also known [7]. The sex ratio was calculated as adult males to adult females,

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Table 1. Immigration pattern of red howler males and their female kin

Case No.	Group No.	Natal group							Immigrated group	
		dispersing males			kin-related females in group				was the immigrant related to the resident male?	did immigrant kill infant(s)?
		ID	age years	class	relation	ID	class	age years		
1	5	2	12.0	adult	daughter	10	adult	4.4	no	no, no infants
2		11	4.9	subadult	mother	4	adult	20.0+	no	present
					sister	7	adult	7.5		
3		8	6.5	adult	mother	9	adult	17.0+	no	no, no infants
					sister	10	large juven.	3.0		present
4	6	6	5.5	adult	mother	3	adult	18.0+	yes; immigrant was the son of resident	no, 2 infants were present but none was killed
5	11	3	11.9	adult	mother	4	adult	18.0+	no	yes (inferred)
6		10	5.8	adult	mother	8	adult	15.0+	no	no infants present
7	12	11	5.4	adult	mother	3	adult	20.0+	no	no infants present
8	14	14	5.3	adult	mother	9	adult	18.0+	no	yes (observed)
9		16	4.2	subadult	mother	8	adult	18.0+	no	yes (observed)
					sister	6	adult	9.0+		
10		17	3.3	juvenile					no	no
					mother	7	adult	19.0+		
11		18	2.3	juvenile	mother	8	adult	18.0+	no	no
					sister	6	adult	9.0+		
12	20	10	6.0	adult	mother	8	adult	18.0+	no	no infants present
13		11	5.0	adult	mother	8	adult	18.0+	no	no infants present
14	24	1	10.7	adult	sister daughter?	8	subadult	3.8	no	yes (inferred)
15		9	4.6	subadult	mother	6	adult	9.0	no	?
16		2	19.0+	adult	daughter?	8	subadult	3.8	yes, immigrant	no, 3 infants were
					daughter	7	adult	4.2	was the father of resident male	present but none was killed
17	29	8	5.2	adult	mother	4	adult	15.0	no	yes (inferred)
18	31	5.1	3.7	juvenile	mother	5	adult	15.0+	no	no, no infants
					sister	8	adult	8.0+		present
19		3.1	3.7	juvenile					no	no, no infants
					mother	3	adult	17.0+		present
20	32	1	15.0+	adult	daughter	6	subadult	3.8	no	yes (inferred)
21		4.1	2.8	juvenile	sister	6	subadult	3.8	no	?

ID = Identification number.

ed each other in aggressive disputes to obtain higher social rank [18].

Male invasions followed by infanticide have been observed or inferred previously for red howlers [7, 10, 19], mantled howlers [20] and black howlers [21]. In this study, infant killing or infant disappearance resulted after male immigration into groups that had infants [see 13, 14 for details], except in 2 cases where the immigrants were related to the resident males. Recognizing kin and behaving preferentially towards them with co-operation and altruism are important aspects of kin-selected behaviour [22]. In case 16 (table 1),

after excluding males that migrated from their natal groups. The non-kin male-to-female sex ratio was calculated after excluding kin-related adult females of males in natal groups or immigrated groups. Cox and Stuart's modified sign test [16] was used to evaluate the increase or decrease in sex ratio of groups in which males emigrated and immigrated.

Results

21 red howler males migrated to join a new social group in 13 dispersal events: 6 singly, 6 in pairs (5 half-brothers and 1 father-son) and 1 with a trio (a male, his son and an individual of unknown status). All of the migrating males had living mothers, mature maternal sisters (the number of paternal sisters was uncertain) and/or mature daughters in their natal groups at the time of their dispersal (table 1). The majority (61.9%) of them dispersed at or before the attainment of sexual maturity (fig. 1). Males usually mature at about 5 years of age [7]. The ages of the dispersed males ranged from 2.3 to 19 years (table 1). In 1 case (No. 5 in table 1), an adult male first left his group at the age of 9 years but returned intermittently over a period of 3 years before finally emigrating definitively at the age of 11.9 years. Two old adult males (aged 15 and 19 years, respectively) were the only ones to disperse for a second time (cases 20 and 16 in table 1). Infant killing was either observed or inferred following the immigration of males into groups that had infants [13], with only 2 exceptions (table 1).

