

## RESEARCH ARTICLES

### Inferring Patterns of Aggression From Red Howler Monkey Injuries

CAROLYN M. CROCKETT<sup>1</sup> AND THERESA POPE<sup>2</sup>

<sup>1</sup>Department of Zoological Research, National Zoological Park, Smithsonian Institution, Washington, D.C., and Departments of Anthropology and Psychology, University of Washington, Seattle; <sup>2</sup>Department of Zoology and Florida State Museum, University of Florida, Gainesville

Venezuelan red howler monkeys in a semideciduous habitat typically survive injuries and disabilities. Intraspecific physical aggression was the most frequently observed and inferred cause of injury. Thirty-eight percent of 119 howlers of all ages examined during capture had scars or other evidence of "damage." Overall, the sexes did not differ significantly in total number of injuries or number of individuals classified as "damaged." The incidence of injury was not independent of age-sex class. The subadult male class had the highest percentage of "damaged" individuals. However, when total injuries per age class were examined for each sex separately, only females showed a pattern that was significantly different than expected based on age (i.e., exposure to injury factors). Subadult females experienced more injuries than expected, whereas adult females had fewer injuries. Troop status (resident troop, natal troop, or extratrop) was not significantly related to the number of injuries in adult and subadult males. This finding was not surprising, because adult and subadult males of all status classes are involved in aggression related to breeding competition. Extratrop females had more injuries than expected, and natal females had the fewest injuries. The higher incidence of injuries on subadult females and extratrop females is consistent with aggression-mediated emigration of some females and observed resistance to female immigration by resident females. Overall, 74% of injuries were located on anterior-ventral portions of the body, consistent with the face-to-face fighting observed in howlers. Sociobiological costs of aggression in red howlers are difficult to assess because many howlers, despite frequent and severe injury, subsequently survive and reproduce. We recommend caution in inferring mortality from injuries, especially when social mobility and emigration out of the study area are common.

**Key words:** *Alouatta seniculus*, reproductive competition, disabilities, age-sex class differences

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Address reprint requests to Dr. Carolyn M. Crockett, 13034 1st Ave. N.E., Seattle, WA 98125-3005.

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## INTRODUCTION

Howler monkeys have been characterized as exhibiting some of the lowest levels of conspecific aggression reported for any social primate: "Virtually all observers of howler monkeys, *Alouatta* spp., have commented on the rarity of conspecific agonistic interactions and aggression" [Klein, 1974, 118]. In general, to characterize aggressiveness, one must not only consider the absolute frequency of aggression but also its severity and frequency relative to other kinds of social interaction [Walters & Seyfarth, 1987]. The infrequency of social interaction within howler monkey troops has frustrated the attempts of many workers to establish clear patterns of rank and social dominance [for reviews see Crockett & Eisenberg, 1987; Klein, 1974]. Also, disagreements regarding which howler behaviors to classify as "agonistic" have further retarded an evaluation of the prevalence of aggression in this genus [Klein, 1974].

Despite howlers' reputation for passivity, reports on incidence of wounding suggest that although aggression may be infrequent, it commonly results in physical injury. Chivers [1969] observed that 15% of mantled howler (*Alouatta palliata*) adult males in his study population had scars or torn lips, which he attributed to aggression among troop males. In the first study of red howler monkeys (*A. seniculus*) at our site (Hato Masaguaral, Venezuela) Neville [1972] reported that about 13% of adult and subadult males had scars or missing fingers. Rudran [1979] subsequently reported extensive wounding in red howler males resulting from observed physical aggression during troop invasions and takeovers by extratroup males. Sekulic [1983a] witnessed considerable within-troop aggression among males in the context of status reversals. In fact, several adult red howler monkeys in our study area are known to have died from injuries sustained in observed or presumed male-male fighting [Rudran, 1979; Sekulic, 1983a; Crockett & Sekulic, 1984].

Although howler aggression was originally thought to involve primarily adult males, more recent evidence has suggested that other age and sex groups also show aggression. Aggression has been observed by troop females toward solitary females [e.g., Sekulic, 1982] and inferred among females in the context of forced dispersal of immature females by reproductive females [Crockett, 1984]. Fatal aggression by adult males toward infant howlers (infanticide) has been reported in red howlers [Rudran, 1979; Sekulic, 1983a; Crockett & Sekulic, 1984] as well as in *A. palliata* [Clarke, 1983] and *A. caraya* [Zunino et al., 1985].

The rarity of observed aggressive interactions makes it difficult to quantify and compare aggression among the different age-sex groups. Thus, we have systematically quantified physical injuries in a sample of captured red howler monkeys. We also describe in detail some of the types of injuries that red howlers in our study area have survived. Although aggressive interactions are relatively infrequent in this species, aggression does occur in circumstances in which the stakes are high, and the price frequently is injury. Specifically, the occurrence of injury is related to intrasexual competition and troop membership status.

## METHODS AND STUDY AREA

These data were collected on red howler monkeys in the *llanos*, or plains, of Venezuela. The study area, Hato Masaguaral, has been described in numerous publications [e.g., Rudran, 1979; Troth, 1979; Crockett, 1984, 1985; Crockett & Rudran, 1987a]. Crockett and Eisenberg [1987] summarize the behavior and polygynous social organization of howler monkeys. Red howlers differ from most primate species in that many immatures of both sexes emigrate from their natal troops [see Pusey & Packer, 1987]. As a consequence, approximately 6% of our study population of about 500 animals are found in extratroup associations (groups that have not

produced offspring) or are solitary [Crockett, 1984, 1985]. Between 1979 and 1983, 15 extratroup associations persisted, produced offspring, and became new troops [Crockett, 1985].

The qualitative observations of aggression and wounding reported here were taken from field notes made during census contacts with many troops and extratroup animals over 6 years and during intensive behavioral observations of selected troops and individuals. Crockett censused 43–54 troops and numerous extratroup animals in two habitats (Woodland and Gallery Forest); Pope censused 33 Woodland troops and all extratroup animals encountered in the Woodland habitat. Crockett observed howlers in both habitats in October 1978, March 1979–February 1981, November–December 1981, February 1983, and February 1984 and recensused the Gallery habitat in March–April 1987. Pope was at the site from January 1981 to January 1982 and from February 1984 to July 1985.

