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Causes of Intraspecific Aggression in *Alouatta palliata mexicana*: Evidence From Injuries, Demography, and Habitat

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Although howlers have been traditionally considered to be pacific, showing one of the lowest rates of aggression among primates, new evidence is emerging to question this image. We present data on injuries in Mexican mantled howlers (Alouatta palliata mexicana) in relation to different sociecological parameters. We censused howler populations in 19 forest fragments over a 17-mo period in the Los Tuxtlas Region, southern Veracruz, Mexico. We conducted detailed observations of scars, torn lips, broken fingers, mutilated tails and other visible injuries. We also collected data on the demography, biogeography and vegetation of each fragment in order to relate injury data to them. We censused 333 howlers, of which we exhaustively observed 254 for injuries. Four resident adult females ($n = 108$*) and 29 adult resident males (*$n = 76$*) had injuries, while none of the solitary males (*$n = 16$*), solitary females (*$n = 1$*), juveniles (*$n = 23$*) and infants (*$n = 30$*) had them. We discuss possible interpretative scenarios for the distribution of injuries. Although some results suggest that food resource concentration may determine intergroup agonistic encounters, we propose that physical injury is primarily associated with male-male agonistic encounters during takeovers, and consequently it could indicate migration among troops.*

KEY WORDS: *Alouatta palliata*; Los Tuxtlas; Veracruz; Mexico; physical injuries; aggressive behavior.

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INTRODUCTION

Bernstein (1981) proposed that obtaining priority of access to limited resources, with its advantages for reproductive fitness, could be the main function of aggressive behaviors. Males and females are fundamentally different in terms of parental investment (Trivers, 1972), and critical resources vary between sexes (Clutton-Brock and Harvey, 1978; Wrangham, 1979, 1982). For females, the most important limiting resource is food, especially high quality food items. For males, fitness depends on mating success, and access to receptive females. Whenever the resources are limited, conflicts of interests emerge and competition can ensue (van Hooff and van Schaik, 1992).

Although aggression may benefit individual interests, these behaviors entail significant costs. Intense competition, aside from the danger of physical injury, can reduce time available for feeding activities, reproduction, and vigilance, which in turn can decrease lifetime reproductive success (Lee, 1994). The costs are even more serious for species having diets that include significant amounts of low-energy food items, since time and energy available for reproduction and feeding is further conditioned by the poor quality of food items (Jones, 1980).

Since the availability of resources that limit the reproductive fitness of the individuals depends on demographic and ecological constraints, it can be expected that the relative importance of aggressive and nonaggressive tactics will vary both intra and interspecifically (van Hooff and van Schaik, 1992; van Schaik, 1989; Wrangham, 1982).

Due to their folivorous-frugivorous diet and lack of a specialized digestive system (Milton, 1980), *Alouatta* spp. have evolved an energy minimizing strategy. Social interaction rates are very low and aggressive behaviors are even more rare. Howlers exhibit some of the lowest levels of conspecific aggression among social primates (Klein, 1974), but reports on incidence of injuries and skeletal pathologies suggest that although aggression may be infrequent, the common result is physical injury (Chivers, 1969; Crockett and Pope, 1988; DeGusta and Milton, 1998). These episodes of aggression are practically restricted to migratory events in *Alouatta. palliata*.

In order to attain group membership, solitary males must defeat the resident alpha male and assume his position. If they lose, they remain solitary (Clarke, 1983; Glander, 1980). The intensity of the aggressive encounters has been described by Glander (1992, p. 427). During group takeovers, males may attack immatures and infanticide may occur (Clarke, 1983; Clarke *et al.*, 1994). Further female-to-female aggression is related to immigration and the subsequent fights for group dominance. Aggression can range from low-level harassment to hair pulling and biting (Glander, 1992).

