GROUP SIZE AND FORAGING EFFORT IN MANTLED HOWLERS AT LOS TUXTLAS, MEXICO: A PRELIMINARY TEST OF THE ECOLOGICAL-CONSTRAINTS MODEL

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ABSTRACT. The ecological-constraints model (ECM) proposes that group size is constrained by travel costs. This model has been seldom demonstrated in folivorous primates, and in the present study we tested it by performing a cross-study analysis (*N* = 13 studies) with populations of mantled howlers (*Alouatta palliata*) inhabiting several rainforest fragments of Los Tuxtlas, Mexico. Specifically, we predicted that as group size increases, individuals should spend more time moving, occupy larger home ranges and, to compensate for increased energy expenditure during traveling, spend more time feeding or increase the consumption of energy-rich foods. As predicted, group size correlated positively with time spent moving. This confirms the ECM and suggests that group size of mantled howlers may be limited by traveling costs. However it did not correlate with home range size, most probably due to the incapability of several of our study groups to increase their home ranges as they were already occupying all their fragments. Finally, the increase in energy expenditure associated with larger group size was not compensated by an increase in feeding time or an increase in feeding quality, which could compromise their fitness. Thus, it is possible that at Los Tuxtlas group size is constrained by the interaction between traveling costs and the effect of spatial restrictions on the use of space and on the access to primary food resources.

Key words: *Alouatta palliata*, grouping patterns, home range

RESUMEN. El modelo de restricciones ecológicas (ECM) propone que el tamaño de los grupos está limitado por los costos de la locomoción. Este modelo ha sido raramente demostrado para primates folívoros, y en el presente estudio nosotros lo analizamos a través de un meta-análisis (*N* = 13 estudios) con poblaciones de monos aulladores de manto (*Alouatta palliata*) habitando varios fragmentos en Los Tuxtlas, México. Específicamente, nosotros predecimos que a medida que el tamaño del grupo aumenta, los individuos dedicarán más tiempo a moverse, ocuparán ámbitos hogareños mayores y, para compensar el gasto energético asociado a la locomoción, dedicarán más tiempo a alimentarse o incrementarán el tiempo de consumo de alimentos más energéticos. Como fue predicho, el tamaño del grupo correlacionó positivamente con el tiempo dedicado a moverse. Esto confirma el ECM y sugiere que en monos aulladores de manto el tamaño grupal puede estar limitado por los costos de la locomoción. Sin embargo, no correlacionó con el tamaño del ámbito hogareño, seguramente porque varios de los grupos estudiados ya ocupan toda el área de su fragmento. Finalmente, el incremento en el gasto energético, asociado con tamaños de grupos más grandes, no fue compensado por un incremento en el tiempo de alimentación o un incremento en la calidad del alimento, lo cual podría comprometer su adecuación biológica. Por tanto, es posible que en Los Tuxtlas el tamaño grupal esté limitado por la interacción entre los costos de la locomoción y el efecto que tienen las restricciones espaciales asociadas a la vida en fragmentos sobre el uso del espacio y el acceso a recursos alimenticios primarios.

Palabras clave: *Alouatta palliata*, patrón de agrupamiento, ámbito hogareño.

INTRODUCTION

The ecological-constraints model (ECM) predicts that primates' foraging effort increases as a function of group size (Milton 1984; Wrangham *et al*. 1993; Chapman *et al*. 1995). Because larger groups deplete food patches faster, individuals will have to visit more patches each day, increase day ranges, and in some cases, expand their home ranges. Therefore, when resource availability is constant, individuals living in larger groups will have to invest more energy to maintain foraging efficiency (Milton 1984; Chapman 1990). However, studies with folivorous primates dispute this possibility, as leaves do not appear limited in distribution and abundance. Thus, many authors have assumed that food competition within folivore monkeys is inconsequential and that populations are not limited by the availability of food (Isbell 1991; but see Borries 1993). Actually, a number of studies have found no relationship between group size and day range among folivores (e.g., Yeager & Kirkpatrick 1998).

Some data suggests that in *Alouatta palliata* – a folivore-frugivore Neotropical primate – group size varies as a function of habitat type (e.g., larger groups in tropical wet forests vs. tropical dry forests; Chapman & Balcomb 1998), and groups adjust the size of feeding aggregates to the size and abundance of food resources (e.g., Leighton & Leighton 1982; Dias & Rodríguez-Luna 2006). Nevertheless, no study has yet tested the relation between group size and foraging effort in *A. palliata*, the central premise of the ECM.

In the present study we perform a preliminary test of the applicability of the ECM to mantled howlers, by examining if there is an increase in foraging effort associated with larger group size. Specifically, if larger groups deplete food patches faster, as group size increases we expect individuals to (1) spend more time moving, (2) occupy larger home ranges, and (3) spend more time feeding or (4) increase the consumption of energy-rich foods, to compensate for increased energy expenditure during traveling.