Quantitative assessment of wounding was made on a sample of 119 captured howlers. In January and December 1981, howlers of all ages (1 week to old adult) were captured for ear tagging, measurement, and blood samples [see Thorington et al., 1979]. This cross-sectional sample was representative of animals in the whole population and was considered to be unbiased with respect to the occurrence of injuries. We attempted to capture entire troops and most extratroup individuals encountered.

Each of 119 captured animals in the sample was carefully inspected for injuries, scars, and other defects, and the location and description of any damage was noted. Some animals also had permanent scars previously recorded on their individual description sheets (as part of the ID system for individual recognition). The total number of injuries for each individual was scored, based on evidence of past injury (scars, damaged bones, etc.) as well as recent wounds. Each "injury" was given a score of 1, except missing teeth (excluding milk teeth), for which a score of 1 was given regardless of the number missing. Any monkey with one or more injuries was considered "damaged." The location of injuries on the body was classified as either anterior-ventral (head, shoulders, arms and hands, throat, and ventrum) or posterior-dorsal (legs and feet, back, rump, and tail).

Each monkey was assigned an age-sex class. Most immatures were of known months of age, although a few ages were approximated. Most adults were of unknown age; for analysis purposes, they were assigned a mean age (see Results). Infant males (IM) and infant females (IF) were 0–12 months of age; juvenile males (JM) were 13–47 months; juvenile females (JF) 13–35 months; subadult males (SAM) 48–71 months; subadult females (SAF) 36–59 months. Males (AM) were considered adult at 6 years; females (AF) at 5 years. (The subadult classes include animals in the large juvenile category of Crockett [1984]; males aged 6–7 years are sometimes classified as adult/subadult or SA+ but are considered adults in the analyses in this paper.)

The adults and subadults were also grouped into sex- and troop-status categories, i.e., extratroup, natal, or resident. Animals classified as extratroup were living outside of an established troop at the time of capture, either alone or in association with other extratroup animals. All had emigrated from their natal troops. Natal individuals were those still living in the troop in which they were born. Most natal animals were immature, but some adults were believed to be natal, based on their immaturity when first observed in their troops. Resident animals (all adults) had either immigrated into the troop in which they were a member or were already present as an adult in that troop at the time of the first census contact. Nearly all resident males were known immigrants. Resident females may have been born in the troop (natal origin), or they may have been one of the troop "founders"

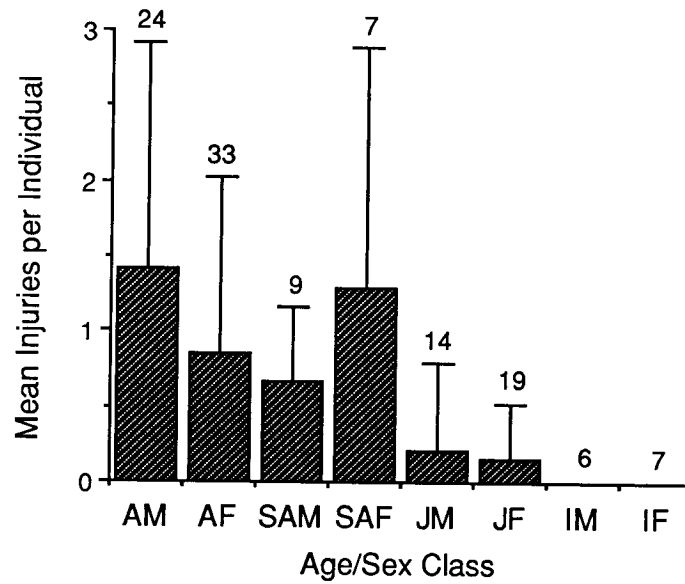


Fig. 1. Mean number of injuries per individual in each age-sex class; error bars present standard deviations; number above bar is sample size.

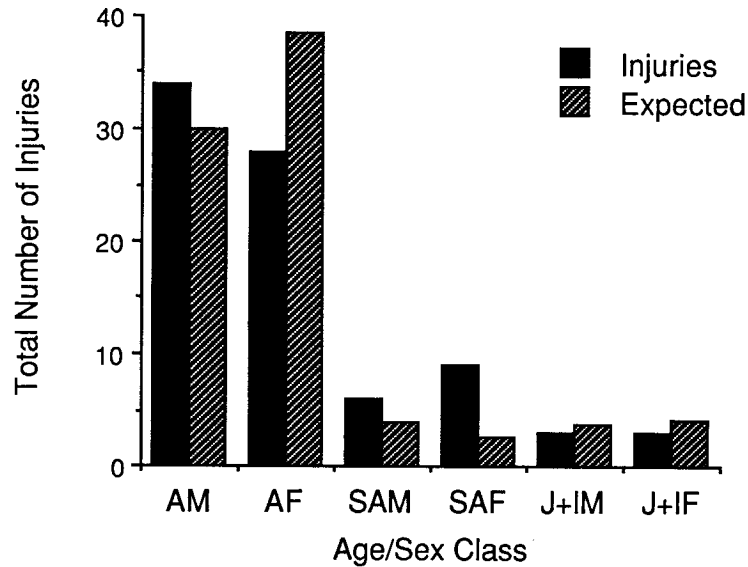


Fig. 2. Observed injuries per age-sex class compared with expected values based on "months of exposure" per class (see text).

from the time the troop was first established from extratrop animals (immigrant origin). However, which of those cases applied to any individual resident female usually could not be determined. One resident female was one of the few examples of a known female immigrant into an established troop [Crockett, 1984].

Specific analyses are described in Results. Probability levels for the chi-square distribution are from Rohlf and Sokal [1981].

## RESULTS

### Injuries by Age-Sex Class

Of the captured howlers, 45 individuals or 38% had evidence of present or past injury, 42% of males and 35% of females (Table I). The damaged individuals included those with broken bones; stiff, bent, or missing digits; a missing limb; torn ears; fresh wounds; and healed scars that indicated past injuries. We also classified missing teeth as evidence of injury because in all cases missing teeth were associated with known past injuries or scars. One juvenile female in the capture sample may have been partially blind as a result of a possible cataract; however, this disability was not classified as an injury.

