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MOVEMENTS OF *ALOUATTA PALLIATA* AMONG FOREST FRAGMENTS IN LOS TUXTLAS, MEXICO

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Introduction

Individual dispersal is part of a reproductive strategy that balances the costs and benefits for an individual as it chooses to stay with or leave its natal group (Jones, 1995). Dispersal in *Alouatta* has been documented in a number of studies (Agoramoorthy and Rudran, 1993; Clarke and Glander, 2004; Glander, 1992; Moore, 1992). However, habitat fragmentation may significantly limit the options available for an individual to move between social groups (Swart and Lawes, 1996). In many cases, this interference with the ability to disperse forces primates to live in small and isolated fragments, which in turn may cause changes in foraging and activity patterns, social organization, and physiological conditions, leading to inbreeding that can diminish genetic variability (Clarke *et al.*, 2002; Gonçalves *et al.*, 2003). The ability to disperse across fragmented landscapes will depend on the characteristics of each species (Bicca-Marques, 2003; Jones, 1999) as well as the spatial configuration of the landscape in question (Fahrig, 2003). Tischendorf *et al.* (2003) defined a specialist disperser as having a low probability of crossing boundaries from habitat to matrix, a high risk of mortality while in the matrix, and fast movement and high inter-step movement correlation (i.e., small turning angles between consecutive movement steps, in matrix). In contrast, generalist dispersers have a higher probability of leaving habitat, lower dispersal mortality and less directed movement paths while traveling through the matrix (i.e., larger turning angles between consecutive movement steps).

Howler monkeys are arboreal quadrupeds and are observed only occasionally to leave the trees and walk along the ground (Glander, 1992). For example, *A. pigra* individuals walk among the naturally patchy vegetation in the Petenes of Yucatán (A. Estrada, pers. comm.) and Tabascan swamps (J. C. Serio-Silva, pers. comm.). The same is true for red howlers, *A. seniculus*, travelling among clumps of trees in the Venezuelan llanos. Data on travel patterns in continuous forest suggest that *A. palliata* uses routes that minimize travel times from feeding to resting trees (Garber and Jelink, 2004). Fedigan *et al.* (1998) mention that the formation of new *A. palliata* groups in Santa Rosa, Costa Rica, occurred as a result of large groups splitting, and the dispersal of lone individuals in search of females. Glander (1992) reported an average travel distance of 700 m for *A. palliata* at Hacienda La Pacifica, Costa Rica. Individuals had to cross open areas to reach a new group; in some cases, these movements occurred in several stages between “stepping stone” fragments. In particular, dispersal success declines with a decrease in habitat and increased fragmentation of the landscape, but the rate of this decline accelerates once the amount of remaining habitat falls below 10-20% (King and With, 2002). Therefore, one might expect that howler monkeys do not travel among fragments randomly, and that the spatial configuration of habitat patches and the nature of the surrounding matrix is critical to successful dispersal.

The tropical rainforest in Los Tuxtlas in the Mexican state of Veracruz has been largely deforested: 75% of native habitat has been lost, 20% now survives only in isolated fragments, and barely 5% is comprised of widespread contiguous rainforest at high elevations (>800 m) (Estrada and Coates-Estrada, 1996). *Alouatta palliata,* the mantled howler monkey native to Veracruz, now survives in archipelagos of forest fragments that vary in size, age, and degree of isolation. Their existence in these scattered forest remnants is precarious both ecologically and demographically, which compounds the dilemma of dispersal (Estrada and Coates-Estrada, 1996; Mandujano *et al.*, in press). Here we present data on the movements of howler monkeys in this region’s highly altered landscape and develop a preliminary model of the probability of interchange between fragments.