Emigration in mantled howlers is not voluntary but is forced by both resident adult males and females (Crocket and Eisenberg, 1987). Juveniles can be forced out of the group via contact aggression (i.e., wounds to extremisties) or aggressive displays by unrelated adults (Clarke and Glander, 1984; Clarke and Zucker, 1989; Cuarón-Orozco, 1997).

For both sexes, once the dominance hierarchies are established, social status relationships are maintained, primarily via spatial regulatory mechanisms and ritualized behaviors, thus allowing a minimal energy expenditure in open competition, i.e., biting, air pulling, and chasing (Jones, 1980).

Reinforcing the idea that howlers minimize aggressive behaviors, Sekulic (1982) suggested that crepuscular howling bouts broadcast group position thus lowering the probability of intergroup encounters and subsequent aggressive episodes.

Despite the evidence of intraspecific aggression in howlers, the rarity of observed aggressive interactions makes it difficult to quantify and to compare aggression among the different age-sex groups (Crockett and Pope, 1988), and to determine how the different socioecological constraints are affecting the expression of the behaviors.

Intense deforestation in Los Tuxtlas Biosphere Reserve has left a mosaic of fragments of different size, shape, grade and age, inhabited by wild populations of howlers of several sizes and composition (Estrada and Coates-Estrada, 1996). The wide range of socioecological conditions with which the howlers must cope makes them of special interest for the analysis of different environmental situations and their influence on social behavior.

Due to the difficulty of direct observation of aggressive behavior and its determinants in field situations, (Crockett and Pope, 1988; DeGusta and Milton, 1998; Jones, 1994), we suggest that physical injuries can be used as an indirect indicator (Crockett and Pope, 1988; DeGusta and Milton, 1998). Accordingly, we quantified facial scars, torn lips, broken fingers, mutilated tails, and protrusions via systematic visual observations, discuss their possible causes, and relate them to different demographic, floristic and biogeographic features of the howler populations and their habitats.

METHODS

Study Site

The study area is in the Los Tuxtlas Biosphere Reserve, (2064129 m., 2042024 m. North and 272772 m., 283819 m. South, zone 15; elevation from sea level to 400 m) in southern Veracruz, Mexico. Mean annual rainfall is 4900 mm, with a drier season from March to May ($X = 111.7 \pm 11.7$ (SD) mm *per* mo), and a wetter season from June to February ($X = 486.25 \pm 87.0$ mm *per* mo). Mean annual temperature is 27°C (Estrada and Coates-Estrada, 1996).

Like many other regions in Central and South America, Los Tuxtlas, has suffered an extensive transformation of its original habitats into pasture and agricultural landscapes. According to Estrada and Coates-Estrada (1996), 1922 km^2 (75%) of the original forest has been destroyed, 514 km^2 (20% of the total area) consists of forest fragments, and only 110 km^2 (5% of total area) contains continuous forest at high elevations.

Data Collection

Census of Howler Populations

We censused howler populations from March to September 2001, and from March to December 2002, in forest fragments surrounding the San Martín Tuxtla Volcano, in the northeastern part of The Los Tuxtlas Biosphere Reserve.

Our census method involved positioning for several days (depending on the size of the fragment) in strategic spots before the sunrise, waiting for the monkeys to howl. Then, we established direct visual contact. The strategic spots were inside or outside the fragments, where we could evaluate sizable forest areas, or near areas where we had heard vocalizations on previous occasions. At the beginning of the fieldwork when we did not hear any vocalizations, we walked throughout the fragment looking for the monkeys for 1-2 h, but this method was not productive.

Once we located howlers, we recorded group composition—[age and sex of all members (Clarke, 1990)]—via 10X42 Swarovski EL binoculars, and documented their location with a GPS. device. In order to avoid data repetition by censusing the same groups more than once, we identified members by drawing its distinguishing color patterns characteristic of the feet and tails of this subspecie.

Finally, we systematically recorded scars, torn lips, broken fingers, mutilated tails or any other sign of physical injury. We registered the subjects as observed for injuries only when appropriate observational conditions allowed us to assess them fully. If any doubt subsisted, we considered them as "unobserved."

