*Journal of Tropical Ecology* (2005) **21**:445–450. Copyright © 2005 Cambridge University Press
doi:10.1017/S0266467405002415 Printed in the United Kingdom

# Food selection by a hyperdense population of red howler monkeys (*Alouatta seniculus*)

Gabriela Orihuela Lopez*, John Terborgh†[1] and Natalia Ceballos‡

* 8415 SW 107 Avenue #238w, Miami, Florida 33173, USA
†Center for Tropical Conservation, Nicholas School of the Environment and Earth Sciences, Duke University, 3705-C Erwin Road, Durham, NC 27705, USA
‡Fauna Terrestre-IZT, Laboratorio de Comportamiento Animal-IBE, Universidad Central de Venezuela, Caracas, Venezuela
(*Accepted 15 December 2004*)

**Abstract:** We studied diet choice by a generalist herbivore, the red howler monkey (*Alouatta seniculus*) under conditions of high and normal population density. Densities equivalent to 800–1000 $km^{-2}$ (roughly 20–40 times normal) occurred in populations trapped on small, predator-free islands in Lago Guri, Venezuela. For three successive years, we studied one such population, a group of six animals living on a 0.6-ha island and compared its feeding ecology to that of two groups living at normal densities on a 190-ha island. The 0.6-ha island supported a total of 351 trees $> 10$ cm dbh of 46 species, whereas $> 100$ species probably occurred within the 16- and 23-ha home ranges of the two large-island howler troops. Small-island howlers were thus predicted to consume fewer resources, in particular less fruit, and to be less selective in diet choice than large-island howlers. As predicted, small-island howlers consumed fewer resources and obtained a smaller fraction of their intake from rare tree species (those contributing $< 1\%$ of basal area). Small-island howlers consumed less fruit (2% of feeding time vs. 22%) and more foliage (73% vs. 55%) than the large-island groups. Diet breadth of small-island howlers was markedly less than that of their large-island counterparts. Tree species not present on the small island contributed $\geq 60\%$ of leaf consumption by large-island howlers. Foliage sources preferred by large-island howlers were different in each of 3 years, whereas foliage of the same species of tree consistently ranked first on the small island. Long-term persistence (17 y) of self-perpetuating howler groups on Lago Guri islets at $> 20$ times normal density strongly suggests that food availability does not limit mainland populations.

**Key Words:** food selectivity, forest fragments, Lago Guri, land-bridge island, population density, population regulation, red howler monkey, Venezuela

## INTRODUCTION

We took advantage of a fortuitous experiment to study diet choice by a generalist herbivore, the red howler monkey (*Alouatta seniculus*), under conditions of high and normal population density. The experiment began in 1986 with the creation of Lago Guri, a hydroelectric impoundment in the Caroní Valley of east-central Venezuela. The impoundment flooded 4300 $km^2$ of hilly terrain, creating hundreds of forested islands ranging in size from $< 1$ ha to $> 700$ ha. As the water rose, animals presumably sought high ground and thereby became concentrated on hilltops that remained emergent as islands.

Faunal surveys conducted a few years after flooding revealed that most Lago Guri islands of $< 15$ ha had already lost 75% or more of the regional vertebrate fauna (Terborgh *et al.* 1997a, b). Among the few vertebrates that were consistently able to persist on small islands was the red howler monkey (hereafter, simply howlers). For example, two howlers survived for 15 y on 0.25-ha Isla Baya, and one survived on 0.25-ha Miedo until the animals of both islands were captured and removed in 2001. Two slightly larger islands, Iguana (0.6 ha) and Cola (0.7 ha), supported reproducing groups that numbered six individuals each in 2001 (Terborgh *et al.* 2001). The density of these two groups is equivalent to 800–1000 individuals $km^{-2}$, a value 20–40-times higher than that of red howler populations living in similar dry tropical forest on the Venezuelan mainland (Crockett & Eisenberg 1987, Kinzey *et al.* 1988, Neville 1972). Our situation is not unique: high densities of folivorous primates persisting on islands or in small forest fragments have been documented previously (Chapman *et al.* 2004,

---

[1] Corresponding author.

Estrada & Coates-Estrada 1988, Rodriguez-Luna *et al*. 2003). At Lago Guri, howlers are one of three generalist herbivores able to persist on small islands, the others being leaf-cutter ants (*Atta* spp., *Acromyrmex* sp.) and common iguana (*Iguana iguana*).

