monkeys. In: *Proceedings of the Sixth Annual International Congress of the International Primatological Society*, D. J. Chivers and W. Lane-Petter (eds.), pp.183–185. Academic Press, London.

Serio-Silva, J. C., Hernandez-Salazar, L. T. and Rico-Gray, V. 1999. Nutritional composition of the diet of *Alouatta palliata mexicana* females in different reproductive states. *Zoo Biol.* 18: 507–513.

Tardif, S. D. and Jaquish, C. E. 1997. Number of ovulations in the marmoset monkey (*Callithrix jacchus*): Relation to body weight, age and repeatability. *Am. J. Primatol.* 42: 323–329.

Teaford, M. F. and Glander, K. E. 1996. Dental microwear and diet in a wild population of mantled howling monkeys (*Alouatta palliata*). In: *Adaptive Radiations of Neotropical Primates*, M. A. Norconk, A. L. Rosenberger and P. A. Garber (eds.), pp.433–449. Plenum Publishing, New York.

Zucker, E. L. and Clarke, M. R. 1998. Agonistic and affiliative relationships among adult female mantled howlers (*Alouatta palliata*) in Costa Rica over a four-year period. *Int. J. Primatol.* 19: 433–449.

Zucker, E. L., Clarke, M. R. and Glander, K. E. submitted. Latencies to first births by immigrating adult female howling monkeys (*Alouatta palliata*) in Costa Rica.

Food Resources and the Survival of a Group of Howler Monkeys (*Alouatta palliata mexicana*) in Disturbed and Restricted Habitat at Los Tuxtlas, Veracruz, Mexico.

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Introduction

In recent decades, a gradual transformation and disappearance of primate habitat has taken place world-wide, placing an increasing number of species in danger of extinction. Mexico, at the northern limit of Neotropical primate distribution, is one of the areas where primates are potentially under the greatest threat. At present, researchers have only a very general idea of the distribution, biology and ecology of the Mexican primates *Ateles geoffroyi vellerosus, A. g. yucatanensis, Alouatta palliata mexicana* and *A. pigra*. There is still a great deal to be learnt (Rodríguez-Luna *et al.*, 1996a).

Primates are profoundly affected by growing pressure from human activity, as well as the implementation of inappropriate development policies that largely ignore environmental consequences. The main pressures affecting the primates and their habitat in south-eastern Mexico are "slash and burn" farming techniques to create cattle pasture (Guevara *et al.*, 1997) or agricultural land for crops (for example, sugar cane and maize), fires, logging and the construction of rural and urban infrastructure (such as dams and highways). The hunting of primates for food and their capture for sale as pets also threaten groups surviving in increasingly small forest fragments (Paré *et al.*, 1992; Peres, 1997). These small groups remaining in forest patches may also be more susceptible to disease and genetic problems. These threats have led to a recent reassessment of the conservation status of the four Mexican primate taxa, prompting the World Conservation Union (IUCN) to list two of them (*Alouatta palliata mexicana*, *Ateles geoffroyi yucatanensis*) as threatened species (Hilton-Taylor, 2000). As new field studies are developed, it will be necessary to revaluate the Mexican primates to determine their conservation status more accurately.

In the Los Tuxtlas region *A. palliata* is found in San Martín Tuxtla Volcano, in Sierra Santa Marta, in San Martín Pajapan and in the fragments of forest surrounding these three areas (Fig. 1). These areas make up the core of the recently established Los Tuxtlas Biosphere Reserve (Presidential Decree in *Diario Oficial de la Federación*, 23 November 1998). The *A. palliata* population is in numerous isolated groups in this area. Besides the destruction and fragmentation of their habitat, the main threat is hunting, and although still surviving, there is an urgent need for plans and conservation measures to ensure the long-term survival of these groups (Rylands *et al.*, 1996/1997). To address this, a Conservation Assessment Management Plan (CAMP) workshop was held (Rodríguez-Luna *et al.*, 1996a) at Puebla (México). Its recommendations led to a Population and Habitat Viability Assessment (PHVA) for *Alouatta palliata mexicana*, which included a simulation of the survival of populations using ecological and demographic parameters (Rodríguez-Luna *et al.*, 1996b).

Factors which must be considered in the conservation and management of primates in fragmented habitats include population densities, home range boundaries and foraging strategies (e.g., minimum foraging area required to maintain a group). A number of estimates for the minimal forest area required have been suggested for both continuous and fragmented habitat (Estrada and Coates Estrada, 1996). These data are useful when estimating the carrying capacity of a particular habitat, but values may vary according to the characteristics of each and the pressures from indirect and direct human activities such as hunting (Neville *et al.*, 1988). These variations explain the different estimates obtained in this study, and it is therefore difficult to define the carrying capacity of any given habitat and/or the minimum area required by a group of this species, as small changes in environmental conditions and anthropogenic pressure can cause significant differences in the demography of primate groups. The incidence of illness and other factors (injuries, loss of variability, genetic defects, behavioral abnormalities) in population regulation also remains unclear, especially in fragmented habitats (Jones, 1994).

Estrada and Coates Estrada (1994) showed the negative effects of habitat fragmentation on the viability and size of the monkey groups living in areas of dense vegetation in Los Tuxtlas. The distance between fragments and the time they have been isolated has a negative effect on the survival chances of monkeys and other groups of animals. Estrada and Coates Estrada (1994) give an estimate of the requirements for a group of 10 howler monkeys as between 30 and 60 hectares of rainforest.