The overall sex difference in number of damaged individuals compared with expected values computed from the proportion of each sex in the capture sample was not significant ( $\chi^2 = 0.09$  with Yates' correction,  $P > .50$ ,  $df = 1$ ). However, the distribution of damaged individuals with respect to age-sex class was significant ( $\chi^2 = 15.46$ ,  $P < .01$ ,  $df = 5$ ; the infant and juvenile classes were combined because no expected value should be less than 1 [Zar, 1984, 49]). In the sample, the proportion of subadult females that was damaged (57%) was higher than that of adult females (48%) and was nearly identical to the percentage of damaged adult males (58%). Subadult males had the highest proportion of damaged individuals of all classes (67%). (The reversal between subadult and adult percentages is not contradictory if damage and survival to adulthood are inversely related.) Few juveniles and no infants were damaged. The scars on one juvenile female (6183) resulted from an injury she received as an infant, which was interpreted as a possible infanticide attempt [Crockett & Sekulic, 1984].

Figure 1 presents the mean number of injuries recorded for each age-sex class. The variances (SDs) tend to be large because a minimum of one-third of the animals in each class had no injuries (range = 0–5 injuries per individual). Although a lower percentage of subadult females was damaged, compared with subadult males, these females had a higher mean number of injuries. As in previous wounding studies [Whitten & Smith, 1984; Ruehlmann et al., 1988], the total number of injuries recorded for each age-sex class was considered an indirect estimate of aggression received. Although some minor wounds will heal completely, the more-severe injuries leave permanent scars (see next section). Because 70% of the injuries scored in the capture sample consisted of evidence of past wounding of the type that accumulates with age (e.g., scarred lips, healed fractures, slit ears, missing teeth), it was necessary to control for this factor when testing the differences among age classes. Therefore, expected values for number of wounds in each class were determined by assuming that the total number of injuries should be randomly distributed among age-sex classes proportional to age, i.e., based on length of exposure to injury factors. (The underlying null hypothesis is that individuals receive injuries whose rate of occurrence and severity is independent of age-sex class.) The technique used to calculate the relative number of animal months of exposure for each class was based on the method described by Altmann & Altmann [1977] for an unknown constant rate of behavior, and a variable population composition. This method was used to assess patterns of wounding in stump-tail macaques (*Macaca arctoides*) [Whitten & Smith, 1984]. The average age of each howler age-sex class was multiplied by the number caught to yield the proportional representation of "exposure to risk." Because adult ages were usually unknown and adequate life table data unavailable, the mean age was estimated in the following manner: animals were assumed to die

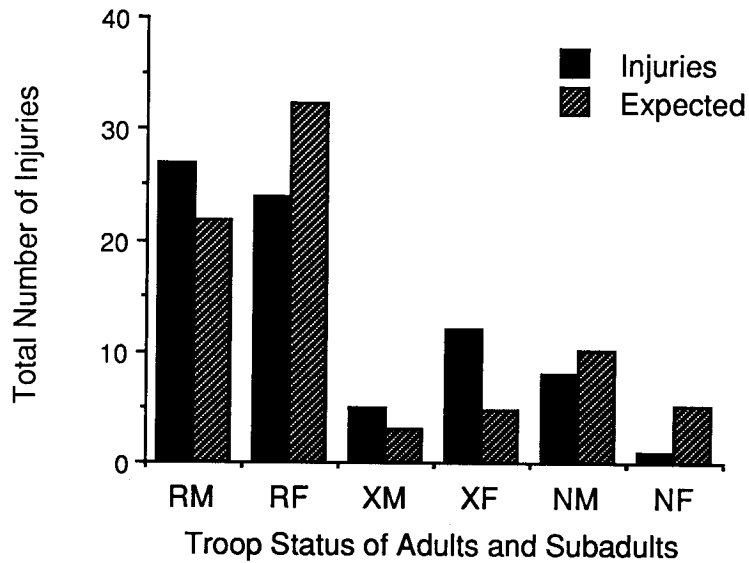


Fig. 3. Observed injuries per troop status-sex class (adults and subadults only) compared with expected values based on "months of exposure" per class (see text).

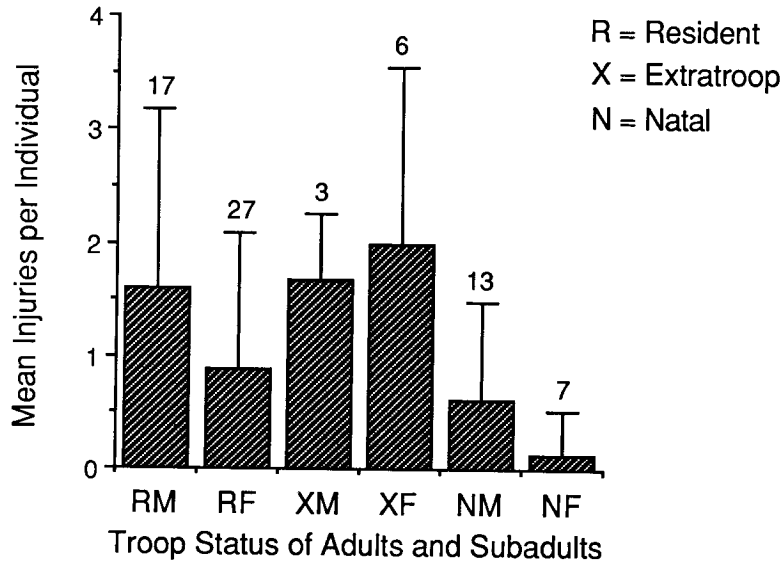


Fig. 4. Mean number of injuries per individual in each troop status-sex class (adults and subadults only); error bars present standard deviations; number above bar is sample size.

at a constant rate from reaching adulthood (100% alive) until age 25 years (0% alive). The average age,  $x$ , was computed as the point on the x-axis at which half the area under the curve (straight line) was reached, i.e., area above  $25 - x =$  area above  $x -$  age of adulthood. For females reaching adulthood at age 5 years, the average age

$x = 10.86$  years, or 130 months, and for males reaching adulthood at 6 years,  $x = 11.56$  years, or 139 months.

