

# Resource availability and habitat use by mantled howling monkeys in a Nicaraguan coffee plantation: can agroforests serve as core habitat for a forest mammal?

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agroforestry; matrix habitat; primates; resource availability; shade coffee; tree community; *Alouatta palliata*.

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## Abstract

Although shade coffee plantations are potentially valuable habitats for wildlife conservation, little information exists on the extent to which they provide resident wildlife populations with resources necessary for survival and reproduction. A 14-month study of the ecology of mantled howling monkeys *Alouatta palliata* living in a Nicaraguan shade coffee plantation was therefore conducted. Trees were surveyed at randomly located enumeration points in the coffee plantation and monitored for phenophase production to characterize resource availability. Day-long focal animal follows were used to characterize the ranging and habitat preferences of the howlers. The study site had a diverse canopy, with over 60 tree species providing shade for coffee cultivation; high tree diversity ensured year-round availability of the howlers' preferred foods. Howlers did not avoid feeding or ranging in areas of shade coffee cultivation. However, when foraging in coffee they favored large shade trees for feeding and were less likely to use areas of shade coffee with small trees and fewer arboreal pathways. Results suggest, in conjunction with controls on hunting and protection of nearby forests, that shade coffee can serve as alternate wildlife habitat and corridors between forest fragments for howling monkeys and possibly other forest mammals. Specific management recommendations to improve the conservation value of shade coffee for primates are made and the potential role of coffee plantations in primate conservation at a regional scale are discussed.

## Introduction

The critical role of matrix habitats in influencing edge effects, successional processes and dispersal between forest fragments has been increasingly recognized (Gascon *et al.*, 1999; Laurance *et al.*, 2002; Perfecto & Vandermeer, 2002). The future conservation of even well-protected species may depend on the ability of anthropogenic landscapes surrounding protected areas to support basic ecological processes (Vandermeer & Perfecto, 1997). Agriculture is the most pervasive of human land uses, with the 5 billion ha of land under cultivation surpassing the extent of forested areas (Robertson & Swinton, 2005). In the tropics, agricultural areas vary considerably in management intensity, degree of planned and associated biodiversity, and hence in conservation value (Vandermeer *et al.*, 1998).

In the Neotropics, shaded coffee plantations have drawn interest as potential reservoirs of tropical biodiversity

(Perfecto *et al.*, 1996; Moguel & Toledo, 1999; Donald, 2004; Somarriba *et al.*, 2004). Traditionally, coffee is grown beneath an understory of native forest trees; in stark contrast, some modern coffee varieties are grown without shade cover. Shade coffee itself varies greatly in management intensity: the most rustic forms resemble native forest with the understory replaced with coffee, the most modernized comprise only a few tree species with heights less than 5 m and a discontinuous canopy (Perfecto *et al.*, 1996; Moguel & Toledo, 1999). There is thus some confusion over the meaning of the term shade coffee; here we use it to refer to coffee agroforestry systems incorporating a diverse and relatively intact shade canopy (types 1–3 in fig. 1 of Moguel & Toledo, 1999). Although shade coffee plantations represent highly modified habitats in comparison with undisturbed forest, they have been suggested to have significant conservation value as reservoirs for biodiversity and corridors between forested areas (Perfecto *et al.*, 1996; Moguel &

Toledo, 1999; Philpott & Dietsch, 2003; Somarriba *et al.*, 2004). Shade coffee plantations support diverse communities of arthropods (Nestel, Dickschen & Altieri, 1993; Perfecto & Snelling, 1995; Perfecto *et al.*, 1997; Perfecto & Vandermeer, 2002), resident and migratory birds (Wunderle & Latta, 1996; Greenberg *et al.*, 1997a; Greenberg, Bichier & Sterling, 1997b; Calvo & Blake, 1998; Johnson, 2000; Tejada-Cruz & Sutherland, 2004) and mammals (Estrada *et al.*, 1994; Gallina, Mandujano & Gonzalez-Romero, 1996; Cruz-Lara *et al.*, 2004). Similarly, several primate species can be found in agroforests (Ganzhorn & Abraham, 1991; Estrada & Coates-Estrada, 1996; Raboy, Christman & Dietz, 2004).

Clearly, traditional agroforestry systems like shade coffee can support diverse wildlife communities. However, little information exists on the extent to which agroforests can support the foraging and reproduction of resident wildlife (Donald, 2004). Although a diverse canopy probably helps prevent temporal gaps in food availability for arboreal taxa (Perfecto *et al.*, 1996), the patterns of resource abundance affecting animals relying directly on shade trees for their foraging have received little attention (Gallina *et al.*, 1996; Carlo, Collazo & Groom, 2004).