In a demography study of howler monkeys in the San Martín Volcano area carried out in 1995 (Garcia-Orduña, in prep.), the sizes of the forests where monkeys were found ranged from 15 ha (not including the fragment in the present study) to 300 ha, with the one exception being the fragment or central core of the San Martín Volcano of approximately 4,000 ha where several groups were observed. There was no correlation (r = 0.5, p = 0.1749) between the number or density of individuals and the area of the fragment, and therefore its particular history, which would make ecological differences between the fragments less significant. There was an approximate mean ecological density of 8.48 howlers/km^2 (SD 6.76, n = 10) for the fragments occupied by *A. palliata*, an average group size of 3.36 animals (SD 2.38; range 1-8), and an average composition, following Clarke's (1990) classification, of 1.27 adult males, 1.45 adult females, 0.09 young and 0.53 infants. Another case observed by the authors that demonstrates a capacity to adapt to restricted habitats was in the Sierra de Santa Marta, where groups of howler and spider monkeys numbering more than 10 individuals each were found in a fragment of less than 10 ha (Garcia-Orduña, 1996). Further examples of the howler monkey's ability to survive in very disturbed or small areas are given by Rodríguez Luna *et al.* (1987), Silva-López *et al.* (1988) and Estrada *et al.* (1996). Estimates of the minimum area required resulting from these studies range from 30-60 ha for a group of 10 howlers (Estrada and Coates Estrada 1984). However, howler monkeys can survive in the long-term in even smaller areas. Perhaps the most striking example of this is a troop of howlers released on Agaltepec Island in Lake Catemaco, which is only 8.3 ha. At the beginning of 1998 the island had a population of over 70 howler monkeys, originating from a group of 10, introduced during 1988-89 (Rodríguez-Luna and Cortés-Ortiz, 1994; Rodríguez-Luna, unpubl. data). The resources on the island seem not only to be sufficient for present needs, but it is also probable that they have yet to be fully exploited (Serio-Silva, 1992). It remains to be seen, however, how these groups fare in the long term.

Here we present an extreme case of survival of a group of seven howler monkeys (one male, five females and one juvenile) in an area of 1.3 ha near Arroyo Liza, north of the San Martín Tuxtla Volcano. This group was of interest for three reasons: 1) it was probably not introduced and is at the northernmost limit of the species' original distribution, proposed by Hall (1981); 2) it has adapted to an extremely small and isolated area; and 3) it has remained in the area for at least eight years.

Study Site

The forest fragment near Arroyo Liza is located at 18° 41' 16" N; 952 pt 11' 12" W, altitude 60–100 m above sea level. It is

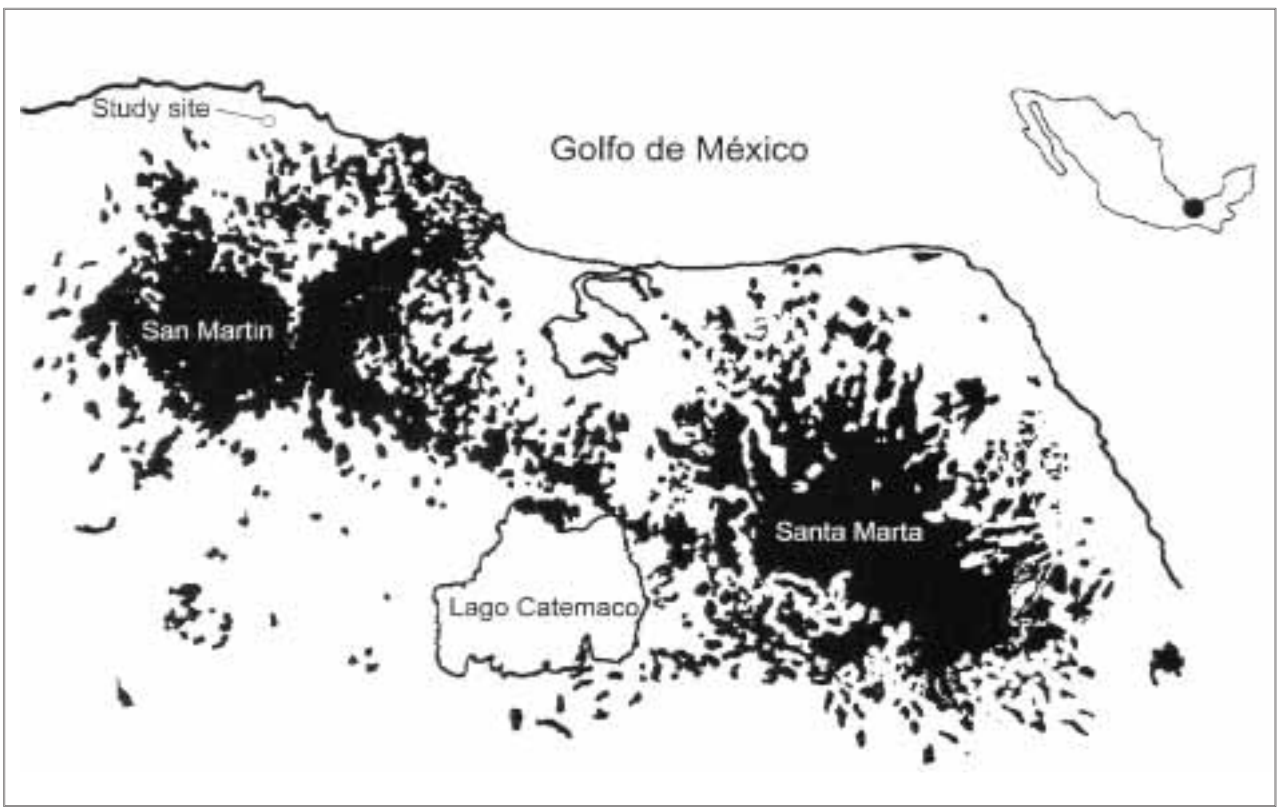

Figure 1. Region of Los Tuxtlas. Dark areas represent remaining forest. Forest fragment near, is located at 18° 41' 16" N, 95° 11' 12" W.