Overall, the distribution of injury among age-sex classes was significantly different from random ( $\chi^2 = 20.58$ ,  $P < .001$ ,  $df = 5$ , Fig. 2); the infant and juvenile classes were combined because no expected value should be less than 1 [Zar, 1984, 49]. Testing each age class separately for males and females revealed that only the females experienced injuries disproportionately across age classes (males,  $\chi^2 = 0.77$ ,  $P > .50$ ,  $df = 2$ ; females,  $\chi^2 = 20.77$ ,  $P < .001$ ,  $df = 2$ ). This result was primarily due to the subadult female class, which had an accumulation of injuries that was  $3\frac{1}{2}$  times the expected value. Adult females exhibited fewer injuries than expected, suggesting a decline in the rate of injury accumulation during the adult years. The total injuries on males vs. females was not significantly different than expected, neither by their proportional months of exposure ( $\chi^2 = 1.10$  with Yates' correction,  $P > .10$ ,  $df = 1$ ) nor by the proportion of males to females in the sample ( $\chi^2 = 1.49$  with Yates' correction,  $P > .10$ ,  $df = 1$ ).

The position of wounds by age-sex class was examined by testing the null hypothesis that half of the wounds would be anterior-ventral. Whitten and Smith [1984], citing data from Hori et al. [1972], presented a figure of a Japanese macaque (*M. fuscata*) indicating that 49% of body surfaces were anterior-ventral. Because howler monkeys have long tails, their anterior percentage is probably slightly less than that of *M. fuscata*. Using 50% of total injuries per age-sex class as the expected values, the class by position  $\chi^2 = 15.61$  ( $P < .01$ ,  $df = 5$ ). Because the heterogeneity chi square [Zar, 1984, 51] was not significant ( $.5 < P < .25$ ), it is legitimate to pool the totals across age-sex classes. Overall, 73.5% of injuries were anterior-ventral ( $\chi^2 = 8.70$  with Yates' correction,  $P < .005$ ,  $df = 1$ ). The prevalence of anterior injuries was shown for all classes but subadult females, for whom seven of nine (78%) injuries were posterior, suggestive of a different pattern of aggression.

### Troop Status

The analysis of injury by each sex-troop status class used expected values calculated by average age (exposure to risk), as described earlier for the age-sex class comparison, except that only adults and subadults were included (Fig. 3). The overall injury by class analysis was significant ( $\chi^2 = 19.53$ ,  $P < .005$ ,  $df = 5$ ). When sexes were tested separately, males' injuries were not significantly related to troop status, whereas females' were highly significant (males,  $\chi^2 = 1.98$ ,  $P > .10$ ,  $df = 2$ ; females,  $\chi^2 = 18.07$ ,  $P < .001$ ,  $df = 2$ ). The number of injuries on extratroop females was  $2\frac{1}{2}$  times the expected value, and natal females had less than one-quarter the expected number of injuries.

Figure 4 presents the mean number of injuries per sex-troop status class for subadults and adults (the resident class only includes adults). Natal adult and subadults of both sexes have the lowest mean number of injuries. Extratroop females (which in this sample included three adults and three subadults) had the most injuries and almost no overlap in error bars with natal adult and subadult females. Over 83% of these extratroop females were damaged, compared with only 14% of natal adult and subadult females. Resident females had about half the mean number of injuries as extratroop females, and 52% of them were damaged. Resident and extratroop males had similar mean number of injuries. The percent damaged for adult and subadult males was 100% for extratroop, 65% for residents, and 46% for natal.

Overall for adults and subadults, 56 of 77 injuries were anterior-ventral (73%), but for the extratroop female class, nine of 12 injuries were posterior-dorsal (75%).

### Survival of Handicapped Howlers

The purpose of this section is to describe qualitatively the nature of the wounds and scars observed in the red howler population and how some of these injuries have affected survival and reproduction in the animals sustaining them. Some of the individuals described below are included in the captured sample (Table I), but others were detected during census and behavior observations.

**Lacerations and punctures.** A number of howlers were seen with multiple severe lacerations that they survived. Some were in association with slashed lips, amputated digits, and/or broken bones, whereas others did not include these additional injuries. For example, a 2½-month-old male (7174) survived a deep slash wound to the base of the tail and onto the right leg that was an apparent infanticide attempt [Sekulic, 1983a]. Solitary subadult male 7751 had a scar on his left wrist that indicated a severe, debilitating injury at one time. However, at the time of capture, the hand seemed to function normally. He successfully invaded troop M72 two months later, and eventually became the alpha male. Adult male 6312 had multiple fresh injuries at the time of his capture, including a deep wound across the right biceps and wounds in his tail pad and behind the left ear. He recovered fully and maintained his position as the breeding male of troop M63.

Although most individuals seen with injuries of a similar nature appeared to recover, breeding potential is sometimes reduced. Male 8200, a member of an extratrop association, was attacked by both adult males from troop M61 in a territory dispute. The fight left him with severe lacerations in the groin, neck, and shoulders and unable to follow the rest of his association on their daily foraging rounds. While in this weakened state, a new male was able to successfully evict male 8200 and take over his association of females. Although 8200 had fully recovered from his injuries 5 months later, he had been unable to regain breeding status elsewhere and remained solitary. His former extratrop association eventually became a troop (i.e., produced offspring).

Slashed lips are common injuries associated with observed and inferred fights in both sexes. Cut lips would appear to be somewhat handicapping injuries, in that they might impair an animal's ability to eat; however, red howlers in the study area generally recovered from lip injuries. One male (6112) [see Fig. 6-2 in Crockett & Eisenberg, 1987] had a deeply slashed lip when captured in January 1981. The cut extended 3 cm next to the right nostril and was completely split 1 cm to the gum line, exposing the right canine. This male was one of the older males in the population, yet he survived this injury. He was also seen with severe injuries on his face in February 1983; he appeared weak and was not expected to live, yet he survived and was still with his troop at the end of the last census in July 1985. Solitary male 4311 was first seen in February 1983 with a lip that was slashed on the left side to above the level of the nostrils and toward the eye. The split was fresh, completely open, and the teeth showed through. His left outer wrist was also injured, and he did not use his left arm. Three days later, his wound had darkened and healed somewhat, and he was seen associating with an adult female and juvenile male. In February 1984 a male with a healed facial scar of similar location and size was seen in a new troop (G14) a few hundred meters away and was probably the same male.