Methods

Fieldwork

This research was conducted in the Sierra Santa Marta in the south of Los Tuxtlas, Veracruz, Mexico (18°22’N, 94°45’W). We defined the study area as the landscape between the Ríos Tecuanapa and Pilapa, covering 4,960 ha, of which only 11% is suitable primate habitat (Fig. 1). Elevation ranges from sea level to 900 m. Corn crops and livestock pasture make up the matrix that surrounds the 92 remaining fragments, most of which are located in riparian zones along rivers and streams, often on slopes steeper than 30°. Some fragments are on hilltops, while others lie in permanently flooded areas. Of these fragments, 81% are smaller than 5 ha, and only five (8%) are between 10 and 75 ha. The mean distance between fragments and the higher elevation continuous forest was 3,625 m, while the mean distance from one fragment to the next was 111 m. The mean distance from any fragment to the nearest town was 880 m.

We carried out fieldwork from January 2001 to July 2003. Three times a year we conducted a census of all fragments identified in the study area noting the presence or absence of *Alouatta* groups in each. Two to five people spent 4-5 hours sampling in small fragments (<10 ha) and 1-2 days in larger fragments (>10 ha). We compiled a catalog of individuals according to their identifying features and facial shapes, plus scars and coloration patterns of the back and tail. Although animal dispersal is broadly defined (see Clobert *et al.*, 2004), for the purpose of this study we consider it be movement between fragments by individuals of any age or sex class. To quantify dispersal, we observed the movement of individuals into adjacent fragments and noted whether or not they later returned to their group of origin. We also recorded the number of solitary individuals inhabiting fragments at the time, plus the number of individuals entering empty fragments. Although we report here all the movements we observed, we recognize that there were other arrivals and departures that we were unable to observe.

Modeling

We divided up all observations of the movements of individuals between adjacent fragments into the following distance classes: 0-100 m, 101-200 m, 201-400 m, and 401-800 m. and then calculated the proportion of the movements in each. We observed no movements greater than 800 m (see Results). We then fitted these data to negative exponential, half-normal, and linear inverse models through the least squares method using the STATISTICA Program (StatSoft, Inc., 1998). These and other dispersal models have been theoretically and empirically used for investigating patterns in a number of animal and plant species (e.g., Urban and Keitt, 2001; Mennechez *et al.*, 2003; Skalski and Gilliam, 2003).

In these three models, the dispersal probability decreased as isolation distance increased between fragments; however, the probability varied among models. For the negative exponential model, the dispersal probability p_{ij} was estimated as

$$p_{ij} = \exp\left(\theta \times \mathrm{d}_{\mathrm{ij}}\right),$$

for the half-normal model, the dispersal probability was

$$p_{ij} = \exp\left(\theta \times \mathrm{d}^2_{\mathrm{ij}}\right),$$

while for the linear inverse model, the dispersal probability was

$$p_{ij} = 1 - \left(\frac{\mathrm{d}_{\mathrm{ij}}}{1000}\right).$$

In all cases, θ is a distance-decay coefficient (θ <0.0) that determines the slope of the relationship (Urban and Keitt,