within the buffer zone of the Los Tuxtlas Biosphere Reserve (Fig. 1). The climate is of type Am: warm and humid, with summer rains and monsoon influence, a mean annual temperature of 24–26° C and a mean annual precipitation of 3,000–4,000 mm, distributed seasonally, with a relatively dry period from March to May. The maximum temperature is 36° C and the minimum is 16°C (Soto, 1997). The soil is volcanic in origin and made up of plioquaternary volcanic rocks (Martín-del Pozo, 1997). The original vegetation was predominantly evergreen rainforest, although it has for the most part been degraded and fragmented by human activities, particularly the creation of pasture for extensive cattle farming. Land ownership in the Arroyo Liza area consists of private ranches and the communal properties of sharecroppers, parcels of which have been recently privatized. Most is given over to extensive cattle farming and some small areas are used for maize (*milpas*) and chili, among other cash crops.

Vegetation

Although the original vegetation was evergreen rainforest, today there is only a small corridor left of 350 m in length bordering a permanent stream (Fig. 2). The maximum width is around 100 m at the highest point of the fragment in the south-west. The forest there, although disturbed, is the most conserved and has the highest species diversity, with trees between 15 and 25 m tall. Further downhill there is a strip of trees bordering grassland (*Bursera simaruba, Ficus* sp. and *Sapium* sp.) which contains a small area of secondary growth. This area in turn extends to a patch of trees, mainly *Bursera simaruba*, ending in a group of six large trees in the pasture, with 10 coconut palms and three other trees near by. The nearest woodland is over 100 m away; it is a fragment totally surrounded by meadows used for pasture, with only herbaceous vegetation.

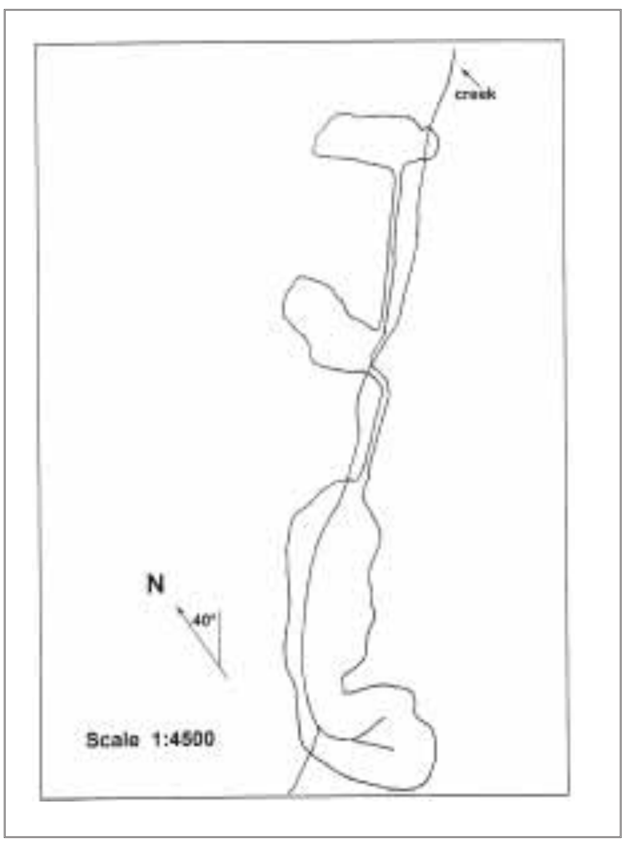

Figure 2. Map of the Arroyo Liza forest fragment.

Potential Food Resources for Howlers in the Fragment

We observed a group of seven *A. palliata*, at what is probably the northernmost limit of their distribution, in conditions of extreme habitat reduction and disturbance. According to local people, the group has lived in these conditions for at least eight years. The monkeys appeared physically normal and healthy when we first observed them (1 December 1997). The group is occasionally harassed by the locals, and individuals are occasionally captured (probably infants) for the pet trade. On our second visit (2 December 1998) nine individuals were found - two adult males, five adult females and two juveniles - demonstrating the group's capacity for survival and reproduction.

The forest is approximately 1.3 ha. The vegetation is disturbed both in terms of species composition and forest layers. Lists of the plant species identified can be found in Tables 1 and 2. One hundred ninety-eight trees were registered; 182 were identified as belonging to 43 genera and 48 different species. As can be seen in Table 1, 37 to 39 of the species identified (77.7% to 81.25%,) provide food for *Alouatta palliata* in other places where the species has been studied (see references in the table). As such, 81.32% to 83.52% (n = 152-162) of the trees in the Arroyo Liza fragment are potentially edible for the howlers. A total of 86 of these trees are important in the howlers' diet (marked Yes* in Table 1); this category includes species (n = 13) reported by other authors as among the ten most important in their studies, and those that in our view may make significant seasonal contributions to their diet. These account for 47.25% of the total number of identified trees in the fragment.

