

Group Takeover by a Natal Male Howling Monkey (*Alouatta palliata*) and Associated Disappearance and Injuries of Immatures

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ABSTRACT. As part of a long-term study on howling monkey behavior and social dynamics, a known natal male was observed taking over his group from his putative sire. Due to the accidental death of one of the adult males, this natal male had matured in a one-male group and had never observed juvenile male emigration nor adult male immigration and associated behaviors. Nevertheless, the behaviors associated with the takeover were indistinguishable from those of an immigrant male, including disappearance of immatures, one of whom was found with extensive injuries. While it cannot be said that the natal male inherited these behaviors from his presumed father, it can be said that he exhibited species-typical behaviors associated with male takeover in the absence of observational learning.

Key Words: *Alouatta palliata*; Infant-killing; Male takeover; Juvenile migration.

INTRODUCTION

Group takeovers by an immigrant male have been associated with infant-killings and infant disappearances in a number of nonhuman primate species (e.g. BLAFFER HRDY, 1974, 1976, 1979; BUTYNSKI, 1982; HAUSEFATER & BLAFFER HRDY, 1984; ROSS, 1993; STRUHSAKER, 1977; SUGIYAMA, 1965, 1966) including three species of howling monkey [*Alouatta palliata* (CLARKE, 1983), *A. seniculus* (CROCKETT, 1984; CROCKETT & SEKULIC, 1984; IZAWA, 1988; IZAWA & LOZANO, 1991; SEKULIC, 1983), *A. caraya* (RUMIZ, 1990; ZUNINO et al., 1985)]. Since these species typically exhibit male emigration/immigration and do not exhibit discrete birth seasons (in sensu MACROBERTS & MACROBERTS, 1966), the removal of nonrelated immature monkeys should reduce resource competition, and it is associated with adult females becoming sexually receptive to the newly dominant male. The function of infant-killing in association with group takeover continues to be a matter of controversy (see HAUSEFATER & BLAFFER HRDY, 1984), but whether it is interpreted as resource competition, social pathology, or a male reproductive strategy, it is a persistent pattern.

For the three species of howling monkeys exhibiting these behaviors, relatedness among adult members of a group is assumed to be low as juveniles of both sexes emigrate to join or form new groups (CLARKE, 1982; CROCKETT, 1984; CROCKETT & EISENBERG, 1987; GLANDER, 1980, 1992; JONES, 1980a, b; RUMIZ, 1990). Long-term studies of *A. palliata* reveal that almost all juveniles emigrate (CLARKE & GLANDER, 1984; GLANDER, 1992), whereas emigration by juvenile female *A. seniculus* is more variable (CROCKETT & POPE, 1993). Emigration is associated with aggression, suggesting it is not voluntary (CLARKE, 1982; CLARKE & GLANDER, 1984; CROCKETT & POPE, 1988; RUMIZ, 1990), and juvenile mantled howling monkeys have been observed receiving contact aggression (i.e. wounds to

extremities), as well as noncontact aggression, from like-sex, nonrelated adults prior to emigration (CLARKE & GLANDER, 1984; CLARKE & ZUCKER, 1989). Thus, a juvenile surviving to the age of emigration in a multi-male howling monkey group should have witnessed behaviors associated with other emigrating juveniles and possibly adult male immigration (see CLARKE, 1990).

Here we report the atypical occurrence of a male maturing in and taking over his natal group, observed as part of a long-term study of howling monkey social dynamics and behavior. The natal male's behavior was indistinguishable from that of a takeover by an immigrating male, indicating that similar behaviors occur despite life history differences and in the absence of opportunities for observational learning.

METHODS

The study site was at Hacienda La Pacifica, Guanacaste Province, Costa Rica, a working cattle ranch (1,330 ha) that was conservatively deforested between 1965 and 1975. La Pacifica is in the deciduous dry tropical forest zone (HOLDRIDGE, 1967), and has both riparian and upland forest habitat. The howling monkeys of La Pacifica have been under study since the mid-1960's (HELTNE et al., 1976; SCOTT et al., 1976, 1978; GLANDER, 1975, 1980, 1982). The data reported here were collected over an 8-year period (May 1978 through August 1986) when the habitat and the size and distribution of approximately 20 groups of free-ranging mantled howling monkeys were unchanged from the early 1970's (CLARKE et al., 1986).