MATERIALS AND METHODS

Study site. Los Tuxtlas is located in southeastern Veracruz, Mexico (18º8′–18º45′N and 94º37′–95º22′W). The climate is warm and humid, with mean annual temperature of 25 ºC, annual rainfall between 3,000 and 4,600 mm (Soto & Gama 1997), and altitudes ranging from 0 to 1,780 m. The original dominant vegetation was tall evergreen rainforest, but this region has been severely fragmented during the last 60 years (Guevara *et al*. 2004).

Data collection. We examined all available studies conducted at Los Tuxtlas until May 2009 with duration of ≥ 9 months, on the diet and activity pattern of *A. palliata*. As daily ranging distances were not available in our sample of studies, we used time spent moving as a surrogate indicator of foraging effort. This measure has been previously used for discussing foraging effort in primates (e.g., Isbell & Young 1993; Knopff & Pavelka 2006). It is expected that, as group size increases, individuals will have to invest more time moving between food patches to cope with faster depletion rates. We used time spent feeding on fruits as an indicator of the consumption of energy-rich foods. Though fruits vary widely in biochemistry and quality, they are in general easily digested and contain energy-rich sugars and nonstructural carbohydrates (Kay & Davies 1994). Therefore, fruits are an important source of readily available energy.

The literature regarding the ECM suggests that to properly test this model it is important to control for differences in habitat quality (Gillespie & Chapman 2001; Snaith and Chapman 2007). In addition to the fact that all groups were located in contiguous areas with similar habitat types, we carried out a preliminary assessment of food availability based on data on the composition and structure of vegetation (i.e. plants with diameter at breast height, dbh > 10 cm) sampled within 0.1 ha (i.e. ten randomly located 50 x 2-m plots) in each study site (see details in Arroyo-Rodríguez *et al*. 2009, Table 1). Particularly, as indicators of food availability within the fragments, we considered tree density and richness of the top food species to mantled howlers at Los Tuxtlas (i.e. those representing > 80% of total feeding time in nine studies carried out in this region; reviewed by Cristóbal-Azkarate & Arroyo-Rodríguez 2007), as these variables are known to influence howler distribution in fragmented landscapes of Los Tuxtlas (Arroyo-Rodríguez *et al*. 2007).

Data analyses. To investigate if the variation in the percentage of time spent moving, feeding, feeding on fruits, and home range size were associated with group size, we used a series of linear correlations (r-Pearson). To relate habitat quality (i.e. tree density and richness of top food species) with group size, time spent moving, feeding, feeding on fruits, and home range we also used linear correlations. However, in these correlations we excluded data from Jiménez-Huerta (1992) and Serio-Silva (1992) because these two studies were done in a very small fragment (10 ha) and a very small island (8.3 ha), respectively, ca. 12 years before the vegetation sampling performed by Arroyo-Rodríguez *et al*. (2009) in these study sites (Table 1). As vegetation in small fragments can be highly dynamic (Laurance 2002), vegetation characteristics may have changed significantly in the past 12 years. Group size and home range size data were normalized using a logarithmic transformation, whereas data on the percentage of time spent moving, feeding, and consuming fruits were normalized using the arcsine transformation (Fowler *et al*. 1998).

RESULTS

Group size data were available for 15 samples of nine studies (Table 1), and groups averaged (± SD) 16.6 ± 17.4 individuals (range = 6–59). The average percentage of time spent moving (reported in 14 samples of eight studies) was 10.0 ± 3.4% (range = 2.0–14.9%). The average home range (available for 15 samples of nine studies) was 19.5 ± 24.9 ha (range = 1.3–60 ha), but after excluding those cases in which home range size corresponded to fragment size (n = 10), the average home range was 44.7 ± 30.9 ha (Table 1). Percentage of time spent feeding averaged 22.9 ± 7.1% (range = 14–40%), and the mean percentage of time dedicated to consuming fruits was 40.3 ± 13.9% (range = 13–59%). Finally, tree density and richness of the top food species to mantled howlers in each site averaged 20.4 ± 7.5 stems/0.1 ha (range = 10-37 stems/0.1 ha) and 10.8 ± 7.5 species (range = 6-15 species), respectively (Table 1).

As predicted, group size was significantly and positively correlated to the percentage of time spent moving (r = 0.55, n = 14, p = 0.04). However, both home range size and time spent feeding did not correlated with group size (home range: r = 0.004, n = 15, p = 0.99; time feeding: r = 0.19, n = 14, p = 0.50). Considering only the cases in which home range differed from fragment size (n = 5), home range was still not related to group size (r = -0.01, p = 0.98). In contrast to our predictions, group size was negatively correlated to the proportion of time spent consuming fruits (r = -0.50, n = 15, p = 0.04).