Biogeography of the Forest Fragments

In addition to the census, we studied the biogeography of the fragments. Analyzing INEGI aerial photographs of the area (year 1999, 1:20000 scale) via ArcView GIS software (version 3.1.), and Patch Analyst 2.2 extension (Rempel *et al.*, 1999), we measured the total area, shortest distance to the nearest fragment (SN), mean shortest distance to the neighboring fragments (SMN) and shortest distance to the nearest fragment with monkeys (SNM).

Census of the Vegetation

For each fragment we censused a total area of 1000 m^2, distributed in 10 randomly located 50 × 2-m transects (Keel *et al.*, 1993). We registered all trees with a diameter at breast height (DBH) $\geq$10 cm, noting species, family, DBH and position in the transect.

We calculated several diversity indices (total number of species and families, relative number of species and families, Shannon-Weaver entropy index), and mean DBH, tree density, and the sum of the importance indices of the 5 most consumed taxa by Los Tuxtlas howlers (Estrada, 1984).

Data Analysis

Statistics

We used 3 techniques to evaluate the relationships between injuries, fragment isolation characteristics, demographic variables, and vegetation variables: the nonparametric Spearman-*R* correlation coefficient (significance level $p < 0.05$); multiple regression analysis (standard method; tolerance level = 0.0001; $p < 0.05$); and discriminant analysis (standard method; tolerance level = 0.01; $p < 0.005$).

RESULTS

We found howlers in 19 forest fragments (2 temporarily containing 1 solitary male), 1 solitary male in continuous forest, and 1 solitary male in a fragment that we did not census extensively.

We censused 45 groups and 334 howlers: 107 resident males, 16 solitary males, 144 resident females, 1 solitary female, 29 juveniles and 37 infants. Among them we observed 254 individuals: 76 resident males, 16 solitary males, 108 resident females, 1 solitary female, 23 juveniles and 30 infants (Table I).

No immature (juvenile and infant) or solitary male showed injury. Two resident females had a broken finger, and another 2 females had protuberances on their backs that looked like abscesses. However, 29 (38%)

Table I. Characteristics of the populations in each fragment

Fragments	No. of groups		No. individuals		Resident males		Solit. males		Resident females		Solit females		Juveniles		Infants			Sex
	Total[a]	Obs.[b]	Total	Obs.	Total	Obs.	Total	Obs.	Total	Obs.	Total	Obs.	Total	Obs.	Total	Obs.	Dens.	ratio
1	5	5	43	35	16	15	1	1	18	13	0	0	2	2	6	4	0.674	1.059
2	9	5	63	37	22	8	5	5	24	16	0	0	5	4	7	5	0.577	0.889
3	5	5	29	24	13	11	2	2	10	7	0	0	1	1	3	3	0.119	0.667
4	1	1	11	11	2	2	0	0	5	5	1	1	1	1	2	2	0.012	2.5
5	1	1	3	3	2	2	0	0	1	1	0	0	0	0	0	0	0.41	0.5
6	1	1	6	6	1	1	0	0	4	4	0	0	0	0	1	1	2.845	4
7	2	2	14	12	4	4	1	1	6	5	0	0	3	2	0	0	0.428	1.2
8	3	2	13	11	3	2	0	0	9	8	0	0	0	0	1	1	2.463	3
9	1	1	4	4	2	2	0	0	2	2	0	0	0	0	0	0	0.553	1
10	1	1	6	6	2	2	0	0	2	2	0	0	2	2	0	0	0.342	1
11	10	8	108	73	29	16	3	3	48	33	0	0	15	11	13	10	0.713	1.5
12	1	1	12	11	4	4	0	0	7	6	0	0	0	0	1	1	1.664	1.75
13	1	1	5	4	2	2	0	0	3	2	0	0	0	0	0	0	1.375	1.5
14	1	1	5	5	2	2	0	0	2	2	0	0	0	0	1	1	0.535	1
15	1	1	3	3	1	1	0	0	1	1	0	0	0	0	1	1	4.349	1
16	1	1	3	3	1	1	0	0	1	1	0	0	0	0	1	1	3.068	1
17	1	1	2	2	1	1	0	0	1	1	0	0	0	0	0	0	0.286	1
18[c,*]	0	0	1	1	0	0	1	1	0	0	0	0	0	0	0	0	—	—
19[c,*]	0	0	1	1	0	0	1	1	0	0	0	0	0	0	0	0	—	—
20[d,*]	—	—	1	1	—	—	1+?	1+?	—	—	—	—	—	—	—	—	?	?
21[e,*]	—	—	1	1	—	—	1+?	1+?	—	—	—	—	—	—	—	—	?	?
Total	45	38	334	254	107	76	16	16	144	109	1	1	29	23	37	30		