Some animals with slashed lips may die or be evicted. An unidentified male that had taken over troop M77 was first observed with a laceration on his upper lip that extended from the center of the lip to beneath the left eye. The skin hung open in a long flap, exposing teeth and bone. The injury was surmised to have occurred during the takeover. He was replaced shortly thereafter by the original troop male



TABLE I. Summary of Injuries Detected in a Sample of Captured Red Howler Monkeys, by Age-Sex Class\*

Injury data	Class										Total
	AM	AF	SAM	SAF	JM	JF	IM	IF	Total		
No. animals captured	24	33	9	7	14	19	6	7	119		
No. (%) animals damaged <sup>a</sup>	14(58)	16(48)	6(67)	4(57)	2(14)	3(16)	0	0	45(38)		
Injury type											
Broken bones <sup>b</sup>	3	2	0	2	0	0	0	0	7		
Damaged digits <sup>c</sup>	5	2	0	0	0	0	0	0	7		
Torn ears	3	4	1	0	0	1	0	0	9		
Missing teeth <sup>d</sup>	4	7	0	0	0	0	0	0	11		
Fresh wounds	8	1	5	2	2	1	0	0	19		
Healed scars	11	11	0	5	1	1	0	0	29		
Missing one arm	0	1	0	0	0	0	0	0	1		
Total injuries	34	28	6	9	3	3	0	0	83		
No. (%) anterior	25(74)	23(82)	6(100)	2(22)	2(67)	3(100)	0	0	61(73)		
Mean injuries	1.42	0.85	0.67	1.29	0.21	0.16	0	0	0.70		
S.D.	± 1.50	± 1.18	± 0.50	± 1.60	± 0.58	± 0.37	0	0	± 1.13		

\*Excluding injuries caused during capture and one partially blinded by possible cataract.

<sup>a</sup>Of those animals captured, the number scored for one or more injury.

<sup>b</sup>Excluding those in damaged digits; all were healed fractures.

<sup>c</sup>Broken, stiff, bent, or amputated fingers and toes.

<sup>d</sup>One count for one or more teeth missing; excludes milk teeth.



Fig. 5. Broken and lacerated left foot of adult male. (Photo by Raymond A. Mendez.)

(7711) and subsequently disappeared from the study area. One tagged solitary male (7831) with a severely slashed lip was not seen again; his fate is unknown.

Many other males received slashed lips of varying degrees of severity, but longtime resident troop males who received badly slashed lips usually recovered fully. After healing, some scars remained to indicate the injury, but in general the scars were subtle compared to original injuries. Females also received slashed lips and body lacerations [e.g., Crockett, 1984], but none was as severe as the most serious male injuries (e.g., no females had lip slashes as severe as the male in Fig. 6-2 in Crockett & Eisenberg [1987]).

Puncture wounds, although observed less frequently than lacerations, appeared to be potentially debilitating injuries. Female 781 was about 1 year old when her left leg was injured, apparently by a puncture wound in the left shin. She limped badly and held her foot curled in subsequent census contacts, during which time the limb appeared to be somewhat atrophied. She was able to survive 9 months before she disappeared from the troop. Adult female 6321 was also crippled by one or several puncture wounds in her left arm. There was evidence of a bad infection including several holes in her forearm at the elbow. Although she had no or limited use of her arm for at least a month, it eventually healed completely. A photograph in Sekulic [1983a] depicts a severe puncture wound penetrating an infanticide victim's skull.

**Broken bones.** The presence of broken bones usually cannot be verified from observation alone. In captured animals, we identified healed fractures in fingers and toes (categorized as damaged digits in Table I), tails, and limbs. For example, old female 5223 had a broken left ankle that had healed crooked; she also had a broken finger that had healed bent and old scars on her lips. Solitary adult female



Fig. 6. Adult female missing right arm above the elbow. (Photo by Raymond A. Mendez.)

7021 had an old break at the distal end of the ulna and radius. This female had spent many months unsuccessfully attempting to integrate into a troop [Sekulic, 1982]. Adult male 5111 had broken his left tibia and probably fibula; that break had also healed crooked. The male also had a scar on the inner left thigh and outside his right foot. His injuries were probably received around July 1978, when he fought with a second adult male in the troop [Mack, 1978].

Solitary adult male 5711 suffered multiple injuries in February 1984. Those injuries were presumably inflicted by two males who apparently evicted him from troop M57, in which he had been the only adult male since its establishment in 1979. When the male was captured for examination (not included in Table I), he was found to have a lacerated and broken left foot (Fig. 5) in addition to two large apparent bite wounds (chunks of flesh removed) and a long slash wound. He also had lost weight, weighing 6 kg, compared with 6.9 kg in January 1981. The male healed and remained solitary through July 1984; in September and October 1984 he was seen with another male, a nulliparous female, and a large juvenile female. By February 1985 they remained in the same area and had been joined by another nulliparous adult female.

Two juvenile females aged 14 and 16 months had their femurs broken in January 1981 by the impact of the tranquilizing dart. Temporary splints were placed on their legs while they were handled for measurement and tagging, but the splints were removed at the time of release. Both juvenile females recovered full use of their injured legs and in December 1981 exhibited no visible signs of past injury. They eventually disappeared from their troops in 1984 at an age when emigration was likely. Although recognizable because of their ear tags, they were not located again. However, dispersing females tend to travel rapidly and leave the study area where they would not be found.



Fig. 7. Nulliparous young adult female missing half of tail. (Photo by Carolyn Crockett.)

**Partial blindness.** Four or five individuals were blinded in one eye. Eight-month-old female 5381 was injured when two new males replaced the resident males, and a similar-aged infant disappeared [Crockett & Sekulic, 1984]. The most likely explanation for her injury is an unsuccessful infanticide attempt. The infant had a bare scar on the right side of her face between her eye and ear; the eye appeared blinded and permanently remained small. The infant survived her injury and stayed with her troop through December 1981, when she was 34 months old. She disappeared between December 1981 and February 1983 at an age when she could have emigrated (permanently identifiable; not located again).

Females 7982.1 and 7982.2, successive offspring to the same mother, were both discovered missing their left eye when infants, apparently as a result of disease or birth defect. Female 7982.1 emigrated at age 40 months and died 8 months later. Female 7982.2 was still in her natal troop at the time of the last census contact at the age of about 30 months. An adult female in the Gallery Forest was found to be missing an eye in 1987. The socket was empty, with a scar above it, and the loss appeared to have occurred when she was approximately full size. She was apparently the same animal as an intact natal juvenile 881 last seen in the troop in 1984. In 1987 this female seemed to be fully recovered and carried an infant of about 5 months of age. A fifth monkey, juvenile female 7882, may have been blind in one eye. During capture in December 1981, her right eye was cloudy, perhaps from a cataract (not included as injury in Table I). She disappeared before the February 1983 census (tagged, not located).