Mantled howling monkeys *Alouatta palliata* are a highly adaptable primate species, found in a wide variety of primary and disturbed habitats (Crockett & Eisenberg, 1987; Neville *et al.*, 1988). Although the subspecies found in Nicaragua (*Alouatta palliata palliata*) has been assessed as Least Concern by the IUCN (Cuarón *et al.*, 2003), as obligate forest dwellers threatened by deforestation and hunting, mantled howlers merit conservation attention (Horwich, 1998). *Alouatta palliata* is listed on CITES Appendix I (Reid, 1997), and populations in Nicaragua's heavily deforested Pacific slope are highly fragmented (Crockett *et al.*, 1997; K. Williams-Guillén, pers. obs.). During a census of the primate community in and around Mombacho Volcano, Nicaragua (McCann *et al.*, 2003), we frequently found groups of mantled howling monkeys in the area's shade coffee. We were unsure whether the howlers really resided in the coffee plantations or were relying more heavily on the many small patches of forest found in the coffee-dominated landscape. To evaluate the value of shade coffee plantations as habitat for primates, we therefore studied the behavioral ecology of three groups of mantled howlers living in a shade coffee plantation on Mombacho.

We describe the tree community, focusing on characteristics known to affect howlers' use of trees at other sites. We then consider aspects of range use, comparing patterns of habitat use to availability. We predicted that if areas of shade coffee cultivation were less suitable for use by howlers than nearby patches of secondary forest, howlers would range and feed in shade coffee less often than expected based on the availability of the habitat. Given that howlers prefer large trees for feeding and travel (Milton, 1980; Leighton & Leighton, 1982; Chapman, 1988), we predicted that the feeding trees located in shade coffee would be larger than a random selection of shade trees. We also predicted that howlers would preferentially use areas of shade coffee with

larger trees, higher tree diversity, higher canopy connectivity and higher densities of food resources.

## Methods

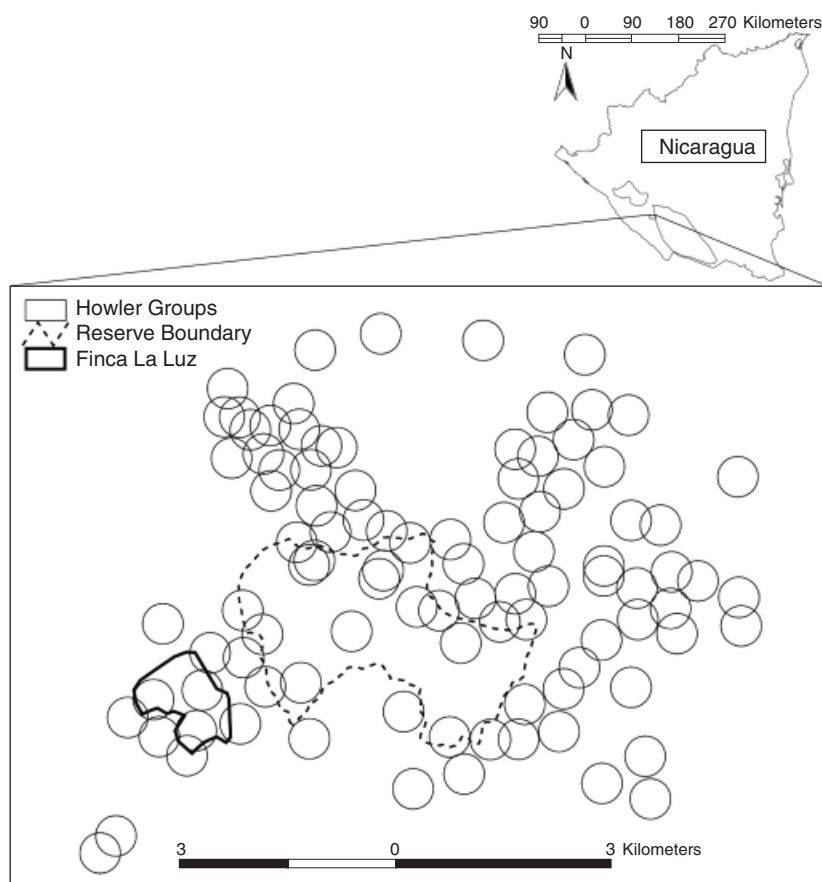
### Study area and species

We conducted this study from September 1999 to November 2000 in Finca La Luz, a shade coffee plantation on the western side of Mombacho Volcano, Nicaragua (Fig. 1). Mombacho is a large, dormant volcano with elevations from 200 to 1345 m a.s.l. (Atwood, 1984). The 650-ha Reserva Natural Volcán Mombacho (RNVM) consists of the volcano's summit above 850 m; the reserve comprises tall and elfin cloud forest and is home to endemic species of salamander, orchid and butterfly. All areas of the volcano experience a dry season from December to April. Mombacho's lower slopes support seasonally dry forest (highly disturbed because of agriculture, cattle ranching and wood extraction), most of which falls within a belt of coffee plantations in the 400–800 m elevation zone. Mombacho supports a population of *c.* 1000 mantled howling monkeys (McCann *et al.*, 2003); despite the greater disturbance at lower elevations, the majority of Mombacho's monkeys are found not in RNVM but in the 25 surrounding shade coffee plantations (Fig. 1).