Here we investigate the consequences and implications of hyperabundance for food selection through comparisons of feeding observations of a howler group inhabiting 0.6-ha Iguana, with observations made on two groups living on Danto Machado, a 190-ha island supporting normal howler densities (Kinzey *et al*. 1988, Peetz 2001).

## METHODS

### Study site

The research was conducted on two islands in Lago Guri: Iguana and Danto Machado (hereafter, simply 'Danto'). Both islands are situated in the west-central sector of the Guri impoundment. Iguana lies approximately 20 km to the south of Danto. The vegetation of both islands is semi-evergreen tropical dry forest dominated by legumes (Aymard *et al*. 1997, Kinzey *et al*. 1988, Peetz 2001).

### Feeding observations

We observed howlers on three successive years, 1999, 2000 and 2001, always between 16 May and 3 August, a period corresponding to the first half of the rainy season at Lago Guri when the forest is in full leaf (Peetz 2001). On Isla Iguana there were six individuals present (five adults and subadults and one juvenile) during each year of observations. On Danto we observed two groups. The 6S group contained six adults and subadults each year; the 7K group was observed only in 2001 when it contained seven adults and subadults. Home ranges of the howler groups consisted of the entire islet of Iguana (0.6 ha) and minimum areas of 16 and 23 ha for the two groups studied on Danto.

Our methodology followed Terborgh (1983). Feeding was observed during dawn-to-dark follows. When a feeding bout began, the observer noted how many animals were feeding, and for how long. The duration of the feeding bout was multiplied by the number of feeding individuals to yield a total number of monkey-minutes for the bout. Food items were assigned to one of the following categories: buds, flowers, mature fruit, immature fruit, mature leaves, immature leaves, petioles, seeds. Contact hours at Isla Iguana totalled 106 in 1999, 101 in 2000 and 118 in 2001. The corresponding values for Danto were 74, 146 and 127.

On Iguana, the social behaviour of the animals was atypical in that individuals often scattered to the far corners of the island, so that just one or two (of the six) individuals could be observed at a time. To increase the rate of data acquisition, as well as better to distribute the feeding observations around the island, we often deployed two observers who simultaneously observed different individuals in different parts of the island. All individual trees $\geq 10$ cm dbh on Iguana were tagged and identified to species, a fact that afforded ready identification of food items.

Three fully identified tree plots on Danto, totalling 2.5 ha, served to characterize forest composition for the island, but most howler feeding trees were outside these plots. Feeding trees were routinely identified by the observer, but when the identity of a tree was in doubt, it was marked with red flagging and later identified by an experienced botanist.

### Resource availability

We used the basal area of trees $\geq 10$ cm dbh to represent the availability of foliage at all locations, ignoring the fact that howlers occasionally use lianas and trees smaller than 10 cm dbh. Basal areas were derived from tree inventories conducted at each site as described above and are considered good surrogates for foliage volume (Enquist & Niklas 2002).

### Analysis

We measured feeding selectivity by comparing the proportion of feeding minutes in each tree species to the proportion of the total basal area of the site made up by that species. Basal areas for most tree species were available from the whole-island inventory (Iguana) or the 2.5 ha of tree plots on Danto. The relative basal area of each tree species at each site was taken as the 'expected' value, whereas the fraction of feeding time was taken as the 'observed' value. The square root of the summed differences squared provided an index of selectivity having potential values between zero and one. Selectivity is thus zero when tree species are used in proportion to their basal areas, and can attain a value approaching one in the unlikely case that all feeding was concentrated in a single rare species.

## RESULTS

### Diversity of plant resources

The flora of Lago Guri is not rich by humid tropical standards but is similar in diversity to other neotropical dry forests (Hubbell 1979). The three sample plots on

Danto included 94 species (50–70 species $ha^{-1}$), but a published flora of the island lists 151 tree species (Aymard *et al.* 1997). Thus, the two howler groups studied on Danto probably had access to > 100 species in home ranges of 16 and 23 ha. In contrast, Isla Iguana offered only 46 tree species.