The study group (SCOTT's No. 7) has been observed since 1970 (see CLARKE, 1982, 1990; GLANDER, 1975, 1980, 1982, 1992). During that time there have been 2 or 3 adult males (with the exception reported here), 7 to 13 adult females, and immatures. Females have no more than two immature offspring in the group at any one time. This group has been routinely captured since 1970 (when all animals were tattooed) and individuals have been marked with collars/tags, leg bands, and ear tags. All new animals that were captured (infants or immigrants) received a unique tattoo number (see GLANDER et al., 1991).

Data for this analysis come from behavioral observations, capture and mark sessions, and census results. Behavioral observations consist of both focal and ad lib sampling (ALTMANN, 1974), and dates and hours of observation are given in Table 1. Capture and marking data come from routine sampling (SCOTT et al., 1976; GLANDER et al., 1991), and census results provide additional information on marked animals at irregular intervals. Identification of animals during observation periods and census periods are absolute. Animals with lost tags can be positively identified by tattoo number following recapture.

Table 1. Observation periods.

Dates	Type of observation	Hours	Total
May 5 - 20, 1978	Focal samples of immatures	20	20
November 1978 - September 1980	Focal on immatures	703	
	Ad lib on group	753	1456
November 1 - 8, 1982	Ad lib on group	20	20
July 12 - August 8, 1984	Focal on males	56	
	Focal on group	374	430
July 13 - August 6, 1985	Focal on males	20	
	Ad lib on group	21	41
Total			1967

Hourly rates and direction of agonistic behaviors and patterns of affiliation (male-male, male-female) were determined from behavioral data. Following disappearance of infants, cessation of lactation and return to estrus were noted for females by both physiological and behavioral criteria. Cessation of lactation was indicated by a "flattening" of mammae (CLARKE, 1982), and return to estrus was indicated by increased vulval swelling (GLANDER, 1980) and by male-directed behaviors, such as initiate affiliation, maintain consort, lingual gesture, and copulate (CLARKE, 1982; CLARKE et al., 1991; GLANDER, 1980). Dominance relationships were determined based on outcomes of competitions for food, preferred sleeping sites, and for the male monkeys, access to females. Demographic data (capture/mark and census) were compiled to characterize changes in group composition.

RESULTS

MALE TAKEOVERS IN GROUP 7

Important events concerning male takeovers and infant/immature disappearances between May 1978 and July 1986, with an emphasis on the history of the male *RO*, are presented in Table 2. Male takeovers in 1978, 1980, and 1985 were all associated with infant disappearances (see CLARKE, 1990). *RO* was identified as a newborn in March 1982 (mean gestation length=186 days, GLANDER, 1980), and was thus conceived after the male *MA* died accidentally in July 1981. *RO* was permanently marked when he was still in association with his mother. This normally multi-male group contained only one adult male (*HO*) while *RO* was maturing. No male juveniles were forced out of the group, nor did a new male immigrate into the group during this time.

Table 2. Social dynamics associated with male takeovers and infant disappearances in Group 7, May 1978 – July 1986.

Date	Social dynamics	Males in Group 7	Sample type/Observer ²⁾
May 1978	<i>MA</i> peripheral	<i>BA, SC</i>	Focal, ad lib/MC Capture, mark/MC, KG
November 1978	22 mo. male leaves ¹⁾ 21 mo. female leaves <i>MA</i> dominant male	<i>MA, BA, SC</i>	Focal, ad lib/MC Capture, mark/MC, KG
December 1978	14 mo. male leaves <i>BA</i> leaves	<i>MA, SC</i>	Focal, ad lib/MC
January 1980	<i>HO</i> peripheral	<i>MA, SC</i>	Focal, ad lib/MC
August 1980	<i>HO</i> takes over ¹⁾ 22 mo. female leaves	<i>HO, MA, SC</i>	Focal, ad lib/MC
November 1980	<i>SC</i> gone (dead)	<i>HO, MA</i>	Census/GW
July 1981	<i>MA</i> dies	<i>HO</i>	Capture, mark/KG
March 1982	<i>RO</i> newborn	<i>HO</i>	Capture, mark/KG
November 1982	<i>RO</i> earnotched, tattooed	<i>HO</i>	Capture, mark/KG, MC
September 1983	<i>RO</i> eartagged	<i>HO</i>	Capture, mark/KG
August 1984	<i>RO</i> maturing, copulates with female <i>MG</i>	<i>HO</i>	Focal, ad lib/MC, EZ, and students
July 1985	<i>RO</i> takes over ¹⁾ <i>LN, GP, RI, PA</i> gone <i>LE, GN, MG, PU, AP</i> solicit <i>RO</i> <i>RI</i> found wounded	<i>RO, HO</i>	Focal, ad lib/MC Capture, mark/KG, MC
July 1986	<i>RO</i> dies	<i>HO</i>	Capture, mark/KG, MC

Leave: The animal was subsequently seen as a solitary or as a group member in another group. 1) Infant disappearances (1978 and 1980 previously reported in CLARKE, 1983). One immature in 1980 and one in 1985 found fatally wounded. See Table 3 for mother-offspring genealogy; 2) MC: CLARKE; KG: GLANDER; GW: GERALD WILKINSON; EZ: ZUCKER.