**Amputations.** The most severely handicapped individual was a one-armed female (9022; Fig. 6). An extra troop subadult female missing one arm was seen in the study area in May 1980 associating with a subadult male for at least 2 days (Sekulic, personal communication). She was first seen by C.C. in August 1980 as a

solitary, and at that time her injury was completely healed. During capture in December 1981, inspection revealed that the right arm was amputated at the middle of the humerus and that the injury appeared to have been received while the female was nearly grown. Her right humerus was 115 mm long, compared with 140 mm for the left, intact upper arm.

This female locomoted adequately, using her tail to compensate for the missing arm. The most remarkable thing about this female is that she successfully bore an infant, which must have been conceived while she was extratroup. This is the first and only documented case of any female (intact or otherwise) conceiving outside a troop situation in our study area. In two other cases an apparently parous female and a juvenile male were found in newly formed extratroup associations. However, it is not known if the juveniles were the females' sons and if they had been conceived while their mothers were not troop members. They could have been members of troops that dissolved, as has occurred in our study area.

The one-armed female was first seen with her infant son of approximately 4 months of age in June 1981 by T.P. Mother and son were in a newly formed group, which also included two nulliparous adult females and an adult male. The infant was healthy, and the mother seemed to be caring for him adequately. However, the infant soon disappeared, coincident with the replacement of one male by a new male. The infant was probably a victim of infanticide. Eventually, the one-armed female had an infant in March 1985 that survived. Despite her obvious handicap, she was able to emigrate successfully from her natal troop (distance unknown), travel alone, join other extratroup individuals, bear an infant, and maintain membership in a newly formed troop for more than 4 years.

Another conspicuously handicapped howler was a nulliparous female missing half her tail, including the entire prehensile tail pad (4223, Fig. 7). The end of the tail was bare and grayish. The injury was completely healed but appeared to have occurred when the animal was approximately fully grown. When crossing from one tree to another, the female used one hind foot to hang on to a branch, much in the way intact howlers normally use their prehensile tails. The female was solitary when first observed in the Gallery Forest on February 9, 1983. By February 14, she had joined an adult male and two other nulliparous females. The extratroup association was seen again on February 16 and 17, 1983. The short-tailed female was not located in February 1984 or in 1987.

**Nonfunctioning limb.** Another permanently handicapped animal was the oldest female of troop M67, who had completely lost the use of her right hand in an injury sustained before the beginning of the study. A long scar that spiraled around the forearm suggested that the tendons leading to the hand had been severed or damaged. She locomoted with the other three limbs and her tail, occasionally resting her weight on her right forearm by placing it transversely across a tree limb. She maintained her status throughout the study period, and two of her daughters succeeded in remaining in the troop to become breeding females.

## DISCUSSION

### Injuries and Aggression

Red howler monkeys in the *llanos* study area often survive serious and debilitating injuries. As estimated by the number of scarred and wounded howlers in the sample of captured animals, the frequency of these injuries is high. Nearly three-fourths of the injuries were on the anterior-ventral portions of the body, the areas most likely to be vulnerable in the face-to-face aggression typical of red howlers [e.g., see Crockett, 1984, 167]. Most of the detected damage was inferred or observed to be from intraspecific aggression, but a few cases may have been the result of

unsuccessful predation attempts, falls, thorny vegetation, or disease. Because of the low interaction rate in red howlers, aggressive encounters are frequently inferred by field workers from the sudden appearance of fresh wounds in two or more animals known to be involved in recent agonistic conflict [e.g., Rudran, 1979; Sekulic, 1983a; Crockett, 1984]. The results of the quantitative injury analysis are consistent with what we know qualitatively of howler aggression. Most physical aggression appears to be of the male-male or female-female type or is infanticide by males [Rudran, 1979; Sekulic, 1982, 1983a,b; Crockett, 1984; Crockett & Sekulic, 1984]. Aggression between males and females is rare and has been observed primarily in the context of defending infants from potential infanticide and chasing new immigrant males [Sekulic, 1983a; Crockett & Sekulic, 1984]. Intertroop encounters usually involve howling and chasing, and only occasional physical contact (usually rough play between juveniles). Territorial disputes between troops and associations of extratroop individuals occasionally escalate to physical aggression, as in the case described for male 8200.

Reproductive competition is fierce for both males and females in this species. For both sexes the benefit gained through intrasexual aggressive competition is the opportunity to enter or remain in a stable troop, which is a prerequisite for successful reproduction in red howlers. The pattern of wounding in red howlers is consistent with expected patterns of aggression involved in reproductive competition.

Males usually gain breeding status within a troop through aggressive invasion and subsequent eviction of resident troop males [Rudran, 1979; Sekulic 1983a; Crockett & Sekulic, 1984]. Although some troops may contain more than one fully adult male, paternity exclusion based on genetic markers and observations on access to estrous females indicates that only one male fathers the majority of troop offspring [Pope, unpublished manuscript; see also Sekulic, 1983a]. This predominantly single-male harem breeding structure permits less than half of the adult males in the population to breed at any time (based on typical adult female/male sex ratios in troops of 2:1, average number of adult males per troop of 1.1–1.7, and the presence of nonbreeding extratroop males [Crockett & Eisenberg, 1987]). The rate of injury observed in adult and subadult males is consistent with their regular participation in aggressive interactions (i.e., in direct proportion to their age). On reaching subadulthood, males begin to participate vigorously in aiding the resident adult male in defending the troop during takeover attempts, and they were observed to pursue invaders actively. Both adult and subadult males have been evicted after successful takeovers by associations of invading males. Although some males remained in their natal troops until adulthood and a few may have bred there, the majority of natal males emigrate at age 4–6 years [Crockett, 1984]. This information is consistent with the finding that the class with the highest proportion of damaged individuals was the subadult males.