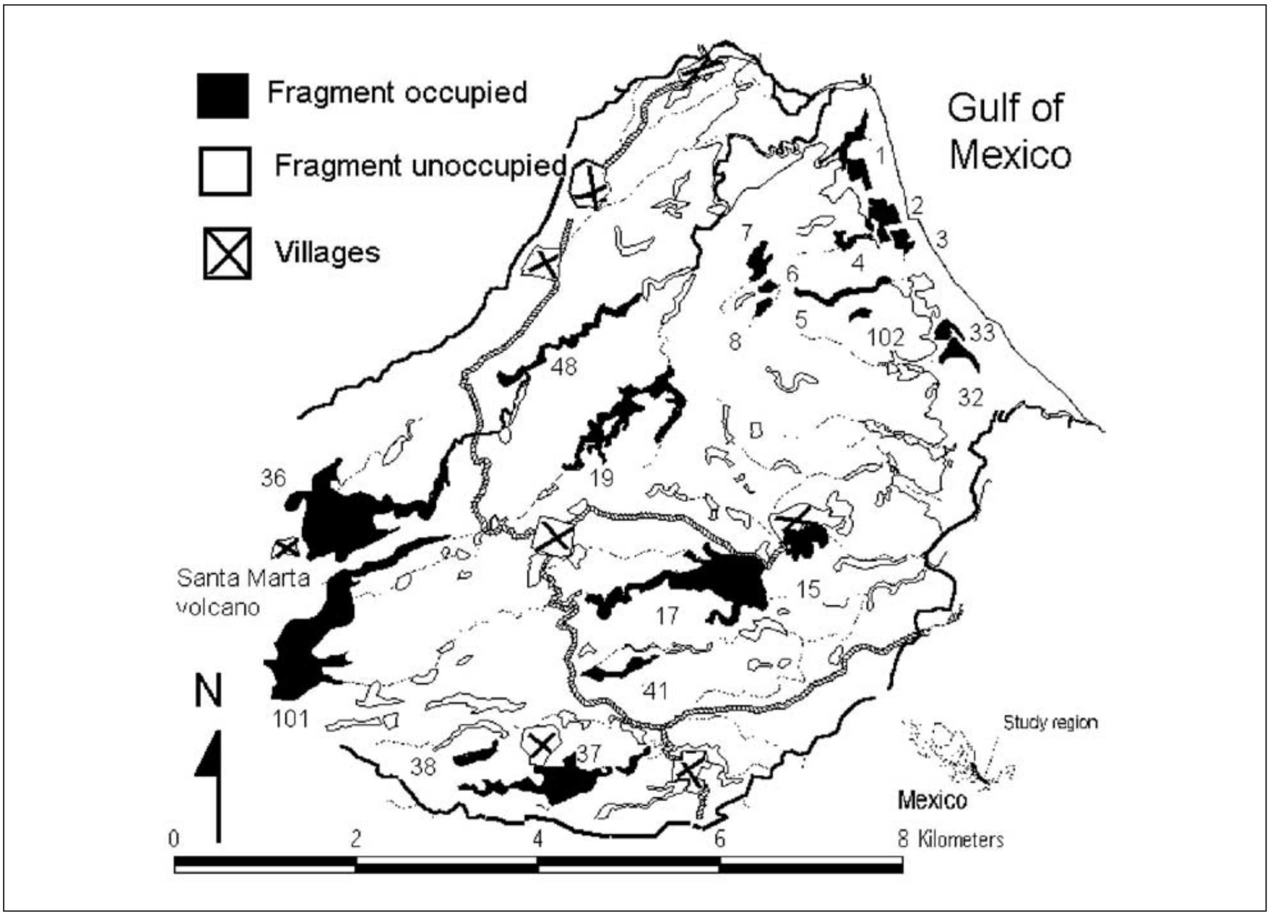

Figure 1. The landscape of the study area in Los Tuxtlas showing the fragments (numbered) occupied by *Alouatta palliata* (in black) and those that were empty (in white). See Table 1 for information on each of the occupied fragments.

2001). To fit the observed data, we made two assumptions. First, if two different primate groups inhabit the same fragment, the probability of dispersal between them is equal to 1.0 because there is no isolation. Second, if two groups inhabit different fragments with an isolation distance equal or greater than 1000 m, the probability of dispersal was equal to 0.0. The 1000 m limit was chosen considering the very few observations of howler monkeys traveling between groups inhabiting fragments at distances of this magnitude (see Glander, 1992).

Results

Overall counts ranged from 71 to 76 howler monkeys inhabiting 19 fragments — 17.5% of the 92 fragments in the study area. Three groups of howlers (of 6, 5 and 3 individuals, respectively) lived in fragment F19 (Fig. 1 and Table 1), while, at the other extreme, one group used four fragments. Eight fragments were each inhabited by a separate group, while five fragments were each inhabited by a separate solitary male. The mean isolation distance of any one occupied fragment to any other was 2.71 ±0.75 km. The mean distance of any one group to the closest fragment was 0.33 ±0.39 km, while the mean distance of the howler groups to continuous forest was 6.18 ±2.31 km.