Coffee (*Coffea arabica* var. *bourbon*) has been cultivated at Finca La Luz for over 100 years. We chose this plantation for study because it seemed intermediate in size and management intensity for the Mombacho area. La Luz comprises 125 ha of active shade coffee cultivation, abandoned coffee, young regeneration and patches of older secondary forest in areas too steep for cultivation; the property also has areas of pasture and other crops. Elevations in the property range from about 450 to 600 m; rainfall at the site was *c.* 1490 mm during the study period and minimum temperatures are relatively constant (20–23 °C). Finca La Luz has a species-rich shade tree community, which includes several native forest species. Although some shade trees are planted (*Gliricidia sepium*, *Inga* spp.), they are not intensively managed, and only limited numbers of the smaller shade trees were pruned. At the time of the study, La Luz had a population of ~65 howlers belonging to three permanent groups of 15–26 individuals. Group sizes and compositions were typical for the species, and we observed births in all groups during the study period (Williams-Guillén, 2003).

### Ecological sampling

Using a 100 × 100 m grid superimposed on aerial orthophotographs (already georeferenced and corrected for orthogonal distortion), we estimated per cent canopy cover in La Luz by counting the number of grid vertices that fell on tree crowns within the property boundaries and then dividing by the total number of vertices (Nowak *et al.*, 1996). Aerial photographs and ground truthing were also used to create a habitat map for La Luz. We defined four habitat types in La Luz. The first, active coffee cultivation, were those areas



**Figure 1** Locations of howling monkey groups (circles), Mombacho Volcano Nature Reserve (dotted line) and study site Finca La Luz (solid line) in Mombacho Volcano, Nicaragua. Group locations from McCann *et al.* (2003).

where coffee predominated in the understory and the coffee was regularly maintained via pruning, application of agrochemicals and clearing of competing ground vegetation. The second, abandoned coffee bushes, comprised the most important understory element, but these were left unmanaged, and there was evidence of forest regeneration (e.g. more tree seedlings and saplings mixed in with the coffee). Third, areas of young regeneration had a dense understory and a broken canopy dominated by *Cecropia*. Finally, older secondary forest included areas that had not been cleared in over 50 years, with a relatively sparse understory, trees with boles typically between 15 and 50 cm diameter at breast height (DBH), and a predominance of *Bursera simaruba*, *Cordia alliodora*, *Lysiloma aurita* and *Guazuma ulmifolia* trees.

To estimate tree species composition, we established 30 randomly located, non-overlapping circular plots with a 25-m radius at randomly selected points separated by > 100 m in areas of active coffee cultivation (total enumeration area of 5.8 ha). We identified and measured the DBH of all trees  $\geq 20$  cm DBH (howlers rarely use smaller trees; Milton, 1980; Leighton & Leighton, 1982; Chapman, 1988). We collected vouchers and made identifications using guidebooks (Croat, 1978; Salas, 1993; Gentry & Vasquez, 1995) at the Herbario Nacional, Managua, Nicaragua. Tree heights were estimated visually and selected estimates were checked by measuring tree height with a clinometer. To characterize

the availability of arboreal pathways between trees, we used a five-point scale to estimate canopy connectivity (0, trees with isolated crowns; 1, crown contiguous with other trees for <25% of circumference; 2, *c.* 25–50%; 3, *c.* 50–75%; 4, >75% contiguous). The same measurements were taken for all trees in which the howlers fed in order to facilitate comparisons between feeding trees and available trees. To characterize phenological patterns, we visited each tree in the vegetation enumerations on a monthly basis to record the production of mature leaves, young leaves, fruits and flowers. We present phenological data as the percentage of trees bearing a given phenophase per month.

### Feeding and ranging behavior

We collected over 1300 h of behavioral data on the howlers. Data were collected using focal animal sampling (Altmann, 1974) between 05:30 and 17:30 h, ideally for four full-day activity cycles per group per month (occasionally, the first day of each cycle was spent locating the group), for 11 cycles for group 1 and 12 cycles for groups 2 and 3. The focal animals to be followed were randomly selected in advance. Focal animals were followed for an entire day; all behavioral states (feeding, resting, travel and social) and their durations were recorded, with particular focus on feeding and foraging bouts (see Williams-Guillén, 2003 for a detailed description

of data collection methods and schedules). We defined feeding bouts as periods of processing or consumption of a single food type within a single feeding tree uninterrupted by other behavior states. Feeding trees were numbered and mapped, the DBH measured, and tree height and crown connectivity estimated; we did not mark or measure vines and epiphytes used as food sources. Approximately 75 feeding trees, accounting for less than 4% of total feeding time, could not be marked or mapped because they were inaccessible due to very steep slopes. In characterizing range size and composition, we excluded data collected on group 2 during the last 3 months of the study because of a dramatic shift in ranging area related to social disturbance (to ensure that this exclusion did not introduce a bias, relevant tests were repeated with the data included; the results of all analyses were consistent with the censored data set). To estimate home range size and location, we used digitized polygons (Ostro *et al.*, 1999). Using ArcView 3.2 GIS software (ESRI Inc., Redlands, CA, USA) we merged the home range and habitat maps to determine the amount of each habitat type in each group's range.