The adult male-to-female sex ratio was not significantly lower in groups into which males immigrated than in those from which males had emigrated (Cox and Stuart test, $x = 0.8$, $p > 0.05$). However, when kin-related females were excluded from the groups from which males had emigrated, the non-kin male-to-female sex ratio was found to be significantly lower in the groups into which males immigrated (Cox and Stuart test, $x = 0.98$, $p < 0.05$, $n = 12$). Among the 13 dispersal events, the sex ratio of the groups into which males migrated was lower in 7, equal in 2 and higher in 4 events than the groups from which males emigrated. All migration events except one were independent. In the exception, 2 males immigrated into a group into which their male relatives had already immigrated a week earlier (cases 10 and 11 in table 1). The number of non-kin-related females in natal groups was significantly lower than the number of females in immigrated groups (binomial test, $p < 0.05$). 12 of the 21 immigrant males transferred to groups with a higher number of females, 7 went to groups with the same number of females, and 2 went to groups with fewer females. However, when the sex ratios were compared among all the neighbouring groups, the groups into which immigration occurred had neither the lowest sex ratio nor the greatest number of mature females (binomial test, $p > 0.05$).

Discussion

The company of a father or a brother appeared to be a factor for dispersal of immature males because only adult males over 5 years of age dispersed singly. In addition, the cost for immature males to migrate on their own seemed to be high because male immigration sometimes resulted in severe wounding or death [7, 13]. Although the presence of a brother or a father may increase competition for mates within a group, the benefits of staying in a kin-related coalition may outweigh the costs of competition for oestrous females. Moreover, kin relatedness may increase the inclusive fitness of such males [17]. In a previous study of red howlers, males that formed a coalition of relatives gained longer tenure than a coalition of non-relatives [11]. Similarly, in rhesus macaques, males that were transferred with their brothers support-

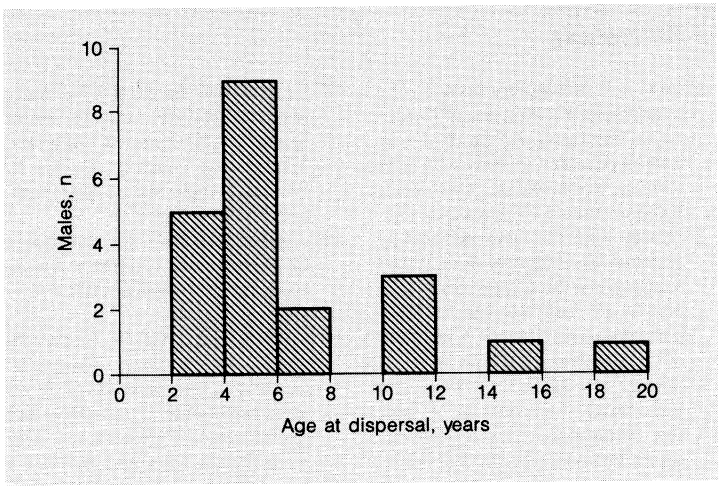

Fig. 1. Male dispersal in free-ranging red howler monkeys *(A. seniculus)* of Venezuela.

an old adult male immigrated into a neighbouring group where his probable son held residency. Three vulnerable infants, less than 3 months old, were present, but the immigrant did not harm them. Indeed, he was observed to groom, lick and play with the infants on several occasions [Agoramoorthy, unpubl. video document]. This kind of interaction between a male immigrant and infants has not been reported previously for howlers. Similarly, in case 4 (table 1) an adult male immigrated to a neighbouring group in which the resident male was his putative father. At that time, 2 infants were present, and neither of them was harmed. These cases of infanticide avoidance suggest co-operation between fathers and sons, which may have increased the probability of survival and reproductive success of close kin [17].

In non-human primates, males usually transfer to neighbouring groups at sexual maturity, whereas females remain in their natal groups through much of their lifetime. It is assumed that the ultimate function of male dispersal is reduction of inbreeding [1]. The presence of a sexually mature kin-related female(s) may have been a factor promoting the dispersal of red howler adult males. Although intergroup male transfer among red howlers may thus obviously reduce the likelihood of incestuous mating, dispersed males in this study eventually succeeded in immigrating into groups that had a greater number of unrelated mature females, as reported for olive baboons [4]. Despite the fact that both males and females routinely emigrate from their natal groups [7, 12], mating between kin-related individuals has not been reported so far among red howlers. It may be possible that a male and a female from the same natal group can simultaneously migrate into the same host group, but this type of migration has not been observed.

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