## Consumption of plant resources

Given the possibility that the most preferred resources are not necessarily the most common, one might expect *a priori* that Danto howlers would use more tree species, and more rare tree species (operationally defined as those contributing < 1% of stand basal area) than the howlers of Iguana.

The number of rare species used can be expected to increase over time. To control for this tendency, we consider the samples available from 2000, when the number of monkey-minutes (m-m) of feeding time was similar for both sites: 4628 m-m for Danto and 4315 m-m for Iguana (Table 1). Rare tree species were equally represented at both sites, making up 15% of basal area on Iguana and 16% on Danto. In 2000, Iguana howlers used 11 rare species for 6% of feeding time and Danto howlers fed on 23 rare species for 19% of feeding minutes. Thus, as predicted, Danto howlers used more tree species and more rare species than did Iguana howlers, even though the latter tended to be more widely dispersed when feeding, a bias that should increase rather than decrease the number of species used.

**Table 1.** Monkey-minutes of feeding observations and food resources used by howlers on two islands in Lago Guri, Venezuela, 1999–2001 (per cent of monkey minutes).

| Category | 1999 | 2000 | 2001 | 3-y mean |
|---|---|---|---|---|
| Danto Machado | | | | |
| Flowers | 12 | 12 | 31 | 18 |
| Buds | 0 | 1 | 8 | 3 |
| Mature leaves | 54 | 26 | 6 | 29 |
| Young leaves | 16 | 28 | 35 | 26 |
| Unripe fruit | 4 | 8 | 11 | 8 |
| Ripe fruit | 10 | 24 | 9 | 14 |
| Other | 3 | 2 | < 1 | 2 |
| Total monkey-minutes | 2249 | 4628 | 7414 | |
| Isla Iguana | | | | |
| Flowers | 16 | 9 | 17 | 14 |
| Buds | 14 | 4 | 16 | 11 |
| Mature leaves | 28 | 13 | 21 | 21 |
| Young leaves | 40 | 72 | 44 | 52 |
| Unripe fruit | 2 | 1 | 2 | 2 |
| Ripe fruit | < 1 | < 1 | 0 | 0 |
| Other | 0 | < 1 | < 1 | 0 |
| Total monkey-minutes | 2308 | 4315 | 3073 | |

Combining results for the 3 y, Danto howlers fed on 56 species of tree, 10 more than existed on Iguana, including 34 rare species, whereas Iguana howlers used a total of 33 species, 18 of which were rare.

Given the lower plant diversity present on Iguana, it could be surmised that the monkeys there would be obliged to consume a less varied diet than those on Danto, where the range of edible materials was manifestly greater. This prediction also proved to be true (Table 1). Iguana howlers consumed less fruit (2%) and more foliage (73%) than those on Danto (22% fruit, 55% foliage). Danto monkeys had access to ripe fruit (64% of fruit consumption), whereas most of the fruit consumed by Iguana monkeys was in immature condition (80%). Flower consumption was similar at both sites (18 and 14%, respectively). The diversity of food items, H′, consumed by Danto howlers was 1.7 (where $H' = -\Sigma p_i \ln p_i$), whereas the diversity of items consumed by Iguana howlers was only 1.2, affirming the prediction of greater diet breadth on Danto.

Given that Danto howlers had access to a wider range of tree species, it could be expected that some foliage sources preferred by Danto howlers were absent on Iguana. Conversely, Iguana monkeys might have been obliged to consume species that were ignored by their Danto counterparts.

Sixty per cent or more of the leaf consumption by Danto howlers in all 3 y was from tree species not present on Iguana (Table 2). Danto howlers often ignored foliage sources that were available to them and used by Iguana howlers in the same year, although the figures are highly variable.

We predicted that Iguana howlers would show less selectivity of foliage sources than Danto howlers. However, the observations contradicted this prediction. Iguana howlers exhibited more selectivity in two out of three years (Table 3). The two most preferred species by the Danto animals in 1999 were *Brosimum alicastrum* (57%) and *Cordia alliodora* (9%), which together contributed 66% of leaf consumption. In 2000, more

**Table 2.** Consumption of young and mature leaves by *Alouatta seniculus* on Danto Machado and Isla Iguana in relation to basal area, 1999–2001. Left column: proportion of leaf consumption by Danto Machado howlers contributed by tree species not present on Isla Iguana; right column: proportion of leaf consumption by howlers on Isla Iguana contributed by tree species present but not eaten by howlers on Danto Machado.