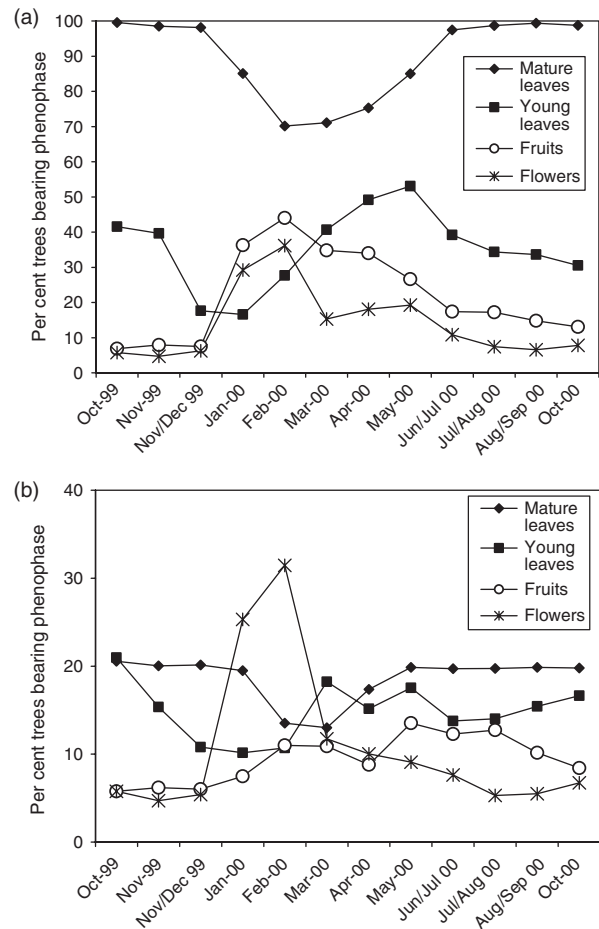
### Statistical analyses

Data were analyzed using SPSS statistical software; all tests are two tailed. To determine whether the howlers visited certain habitats more frequently than expected, we used a  $\chi^2$  goodness-of-fit test to compare the number of days spent in each habitat with the expected number based on habitat availability within the home range (Stoner, 1996; Raboy *et al.*, 2004); each group was tested separately. The amount of time spent in each habitat was determined by the location of the focal animal at a randomly chosen time for each sampling day; the howlers could traverse their ranges within a day, and we assume that these randomly selected locations are statistically independent and reflect habitat preference. Similarly, to determine whether the howlers exploited certain habitats for feeding more often than expected, we used the same test to compare the observed frequency of feeding bouts in each habitat type with the expected frequency. Again, we randomly selected one feeding bout from each day for the  $\chi^2$  test. We used a Mann-Whitney *U*-test to test for differences between feeding trees and trees available in the habitat and to test for differences in tree characteristics between vegetation plots that were used versus unused by study groups for feeding. We used  $\alpha = 0.05$  for all tests; mean values are followed by  $\pm$  standard deviation (SD).

## Results

### Tree community composition and phenology

On the basis of assessment of aerial photographs, the La Luz property as a whole had a canopy cover of 57%, and areas of active shade coffee cultivation had 67% canopy cover. In the enumeration points we located 492 trees of 48 species with a DBH of  $\geq 20$  cm, for a density of 83.5 trees  $\text{ha}^{-1}$  and a basal area of 30.6  $\text{m}^2 \text{ha}^{-1}$ . A few rare species were not found



**Figure 2** (a) Percentage of trees in vegetation points bearing mature leaves, young leaves, fruits and flowers; (b) percentage of trees in vegetation points bearing mature leaves, young leaves, fruits and flowers of species used by the howlers as primary food sources.

in the plots, and we estimate that there were 60–65 tree species present in the plantation. In terms of stem numbers, the tree community was dominated by a few common species (*G. sepium*, *Cecropia peltata* and *Cedrela odorata*); the 10 most common trees comprised more than 75% of stems. Considering species composition as a proportion of total basal area (Supplementary Material Table S1), *G. sepium* still made the largest contribution to the shade tree community. However, species such as *Enterolobium cyclocarpum* and *Ficus costaricana* contributed more to basal area than stem counts alone would suggest. The mean DBH of marked trees was  $55.1 \pm 40.7$  cm. Several species, such as *E. cyclocarpum*, had DBHs of 200 cm or more (Supplementary Material Table S1). Tree heights ranged from 5 to 35 m, with most trees 10–15 m in height; only 9% of trees exceeded 20 m in height.

Most trees bear mature leaves throughout the year, although *G. sepium* and a few other species were deciduous during the dry season (Fig. 2a). At the beginning of the dry season, many tree species produced flowers and fruits, with

young leaf production peaking later in the dry season. Fruit production remained relatively high through the rainy season. Most species had synchronous phenological patterns. Important exceptions were *F. costaricana* and *Cec. peltata*, both of which were important food sources for howlers (Williams-Guillén, 2003); individuals of these species varied in the timing of the production of leaves, fruits and flowers. To better characterize the availability of important food sources, we considered the production of leaves, fruits and flowers that comprised primary (> 10% of feeding time) food sources (Fig. 2b). Preferred foods, such as fleshy fruits and young leaves of *Ficus* spp. and *Cec. peltata*, were produced throughout the year.