TAKEOVER BY *RO*

Adult females and their offspring in the group at the beginning of the 1984 observation period (when *RO* was maturing) and the 1985 observation period (when *RO* took over) are listed in Table 3. Immatures' ages, sexes, and status in the group (present/absent) at the end of 1985 observation period are presented.

Table 3. Adult females and immature offspring.

Adult female	Offspring	Sex	Age in July 1984 (months)	Age in July 1985 (months)	Status in August 1985
<i>Green (GN)</i>	<i>Greta (GT)</i>	F	16	28	Present
	<i>Gopher (GP)</i>	U	—	8	Absent
<i>Lemon (LE)</i>	<i>Lily (LY)</i>	F	9	21	Present
	<i>Lincon (LN)</i>	U	—	2	Absent
<i>Magnolia (MG)</i>	<i>Moxie (MX)</i>	F	6	18	Present
	<i>Mickey (MK)</i>	U	—	<1	Present
<i>Greenred (GR)</i>	<i>Roddy (RO)</i>	M	28	40	Present
	<i>Ripple (RI)</i>	M	2	14	Absent
<i>Apricot (AP)</i>	<i>Anemone (AN)</i>	F?	<1	Gone ¹⁾	Absent
<i>Purple (PU)</i>	<i>Patches (PA)</i>	M?	1	13	Absent
<i>Scarlett (ST)²⁾</i>	None				

1) Seen in group at 10 months of age; 2) immigrant in 1985. F: Female; U: unknown; M: male; ?: animal sexed from distance rather than when captured.

Male-male Interactions

In 1984, focal observations revealed that the male *HO* supplanted *RO* at a rate of 0.27/hr, and that *RO* never supplanted *HO*. Ad lib notes made during focal observations sessions in 1984 indicate that whenever *HO* approached within 10 m of *RO*, *RO* increased the distance to 15 m. In 1985, ad lib notes reveal that *RO* still avoided *HO* when the animals were first observed, but they sat less than 3 m apart and howled in unison on one morning and two afternoons. After focal sampling began, *RO* supplanted *HO* at a rate of 0.45/hr, and *HO* avoided *RO* at a rate of 0.75/hr, indicating a dominance reversal. After that, *HO* never supplanted *RO*, and *RO* never avoided *HO*. In addition, a "greeting" was initiated by *RO*, a behavior usually initiated by the dominant male (GLANDER, 1975; ZUCKER & CLARKE, 1986).

Disappearances of Immatures

While one immature (*AN*) present in May 1985 was not seen in the group during the 1985 study period, four immatures disappeared in the three weeks following *RO*'s takeover (Tables 2 & 3). *LN* and *GP* were gone the same day *RO* first supplanted *HO*, and *RI* and *PA* were gone one day after the male dominance reversal was complete. Two days later, *RI* (14-month old male offspring of *GR*) was found on the ground away from the group. This juvenile had extensive dried wounds and injuries, including a slash wound which crossed the right ear and ended in a puncture wound at the base of the skull. The puncture wound was too deep to have been inflicted by a female's canine tooth. There were scratches on the head and rear quarters, a deep cut on the left foot, and the right arm was broken. This animal was subsequently seen 10 and 22 days later, sitting low (1.5 m off the ground) in a tree about 200 m from the initial sighting, appearing disoriented. The next day,

hair and a small hand the size of *RP*'s was found in the area, suggesting that he had been taken by a predator. None of the other missing immatures were sighted. The only two immatures under 22 months of age that did not disappear (*MX* and *MK*) were the offspring of *MG* (see Table 3). In 1984, *MG*, a nonestrous female with a dependent offspring, was the adult female with whom *RO* copulated (see Table 2).