| Year | Danto Machado | Isla Iguana |
|---|---|---|
| 1999 | 0.98 | 0.95 |
| 2000 | 0.60 | 0.07 |
| 2001 | 0.63 | 0.51 |

**Table 3.** Selectivity of foliage sources by *Alouatta seniculus* on Danto Machado and Isla Iguana.

| Year | Danto Machado | Iguana |
|---|---|---|
| 1999 | 0.53 | 0.50 |
| 2000 | 0.24 | 0.52 |
| 2001 | 0.29 | 0.46 |

species were eaten and the two most preferred were *Pradosia caracasana* (29%) and *Lonchocarpus sericeus* (9%). In 2001, the three species most used for foliage were *Brosimum alicastrum* (22%), *Lonchocarpus dipteronervus* (17%) and *Brosimum guianensis* (12%). Thus there was little constancy from year to year in the choice of foliage sources by Danto howlers.

In contrast, a single species, *Tabebuia serratifolia* (Bignoniaceae), was preferred by Iguana howlers in all 3 y (50% in 1999, 48% in 2000 and 32% in 2001). Scant use of *T. serratifolia* by Danto howlers cannot be attributed to lack of availability, although it was more abundant on Iguana where it ranked 4th in basal area vs. 18th on Danto. However, the option of consuming *Brosimum*, *Cordia* or *Pradosia* leaves was simply not available to Iguana howlers, because none of these species occurred on the island.

Howler monkeys are known to prefer young foliage to mature leaves, so could be expected to switch species preferences in accord with seasonal or year-to-year variation in phenology. This proposition can be tested by correlating foliage use by species across the 3 y of observations. As indicated above, Danto howlers used different leaf sources in different years, so the mean between-year (Pearson) correlation in foliage consumption was only 0.29. In contrast, Iguana howlers showed a strikingly consistent use of a few species, leading to a much higher between-year correlation of 0.82.

## DISCUSSION

Long-term persistence of howler groups in forest fragments as small as 0.25 ha is doubly remarkable, first, because the densities of individuals exceed the normal range by more than an order of magnitude, and second, because the diversity of resources available in such reduced areas is substantially less than is available in continuous habitat (De Thoisy & Richard-Hansen 1997, Estrada & Coates-Estrada 1988, Galetti *et al.* 1994, Lovejoy *et al.* 1986, Neves & Rylands 1991, Rumiz 1990, Serio-Silva *et al.* 2002).

Compared with counterparts living on 190-ha Danto Machado, Iguana howlers showed (1) less use of rare trees for feeding (6% vs. 19%); (2) increased leaf consumption (73% vs. 55%); (3) decreased fruit consumption (2% vs. 22%); (4) greater use of unripe fruit (80% vs. 36% of all fruit consumed); (5) a lack of access to several tree species that were preferred as foliage sources by Danto howlers; and (6) heavy reliance on a single species (*Tabebuia serratifolia*) as a foliage source.

These responses to resource scarcity entailed a clear contraction of diet breadth. Fruit consumption was almost nil on Iguana, and fewer species were exploited for foliage and other resources. These concomitants of scarcity, quite conspicuous by other measures, were not reflected in a statistical measure of food selectivity. Iguana monkeys were predicted to be less selective, but proved to be more selective than Danto monkeys in 2 y out of 3. The selectivity statistic failed to reflect obvious differences in resource use because it does not distinguish between concentrated use of a single resource (high selectivity) that is seasonally abundant and highly preferred, and concentrated use of a resource because suitable alternatives are not available.

The responses to persistent resource scarcity shown by Iguana howlers are strikingly different from responses to seasonal scarcity shown by several primate species at Cocha Cashu in the Peruvian Amazon. As fruit abundance declined at the end of the wet season, Cocha Cashu primates broadened their diets through increased consumption of resources that were used little or not at all at other seasons: seeds, nectar, pith, foliage, exudates, small prey, etc. (Terborgh 1983). In both situations, less-preferred resources are used, but where resources of all kinds were chronically scarce, as on Isla Iguana, diet breadth contracted rather than expanded.