The following are some examples of movements that we recorded:

1. A male moved from his group in fragment F6 into fragment F8, 78 m away; he remained for almost a year, then returned to F6.
2. Another adult male left fragment F6 to inhabit fragment F7, 79 m away. He remained in this fragment for less than six months before returning to F6.
3. The entire group inhabiting F6 moved to F5, 120 m away, and stayed there for less than one month before returning to their original fragment.
4. At the beginning of the study, a solitary male was found inhabiting F48. According to the field assistant and local landowners, this individual had moved from F19, 656 m away.
5. There were no howlers in F37 when it was first surveyed, but one male who had not been recorded in the next nearest groups, F41 and F17, subsequently took up residence. We suspect that he moved from an unstudied group located 80 m away.
6. Another male appeared in F37, probably from the nearest fragment 80 m away as well.
7. An older male arrived in F37 and then moved on to F38. Again, we suspect that this individual was from an unstudied group located 80 m away. Local people supported this supposition.
8. One group of six individuals initially occupied F32. This group later divided into two, each with three individuals; one group moved out and took up residence in the nearest fragment, F33, 47 m away.
9. Fragment F4 was empty at the beginning of the study; six to eight months later, individuals were continuously observed there. It is probable that they moved from fragments F2 or F3, located 41 m and 92 m away, respectively.
10. An adult male moved 171 m from F5 to F102.

Table 1. Characteristics of the study area. Annual numbers and group composition of howler monkeys and of forest fragments characteristics in the study area. Fragments are labeled in Figure 1.

Fragment	Size (ha)	Isolation distance (m) to nearest			Number of individuals		
		Fragment	Town	Continuous forest	2001	2002	2003
1	11	96	1438	6704	3	4	3
2	9.3	34	2125	6169	5	5	5
3	4.7	34	2542	5900	7	8	7
15	11.8	115	4	3675	10	15	14
17	57.2	18	307	3364	5	5	6
19[1]	29.9	196	562	3197	11	14	11
32	5.3	24	1988	4426	6	5	6
33	3.67	12	2186	4817	6	3	4
36	75.5	75	81	144	1	1	1
38	5	23	192	1184	0	0	1
41	6.5	57	625	2850	5	5	5
48	13	15	557	2660	1	1	1
5, 6, 7, 8[2]	14.6	43	1941	5634	10	7	8
101[3]	71.0	75	438	206	?	?	2
102[3]	1.4	171	1970	6624	?	?	1

[1]Fragment 19 inhabited by 3 groups.
[2]Fragments 5, 6, 7 and 8 were used by one group; therefore the size is the sum of each fragment, and isolation is the mean distance.
[3]Fragments 101 and 102 were sampled only once at the end of 2003; thus there is no precise data for previous years.

Distance of movement ranged from 15 to 656 m, but 70% were under 100 m (Fig. 2). Data fit the negative exponential (r^2 = 0.90, *F* = 28.6, df = 1, 3, *P* = 0.01) and half-normal (r^2 = 0.89, *F* = 24.6, df = 1, 3, *P* = 0.02) models (Fig. 2). In contrast, data did not fit the linear inverse model (r^2 = 0.47, *F* = 2.7, df = 1, 3, *P* = 0.20). The θ coefficients were –0.007 and –0.000035 for the negative exponential and half-normal models, respectively.

Discussion

The landscape of our study area is characterized by considerable destruction and fragmentation of the natural habitats; the remaining forest occurs predominantly in small fragments with a lack of corridors between the fragments (e.g., riparian vegetation, live fences), and a homogeneous matrix consisting mainly of pastures and seasonal agriculture. As a result, *Alouatta palliata* is scarce, and the remaining individuals inhabit only a few fragments (19 of the 92 fragments we investigated), which are isolated from one another and from continuous forest (Rodriguez-Toledo *et al.*, 2003; Mandujano *et al.*, in press). As such, the probability that animals will disperse from one group to another is sharply limited by isolation distances. Considering Tischendorf *et al.*'s (2003) definition of specialist and generalist dispersers, we initially expected that each of the three dispersal models in this study (negative exponential, half-normal, and linear inverse) would represent the hypothetical facility with which the monkeys could disperse from one fragment to another. If a generalist species, the howler monkey would have a greater capacity to move along the ground in the matrix as it disperses from one fragment to other; in this case, the data should be adjusted to a linear inverse model. But if the howler monkey is a habitat specialist and more limited in its dispersal ability, then field data should be adjusted to a negative exponential or half-normal model. The difference between negative exponential and half-normal models is that in the first, the probability of dispersal decreases exponentially with a small increase in isolation distance; in the second model, there is an isolation distance where the dispersal probability is high, and then the probability decreases slowly. The few data obtained during field work showed that the most frequent movements were towards fragments located a very short distance away (<100 m); beyond this distance the frequency of movements dropped. Thus, data fit better into the negative exponential or half-normal models, indicating, therefore, that *A. palliata* may be classified as a specialist disperser.