Post-takeover Sexual Behavior and Aggression

Five of the six adult females sexually solicited *RO* after he became dominant. There had been no evidence of sexual behavior prior to the disappearance of the two youngest immatures, and each female initiated sexual behavior only after her immature offspring had disappeared. While *RO* supplanted one high-ranking female twice while he was still subordinate to *HO*, there was no evidence for any female-directed aggression from males at any time. Females, however, supplanted each other to gain proximity to *RO* after *RO* became clearly dominant to *HO*.

DISCUSSION

From the perspective of the observer, *RO*'s takeover appeared to be typical, i.e. a new male immigrating into a group, overthrowing the dominant male, and then copulating with females, with associated disappearances of immatures. However, *RO* had been identified as *GR*'s offspring soon after birth and was permanently tattooed, so we know that this apparent "invading" male was actually a natal male, and probably the offspring of the newly defeated male. Although paternity is never certain without confirmation by DNA fingerprinting (see OHSAWA et al., 1993) the fact that *RO* was conceived after *MA* died increases the probability that *RO* was *HO*'s offspring¹⁾, as were most offspring sired after *MA*'s death (a potential paternal sibship, ALTMANN, 1979). Even if *RO* were not *HO*'s offspring, *RO* exhibited species typical behavior in the absence of observational learning. *RO* lived his complete life in a one-male group, never observed the emigration of other male juveniles (see CLARKE, 1990), nor observed or experienced the behaviors associated with a takeover by an invading male. Despite this lack of experience and lack of opportunity for observational learning, *RO* successfully defeated the dominant male (his putative father) and proceeded to behave in a manner typical of an invading male.

While the most logical argument for the existence and persistence of infant-killing and disappearances of immatures is for male reproductive advantage, in this case at least one maternal relative of the newly dominant male was injured, and other potential paternal relatives disappeared. *RO*'s individual fitness was protected as the immature offspring of the female with whom *RO* consorted prior to group takeover remained in the group. This same pattern was exhibited when *HO* took over the group in 1981 (CLARKE, 1983). The most important point, however, is that *RO* behaved like an invading male, i.e. he exhibited the same behaviors that had increased *HO*'s reproductive fitness when he

1) DNA fingerprinting technology was unavailable in field conditions at the time of these observations. Attempts were made at paternity exclusion analysis, but blood samples taken from these animals and others on La Pacifica indicate that this population of howling monkeys is highly monomorphic (BOWEN, pers. comm., in 1978; SMITH & RICH, pers. comm., in 1982 & 1986).

joined the group in 1980, and would have functioned similarly for *RO* if *RO* had emigrated and later joined a group of nonrelatives. It is unfortunate that *RO* was killed accidentally before his tenure ran its normal course and the number of offspring he produced was known. Since most dominant males in this group have had over ten surviving offspring (CLARKE, pers. obs.), the potential advantage of taking over a natal group (i.e. avoiding solitary phase and beginning reproduction at an earlier age) might offset the immediate loss of a relative.

There was no evidence to suggest that the injuries to *RI* were random, accidental, or a byproduct of female-directed male aggression. The injuries to *RI* were almost identical to those previously described in association with *HO*'s takeover (CLARKE, 1983), and also identical to injuries described for red howlers (CROCKETT, 1984; CROCKETT & SEKULIC, 1984; SEKULIC, 1983). All exhibited the life-threatening craniocervical bite (STEKLIS & KING, 1978) and additional injuries. These are qualitatively and quantitatively different from injuries received from like-sex nonrelated adults in association with juvenile emigration. Female-directed male aggression is also not characteristic of howling monkey male takeovers. Four takeovers have been observed, and no contact aggression or chases have ever been directed toward females (CLARKE, pers. obs.). In only one takeover was the deposed male actually injured, but in all cases, the direction of aggression and harassment was clear, and did not directly involve adult females.

As the group and monkey population and habitat had been stable since at least 1974, there was no evidence to support resource competition as the reason for infant-killing. Without concomitant feeding data, however, it cannot be eliminated completely as an explanation.

This takeover by a natal male appears to have been opportunistic, and only a transient deviation from typical howling monkey social dynamics. *HO* and a new adult male have been co-residents in Group 7 since 1989, and while it is unknown if the new male is an unmarked natal male or an immigrant male, the group once again exhibits the species-typical multi-male group with juvenile emigration (CLARKE, pers. obs.; GLANDER, 1992). A similar pattern was observed in a group which was formed by a known (marked) emigrant male from Group 7 who established a home range and attracted females. The first male offspring remained in the group, and became dominant (CLARKE, pers. obs.; GLANDER, 1992). While the behavioral details for that takeover are unknown, the original (now-subordinate) male continues to take an active part in aiding juvenile emigration (CLARKE, pers. obs.; GLANDER, 1992). The presence of two males, even though presumably related, appears to be enough to foster the species-typical juvenile emigration pattern.