Troop status should have little effect on the accumulation of injuries in males: both invading and defending males may become injured during takeover attempts. Resident troop males that successfully maintain their status will experience aggressive encounters at the rate at which they are attacked by extratroop males attempting invasion or are challenged by coresidents. A resident male may successfully deter several such attempts during his troop tenure. Furthermore, because average troop tenure by a breeding male is estimated to be about 5–7 years [Crockett & Sekulic, 1984], a male can enter the extratroop population of floating males more than once during his lifetime. He may also be successful at entering a new troop a second or possibly even a third time. Rudran [1979] extensively documents this cycle over a 2-year period for individual males living in the Woodland habitat.

The situation is different for females. Unlike howler males (and unlike females of most other nonhuman primates, which rarely emigrate [Pusey & Packer, 1987]), only some maturing females emigrate. For example, in the Woodland population between January 1981 and July 1985, 55% of maturing females emigrated from their natal troops. However, an emigrating female's chances for successful reproduction are considerably lower than those of a female that succeeds in staying in her natal troop, and her age of first reproduction is probably older [Crockett, 1984]. This is because emigrant females must find a troop in which to breed, and because resident females repel attempts of females to immigrate they usually must establish a new troop [Crockett, 1984; Sekulic, 1982]. Furthermore, there is evidence that juvenile and subadult females suffer higher mortality than do maturing males; however, female mortality figures are complicated by the fact that emigrant females tend to travel rapidly beyond the study area, and their fates are difficult to quantify [Crockett & Rudran, 1987b].

Logic and theory suggest, then, that maturing females would "prefer" to breed natively. However, their own reproductive interests may be in conflict with those of resident reproductive females. As elaborated by Crockett [1984] and Crockett and Eisenberg [1987], maintaining an "optimal troop size" (e.g., in terms of foraging strategy) is in the interests of reproductive females. Consistent with these interests, there is evidence that females limit troop size by vigorously excluding outside females from joining the troop and by aggressively coercing natal females other than their own daughters to emigrate when they reach reproductive age; subadult females may also compete with one another over natal breeding opportunities [Crockett, 1984; Sekulic, 1982].

Much of this evidence for female-female reproductive competition has been indirect, but the data on injury patterns further supports the idea that subadult and extratroup females receive a disproportionate amount of physical aggression. Solitary females were usually observed attempting to affiliate with an established troop or extratroup association by way of persistent approach and appeasement, during which they would be repeatedly chased by resident troop females and occasionally caught and bitten [see also Rudran, 1979; Sekulic, 1982]. In fact, solitary females rarely successfully enter an established troop [Rudran, 1979; Crockett, 1984]. However, persistent following sometimes leads either to acceptance in an extratroup association that subsequently develops into a troop or to the establishment of a consortship with a subadult troop male that results in a new extratroup association. A troop or association may be trailed by a solitary female for days or months, potentially subjecting her, on average, to more prolonged, repeated aggression than a male attempting a takeover.

The incidence of injury suggests that the rate of physical aggression involving resident troop females is low, compared with dispersing females. Although many residents must have experienced an extratroup phase, injuries that were received years previously sometimes leave no permanent scars. Also, females that successfully attain adulthood and reproduce may actually have experienced less aggression while young (i.e., this reduced level of injury may be a correlate of reproductive success). The aggression between breeding adult and natal females appears to occur during a limited period of maturation; its incidence therefore tends to be low relative to the total adult life span of a female. Rank interactions among adult troop females are subtle, ambiguous, and infrequent, so that dominance hierarchies are often difficult or impossible to establish [Crockett & Eisenberg, 1987]. Unlike resident adult males, females show no evidence of emigrating from a troop in which they have succeeded in breeding (unless the troop dissolves, which rarely happens). A

resident adult female can generally expect to remain in the same troop for the remainder of her reproductive life without fighting to maintain membership (in contrast to *A. palliata* [Jones, 1980]).

Females that remained in their natal troops experienced the lowest levels of injury of all adults and subadults. About half of the natal females in the sample had already given birth to one or more infants. Only one was old enough to have produced a daughter of recruitment-emigration age that might have needed agonistic support.

The fact that so many howlers do survive injuries makes it difficult to assess the sociobiological costs of escalation in fights. Both sexes will escalate to severely damaging physical aggression that often injures both participants in a fight. Although the cost of injury is sometimes death, individuals usually survive. Even severe injury may minimally impair a howler's ability to find food or avoid predation. The herbivorous foods that comprise the howler diet, particularly leaves, are often abundant and easily consumed with a minimum of energy expenditure and contest feeding competition. Predator avoidance seems to be achieved mainly through group surveillance, freezing silently in dense clumps of vegetation, and minimizing travel on the ground and in open canopy. Male 8200 remained in the canopy of the same two adjacent *Lonchocarpus* trees for 3 consecutive days after receiving his injuries in the fight with the M61 troop males described previously. He moved very little during this period, and ate only the available *Lonchocarpus* leaves.

For both sexes, the benefits of aggressive competition may be the opportunity to enter or remain in a stable troop—usually a prerequisite for successful reproduction. It is likely that if fatalities more commonly resulted from injuries, natural selection might have favored more inhibition of escalation of aggression than seen among red howlers. It would be interesting to see if physical aggression is less common among the mantled howlers (*A. palliata*) of Barro Colorado Island, where screwworm larvae can infect even minor openings caused by abandoned botfly cavities and cause death by boring into the spinal area or brain [Milton, 1982]. However, the percentages of damaged males reported by Chivers [1969] for *A. palliata* and by Neville [1972] for *A. seniculus* were similar (but much lower than our figure for red howlers in the same study area).

### Other Causes of Injury

In addition to intraspecific aggression, unsuccessful predation attempts may be a cause of physical damage. This may have been the source of limb amputation in the one-armed and short-tailed females. Both were emigrants and because of the nature of the *llanos* habitat, they must have traveled considerable distances on the ground in unfamiliar territory. This may have made them more vulnerable to predation. One possibility is the spectacled caiman (*Caiman crocodilus*), which is common in the area [Marcellini, 1979]. Traveling terrestrially through flooded terrain would bring howlers in contact with caimans. Crocodile predation has been reported on longtailed macaques (*M. fascicularis*) [Galdikas & Yeager, 1984].