Little attention has been paid to lianas and vines in most studies on the diet and foraging of *A. palliata.* Few are identified or even observed. However, Rodríguez-Luna (2000) showed that the number of species consumed is comparable to tree species and some may even be more important in the diet. Habitat disturbance favors growth of vines and lianas, owing to their greater proliferation in areas of light and at the edges of the rainforest or on slopes. This potentially increases the diversity of species available as a resource for the howlers and possibly the biomass (although it may diminish the resource potential of the trees supporting them due to competition for nutrients, light and space). Tree species that are not a potential food source for the howlers may support vines or creepers they use, thus increasing the food sources available. For example, an increase in the howler population on Agaltepec Island was correlated with an increase in the use of lianas and vines as food sources. In 1990, lianas and vines comprised 12.2% of the time a group

Table 1. Potential feeding resources for *A. palliata* at the Arroyo Liza, Los Tuxtlas, Mexico.

Species	Number of individuals	Habit	Potential resource	References	Family
Albizia purpusii	1	Tree	Yes	8	Mimosaceae
Alchornea latifolia	1	Tree			Euphorbiaceae
Annona glabra	3	Tree	Yes	8	Annonaceae
Aspidosperma megalocarpon	1	Tree	Yes*	10	Apocynaceae
Brosimum alicastrum	2	Tree	Yes*	2,3,4,5,6,8,9,10,12,13	Moraceae
Bursera simaruba	45	Tree	Yes*	1,2,3,5,6,7,8,9,11,12,13	Burseraceae
Castilla elastica	1	Tree	Yes	3	Moraceae
Cecropia obtusifolia	2	Tree	Yes*	1,2,4,5,6,8,9,11,12,13	Cecropiaceae
Citrus sinensis	2	Tree	Yes	8	Rutaceae
Coccoloba hondurensis	3	Tree	Yes	1,6,8,12	Polygonaceae
Cocos nucifera	10	Palm			Arecaceae
Conostegia xalapensis	1	Shrub	Yes	8,9	Melastomataceae
Cordia alliodora	1	Tree	Yes	6, 7, 8, 10	Boraginaceae
Crataeva tapia	2	Tree	Yes	6,13	Capparaceae
Croton pyramidale	1	Tree	Yes	4	Euphorbiaceae
Croton schiedanus	5	Tree	Yes	4 ,8	Euphorbiaceae
Cupania glabra	2	Tree	Yes	6,11	Sapindaceae
Dendropanax arboreus	1	Tree	Yes	2,3,11	Araliaceae
Eugenia acapulcensis	1	Tree	Yes	1,6,8	Myrtaceae
Ficus lundellii	2	Tree	Yes*	8	Moraceae
Ficus petenensis	2	Tree	Yes*	8	Moraceae
Ficus sp.	14	Tree	Yes*	All references	Moraceae
Ficus yoponensis	3	Tree	Yes*	8,10	Moraceae
Gliricidia sepium	1	Tree	Yes	1,7,11	Fabaceae
Guarea grandifolia	1	Tree	Yes	7	Meliaceae
Hampea nutricia	1	Tree			Malvaceae
Bernoullia flammea	2	Tree			Bombacaceae
Nectandra colorata	11	Tree	Yes		Lauraceae
Omphalea oleifera	2	Tree	Yes	6	Euphorbiaceae
Pimienta dioica	1	Tree			Myrtaceae
Piper sanctum	1	Shrub	Yes	13	Piperaceae
Pleuranthodendron lindenii	2	Tree			Flacourtiaceae
Posoqueria latifolia	1	Tree			Rubiaceae
Poulsenia armata	4	Tree	Yes*	6,8,9,10	Moraceae
Pouteria sp.	1	Tree	Yes	2,5,6,8,13	Sapotaceae
Psychotria flava	1	Tree			Rubiaceae
Pterocarpus rohrii	3	Tree	Yes*	6,8,9,10	Fabaceae
Robinsonella mirandae	1	Tree	Yes	6	Malvaceae
Rollinia mucosa	5	Tree	Yes	6,8	Annonaceae
Sapium sp.	13	Tree	Yes	6	Euphorbiaceae
Spondias radlkoferi	4	Tree	Yes*	1,2,6,8,10,12,13	Anacardiaceae
Tabernaemontana arborea	3	Tree	Yes	10	Apocynaceae
Tetrorchidium rotundatum	6	Tree	Yes	6	Euphorbiaceae
Trichilia martiana	1	Tree	Yes?	1,7,10	Meliaceae
Trichospermum galeottii	7	Tree	Yes	9	Tiliaceae
Trophis mexicana	1	Tree	Yes	10,11	Moraceae
Zanthoxylum caribaeum	1	Tree	Yes*	1,2,6,11,13	Rutaceae
Zanthoxylum kellermanii	2	Tree	Yes	6, 8	Rutaceae
Other unidentified species	16	Tree			
Total: 49 Species	**198 trees**		**37-39 species**		**27 Families**

References: 1. Glander (1981); 2. Gaulin *et al.* (1980); 3. Chapman (1987); 4. Silva-López (1982); 5. Estrada & Coates-Estrada (1984); 6. Estrada (1984); 7. Glander (1975); 8. Gómez-Marin (in prep.); 9. Jiménez (1992): 10. Milton (1980); 11. Serio (1992); 12. Estrada *et al.*(1984); 13. Estrada & Coates-Estrada (1986). See text for explanation.

Table 2. Potential food resources (vines and lianas).