Thus infant-killing, which has been described for at least three species of howling monkeys, occurs too frequently in stable populations to be considered social pathology, and occurs too predictably in association with male takeovers to be considered due to resource competition alone. While we cannot demonstrate that the behavior pattern was genetically transmitted to *RO* from his presumed father *HO* (an infanticidal, immigrating, reproductively successful male howling monkey), *RO* did express species-typical behavior in the absence of observational learning.

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REFERENCES

- ALTMANN, J., 1974. Observational study of behavior: sampling methods. *Behaviour*, 49: 227–265.
- , 1979. Age cohorts as paternal sibships. *Behav. Ecol. Sociobiol.*, 6: 161–164.
- BLAFFER HRDY, S., 1974. Male-male competition and infanticide among the langurs (*Presbytis entellus*) of Abu, Rajasthan. *Folia Primatol.*, 22: 19–58.
- , 1976. The care and exploitation of nonhuman primate infants by conspecifics other than the mother. *Adv. Stud. Behav.*, 6: 101–158.
- , 1979. Infanticide among animals: a review, classification, and examination of the implications for the reproductive strategies of females. *Ethol. Sociobiol.*, 1: 13–40.
- BUTYNSKI, T. M., 1982. Harem-male replacement and infanticide in the blue monkey (*Cercopithecus mitis* STUHLMANNI) in the Kibale Forest, Uganda. *Amer. J. Primatol.*, 3: 1–22.
- CLARKE, M. R., 1982. Socialization, infant mortality, and infant-nonmother interactions in howling monkeys (*Alouatta palliata*) in Costa Rica. Doc. Diss., Univ. of California, Davis.
- , 1983. Infant-killing and infant disappearance following male takeover in a group of howling monkeys (*Alouatta palliata*) in Costa Rica. *Amer. J. Primatol.*, 5: 241–247.
- , 1990. Behavioral development and socialization of infants in a free-ranging group of howling monkeys (*Alouatta palliata*). *Folia Primatol.*, 54: 1–15.
- & K. E. GLANDER, 1984. Female reproductive success in a group of free-ranging howling monkeys (*Alouatta palliata*) in Costa Rica. In: *Female Primates: Studies by Women Primatologists*, M. F. SMALL (ed.), Alan R. Liss, New York, pp. 111–126.
- & E. L. ZUCKER, 1989. Social correlates of timing of sexual maturity in free-ranging howling monkeys (*Alouatta palliata*). *Amer. J. Primatol.*, 18: 140.
- , ———, & R. M. HARRISON, 1991. Fecal estradiol, sexual swelling and sociosexual behavior of free-ranging female howling monkeys in Costa Rica. *Amer. J. Primatol.*, 24: 93.
- , ———, & N. J. SCOTT, JR., 1986. Population trends of the mantled howler groups of La Pacifica, Guanacaste, Costa Rica. *Amer. J. Primatol.*, 11: 79–88.
- CROCKETT, C. M., 1984. Family feuds. *Natural History*, 93: 54–63.
- & J. F. EISENBERG, 1987. Howlers: variation in group size and demography. In: *Primate Societies*, B. B. SMUTS, D. L. CHENEY, R. M. SEYFARTH, R. W. WRANGHAM, & T. T. STRUHSAKER (eds.), Univ. of Chicago Press, Chicago, pp. 54–68.
- & T. POPE, 1988. Inferring patterns of aggression from red howler monkey injuries. *Amer. J. Primatol.*, 15: 289–308.
- & ———, 1993. Consequences of sex differences in dispersal for juvenile red howler monkeys. In: *Juvenile Primates: Life History, Development, and Behavior*, M. PEREIRA & L. A. FAIRBANKS (eds.), Oxford Univ. Press, New York, pp. 104–118.
- & R. SEKULIC, 1984. Infanticide in red howler monkeys (*Alouatta seniculus*). In: *Infanticide: Comparative and Evolutionary Perspectives*, G. HAUSFATER & S. B. HRDY (eds.), Aldine, Chicago, pp. 173–191.
- GLANDER, K. E., 1975. Habitat and resource utilization: an ecological view of social organization in mantled howling monkeys. Doc. diss., Univ. of Chicago, Chicago.
- , 1980. Reproduction and population growth in free-ranging mantled howling monkeys. *Amer. J. Phys. Anthropol.*, 53: 25–36.
- , 1982. The impact of plant secondary compounds on primate feeding behavior. *Ybk. Phys. Anthropol.*, 25: 1–18.