Although extratroop howlers in general may be more susceptible than animals living in troops to predation attempts, and thereby contribute to the higher incidence of injury observed in this group, predation did not appear to be a significant source of mortality in our study area. The majority of disappearances that occurred during the study period took place during or immediately following male takeover (primarily adult and subadult males or infants) or were disappearances by young animals that had reached emigration age. Rudran [1979] also concluded that death caused by predation probably occurred infrequently in this population. The major predator on howlers may be the harpy eagle (*Harpia harpyja*) [Terborgh, 1986], which is absent from Hato Masaguaral [Thomas, 1979].



Falling was a suspected cause of death for several mantled howlers in a tall forest [Milton, 1982] and possibly for one red howler with an abdominal wound [Rudran, 1979]. Although falls perhaps caused a few of the injuries listed in Table I, they appear to be uncommon, and 15–20 m is the maximum canopy height on our study area. Crockett observed two falls in over 1,600 hr of observation, and Pope observed one fall in over 2,000 hr. None of those monkeys was injured. Furthermore, although we made an effort to catch drugged howlers in hammocks during capture procedures, several collided with branches or the ground, receiving minor scratches or no injuries. Scratches obviously caused during capture were not scored as injuries.

### Comparisons With Other Species

Although the red howler males in our sample had a few more injuries than did females, we found no statistically significant sex difference in total number of injuries nor proportion injured. Most studies have reported more injuries on males than females [reviewed by Smuts, 1987]. Previous primate studies correlating aggression and associated injury with age or sex classes primarily have examined *Macaca* species [e.g. Bernstein et al., 1983; Ruehlmann et al., 1988; Whitten & Smith, 1984; Wilson & Boelkins, 1970], a genus characterized by high levels of aggressive interaction. In those studies, the majority of injuries were attributed to precisely the sort of agonistic rank encounters that are rarely observed in howler troops. Whitten & Smith [1984] found that adult male stumptail macaques (*M. arctoides*) suffered more injuries than expected, based on the time that they had been in the group, whereas adult females did not. Injuries occurred more frequently than expected on the head, but unlike howlers, the stumptails experienced significantly more back injuries, and for females, foot injuries. Only 8% of the wounds incurred during a 1-year study of the Cayo Santiago rhesus macaques (*M. mulatta*) could be attributed to intergroup aggression [Hausfater, 1972].

The old world colobines are similar to howlers, in displaying low levels of intragroup aggression and dominance interactions [Struhsaker & Leland, 1987; Poirier, 1974]. However, intertroop interactions are usually aggressive, and in several species, extreme male-male aggression during invasions, as well as infanticide, have been observed [Struhsaker & Leland, 1987; Hrdy, 1977; Poirier, 1974; Rudran, 1973].

Hrdy [1977] reported that many langurs (*Presbytis entellus*) had injuries of a sort suggesting intraspecific aggression (e.g., wounds on the face, scalp, and body, and torn ears). She found that 81% of adult males and 33% of adult females showed signs of having been injured—more males and fewer females than we found for red howlers. In both populations, male takeovers and infanticides are a regular feature of society. However, langur females do not emigrate, which perhaps accounts for their lower percentage of injured females. In general, the langur and red howler populations showed a similar range and frequency of injuries and disabilities that the individuals often survived. Both areas are dry for part of the year, which may reduce the number of disease and parasitic agents that might make even minor injuries fatal in other areas.

Severe injuries have been survived by a number of species in a variety of habitats. Amputations of limbs were survived by langurs [Hrdy, 1977]; spider monkeys (*Ateles geoffroyi*) [Chapman & Chapman, 1987]; a Japanese macaque (*M. fuscata*) [Nakamichi et al., 1983], and a dwarf mongoose (*Helogale parvula*) [Rood, 1983]. Being blind in one eye appears to be a defect that also can be overcome, although it is more likely to be detrimental to an arboreal primate specializing in great agility and long leaps. Hrdy's [1977] population included seven individuals with cataracts. Total blindness is probably a death warrant. An infant baboon (*Papio ursinus*) was born blind and died at 74 days of age [Collins et al., 1984].

### Inferring Mortality From Injury

Red howlers in the *llanos* habitat appear to be resilient. Both amputees reported here immigrated into the study area. Had they instead emigrated, freshly injured, their disappearances probably would have been attributed to death. In retrospect, caution in inferring mortality from wounds seems appropriate. Reproductive competition in both males and females can be intense, resulting in extensive wounding. The costs of such escalation of fights is difficult to assess because individuals often recover from severe injuries and survive to reproduce, despite such conspicuous disabilities as losing use of a limb. Although the reproductive success of some injured individuals was reduced, participation by both sexes in potentially injurious competition is often a prerequisite to successful reproduction in this species. Clearly, it is time to abandon the misconception that howlers are passive, nonaggressive primates.

### CONCLUSIONS

1. Venezuelan red howler monkeys in a semideciduous habitat typically survive injuries and disabilities. Intraspecific physical aggression was the most frequently observed and inferred cause of injury.

2. Thirty-eight percent of 119 howlers of all ages examined during capture had scars or other evidence of "damage." Overall, the sexes did not differ significantly in total number of injuries or number of individuals classified as damaged.

3. The incidence of injury was not independent of age-sex class. The subadult male class had the highest percentage of damaged individuals. However, when total injuries per age class were examined for each sex separately, only the females showed a pattern significantly different than expected, based on age (i.e., exposure to injury factors). Subadult females experienced more injuries than expected, whereas adult females had fewer injuries.

4. Troop status (resident troop, natal troop, or extratrop) was not significantly related to the number of injuries in adult and subadult males. This finding was not surprising because adult and subadult males of all status classes are involved in aggression related to breeding competition (e.g. repelling invaders or attempting a takeover).

5. Extratrop females had more injuries than expected and had the highest mean number of injuries; natal females had the fewest injuries. The higher incidence of injuries on subadult females and extratrop females (half were subadults) is consistent with aggression-mediated emigration of some females and observed resistance to female immigration by resident females.

6. Overall 74% of injuries were located on anterior-ventral portions of the body, consistent with face-to-face fighting observed in howlers. However, subadult and extratrop females showed the opposite pattern of 78% and 75% posterior-dorsal injuries, respectively.

7. Sociobiological costs of physical aggression in red howlers are difficult to assess because many howlers, despite frequent and severe injury, subsequently survive and reproduce.

8. We recommend caution in inferring mortality from injuries, especially when social mobility and emigration out of the study area are common.

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