Species	Habit	Potential Resource	References	Family
Salacia megistophylla	Vine	?		Hippocrataceae
Ipomoea phillomega	Vine/climber	Yes	2	Convolvulaceae
Philodendron radiatum	Climber	Yes	2, 3	Araceae
Philodendron scandens	Climber	Yes	2	Araceae
Pisonia aculeata	Vine	?		Nyctaginaceae
Syngonium podophyllum	Climber	Yes	2	Araceae
Smilax aristolochiifolia	Vine	Yes	1	Smilacaceae

References. 1. Estrada (1984); 2. Gómez-Marin (in prep.); 3. Milton (1980).

of 10 howlers spent feeding (Serio 1992). In 1997 this had increased to 22% in a group of 57 (Rodríguez-Luna 2000). At Arroyo Liza we noted seven species of vines and lianas, all potentially eaten by howlers, but we were not able to compile a more complete list (Table 2).

Forest loss and fragmentation lead to a greater proportion of trees being located on the forest edge where they are more exposed to wind, solar radiation and dry microclimates, increasing tree mortality and causing changes in fruit and leaf production. (Gascon *et. al.*, 2000). This may be disadvantageous, but more leaves falling due to wind and/or drying may be followed by the production of new shoots and young leaves which howlers favor (as we have observed in other fragments of the region). The majority of these trees are shorter and have less foliage than trees found in less disturbed areas, and it is possible that the trees in this fragment provide fewer resources (when available) than taller trees of mature undisturbed forests.

Discussion

Estrada and Coates-Estrada (1994) and Estrada *et al.* (1994) showed that there is a positive correlation between the size of a forest fragment and the number of monkeys that live there. This is reasonable due to the greater quantity and diversity of food sources in larger fragments, greater opportunities to escape from humans (which increases the difficulty of hunting the monkeys), greater chances of surviving occurrences such as fires and a reduced incidence of genetic or demographic problems, among others. However, according to Garcia-Orduña (in prep.), no such correlation was observed in the San Martín Volcano area, and we did not observe this correlation with the Arroyo Liza group of nine in 1.3 ha. This indicates that the amount of direct or indirect human activity in a forest fragment, such as monkey harrassment or fire setting, may influence the presence and number of monkeys more decisively than ecological characteristics and the size of the fragment.

On the other hand, the presence or absence of monkeys in a fragment depends on whether or not they were already there at the time of isolation. Undoubtedly, a large fragment will have a better probability of containing monkeys than a small fragment. Estrada *et al.* (1994) found that the distance to the nearest fragment is negatively correlated to the number of monkeys that can inhabit it because of fewer opportunities for migration and fewer opportunities for escape from catastrophes such as fires and large-scale disturbances. Howler monkeys appear reluctant to cross pasture and areas with little vegetation - local people reported seeing monkeys moving from one fragment to another, crossing up to 150 m of pasture. There are also instances where males have been seen to remain isolated for long periods of time while only 150 m away from other monkeys in another fragment (authors' observation). Factors contributing to why monkeys remain in a fragment or decide to leave include: resource availability in both fragments; health of the individuals; knowledge of the destination (acquired prior to isolation); distance and availability of trees for locomotion; presence and composition of other groups at the destination; and degree of attachment to the home range. To date, we do not know if the Arroyo Liza group has ever left their fragment.

Howler monkeys appear to adapt well to adverse conditions. These and other examples in the region (Rodríguez-Luna *et. al.*, 1987, Garcia-Orduña, 1996) prompt us to question whether fragmentation, disturbance, isolation and reduction and loss of habitat diversity are the most influential factors affecting the disappearance of howler monkeys within a fragment (Estrada *et al.*, 1994, 1996). Milton (1985) suggested that seasonal factors or weather conditions can restrict the availability and abundance of resources, and may be causal factors in nutritional stress, contributing to mortality. According to Milton, the most probable mortality factor is parasitism, especially botfly infestation (*Alouattamya baer* and *Dermatobia hominis*). In Los Tuxtlas, mortality and/or poor health, especially in infants, has been observed as a result of these infestations (Gómez-Marín, pers. obs.; Stuart *et. al.*, 1998; Canales-Espinosa, 1992). However, Coelho *et al.* (1976), in their study of resource availability and nutritional requirements of *Alouatta pigra* in Tikal, indicated a superabundance of available resources and suggested that the concept of resource limitation is a myth among primatologists. However, we believe the results and conclusions of Coelho *et. al.* to be premature, as the study was limited to a mere three months (June-August 1973), and a seasonal and/or annual superabundance of resources cannot be ruled out. In other years or during certain times, there are limited resources which affect the size of the population, as seen at Barro Colorado, Panama (Milton, 1985).

This study and others of monkeys living at high densities in small rainforest fragments demonstrate that the values obtained for ecological density in less restricted areas are not universally suitable for estimating survival and densities in fragments. Habitat carrying-capacity parameters used in the PHVA simulations (Rodríguez-Luna *et al.*, 1995), which give only short-term viability for groups in very fragmented habitats, need to be reviewed.

Priority measures for the conservation of howler monkeys, as in other species (Laborde, 1996, Guevara, 1997), should take account of small areas (often the only available), such as gallery forests, forest patches and remnant hillside forests. The establishment of corridors and the maintenance of appropriate habitat mosaics which can allow for dispersal could create conditions for a functional demographic connection for otherwise isolated groups (Forman and Godron, 1986). In the llanos, red howlers (*A. seniculus*) occupy and regularly move through grassland and swamps between very small forest patches (Braza *et al.*, 1983), and there is no reason to suppose that *A. palliata* could not do the same. We would argue that the key factor influencing the survival of primates in fragmented habitats is hunting. This obviates the need for environmental awareness campaigns and measures which can reduce the pressure on the primate populations. Future projects need to comply with the recommendations of the CAMP workshop (Rodríguez-Luna *et al.,* 1995) which recommend integrated rural development, alternatives and improvements in land use and natural resources and a strengthening of legal and penal measures on the hunting, capture, trafficking and ownership of primates.