[a]Number of individuals censused.
[b]Number of individuals observed for aggression signs.
[c]Fragments temporarily with solitary males.
[d]Uncensused fragment.
[e]Continuous forest.
*Not considered for analysis.

Table II. Relations between number of groups per fragment and number of males per group with the existence of aggression (not considering broken fingers and protuberances)

No. of groups	No. of males	Aggression evidences Yes	No	Total
Single group	1 male	0	4	4
	≥2 males	1	6	7
Many groups	≥2 males[a]	5	1	6
Total		6	11	17

[a] All fragments with >1 group had ≥2 resident males.

of the resident males showed some kind of injury. Most ($n = 23$) had ≥1 scar on the face, 1 male had one scar on the face and a broken finger, 2 had mutilated tails, 2 had a broken finger, and 1 had a protuberance on the back. In males, almost all the injuries were facial (87%, $n = 41$): scars on the lower lip (30%, $n = 14$), on the upper lip (43%, $n = 20$), or somewhere else on the face (15%, $n = 7$). Others consisted of mutilated tails (4% $n = 2$), broken fingers (6%, $n = 3$) and bodily protuberances (2%, $n = 1$). The broken fingers and protuberances could very probably be due to causes other than fights; therefore, we excluded them from our analysis.

Eleven of the 17 fragmented howler populations showed no injury; 10 of them were single groups, and 1 comprised 2 groups. Five of the 6 fragments where howlers showed injuries had >1 group. Ninety percent ($n = 9$) of the groups living in single-group fragments showed no injury, while 59% ($n = 16$) of the groups living in multigroup fragments had no injury. Finally, no population containing 1 male *per* group had an injury attributable to agonism ($n = 4$) (Table II).

As an indicator of food availability, and therefore, resource competition, we analyzed population densities and multiple vegetation variables [number of species, relative density of species, Shannon-Weaver entropy index, tree density, tree DBH, number of families, relative diversity of families, and importance of the 5 most consumed taxa in Los Tuxtals (Estrada, 1984)]. Via a step-by-step method, we regressed each vegetation variable with the injury variables, total number of injured resident males (NIRM) and total number of injuries (NI). No food availability indicator showed a significant relation with injury variables. Only DBH by itself correlated significantly with total number of injured males ($R^2 = 0.643$, $p = 0.001$) and with the total number of injuries ($R^2 = 0.553$, $p = 0.018$).

To test for a relation between the number of groups in a fragment and both (NIRM) and (NI), we ran a Spearman rank correlation analysis, which showed strong relations in both cases ($r_s = 0.812$, $p < 0.001$; $r_s = 0.803$, $p < 0.001$). But in an analysis only considering fragments with $j > 1$ group

($n = 6$) there was no significant relationship ($r_s = 0.522$, $p = 0.288$; $r_s = 0.667$, $p = 0.148$). Similarly, there was no significant relationship between group density (number of groups *per* ha) and the injury variables mentioned ($r_s = -0.455$, $p = 0.364$; $r_s = -0.418$, $p = 0.414$).