Table 1. Group size, home range size (ha), time spent moving and feeding, and species richness and density (ind./1000 m^2) of top food resources of mantled howlers (*Alouatta palliata*) at Los Tuxtlas, Mexico

Site	Group size	Home range	% Time moving	% Time feeding	% Time feeding fruits	Top food trees[a]		Refs.
						Richness	Density	
Field Station*	9.12	60	—	—	49.9	11	31	1
Santa Marta	10	10	10.0	28.0	30.0	[b]	[b]	2
Balzapote	6	3.6	2.0	17.0	41.0	12	25	3
Agaltepec Island	19	8.3	12.0	22.0	59.0	[b]	[b]	4
Santa Marta	22	8	10.0	40.0	13.0	10	19	5
Agaltepec Island	59	8.3	14.3	29.0	21.4	13	21	6
Playa Escondida*	7	14.7	11.0	26.0	57.3	10	14	6
Arroyo Liza	6	1.3	6.3	24.2	51.2	8	10	6
Agaltepec Island-t1	10	8.3	11.8	22.7	52.5	13	21	7[c]
Agaltepec Island-t2	57	8.3	13.3	16.9	31.0	13	21	7[c]
Rancho Huber*	8	40	7.0	14.0	46.0	15	37	8
Montepío*	13	19.3	8.0	14.0	23.0	6	21	8
Ruiz Cortinez	6	6.4	9.0	22.0	40.0	8	11	8
Rancho Huber*	9	89.5	10.2	17.7	49.4	13	19	9
Ruiz Cortinez	8	5.8	14.9	27.7	39.1	8	15	9

References: 1. Estrada (1982, 1984); 2. Jiménez-Huerta (1992); 3. Estrada *et al*. (1999); 4. Serio-Silva (1992); 5. García-Orduña (2002); 6. Asensio (2003); Asensio *et al*. (2006); 7. Rodríguez-Luna *et al*. (2003); 8. B. Hervier (unpublished data); 9. Dunn *et al*. (2009).

* Cases in which home range differed from fragment size.

[a] The top food trees are those representing > 80% of feeding time in 9 studies carried out in Los Tuxtlas (reviewed by Cristóbal-Azkarate & Arroyo-Rodríguez 2007). Here, we report vegetation sampled within 0.1 ha (i.e. ten randomly located 50 x 2-m plots) in each study site (Arroyo-Rodríguez *et al*. 2009).

[b] These cases were not considered in the analyses (see Methods).

[c] Studies the same group of howlers but in different times (t1 and t2). —, unavailable data.

Tree density and richness of top food species were not related to group size (r = 0.11, p = 0.72; r = 0.31, p = 0.31, respectively), time feeding (r = -0.46, p = 0.13; r = -0.20, p = 0.54, respectively) nor time consuming fruits (r = -0.002, p = 0.99; r = 0.17, p = 0.58, respectively). Home range size was only positively related to the density of top food resources (r = 0.58, p = 0.04), but considering only the cases in which home range size differed from fragment size, home range was not related to tree density or richness of top food resources (r = 0.40, p = 0.51; r = 0.61, p = 0.28, respectively).

DISCUSSION

Our findings suggest that, like other folivore primates (e.g., *Gorilla beringei beringei*: Ganas & Robbins 2005; *Piliocolobus tephrosceles*: Gillespie & Chapman 2001; *Presbytis thomasi*: Steenbeck & van Schaik 2001), mantled howlers living in larger groups at Los Tuxtlas spend more time moving. As larger groups did not inhabit fragments with higher food availability (i.e., tree density and richness of top food species were not related to group size), our results are consistent with the ECM and suggest that individuals in larger groups need to increase time traveling to maintain foraging efficiency (Gillespie & Chapman 2001).

Contrary to our expectations, home range size did not increase with increasing group size. In our sample, five out of nine sites (i.e. Agaltepec, Arroyo Liza, Balzapote, Ruiz Cortinez and Santa Marta; Table 1) consisted of single groups living in forest fragments where home range size equaled forest block size. For these cases home range expansion is not possible, which would explain the lack of relationship with group size. Under these circumstances, individuals may respond to increasing foraging demands by exploiting more intensively the resources already present inside their home ranges, or by increasing the quality of their diet. However, with increasing group size howlers neither increased the time spent feeding nor the consumption of fruit. Additionally, a previous study demonstrated that at Los Tuxtlas groups living in smaller fragments spent more time consuming non-tree growth forms (Cristóbal-Azkarate & Arroyo-Rodríguez 2007), which are second choice foods of presumably lower quality. Overall, this evidence suggests that mantled howlers living in larger groups may not able to balance increases in foraging effort by enhancing energetic input; this could ultimately result in compromised nutrition, fecundity and birth rates (Snaith & Chapman 2007). Therefore, it is possible that at Los Tuxtlas group size is constrained by the interaction between traveling costs, and the effect of spatial restrictions on ranging behavior (e.g., canopy discontinuity, presence of neighboring groups) on the access to primary food resources.

Although further data are required to test more conclusively the ECM as applied to mantled howlers, this preliminary study suggests that at Los Tuxtlas the ECM may help to explain the grouping patterns of *A. palliata* based on ecological grounds. Future studies should incorporate additional measures of foraging effort (like daily ranging distances), quantify differences in food availability and distribution across study groups and replicate our findings in populations living in undisturbed habitats.

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