### Patterns of habitat use

The home ranges of all groups included areas of active shade coffee cultivation, early regeneration and older secondary forest (Table 1). For all groups, the frequency with which they were located in each habitat was not significantly different from expected (G1:  $\chi^2 = 3.70$ ,  $P = 0.30$ , d.f. = 3; G2:  $\chi^2 = 3.67$ ,  $P = 0.16$ , d.f. = 2; G3:  $\chi^2 = 2.24$ ,  $P = 0.32$ , d.f. = 2). Similarly, the number of feeding bouts in each habitat did not differ significantly from expected (G1:  $\chi^2 = 2.54$ ,  $P = 0.47$ , d.f. = 3; G2:  $\chi^2 = 3.34$ ,  $P = 0.19$ , d.f. = 2; G3:  $\chi^2 = 2.21$ ,  $P = 0.33$ , d.f. = 2).

The howlers were observed feeding in 722 trees of at least 57 species. Nearly 70% of feeding trees were located in areas of active coffee cultivation, and feeding on trees used to shade coffee in these areas accounted for 76% of total observed feeding time. The howlers relied heavily on a few trees that accounted for at least 1% of total feeding time; most of these key trees were in areas of active coffee cultivation (Table 1). In comparison to the trees in the randomly placed vegetation enumerations, the feeding trees located in shade coffee were on average taller (feeding trees  $15.5 \pm 5.8$  m, enumeration trees  $12.7 \pm 4.3$  m) with a larger DBH (feeding trees  $87.7 \pm 71.8$  cm, enumeration trees

$55.6 \pm 40.8$  cm), although the large standard deviations for DBH values indicate great variation in feeding tree size. Feeding and random trees differed significantly in DBH ( $U = 73\,488.5$ ,  $P < 0.001$ ,  $n = 907$ ) and height ( $U = 53\,742.0$ ,  $P < 0.001$ ,  $n = 798$ ); there was no significant difference in canopy connectivity. Although the majority of both random and feeding trees have < 75 cm DBH, no randomly selected tree had a DBH > 250 cm, whereas there were a number of feeding trees (*F. costaricana*, *E. cyclocarpum*, *Ceiba pentandra*) in shade coffee with DBH > 250 cm.

Several of the vegetation plots fell within the howlers' home ranges, and the monkeys were observed feeding in 15 of the 30 plots. Contrasting the vegetation characteristics between used and unused plots ( $n = 15$  for each), there were no significant differences in number of stems, total basal area, average DBH or basal area of the howlers' top five food species, although average values for these variables were higher in the used plots. Plots used for feeding had significantly taller trees ( $U = 62.0$ ,  $P = 0.036$ ,  $n = 30$ ); they also had higher canopy connectivity (i.e. more arboreal pathways between trees) and higher species richness, differences that approach significance (connectivity:  $U = 66.5$ ,  $P = 0.056$ ; species richness:  $U = 68.0$ ,  $P = 0.067$ ;  $n = 30$ ).

### Discussion

Our results demonstrate that Mombacho's howling monkeys are able to use shade coffee plantations as their core ranging areas. Large trees of forest species were particularly important to foraging, and their abundance in La Luz results from a number of factors. Owners of large coffee plantations in Mombacho use a low-risk production strategy of less intensive management, coupled with temporary abandonment of coffee during price depressions and subsequent rehabilitation during price increases (J. C. Martínez Sánchez, pers. obs.); forest trees can grow to very large sizes, without being replaced by planted shade trees such as *Inga* or *Gliricidia*. A less diverse shade plantation comprising mostly *Inga* or *Gliricidia* probably would not provide sufficiently diverse resources throughout the year for howlers to survive. Secondly, relatively stable land tenure in the area has precluded shifts in management practices, and vegetation characteristics in the plantations have not changed much during the last 20 years (J. C. Martínez Sánchez, pers. obs.). The tree diversity in Finca La Luz is particularly high: the number of shade tree species rivals that of more rustic shade coffee plantations in Mexico (40–70 tree species; Perfecto *et al.*, 1996; Moguel & Toledo, 1999) and in coffee landscapes of El Salvador and Carazo, Nicaragua (36–80 species; Somarriba *et al.*, 2004).

Although two study groups did not rely heavily on secondary forest patches for foraging, we believe that the mosaic of forest fragments in Mombacho's coffee plantations is probably critical for the area's wildlife, particularly in areas with less diverse shade and for other species subject to higher hunting pressure. The long-term viability of managed shade systems may be threatened by the slow die-off of climax trees (Rolim & Chiarello, 2004); Mombacho's

**Table 1** Home range compositions and patterns of range use in relation to habitat type by howlers in Finca La Luz

	Group 1	Group 2	Group 3
<i>Home range characteristics</i>			
Home range size (ha)	20.3	13.7	17.3
% Shaded coffee	31.6	89.6	74.3
% Young regeneration	24.7	8.0	23.3
% Secondary forest	38.0	2.4	2.4
% Abandoned coffee	5.7	0	0
<i>Range use</i>			
% Location records in coffee	45.9	86.4	68.9
% Feeding bouts in coffee	38.4	84.2	74.3
Number of feeding trees	210	248	264
Number of key <sup>a</sup> feeding trees	19	28	24
% Feeding trees in coffee	42.2	61.7	73.5
% Key trees in coffee	57.9	85.7	91.6