An unexpected finding was that Iguana howlers consistently ate more young leaves and a higher proportion of young leaves than did Danto howlers (71% vs. 47% of all foliage consumed). Iguana howlers had greater access to young leaves because *Tabebuia serratifolia* trees were induced by frequent defoliation to flush new leaves repeatedly during a season (Feeley & Terborgh 2005, Rao *et al.* 2001).

Howlers studied on the neotropical mainland often exhibit pronounced food selectivity, showing clear preferences for the leaves of certain individual trees of a given species over those of other individuals (Glander 1978, 1981). Such selective feeding has been interpreted, no doubt correctly, as avoidance of plant chemical defences (Milton 1979, 1980). Our results raise the deeper issue of whether the rejection of unpalatable foliage by mainland howlers is a necessity, or a luxury made possible by a high relative abundance of resources and low consumer densities. The results from Lago Guri strongly suggest the latter interpretation.

Circumstantial evidence suggests that the howlers of Iguana, and presumably other small islands in Lago Guri, are under severe nutritional stress. Birth rates of adult females on Iguana and Cola (an adjacent island of similar size) were only one quarter of those observed on Danto (Terborgh *et al*. 2001). Reduced reproduction of howlers occupying small forest fragments has also been noted in Argentina (De Luycker 1995). Weights of adult howlers captured on five small Lago Guri islets were substantially below those of individuals captured on the Venezuelan mainland (K. Glander, unpublished results). All these observations point to a scenario of severe resource limitation, as has also been noted for howlers occupying small forest fragments in Brazil (Neves & Rylands 1991).

If howlers can persist and reproduce (albeit slowly) on small islands at densities an order of magnitude or more above those found on the mainland, what is limiting mainland populations (Chapman *et al*. 2004, Wasserman & Chapman 2003)? The fact that Iguana howlers survive on food resources that are largely rejected by Danto howlers strongly implies that howlers living in normal-sized ranges on the mainland are not ordinarily food limited (De Thoisy & Richard-Hansen 1997).

Howlers are known to be preyed upon by harpy eagles and perhaps other predators (Peetz *et al*. 1992, Peres 1990), but we have no evidence that they are ever attacked on the small islands we studied, which lie across several km of open water from the mainland. Over the period 1994–2001, we monitored the fates of every individual howler on seven small islands (except perhaps for unrecorded babies that might have died in infancy). All missing individuals were recovered as intact, fully articulated skeletons. The intact skeletons provide *prima facie* evidence that the animals were not predated. However, the question of how important predation is to the demography of mainland howlers remains open.

Isolation and the absence of contact with other howlers may protect against parasites and disease, thereby reducing mortality. Bot fly (*Alouattamyia* spp.) and screw worm (*Cochliomyia* spp.) infestations have been shown to be major sources of mortality of *Alouatta palliata* in Panama (Milton 1996). Howlers of small Lago Guri islands have not been observed with bot flies, whereas Danto howlers bear telltale scars and are often actively infested. In contrast, Gilbert (1974) and Stoner (1996) report higher levels of parasitic infection among red howlers occupying small vs. large habitat patches. Investigation of the parasite loads of Guri howlers would be useful in this context.

A final possibility is that mainland howlers are limited by infanticide (Agoramoorthy & Rudran 1995). Small-island groups contain only one dominant male and are isolated from other howler groups, thereby precluding male takeovers and infanticide (Crockett & Janson 2000). More generally, the density dependence of infanticide remains little studied (van Schaik & Janson 2000).

Clearly, there is much yet to learn about the mechanisms of population regulation in howlers under 'normal' circumstances. It seems likely that predation, parasitosis and infanticide all contribute to the mortality of mainland howlers, though just which of these factors are density-dependent, and how strongly so, cannot be stated at present. The advantage offered by small islands is that each of these factors can potentially be controlled or measured in a way that helps shed light on the more complex mainland situation.

## ACKNOWLEDGEMENTS

We thank Dagmar Koebbler, Gutzi Zimmer, Erin Campbell, Mailén Riveros C., and Lisa Davenport for help in habituating howlers at Lago Guri. Percy Nuñez kindly provided plant identifications. We thank EDELCA, the hydroelectric company that manages the Guri impoundment, for permission to conduct the research and for providing valuable logistical support. Blgo. Luis Balbas is warmly thanked for his many contributions to the project. JT acknowledges the financial support of the National Science Foundation (DEB97-09281, DEB01-08107).