There was association between injury variables (NIRM and NI) and other demographic parameters: population densities ($r_s = 0.055$, $p = 0.835$; $r_s = 0.086$, $p = 0.7435$); female-to-male ratio in the populations ($r_s = 0.021$, $p = 0.938$; $r_s = 0.067$, $p = 0.797$); and sex ratios of groups ($r_s = 0.155$, $p = 0.352$; $r_s = 0.161$, $p = 0.335$). It could be expected that the probabilities for a group to receive a solitary male, resulting in possible aggressive episodes that may lead to injuries, would be related to the number of groups in the fragment and to their degree of isolation (Table III). Hence, the chances of finding injuries in howlers in an isolated fragment with one or few groups should be minimal. To test these predictions (Fig. 1) we ran a discriminant function analysis relating the number of groups and the degree of isolation of the fragments with the injury variables. SNM was the best discriminating isolation parameter with an 88% predictive value of the expected over the observed cases [$\lambda = 0.40$ $F(2.14)$, $p < 0.001$]. The model seems to confirm the influence of immigration probabilities, within or between fragments, with respect to injury.

Table III. Isolation grade of fragments

Fragments	SN	SMN	SNM
1	24	442	24
2	24	304	24
3	58	287	53
4	400	700	3000
5	225	423	2000
6	228	835	4000
7	208	1294	208
8	462	1090	470
9	671	1245	780
10	123	602	500
11	53	463	53
12	214	720	220
13	159	506	165
14	174	903	660
15	209	863	480
16	746	1603	431
17	1583	2261	1541

Note. SN = shortest distance to the nearest fragment; SMN = mean shortest distance to the surrounding fragments; SNM = shortest distance to the nearest fragment inhabited by howlers (all measures in meters).

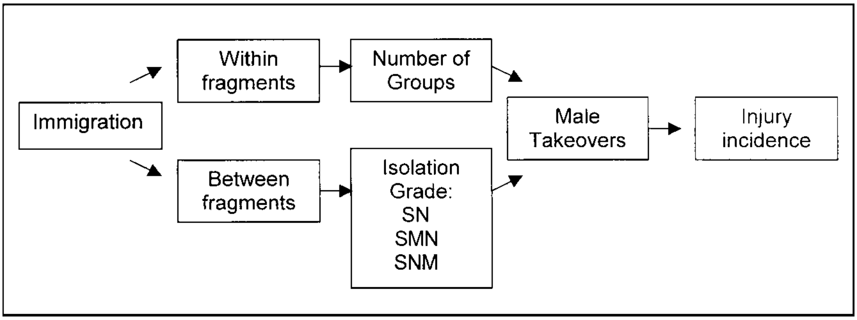

Fig. 1. Schematic representation of injury incidence as a consequence of male immigration associated events.

DISCUSSION

Howlers have low rates of aggression, which impedes the direct study of the behavior and the circumstances which may lead to it. A possible approach to cope with the difficulties of direct observation is to use an indirect method. Scars and other injuries, are a useful way to survey frequency, age/sex distribution, social context, and socioecological influences of intense agonistic behaviors (Crockett and Pope, 1988; DeGusta and Milton, 1998).

The fact that 90% ($n = 41$) of all observed injuries were facial could be an artifact of our observational method . Crockett and Pope (1988) noted several postcranial injuries in anesthetized *Alouatta seniculus*, and it is possible that we missed some scars obscured by the pelage, but this does not affect the main point of our study. Why do resident males have so many facial injuries, while other age-sex classes do not? Injuries are expected to arise from different circumstances: diseases; accidents, e.g., falls from trees (Jones, 1994); interspecific encounters (predation or other conflicts); and intraspecific competition.