- , 1992. Dispersal patterns in Costa Rican mantled howling monkeys. *Int. J. Primatol.*, 13: 415–436.
- , L. M. FEDIGAN, L. FEDIGAN, & C. CHAPMAN, 1991. Field methods for capture and measurement of three monkey species in Costa Rica. *Folia Primatol.*, 57: 70–82.
- HAUSFATER, G. & S. BLAFFER HRDY (eds.), 1984. *Infanticide: Comparative and Evolutionary Perspectives*. Aldine, Chicago.
- HELTNE, P. G., D. C. TURNER, & N. J. SCOTT, JR., 1976. Comparison of census data on *Alouatta palliata* from Costa Rica and Panama. In: *Neotropical Primates: Field Studies and Conservation*, R. THORINGTON, JR. & P. HELTNE (eds.), National Academy of Sciences, Washington, D.C., pp. 10–19.
- HOLDRIDGE, L. R., 1967. *Life Zone Ecology*. Tropical Science Center, Costa Rica.
- IZAWA, K., 1988. Preliminary report on social changes of red howler monkeys (*Alouatta seniculus*): *Field Studies of New World Primates. La Macarena Colombia*, 1: 29–33.
- & H. LOZANO, 1991. Social changes within a group of red howler monkeys (*Alouatta seniculus*): III. *Field Studies of New World Monkeys. La Macarena Colombia*, 5: 1–16.
- JONES, C. B., 1980a. Seasonal parturition, mortality and dispersal in the mantled howler monkey, *Alouatta palliata* GRAY. *Brenesia*, 1: 1–10.
- , 1980b. The functions of status in the mantled howler monkey (*Alouatta palliata* GRAY): intraspecific competition for group membership in a folivorous neotropical primate. *Primates*, 21: 389–405.
- MACROBERTS, M. & B. MACROBERTS, 1966. The annual reproductive cycle of the Barbary ape (*Macaca sylvanus*). *Amer. J. Phys. Anthropol.*, 25: 299–304.
- OHSAWA, H., M. INOUE, & O. TAKENAKA, 1993. Mating strategy and reproductive success of male Patas Monkeys (*Erythrocebus patas*). *Primates*, 34: 533–544.
- ROSS, C., 1993. Takeover and infanticide in South Indian Hanuman Langurs (*Presbytis entellus*). *Amer. J. Primatol.*, 30: 75–82.
- RUMIZ, D. I., 1990. *Alouatta caraya*: population density and demography in northern Argentina. *Amer. J. Primatol.*, 21: 279–294.
- SCOTT, N. J., JR., L. A. MALMGREN, & K. E. GLANDER, 1978. Grouping behavior and sex ratio in mantled howling monkeys. In: *Recent Advances in Primatology I*, D. CHIVERS & J. HERBERT (eds.), Academic Press, New York, pp. 183–185.
- , A. F. SCOTT, & L. MALMGREN, 1976. Capturing and marking howler monkeys for field behavioral studies. *Primates*, 17: 527–534.
- SEKULIC, R., 1983. Male relationships and infant deaths in red howler monkeys (*Alouatta seniculus*). *Z. Tierpsychol.*, 61: 185–202.
- STEKLIS, H. & G. KING, 1978. The craniocervical bite: toward an ethology of primate predatory behavior. *J. Human Evol.*, 7: 567–581.
- STRUHSAKER, T., 1977. Infanticide and social organization in the redtail monkey (*Cercopithecus ascanius* SCHMIDT) in the Kibale Forest, Uganda. *Z. Tierpsychol.*, 45: 75–84.
- SUGIYAMA, Y., 1965. On the social change of Hanuman langurs (*Presbytis entellus*) in their natural condition. *Primates*, 6: 381–418.
- , 1966. An artificial social change in a Hanuman langur troop (*Presbytis entellus*). *Primates*, 7: 41–72.
- ZUCKER, E. L. & M. R. CLARKE, 1986. Male-male interactions in a group of free-ranging howling monkeys. *Amer. J. Primatol.*, 10: 443.
- ZUNINO, G. E., S. C. CHALUKIAN, & D. I. RUMIZ, 1985. Infanticidio y desaparicion de infantes asociados al reemplazo de machos en grupos de *Alouatta caraya*. *Primatologia No. Brasil*, 2: 185–190.

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