## LITERATURE CITED

AGORAMOORTHY, G. & RUDRAN, R. 1995. Infanticide by adult and subadult males in free-ranging red howler monkeys, *Alouatta seniculus*, in Venezuela. *Ethology* 99:75–88.

AYMARD, G., NORCONK, M. A. & KINZEY, W. G. 1997. Composición florística de comunidades vegetales en islas en el embase de Guri, Río Caroní, Estado Bolivar, Venezuela. *BioLlania*, Edición Especial No. 6:195–233.

CHAPMAN, C. A., CHAPMAN, L. J., NAUGHTON-TREVES, L., LAWES, M. J. & MCDOWELL, L. R. 2004. Predicting folivorous primate abundance: validation of a nutritional model. *American Journal of Primatology* 62:55–69.

CROCKETT, C. M. & EISENBERG, J. F. 1987. Howlers: variations in group size and demography. Pp. 54–68 in Smuts, B. B., Cheney, D. L., Seyfarth, R. M., Wrangham, R. W. & Struhsaker, T. T. (eds). *Primate societies*. University of Chicago Press, Chicago.

CROCKETT, C. M. & JANSON, C. H. 2000. Infanticide in red howlers: female group size, male membership, and a possible link to folivory. Pp. 75–98 in van Schaik, C. P. & Janson, C. H. (eds). *Infanticide by males and its implications*. Cambridge University Press, Cambridge.

DE LUYCKER, A. 1995. Deforestation, selective cutting and habitat fragmentation: the impact on a black howler monkey (*Alouatta caraya*) population in northern Argentina. *Latin American Primatological Bulletin* 5:17–24.

DE THOISY, B. & RICHARD-HANSEN, C. 1997. Diet and social behavior changes in a red howler monkey (*Alouatta seniculus*) troop in a highly degraded rain forest. *Folia Primatologica* 68:357–361.

ENQUIST, B. J. & NIKLAS, K. J. 2002. Global allocation rules for patterns of biomass partitioning in seed plants. *Science* 295:1517–1520.

ESTRADA, A. & COATES-ESTRADA, R. 1988. Tropical rainforest conversion and perspectives in the conservation of wild primates (*Alouatta* and *Ateles*) in Mexico. *American Journal of Primatology* 14:315–327.

FEELEY, K. J. & TERBORGH, J. W. 2005. The effects of herbivore density on soil nutrients and tree growth in tropical forest fragments. *Ecology* 86:116–124.

GALETTI, M., PEDRONI, F. & MORELLATO, L. P. C. 1994. Diet of the brown howler monkey *Alouatta fusca* in a forest fragment in southeastern Brazil. *Mammalia* 58:111–118.

GILBERT, K. A. 1974. Parasitic infection in red howling monkeys in forest fragments. *Neotropical Primates* 2:10–12.

GLANDER, K. E. 1978. Howling monkey feeding behavior and plant secondary compounds: a study of strategies. Pp. 561–574 in Montgomery, G. G. (ed.). *The ecology of arboreal folivores*. Smithsonian Institution Press, Washington, DC.

GLANDER, K. E. 1981. Feeding patterns in mantled howling monkeys. Pp. 231–257 in Kamil, A. C. & Sargent, T. D. (eds). *Foraging behavior: ecological, ethological and psychological approaches.* Garland Press, London.

HUBBELL, S. P. 1979. Tree dispersion, abundance, and diversity in a tropical dry forest. *Science* 203:1299–1309.

KINZEY, W. G., NORCONK, M. A. & ALVAREZ-CORDERO, E. 1988. Primate survey of Eastern Bolivar, Venezuela. *Primate Conservation* 9:66–70.

LOVEJOY, T. E., BIERREGAARD, R. O., RYLANDS, A. B., MALCOLM, J. R., QUINTELA, C. E., HARPER, L. H., BROWN, K. S., POWELL, A. H., POWELL, G. V. N., SCHUBART, H. O. R. & HAYS, M. B. 1986. Edge and other effects of isolation on Amazon forest fragments. Pp. 257–285 in Soulé, M. E. (ed.). *Conservation biology: the science of scarcity and diversity*. Sinauer Assoc., Sunderland, MA.