<sup>a</sup>Key trees = trees accounting for > 1% of a group's total feeding time.

forest fragments are the only areas where tree recruitment proceeds naturally. Loss of the larger, older trees could severely impact the utility of the area's shade coffee plantations as wildlife habitat, although the howlers themselves may offset some loss through acting as seed dispersers (Estrada & Coates-Estrada, 1984; Julliot, 1997; Andresen, 2002). Howler seed dispersal in Mombacho could play an important role in long-term maintenance of tree species diversity, particularly through dispersal into unmanaged areas.

Howlers have been found in Mombacho's coffee plantations for decades (J. C. Martínez Sánchez, pers. obs.), and locals report increasing populations during the past 20 years (McCann *et al.*, 2003), suggesting that the monkeys are able to survive and reproduce in shade coffee plantations, apparently without ill effect. The foraging patterns of the Mombacho howlers were similar to conspecifics in less disturbed areas. Home ranges fell well within the range of variation for the species (typically 10–60 ha; Glander, 1978; Milton, 1980; Estrada, 1984), whereas average feeding tree size exceeds that in a dry forest reserve (average DBH 62.6; Chapman, 1988). Given Mombacho's isolation from other forested areas in south-western Nicaragua and RNVM's small size and low howler density, we do not believe that there is much howler migration into the shade coffee. Other primates were rare or absent in Mombacho (McCann *et al.*, 2003), even though capuchins occupy agricultural areas in nearby areas of Central America (Williams & Vaughan, 1998) and may be better able to exploit disturbed habitat (Sorensen & Fedigan, 2000). Throughout Nicaragua howlers are rarely hunted because of their unpalatable meat and lack of suitability for the pet trade (K. Williams-Guillén, pers. obs.), whereas capuchins and spider monkeys are preferred hunting targets. Hunting pressure rather than lack of suitable resources may best explain the rarity of other primates in Mombacho (McCann *et al.*, 2003).

Within the context of south-western Nicaragua, the Mombacho howlers are one of the largest remaining primate populations; managing the region's anthropogenic habitats so that they can support howlers may be critical for maintaining gene flow between isolated populations and allowing recolonization of forest fragments. The extent to which mantled howlers inhabit managed forest areas throughout their range is unknown, although they have been reported in agroforests in Mexico (Estrada & Coates-Estrada, 1996) and are found in shade coffee in several other areas of Nicaragua (K. Williams-Guillén, pers. obs.). That primates are not more common in agroforests throughout Central America (presuming the lack of reports reflects a lack of primates) probably results from shade management practices that make these areas unsuitable for primates (e.g. extensive use of planted trees and pruning) and over-hunting resulting in local extirpations. These factors can work synergistically: hunting can eliminate primates from forested areas (Mittermeier, 1991; Peres, 2001), while reduced matrix quality can prevent recolonization by primates (Gilbert & Setz, 2001). However, with controls on hunting and management of agroforests to maximize resources for

primates, these areas could comprise significant alternate habitat in an increasingly fragmented landscape.

To promote the integration of production and conservation goals, certification programs have been developed that reward sustainable practices and the maintenance of biodiversity in coffee plantations (Mas & Dietsch, 2004). Our results suggest that several criteria (see Rice & McLean, 1999) used in certification programs, such as tree species composition and size, are appropriate with respect to maintenance of resident wildlife populations. Certification programs could be improved by incorporating preservation of tree species particularly important to arboreal herbivores, such as *Ficus* spp., and ensuring that arboreal pathways are maintained to large trees. Of major certification programs, only Rainforest Alliance's includes prohibitions on hunting; controls on hunting should be more widely included to maintain biodiversity of large vertebrates in these landscapes. Although La Luz supports howlers and other species of mammals and birds, the plantation would not meet many programs' certification criteria. This situation underscores the importance of incorporating the areas surrounding the most rustic plantations into such market-based conservation initiatives, both to include wildlife habitat outside of compliant plantations and to encourage owners of surrounding agroforested lands to change management practices with an eye towards future inclusion.

Regional conservation plans such as the Mesoamerican Biological Corridor rely on wildlife use of anthropogenic habitat to connect reserves (Kaiser, 2001). The long-term persistence of the Mombacho howlers in the absence of explicit management plans is thus an occasion for some optimism: these areas can have conservation value. However, the extent to which other primates can make use of these matrix habitats, either as corridors of dispersal or as core habitat, remains unknown. Future research must address how agricultural areas can be incorporated into landscape-level management plans for Central American primates. The question is thus not one of whether wildlife can survive in anthropogenic habitats, but rather how can anthropogenic habitats be managed in order to maximize survival.