Los Tuxtlas howlers show signs of bot fly (Diptera order, Oestridae family), intense infestation most probably *Alouattamyia baeri* (Cristóbal-Azkarate, *in prep.*): large and conspicuous nodules that leave round wounds which can easily become abscessed (Milton, 1996). Accordingly we consider that the dorsal protuberances on the monkeys are best explained as being abscess nodules caused by a bot fly.

The broken fingers could be due to falls or other random accidents because they are equally distributed between sexes. There is no reason to believe that one sex is clumsier than the other, though males are heavier. Falls are more common among immatures than among adults (Glander, 1975), but for cumulative reasons, their consequences—(injuries)—should be more common among the elderly. This could explain why we saw no immature individual with broken fingers or any other injury.

The fact that only adult resident males (34%) had facial scars, torn lips and mutilated tails, would suggest that it is unlikely that they are due to disease or other random accidents.

DeGusta and Milton (1998) suggested that interspecific conflict with spider monkeys (*Ateles geoffroyi)* might explain some of the skeletal trauma in howler populations on Barro Colorado Island (BCI), Panama, though they attribute most of it to intraspecific aggression. Spider monkeys (*Ateles geoffroyi vellerosus*) are extinct in our study site. Cranial injuries were also confined to adult male BCI howlers, in concordance with the our results.

Potential predators for *Alouatta* include harpy eagles (*Harpia harpyja)*, crested eagles (*Morphus guianensis)*, jaguars (*Panthera onca)*, ocelots (*Feliz pardalis)*, tayras (*Eira barbara)*, boa constrictors (*Boa constrictor)*, and anacondas, (*Eunectes marinus)* (Asensio and Gómez-Marín, 2002). At Los Tuxtlas, only ocelots, tayras and boas are present. It is very unlikely that a boa, with its small teeth, could leave conspicuous scars. The ocelots, due to their small size and solitary habits, usually hunt by surprise, focusing on the most vulnerable individuals and avoiding the stronger. Asensio and Gómez-Marín (2002) describe how the predator avoidance behavior of one howler group in response to an aggressive approach by 4 tayras was displayed by the adult females, successfully chasing them away, and that the adult males did not participate in this event. Therefore, even if the predatory hypothesis could explain why the adults show more injuries than the immatures, because they have a greater chance to escape alive from the predators, it would fail to explain the great differences in injury prevalence between adult females and males.

The fact that almost all injuries, excluding broken fingers and protuberances, were located in the facial region (92.3% males, 95.3% of injuries), is consistent with the face-to-face fighting of howlers (Crockett, 1984; Crockett and Pope, 1988) and suggests that they are mostly consequence of inter-male agonistic encounters. Moreover, no male in single-male populations showed injuries.

The aggressive episodes could happen during group encounters (Chivers, 1969). In forest fragments with high group densities inter-group encounters are more probable, and more intergroup agonism could be expected, resulting in increased injury. Accordingly, the significant relationship between the total number of groups across all forest fragments and the injury variables at Los Tuxtlas could indicate that intergroup competition is associated with serious physical damage. But our analysis of only fragments with >1 group revealed no significant relationship between injury variables and number of groups in fragments or group density. Therefore direct intergroup competition events *per se* cannot be responsible for the large number of injuries and injured males in groups, even in fragments with high densities. Another possible interpretation for the injuries could be fights associated with intra-group competition, but the absence of significant relationships between the injury indicators (NIRM, NI) and population densities, sex ratio, and the food availability (measured by the combination of population density and the vegetation parameters), rejects this possibility. In contrast to other populations of *Alouatta palliata* (Clarke, 1982), in Los Tuxtlas, emigration episodes do not seem to be related to intense aggressive behavior, as none of the solitary males showed any sign of injury. Crockett and Pope (1988) related the presence of injuries in subadult *Alouatta seniculus* to their participation in troop defense during male takeovers, but in Los Tuxtlas, only the adult males seem to be taking part in the events, because no subadult male had a visible injury.

Our results support the view that for howlers, the most aggressive episodes are group takeovers by solitary males (DeGusta and Milton, 1998; Klein, 1974; Otis *et al.*, 1981). The number of aggressive encounters that resident males of established groups have to face should depend on intruder pressure, in other words, the chance of encountering candidates willing to fight to join the group. In fragmented habitats the contestants—extragroup males—may mostly arrive from groups located in the same fragment, as shown by the strong relationship between the number of solitary males and the total number of groups in the fragment. Accordingly, 10 of 11 populations composed of a single group showed no injury, whereas 5 of 6 populations containing >1 group did. Similarly 90% of the groups in single-group populations showed no injury in contrast to the 59% of the groups in multigroup populations. Even if the majority of the candidates for group membership are likely to come from another group in the same fragment, some are expected to come from other fragments through the pasture land, as shown by the relation between the probability of finding injured males in a group and the combination of the number of groups in the fragment and its grade of isolation (measured as the shortest distance to the nearest fragment with monkeys).

Considering the food resources that howlers exploit, their digestive physiology imposes serious restrictions in terms of energy available for social activities (Milton, 1980), a strategy that concentrates aggressive episodes in specific periods might be a good alternative. This underlines the idea that males are not fighting directly for resource monopolization, but instead they are aggressively competing at the moment of their entry for the rank that provides access to resources. Once the new social hierarchy is established, intragroup inter-male competitive social interactions must be reduced to a minimum. Other causes, such as intergroup encounters related to food resource concentration, should not be rejected as important causes for some of the injuries.

Although, immigration related events seem to be the best interpretation for injury incidence, our results suggest that other factors may be affecting the expression of aggressive behavior. Direct competition for limited food resources can trigger agonistic encounters. DBH is the only vegetation variable that relates to injury variables. High DBH indicates large trees, and therefore, large amounts of food concentrated at certain times. Therefore, the relationships between DBH and injuries, may suggest that where and when resource concentration occurs, aggression may occur more frequently. Further, population densities in the fragments are higher than those in continuous forests (Veà and Cristóbal-Azkarate, 2002), which may increase troop encounter probabilities. Considering that in forests food availability varies spatiotemporally, the effects of habitat perturbation over patch distribution, size, and density can cause alterations in howler group spatial organization and intertroop competitive regime. In perturbed habitats large food patches are even more limited, and the access to feeding sites may lead to intense competition between neighboring groups.

The absence of injuries (excluding broken fingers and protuberances) in females may suggest the use of a non-aggressive strategy for attaining and maintaining social ranks and for accessing resources. This differs from the situation in mantled howlers at other sites, where there is strong competition associated with immigration by extratroop females (Glander, 1992), rank definition (Zucker and Clarke, 1998) and emigration of subadult females (Glander, 1992).

Our results are even more distinctive when compared with the ones by Crockett and Pope (1988) concerning *Alouatta seniculus*: 35% of captured females had injuries, which they interpreted as a consequence of intraspecific competition between females to maximize their reproductive success.

Perhaps like BCI howlers (DeGusta and Milton, 1998), the Los Tuxtlas females are remaining in their natal groups, which is probably reinforced by the fragmentation of their habitat. This hypothesis is further supported by the fact that we found only 1 solitary female. It would also fit with the results of Crockett and Pope (1988), who found that natal females had fewest injuries.

Finally, if injuries are mostly related to immigration events, they could be useful to assess the degree of isolation in which the populations live in fragmented landscapes. This approach is supported by the negative relationship between the degree of isolation—number of groups sharing the same fragment and distance to the nearest fragment with monkeys—and the existence of injuries in the groups. If we consider injuries as indicators of immigration, the fragmentation of the howlers's original habitat is significantly affecting males, and also most probably female migratory patterns. Note that 64.7% ($n = 11$) of the populations might be isolated in their fragments with all the attendant genetic and demographic consequences.

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