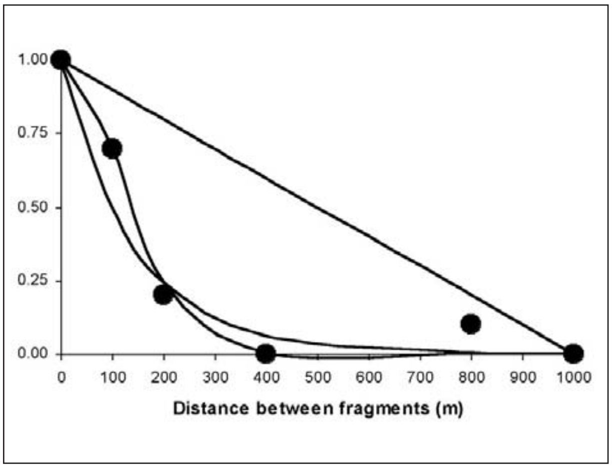

Figure 2. Relationship between dispersal probability and isolation distance. The points represent the proportion of *Alouatta palliata* movements at different isolation distances. Note our assumptions (see methods) that at 0 m the dispersal probability is 1.00; and at 1000 m the probability is 0.00. Lines represent, from left to right, the expected probability of movements in the exponential negative, half-normal, and linear inverse models. Note the field data fit better to the negative exponential and half-normal models.

Our analysis suggests that the degree of structural heterogeneity in the landscape may be an important factor determining the possibility of dispersal by primates across it. In heterogeneous landscapes, primates may use forest fragments as well as tree plantations (for example, shade coffee and cacao agroecoystems) as stepping stones or corridors when moving from one forest patch to another (Estrada *et al.*, in press). In highly homogeneous landscapes (i.e., dominated by pasture or other monocultures, with scant tree cover) exchange of individuals among fragments is more difficult. Using percolation models, it has been found that dispersal success declines with increasing fragmentation of the landscape, with this decline accelerating once the amount of suitable habitat falls below 10–20% (King and With, 2002). The connectivity of habitat patches in a landscape, therefore, depends on the dispersal capacity of the individuals. In the study landscape, connectivity is currently low (<30%) given the high rate of habitat destruction and loss, with only 11% of the original vegetation remaining, and the relatively low dispersal capacity of howler monkeys through the matrix (Palacios-Silva and Mandujano, in press).

Habitat connectivity is a central theme in both metapopulation ecology and conservation biology (Bennett, 2004). As the number of occupied fragments decreases, so too does the probability of persistence on a regional level decline, due to a possible imbalance between the extinction rate of local populations and the colonization rate (Ovaskainen and Hanski, 2004). Therefore, if the dispersal rate proves lower than the deforestation rate, the only conservation alternative on a regional level would involve habitat rehabilitation in an effort to create corridors and stepping stones, plus the translocation of individuals and/or groups to other fragments offering better survival conditions. In particular, the creation of stepping stone fragments could be an alternative management action that increases connectivity and could allow movement among primate groups (Mandujano *et al.*, in press). Basically, a stepping stone can be any landscape element that the animal perceives as a transitional step leading toward a habitat patch (Bennett, 2004). For primates, a stepping stone can be a group of isolated trees, live fences that separate strips of land, riparian zones, corridors, remnants of arboreal vegetation and/or habitat patches that are substantially smaller than an animal's home range. Studies showed that for species with limited dispersal ability and a landscape with isolated habitat, stepping stone habitat patches greatly increase a species' ability to disperse (Bennett, 2004; King and With, 2002).