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## References

- Altmann, J. (1974). Observational study of behaviour: sampling methods. *Behaviour* **49**, 227–267.
- Andresen, E. (2002). Primary seed dispersal by red howler monkeys and the effect of defecation patterns on the fate of dispersed seeds. *Biotropica* **34**, 261–272.
- Atwood, J.T. (1984). A floristic study of Volcano Mombacho, Department of Granada, Nicaragua. *Ann. Mol. Bot. Gard.* **71**, 191–209.
- Calvo, L. & Blake, J. (1998). Bird diversity and abundance in two different shade coffee plantations in Guatemala. *Bird Conserv. Int.* **8**, 207–308.
- Carlo, T.A., Collazo, J.A. & Groom, M.J. (2004). Influences of fruit diversity and abundance on bird use of two shaded coffee plantations. *Biotropica* **36**, 602–614.
- Chapman, C.A. (1988). Patch use and patch depletion by the spider and howling monkeys of Santa Rosa National Park, Costa Rica. *Behaviour* **105**, 99–116.
- Croat, T. (1978). *Flora of Barro Colorado Island*. Stanford: Stanford University Press.
- Crockett, C.M., Brooks, R.D., Meacham, R.C., Meacham, S.C. & Mills, M. (1997). Recent observations of Nicaraguan primates and a preliminary conservation assessment. *Neotrop. Primates* **5**, 71–74.
- Crockett, C.M. & Eisenberg, J.F. (1987). Howlers: variations in group size and demography. In *Primate societies*: 54–68. Smuts, B.B., Cheney, D.L., Seyfarth, R.M., Wrangham, R.W. & Struhsaker, T.T. (Eds). Chicago: University of Chicago Press.
- Cruz-Lara, L.E., Lorenzo, C., Soto, L., Naranjo, E. & Ramírez-Marcial, N. (2004). Diversidad de mamíferos en cafetales y selva mediana de las canadas de la Selva Lacandona, Chiapas, México. *Acta Zool. Mex.* **20**, 63–81.
- Cuarón, A.D., de Grammont, P.C., Cortés-Ortiz, L., Wong, G. & Silva, J.C.S. (2003). *Alouatta palliata*. In *IUCN 2006. 2006 IUCN Red List of threatened species*. <http://www.iucnredlist.org>. Downloaded 16 January 2006.
- Donald, P.F. (2004). Biodiversity impacts of some agricultural commodity production systems. *Conserv. Biol.* **18**, 17–37.
- Estrada, A. (1984). Resource use by howler monkeys (*Alouatta palliata*) in the rain forest of Los Tuxtlas, Veracruz, Mexico. *Int. J. Primatol.* **5**, 105–131.
- Estrada, A. & Coates-Estrada, R. (1984). Fruit eating and seed dispersal by howling monkeys (*Alouatta palliata*) in the tropical rain forest of Los Tuxtlas, Mexico. *Am. J. Primatol.* **6**, 77–91.
- Estrada, A. & Coates-Estrada, R. (1996). Tropical rain forest fragmentation and wild populations of primates at Los Tuxtlas, Mexico. *Int. J. Primatol.* **17**, 759–783.
- Estrada, A., Coates-Estrada, R., Meritt, J. & Dennis, A. (1994). Non-flying mammals and landscape changes in the tropical rain forest region of Los Tuxtlas, Mexico. *Ecography* **17**, 229–241.
- Gallina, S., Mandujano, S. & Gonzalez-Romero, A. (1996). Conservation of mammalian biodiversity in coffee plantations of Central Veracruz, Mexico. *Agroforest. Syst.* **33**, 13–27.
- Ganzhorn, J.U. & Abraham, J.-P. (1991). Possible role of plantations for lemur conservation in Madagascar: food for folivorous species. *Folia Primatol.* **56**, 171–176.
- Gascon, C., Lovejoy, T.E., Bierregaard, R.O., Malcolm, J.R., Stouffer, P.C., Vasconcelos, H.L., Laurence, W.F., Zimmerman, B., Tocher, M. & Borges, S. (1999). Matrix habitat and species richness in tropical forest remnants. *Biol. Conserv.* **91**, 223–229.
- Gentry, A.H. & Vasquez, R. (1995). *A field guide to the families and genera of woody plants of Northwest South America*. Chicago: University of Chicago Press.
- Gilbert, K.A. & Setz, E.Z.F. (2001). Primates in a fragmented landscape: six species in central Amazonia. In *Ecology and conservation of a fragmented landscape: lessons from Amazonia*: 262–270. Bierregaard, R.O. Jr., Gascon, C., Lovejoy, T.E. & Mesquita, R. (Eds). New Haven: Yale University Press.
- Glander, K.E. (1978). Howling monkey feeding behavior and plant secondary compounds: a study of strategies. In *The ecology of arboreal folivores*: 561–574. Montgomery, G.G. (Ed.). Washington, DC: Smithsonian Institution Press.
- Greenberg, R., Bichier, P., Angon, C. & Reitsma, R. (1997a). Bird populations in shade and sun coffee in central Guatemala. *Conserv. Biol.* **11**, 448–459.
- Greenberg, R., Bichier, P. & Sterling, J. (1997b). Bird populations in rustic and planted shade coffee plantation of eastern Chiapas, Mexico. *Biotropica* **29**, 501–514.
- Horwich, R.H. (1998). Effective solutions for howler conservation. *Int. J. Primatol.* **19**, 579–598.
- Johnson, M.D. (2000). Effects of shade-tree species and crop structure on the winter arthropod and bird communities in a Jamaican shade coffee plantation. *Biotropica* **32**, 133–145.
- Julliot, C. (1997). Impact of seed dispersal by red howler monkeys *Alouatta seniculus* on the seedling population in the understorey of tropical rain forest. *J. Ecol.* **85**, 431–440.
- Kaiser, J. (2001). Bold corridor project confronts political reality. *Science* **293**, 2196–2199.
- Laurance, W.F., Lovejoy, T.E., Vasconcelos, H.L., Bruna, E.M., Didham, R.K., Stouffer, P.C., Gascon, C., Bierregaard, R.O., Laurance, S.G. & Sampaio, E. (2002). Ecosystem decay of Amazonian forest fragments: a 22-year investigation. *Conserv. Biol.* **16**, 605–618.
- Leighton, M. & Leighton, D.R. (1982). The relationship of size of feeding aggregate to size of food patch: howler monkeys (*Alouatta palliata*) feeding in *Trichilia cipo* fruit trees on Barro Colorado Island. *Biotropica* **14**, 81–90.
- Mas, A. & Dietsch, T.V. (2004). Linking shade coffee certification to biodiversity conservation: butterflies and birds in Chiapas, Mexico. *Ecol. Appl.* **14**, 642–654.
- McCann, C., Williams-Guillén, K., Koontz, F.W., Roque Espinoza, A.A., Martínez Sánchez, J.C. & Koontz, C. (2003). Shade coffee plantations as wildlife refuge for mantled howler monkeys (*Alouatta palliata*) in Nicaragua.

- In *Primates in fragments*: 321–341. Marsh, L.K. (Ed.). New York: Kluwer Academic Press.
- Milton, K. (1980). *The foraging strategy of howler monkeys: a study in primate economics*. New York: Columbia University.
- Mittermeier, R. (1991). Hunting and its effects on wild primate populations in Suriname. In *Neotropical wildlife use and conservation*: 93–107. Robinson, J.G. & Redford, K.H. (Eds). Chicago: University of Chicago Press.
- Moguel, P. & Toledo, V.M. (1999). Biodiversity conservation in traditional coffee systems of Mexico. *Conserv. Biol.* **13**, 11–21.
- Nestel, D., Dickschen, F. & Altieri, M.A. (1993). Diversity patterns of soil macro-Coleoptera in Mexican shaded and unshaded coffee agroecosystems: an indication of habitat perturbation. *Biodiv. Conserv.* **2**, 70–78.
- Neville, M.K., Glander, K.E., Braza, F. & Rylands, A.B. (1988). The howling monkeys, genus *Alouatta*. In *Ecology and behavior of neotropical primates*: 349–453. Mittermeier, R.A., Coimbra-Filho, A. & da Fonseca, G.A.B. (Eds). Washington, DC: World Wildlife Fund.
- Nowak, D.J., Rowntree, R.A., McPherson, E.G., Sisinni, S.M., Kerkmann, E.R. & Stevens, J.C. (1996). Measuring and analyzing urban tree cover. *Landscape Urb. Plann.* **36**, 49–57.
- Ostro, L.E.T., Young, T.D., Silver, S.C. & Koontz, F.W. (1999). A geographic information system method for estimating home range size. *J. Wildl. Mgmt.* **63**, 748–755.
- Peres, C.A. (2001). Synergistic effects of subsistence hunting and habitat fragmentation on Amazonian forest vertebrates. *Conserv. Biol.* **15**, 1490–1505.
- Perfecto, I., Rice, R.A., Greenberg, R. & Van der Voort, M.E. (1996). Shade coffee: a disappearing refuge for biodiversity. *BioScience* **46**, 598–608.
- Perfecto, I. & Snelling, R. (1995). Biodiversity and the transformation of a tropical agroecosystem: ants in coffee plantations. *Ecol. Appl.* **5**, 1084–1097.
- Perfecto, I. & Vandermeer, J. (2002). Quality of agroecological matrix in a tropical montane landscape: ants in coffee plantations in southern Mexico. *Conserv. Biol.* **16**, 174–182.
- Perfecto, I., Vandermeer, J., Hanson, P. & Cartín, V. (1997). Arthropod biodiversity and the transformation of a tropical agro-ecosystem. *Biodiv. Conserv.* **6**, 935–945.
- Philpott, S.M. & Dietsch, T. (2003). Coffee and conservation: a global context and the value of farmer involvement. *Conserv. Biol.* **17**, 1844–1846.
- Raboy, B.E., Christman, M.C. & Dietz, J.M. (2004). The use of degraded and shade cocoa forests by endangered golden-headed lion tamarins *Leontopithecus chrysomelas*. *Oryx* **38**, 75–83.
- Reid, F.A. (1997). *A field guide to the mammals of Central America and Southeast Mexico*. New York: Oxford University Press.
- