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Howler Subgroups as Homeostatic Mechanisms in Disturbed Habitats

The size and composition of groups may have important consequences for the survival and fecundity of organisms (Terborgh and Janson, 1986; Pulliam and Caraco, 1984). A *subgroup* may be defined as a unit (>1) of a demographic group whose functions may be similar to or different from the functions of demographic groups. Cohen (1971) has studied the statistical properties of frequency distributions of primate subgroups of variable size and found that, in general, a zero-truncated binomial distribution provides a good fit where the rate of replacement is >0. Thus, by definition, a subgroup must have the potential to increase in size, and subgroup size may be inherently unstable where solitary individuals or individuals from other groups join subgroups (Rannala and Brown, 1994; Pulliam and Caraco, 1984). Expansion is expected to cease where subgroup size approximates some equilibrium value (Rannala and Brown, 1994).

Subgroup sizes of one demographic group of mantled howler monkeys (*Alouatta palliata* Gray) in tropical dry forests were sampled using *ad libitum* methods over an 18-month period in 1976 and 1977 at Hacienda La Pacífica, Cañas, Guanacaste, Costa Rica. The resulting distribution was analyzed. Only adults were counted (N=18). Figure 1 shows the subgroup sizes and their frequency (mean = 4.46 ± 1.99, N = 120). The coefficient of dispersion is 0.89, representing a repulsed (or overdispersed) distribution with more observations at the center of the distribution than at the extremes and with variance smaller than one would expect by chance alone, suggesting an optimal subgroup size.

Table 1 gives the frequency of subgroups with and without male membership. Males are identified by dominance rank (1, 2, 3, highest rank to lowest; Jones, 1980). Also shown are the mean, standard deviation, and coefficients of dispersion for each category. Female subgroups exhibit the lowest mean group size. Single males subgroup with about equal frequency, and, likewise, mean group size of single male subgroups is approximately equivalent. Two-male subgroups reflect the dominance hierarchy, whereby subgroups including the second and third-ranked males are more frequent than subgroups including the first and third-ranked males. Following this, subgroups including the first

Table 1. Identity (I), frequency (f), mean±standard deviation ($\overline{M}$±SD), and coefficients of dispersion (CD) of subgroups of one demographic group of mantled howler monkeys in tropical dry forest.

I	f	$\overline{M}$±SD	CD
Females	33	3.03±1.24	.51
2	28	4.71±1.72	.63
1	26	4.85±1.43	.42
3	24	5.17±2.08	.84
2, 3	5	7.60±2.50	.82
1, 3	4	2.75±1.50	.82

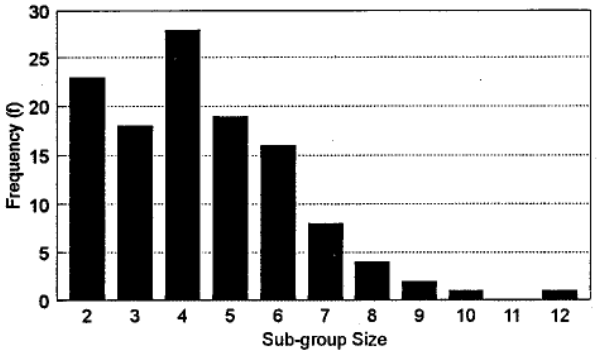

Figure 1. Frequency and size of subgroups for one demographic group of mantled howler monkeys at Hacienda La Pacifica, Costa Rica.

and second-ranked males appear to be rare (see Noë, 1994), although these males were observed to subgroup seven times on occasions when counts were not made. All coefficients of dispersion are repulsed. A "t-test" (one-tailed) of mean subgroup size for subgroups with and without males showed male subgroup size to be larger ($\leq .001$, $t = 7.88$, $df = 118$), suggesting that those with males are more "attractive" than those without, possibly because males subgrouped primarily in association with "preferred" and ephemeral food (flowers 35%; fruit 39%; and new leaves 26%; N = 108) or because there is less conflict in subgroups with males (see Rannala and Brown, 1994).

Howlers occupy a broad range of habitats (Wolfheim, 1983; pers. obs.), and consequently encounter significant environmental heterogeneity. Changing costs and benefits to individual subgroup members may yield differential gains for varying subgroup sizes, presumably in response to variations in environmental conditions. Howler environments may be heterogeneous with respect to macro- and microclimates; the structure of the forest, including tree architecture, patch size, resting sites, treefall gaps, and habitat fragmentation; predation pressure; disease, reproductive opportunities; food availability and quality; "information centers"; and population density. These and other factors, as well as the individual composition of subgroups vary over time and space, conditions which would continuously modify the costs and benefits of subgrouping. Habitat disturbance is expected to increase the rate at which costs and benefits change.

Lewontin (1957) discussed the adaptations of populations to environmental heterogeneity and posited that such regimes may select for homeostatic responses. Subgrouping may represent such a homeostatic response where the benefits of remaining with the demographic group decrease to a point favoring "temporary" or "semi-permanent" subgrouping. Such processes may lead to permanent subdivision, including the establishment of new groups and the colonization of marginal habitats (see Malmgren, 1979; Jones, 1980, p. 396). Subgrouping in mantled howlers may contribute to their survival capacities in disturbed regimes.

La Pacifica is a disturbed area, including significant deforestation, habitat fragmentation, and selective cutting (Clarke and Zucker, 1994; Malmgren, 1979; pers.obs.) where the howler population may be maintained by immigration (i.e., metapopulation effects). Howlers have thrived at this site where no other monkey species reside. Mantled howlers are listed as "endangered" in the United States Endangered Species Act (Groves, 1993), primarily due to habitat destruction in areas outside of Costa Rica (Wolfheim, 1983). La Pacifica may be viewed as a conservation experiment where mantled howlers show no apparent signs of local extinction (Clarke and Zucker, 1994). Local extinctions of fragmented populations are common (Fahrig and Merriam, 1994), and it will be important to conduct continuing studies of the La Pacifica metapopulation to document changes as disturbance continues, especially the flexibility of howler behavior, social organization, and population dynamics. This note proposes that patterns of subgrouping in mantled howlers indicate homeostasis in response to environmental heterogeneity which may maximize the opportunities for success of these monkeys in disturbed and managed areas. Animals with similar characteristics (e.g., *Ateles* and *Cebus*) may also employ subgrouping as a flexible homeostatic response.

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RED HOWLING MONKEY (*ALOUATTA SENICULUS*) REINTRODUCTION IN A GALLERY FOREST OF HATO FLORES MORADAS, VENEZUELA

Introduction: Red howling monkeys, *Alouatta seniculus*, are one the largest cebids, and are widely distributed in the neotropics (Wolfheim, 1983). A large number of field studies have focussed on the population and behavioral ecology of free-living red howlers (Izawa, 1988; Drubbel and Gautier, 1993; Agoramoorthy, 1994), However, little is known about the reintroduction of these animals into their original habitat. In this paper, I will describe the reintroduction of a pet female red howler into the wild in a gallery forest on a ranch in Venezuela.

History of the pet red howler: A wild-born, juvenile, female red howler had been kept as a pet for about 15 months. During that time, she was tied with a leash and chain, and kept outdoors. She was able to eat leaves, flowers, and fruits from the garden. She was fed with such as vegetables, fruits, rice, and crackers. The owner was interested in releasing her back into the wild, and she was, as a result, brought to me in February 1988, while I was conducting a field study on the howling monkey population at Hato Masaguaral, Venezuela (Agoramoorthy and Rudran, 1992, 1993, 1994).

The pet howler was kept in a cage of 2.5 m x 2.5 m x 3.5 m at the study site, adjacent to a social group of captive red howlers, during approximately 12 months. The captive group were wild-caught, and were being kept to conduct nutritional studies on fiber digestibility and digesta passage (Crissey *et al.*, 1989). Both the captive group and the pet female were fed mainly on natural vegetation. They also received monkey chow as a supplement on a regular basis. In captivity, the pet howler had visual contact with the captive group as well as a neighboring wild group. She learned to feed on local, naturally-occurring food items offered to her. Whenever the wild group approached the cage, the captive social group would howl vigorously, occasionally being accompanied by the pet female.

Reintroduction Process: During the first week of August 1989, an association of five individuals (two adult males, two adult females, and one juvenile female) was located in a neighboring forest called Hato Flores Moradas. The habitat was classified as gallery forest (Troth, 1989). A red howler association is a loose gathering of four or five individuals from different social groups, often having one or two adult males and females plus immatures. Associations usually roam around the territories of several social groups. Once an association establishes a definite home range and starts to breed, it becomes a group. The established social groups are territorial, and often show aggressive behavior towards intruding solitary animals as well as neighboring rival groups. Males and females usually disperse from their natal groups to immigrate into neighboring social groups or join a nearby association (Rudran, 1979; Crockett, 1984; Agoramoorthy and Rudran, 1993).

The Flores Moradas association was followed between 12 August and 27 September to determine