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References

Braza, F., Alvarez, F. and Azcarate, T. 1983. Feeding habits of the red howler monkeys (*A. seniculus*) in the llanos of Venezuela. *Mammalia* 41: 205–214.

Canales-Espinosa, D. 1992. Programa piloto de translocación del mono aullador (*Alouatta palliata*). Tesis de licenciatura, Universidad Veracruzana, Veracruz, Mexico.

Castillo-Fernández, M. and García Orduña, F. 1990. Estudo poblacional del mono araña (*Ateles geoffroyi*) y mono aullador (*Alouatta palliata*) en 4 ejidos de la Sierra de Santa Marta, Veracruz, México. *VIII Simposio sobre Fauna Silvestre*, Instituto de Neuroetología, Universidad Veracruzana, Xalapa, Veracruz, Mexico, 23–32.

Chapman, C. A. 1987. Flexibility in diets of three species of Costa Rica primates. *Folia Primatol.* 49: 90–105.

Clarke, M. R. 1990. Behavioral development and socialization of infants in free-ranging howling monkeys (*Alouatta palliata*). *Folia Primatol.* 54: 1–15.

Coelho, A. M. Bramblett, C. A. and Quick, L. B**.** 1976. Resource availability and population density in primates: A socio-bioenergetic analysis of the energy budgets of Guatemalan howler and spider monkeys. *Primates* 17(1): 63–80.

Crockett, C. M. and Eisenberg, J. F. 1986. Howlers: Variation in group size and demography. In: *Primate Societies*, B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham and T. T. Struhsaker (eds.), pp.54–68. University of Chicago Press, Chicago.

Estrada, A. 1982. Survey and census of howler monkeys (*Alouatta palliata*) in the rain forest of Los Tuxtlas, Veracruz. *Am. J. Primatol.* 2: 363–372.

Estrada, A. 1984. Resource use by howler monkeys in the rain forest of Los Tuxtlas, Veracruz, Mexico. *Int. J. Primatol.* 2: 105–131.

Estrada, A. and Coates-Estrada, R. 1984. Fruit eating and seed dispersal by howling monkeys in the tropical rain forest of Los Tuxtlas, México. *Am. J. Primatol.* 6: 77–91.

Estrada, A. and Coates-Estrada, R. 1986. Use of leaf resources by howling monkeys (*Alouatta palliata*) and leaf cutting ants (*Atta cephalotes*) in the tropical rain forest of Los Tuxtlas, Veracruz, Mexico. *Am. J. Primatol.* 10: 51–56.

Estrada, A. and Coates-Estrada, R. 1989. La destrucción de la selva y la conservación de los primates silvestres de México (*Alouatta* y *Ateles*). *Memorias del I Simposio Nacional de Primatología*. México, pp.211–233. Universidad Veracruzana, Xalapa, Veracruz.

Estrada, A. and Coates-Estrada, R. 1994. La contracción y fragmentación de las selvas y las poblaciones de primates silvestres: El caso de Los Tuxtlas, Veracruz. *La Ciencia y el Hombre. Revista de la Univ. Veracruzana* 18: 45–70.

Estrada, A. and Coates-Estrada, R. 1996. Tropical rain forest fragmentation and wild populations of primates at Los Tuxtlas, Mexico. *Int. J. Primatol.* 17(5): 759–783.

Estrada, A., Coates-Estrada, R., Vasquez-Yañez, C. and Orozco-Segovia, A. 1984 Comparison of frugivory by howling monkeys (*Alouatta palliata*) and bats (*Artibeus jamaicensis*) in the tropical rain forest of Los Tuxtlas, Veracruz, Mexico. *Am. J. Primatol.* 7: 3–13.

Estrada, A., Coates-Estrada, R. and Meritt, D., Jr., 1994. Non flying mammals and landscape changes in the tropical rain forest region of Los Tuxtlas, Mexico. *Ecography* 17: 229–241.

Forman, R. T. T. and Godron, M. 1986. *Landscape Ecology*. John Wiley & Sons.

Garcia-Orduña, F. and Canales-Espinosa, D. 1995. Situación de poblaciones de *Alouatta palliata* (Mono aullador) en dos localidades del Estado de Veracruz, Mexico. *Neotrop. Primates* 3(29): 37–40.

Garcia-Orduña, F. 1996. Distribución y abundancia del mono aullador (*Alouatta palliata*) y el mono araña (*Ateles geoffroyi*) en fragmentos de selva del municipio de San Pedro Soteapan, Veracruz. Tesis de Licenciatura, Universidad Veracruzana, Xalapa, Veracruz, Mexico.

Garcia-Orduña, F. en prep. Ecología trófica del mono aullador (*Alouatta palliata*) y el mono araña (*Ateles geoffroyi*) en un fragmento de selva. *Tesis de Maestria*. Universidad Veracruzana, Xalapa, Veracruz, Mexico.

Gason, C., Williamson, G. B. and Fonseca, A. B. da, 2000. Receding forest edges and vanishing reserves. *Science* 288(5470): 1356–1358.

Gaulin, S. J. C., Knight, D. J. and Gaulin, C. K. 1980. Local variance in *Alouatta* group size and food availability on Barro Colorado Island. *Biotropica* 12(2): 137–143.

Glander, K. E. 1975. Habitat description and resource utilization: A preliminary report on mantled howling monkey ecology. In: *Socioecology and Psychology of Primates*, R. H. Tuttle (ed.), pp.37–57. Mouton, The Hague.

Glander, K. E. 1980. Reproduction and population growth in free-ranging mantled howling monkeys. *Am. J. Phys. Anthropol.* 53: 25–36.

Glander, K. 1981. Feeding patterns in mantled howler monkey. In: *Foraging behavior: Ecological, Ethological and Psychological Approaches*, A. C. Kamil and T. D. Sargent (eds.), pp.231–257. Garland, New York.

Gómez Pompa, A. 1977. *Ecología de la Vegetación del Estado de Veracruz*. C.E.C.S.A.-INIREB, México. 91pp.

Guevara, S., Laborde, J., Liesenfeld, D. and Barrera, O. 1997. Potreros y ganadería. In: *Historia Natural de Los Tuxtlas*, E. González, R. Dirzo and R. C. Vogt (eds.), pp.43–58. UNAM, Mexico.

Hall, E. R. 1981. *The Mammals of North America*. John Wiley, New York.

Hilton-Taylor, C. (Compiler). 2000. *2000 IUCN Red List of Threatened Species*. IUCN, Gland, Switzerland, and Cambridge.

Jimenez-Huerta, J. 1992. Distribución y abundancia del recurso alimenticio en un fragmento de selva alta perennifolia y su uso por *Ateles* y *Alouatta* en el ejido Magallanes (municipio de Soteopan, Veracruz). Tesis de Licenciatura. Facultad de Biologia, Universidad Veracruzana, Xalapa, Veracruz, Mexico.

Johns, A. D. and Skorupa, J. P. 1987. Responses of rain-forest primates to habitat disturbance: A review. *Int. J. Primatol.* 8(2): 157–191.

Jones, C. B. 1994. Injury and disease of the mantled howler monkey in fragmented habitats. *Neotrop. Primates* 2(4): 4–5.

Jones, C. B. 1995. The potential for metacommunity effects upon howler monkeys. *Neotrop. Primates* 3(2): 43–45.

Laborde, J. 1996. Patrones de vuelo de aves frugívoras en relación a los árboles en pie de los pastizales. *Tesis Facultad de Ciencias*, UNAM, México, D.F.

Milton, K. 1980. *The Foraging Strategy of Howler Monkeys: A Study in Primate Economics*. Columbia University Press, New York. 165pp.

Milton, K. 1985. Dietary quality and demographic regulation in a howler monkey population. In: *The Ecology of a Tropical Forest: Seasonal Rhythms and Long-term Changes*, E. G. Leigh, S. A. Rand and D. M. Windsor (eds.), pp.273–289. Smithsonian Institution Press, Washington, DC.

Neville, M. K., Glander, K. E., Braza, F. and Rylands, A. B. 1988. The howling monkeys, genus *Alouatta*. In: *Ecology and Behavior of Neotropical Primates*, Vol. 2, R. A Mittermeier, A. B. Rylands, A. F. Coimbra-Filho and G. A. B. da Fonseca (eds.), pp.349–453. World Wildlife Fund, Washington, DC.

Paré, L., Portilla, E., Ramírez, F., Rodríguez E., Narave, H. and Guevara, S. 1992. *Los Tuxtlas: Plan para Su Conservación y Desarrollo Integral*. Gobierno del Estado de Veracruz y Universidad Veracruzana, Xalapa, Veracruz, Mexico. 135pp.

Peres, C. A. 1997. Effects of habitat quality and hunting pressure on arboreal folivore densities in Neotropical forests: A case study of howler monkeys (*Alouatta* spp.). *Folia Primatol.* 68: 199–222.

Rodríguez-Luna, E. 2000. Cambios en la estrategia de forrajeo del mono aullador (*Alouatta palliata mexicana*): estudio de una población en un fragmento de selva. Tesis de Maestria. Universidad Veracruzana, Xalapa, Veracruz, Mexico.

Rodríguez-Luna, E. and Cortés-Ortíz, L. 1994. Translocacion y seguimiento de un grupo de monos *Alouatta palliata* liberado en una isla (1988-1994). *Neotrop. Primates* 2(2): 1–4.

Rodríguez-Luna, E., Fa, J. E., García-Orduña, F., Silva-López, G. and Canales-Espinosa, D. 1987. Primate conservation in México. *Primate Conserv.* (8): 114–118.

Rodríguez-Luna, E., García-Orduña, F. and Canales-Espinosa, D. 1993. Translocación del mono aullador (*Alouatta palliata*): Una alternativa conservacionista. In: *Estudios Primatológicos en México,* Vol. 1, A. Estrada, E. Rodríguez Luna, R. López-Wilchis and R. Coates-Estrada (eds.), pp.120–178. Biblioteca Universidad Veracruzana, Veracruz, Mexico.

Rodríguez-Luna, E., Cortés-Ortíz, L., Ellis, S. and McCance, E. 1996. Taller de conservación, análisis y manejo planificado para primates mexicanos. *Neotrop. Primates* 4(suppl.): 113–141.

Rodríguez-Luna, E., Cortés-Ortíz, L., Ellis, S. and McCance, E. (eds.). 1996a. Conservation assesment and management plan workshop (CAMP) for Mexican primates: Working draft. Unpublished, Universidad Veracruzana, Xalapa, Veracruz, Mexico.

Rodríguez-Luna, E., Cortés-Ortíz, L., Ellis, S. and McCance, E. (eds.). 1996b. *Population and habitat viability assessment for the mantled howler monkey (Alouatta palliata mexicana)*. IUCN/SSC Conservation Breeding Specialist Group (CBSG), Apple Valley, MN.

Rylands, A. B., Rodríguez-Luna, E. and Cortés-Ortíz, L. 1996/1997. Neotropical primate conservation - The species and the IUCN/SSC Primate Specialist Group Network. *Primate Conserv.* (17): 46–69.

Rylands, A. B., Mittermeier, R. and Rodríguez-Luna, E. 1997. Conservation of Neotropical primates: Threatened species and an analysis of primate diversity by country and region. *Folia Primatol.* 68: 134–160.

Serio-Silva, J. C. 1992. Patrón diario de actividades y hábitos alimenticios de *Alouatta palliata* en condiciones de semilibertad. Tesis de Licenciatura, Facultad de Biología, Universidad Veracruzana, Córdoba, Mexico. 67pp.

Silva-López, G. 1982. La situación actual del mono araña y aullador en la selva de Santa Marta, Ver. México. Tesis de licenciatura en Biología, Universidad Veracruzana, Xalapa, Veracruz, México. 162pp.

Silva-López, G., García-Orduña, F. and Rodríguez-Luna, E. 1988. The status of *Ateles geoffroyi* and *Alouatta palliata* in disturbed forest areas of Sierra de Santa Marta, México. *Primate Conserv.* (8): 53–61.

Silva-López, G., Benítez-Rodríguez, J. and Jiménez-Huerta, J. 1993. Uso del hábitat por monos araña (*Ateles geoffroyi*) y aullador (*Alouatta palliata*) en áreas perturbadas. In: *Avances en el Estudio de los Mamíferos de México,* A. Medellín, G. Rodrigo and G. M. Ceballos (eds.), Asociación Mexicana de Mastozoología, A.C., Mexico.

Stuart, M., Pendergast, V., Rumfelt, S., Pierberg, S., Greenspan, L., Glander, K. and Clarke, M. 1998. Parasites of wild howlers (*Alouatta* spp.). *Int. J. Primatol.* 19: 493–512.

Toledo, V. M. 1976. El ejido y la selva tropical húmeda: una contradicción ecológica y social. In: *Regeneración de Selvas*, A. Gómez Pompa, S. del Amo, C. Vázquez Yañes and S. Guevara (eds.), pp.56–61. INIREB, Mexico.

MULTIPLE BREEDING FEMALES AND ALLO-NURSING IN A WILD GROUP OF MOUSTACHED TAMARINS (*SAGUINUS MYSTAX*)

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Introduction

Callitrichines show flexible social organization and mating patterns (Goldizen, 1988; Ferrari and Lopes Ferrari, 1989). Instances of multiple breeding females have been reported in all genera (Table 1) except *Cebuella* and seem to be the rule in *Callimico* (Christen, 1998; Encarnación and Heymann, 1998). Except for *Callimico*, this circumstance has been observed to result in reduced offspring survival or live births for one of the breeding females. However, allo-nursing, a highly co-operative behavior, has also been reported in *Callithrix jacchus*, *C. aurita* and *C. flaviceps* groups with multiple breeding females (Table 1). Here, we present observations of two female *Saguinus mystax* breeding simultaneously and the subsequent allo-nursing of the surviving offspring.

Methods

Data were collected *ad libitum* on a group of *S. mystax* during on-going studies at the Estación Biológica Quebrada Blanco (4°21'S, 73°09'W) in northeastern Peru (for details see Heymann and Hartmann, 1991). The tamarins were observed for 14–20 days each month from 14 February to 28 June 2000. The group consisted of two adult females (labeled 1 & 2), two adult males and a subadult male. The group was never trapped and was fully habituated to the presence of humans. Individuals were recognized by natural distinguishing characteristics. The group was first seen in the area in May 1999, without the second adult male who immigrated in late August/early September 1999 (Tirado Herrera, pers. obs.).

Results

On the morning of 21 February, 2000, a single male infant was seen (born to female 1). He fell to the ground shortly after the group left its sleeping site, and was later recovered by a member of the group, only to fall again shortly thereafter. He was not retrieved the second time and died at 10:10 hrs. That night, female 2 gave birth to male twins and the following morning they were observed being carried separately. Female 1 repeatedly tried to take an infant from his mother's back, but the mother resisted. Later in February the infants of female 2 were seen being nursed on five occasions by their mother and twice by female 1. The mother nursed only with her left nipple. Her right nipple did not produce milk and her breast remained unswollen and unmarked by any effects of suckling. Female 1 nursed with both nipples normally. Their swollen breast(s) indicated that both females continued to lactate until the end of May. Both infants survived to at least one year of age.

Discussion

Factors underlying the occurrence of multiple breeding females in callitrichines are largely unknown. High population density and limited opportunities for dispersal have been suggested as influencing factors in *C. jacchus* and *Leontopithecus rosalia* (De Vleeschouwer *et al*., 2001; Digby and Ferrari, 1994; Dietz and Baker, 1993). However, in *C. aurita* polygyny occurred despite much lower population densities (Coutinho and Corrêa, 1995). Dietz and Baker (1993) found a correlation between the occurrence of polygyny and some habitat parameters in *L. rosalia*, but nevertheless excluded the polygyny threshold model as an explanation. They suggested that the balance of costs and benefits to the dominant female determines whether or not she allows a subordinate female (daughter) to breed (see also Rylands, 1996). The presence of males unrelated to the daughter may play a key role in this decision. This agrees with Savage *et al*.'s (1996) findings that incidences of two pregnant female *S. oedipus* in the same group were associated with the immigration of a novel male. It is also consistent with a greater success of multiple breeding females in captive groups of *L. chrysomelas* with unrelated males (De Vleeschouwer *et al*., 2001).

In our case, population density and habitat quality have not changed noticeably since 1994, and hence are unlikely