Evidently, more factors than isolation distance contribute to an individual's dispersal between habitat fragments (Clobert *et al.*, 2004). For example, in a 30-year study of *A. palliata* at La Pacifica, Clarke and Glander (2004) found that female migration patterns were primarily associated with environmental variables (habitat, rainfall) and secondarily with social variables (number of females in the group, sex ratio); while male migration patterns were only associated with social variables (i.e., male-female ratio and male age). In contrast, from a census of 333 howlers in a recent study in the northern part of Los Tuxtlas, Cristobal-Azkarate *et al.* (2004) found 16 solitary males and only one solitary female. These authors suggest that females remain in their natal groups, probably reinforced by habitat fragmentation. Thus, the relationships between intrinsic factors (social, demographic, and genetic), habitat factors (quantity, quality, and spatial configuration), and human factors (deforestation, hunting, and others) that influence the decision of an individual monkey to stay or leave its natal group are complex. In consequence, the dispersal models presented here, based only on isolation distance between fragments, are preliminary, and field and experimental data will be required to test their accuracy and general application.

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ASPECTS OF THE BEHAVIORAL AND ENDOCRINE ONTOGENY OF SIX MOUSTACHED TAMARINS, *SAGUINUS MYSTAX* (CALLITRICHINAE)

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Eckhard W. Heymann, Michael Heistermann

Introduction

In order to recognize differences in ontogeny between species and between their life history trajectories, it is necessary to have an understanding of the timing of milestone events in behavior and physiology (Pereira and Leigh, 2003). Assessing when and how individuals become independent from their mother and other caregivers is necessary to evaluate costs of varying parental strategies, which in turn allows broader issues to be addressed, such as the evolution of non-maternal care in anthropoid primates (Ross and Maclarnon, 2000). Patterns of ontogeny may also explain aspects of individual differences in behavior, especially, for example, when same-sexed adults become competitors. Ventura and Buchanan-Smith (2003) have stressed that a good understanding of the species' development and behavior in the wild is essential to assess and ensure the well-being of maturing individuals in captivity. Observations are often anecdotal, but the difficulties and imprecision in obtaining data of this sort under field conditions can be overcome by repeated studies of groups of the same or related species.

The ontogeny of immature primates is tied to endocrinological changes. Typically the gonads are only partially developed at birth. The production of sex hormones such as testosterone increases during puberty until adult levels are reached (Plant, 1988). In adult males, testosterone and other androgens are important in the control of spermatogenesis (Wickings *et al.*, 1986) and seem to play a role in the expression of aggressive behavior and in the achievement of social status, though this latter relationship might be less pronounced in primates (Dixson, 1980; Bouissou, 1983). In three callitrichine species (*Callithrix jacchus*, *Callithrix kuhlii,* and *Saguinus oedipus*), however, newborn males show relatively high testosterone levels that drop after two to six months and rise slowly again thereafter (Abbott, 1984; French and Schaffner, 1995; Ginther *et al.*, 2002). Ginther *et al.* (2002) speculated that this neonatal elevation might be related to the sexual maturation of the gonads, endocrine system, and behavior, but it is not known how representative this pattern may be of other callitrichine species.

During a field study on moustached tamarins (*Saguinus mystax*), we were able to observe some aspects of the development of six immature individuals (five males and one female). For some of them we were able to record, for the first time, the onset and final appearance of a number of behaviors — in particular, the first observations of feeding on solid food, foraging, social play, and marking behavior, and the last days they were carried and successfully begged for food.

We expected that the patterns of testosterone and androgen in the five male immatures would be similar to those of the three callitrichines mentioned above. In addition, the immigration of a new female into one of the groups on 5 December 2001 provided the opportunity to study whether this caused endocrinological changes in the immature males. Given that one subadult male was evicted from the group following the new female's arrival, we also tested whether he and his twin differed in their testosterone levels, and whether their values differed from those of adult males in general. If co-twins differ in their sexual maturation, it might be supposed that the more mature of the two would be forced to leave the group in order to remove a potential competitor. If this is true, it might be expected that the evicted twin had higher testosterone levels than the remaining one. Different testosterone levels due to different aggression levels in the