MILTON, K. 1979. Factors influencing leaf choices by howler monkeys: a test for some hypotheses of food selection by generalist herbivores. *American Naturalist* 114:362–377.

MILTON, K. 1980. *The foraging strategy of howler monkeys.* Columbia University Press, New York. 165 pp.

MILTON, K. 1996. Effects of bot fly (*Alouattamyia bueria*) parasitism on a free-ranging howler monkey (*Alouatta palliata*) population in Panama. *Journal of Zoology* (*London*) 239:39–63.

NEVES, A. M. S. & RYLANDS, A. B. 1991. Diet of a group of howling monkeys, *Alouatta seniculus*, in an isolated forest in central Amazonia. *Annais do Primatologia do Brasil* 3:263–274.

NEVILLE, M. K. 1972. The population structure of red howler monkeys (*Alouatta seniculus*) in Trinidad and Venezuela. *Folia Primatologica* 17:56–86.

PEETZ, A. 2001. Ecology and social organization of the bearded saki *Chiropotes satanas chiropotes* (Primates: Pitheciinae) in Venezuela. *Ecotropical Monographs* No. 1, Bonn, Germany. 170 pp.

PEETZ, A., NORCONK, M. A. & KINZEY, W. G. 1992. Predation by jaguar on howler monkeys (*Alouatta seniculus*) in Venezuela. *American Journal of Primatology* 28:223–228.

PERES, C. 1990. A harpy eagle successfully captures an adult male red howler monkey. *Wilson Bulletin* 102:560–561.

RAO, M., TERBORGH, J. & NUÑEZ, P. 2001. Increased herbivory in forest isolates: implications for plant community structure and composition. *Conservation Biology* 15:624–633.

RODRIGUEZ-LUNA, E., DOMINGUEZ-DOMINGUEZ, L. E., MORALES-MAVIL, J. E. & MARTINEZ-MORALES, M. 2003. Foraging strategy changes in an *Alouatta palliata mexicana* troop released on an island. Pp. 229–247 in Marsh, L. K. (ed). *Primates in fragments: ecology and conservation*. Kluwer Academic/Plenum Press, New York.

RUMIZ, D. I. 1990. *Alouatta caraya*: population density and demography in northern Argentina. *American Journal of Primatology* 21:279–294.

SERIO-SILVA, J. C., RICO-GRAY, V., HERNANDEZ-SALAZAR, L. T. & ESPINOSA-GOMEZ, R. 2002. The role of *Ficus* (Moraceae) in the diet and nutrition of a troop of Mexican howler monkeys, *Alouatta palliata mexicana*, released on an island in southern Veracruz, Mexico. *Journal of Tropical Ecology* 18:913–928.

STONER, K. E. 1996. Prevalence and intensity of intestinal parasites in mantled howling monkeys (*Alouatta palliata*) in northeastern Costa Rica: implications for conservation biology. *Conservation Biology* 10:539–546.

TERBORGH, J. 1983. *Five new world primates: a study in comparative ecology.* Princeton University Press, Princeton. 260 pp.

TERBORGH, J., LOPEZ, L. & TELLO, J. S. 1997a. Bird communities in transition: the Lago Guri Islands. *Ecology* 78:1494–1501.

TERBORGH, J., LOPEZ, L., TELLO, J., YU, D. & BRUNI, A. R. 1997b. Transitory states in relaxing land bridge islands. Pp. 256–274 in Laurance, W. F. & Bierregaard, R. O. (eds). *Tropical forest remnants: ecology, management, and conservation of fragmented communities*. University of Chicago Press, Chicago.

TERBORGH, J., LOPEZ, L., NUÑEZ P., RAO, M., SHAHABUDDIN, G., ORIHUELA, G., RIVEROS, M. C., ASCANIO, R., ADLER, G. H., LAMBERT, T. D. & BALBAS, L. 2001. Ecological meltdown in predator-free forest fragments. *Science* 294:1923–1926.

VAN SCHAIK, C. P. & JANSON, C. H. (eds). 2000. *Infanticide by males and its implications.* Cambridge University Press, Cambridge. 354 pp.

WASSERMAN, M. D. & CHAPMAN, C. A. 2003. Determinants of colobine monkey abundance: the importance of food energy, protein and fibre content. *Journal of Animal Ecology* 72:650–659.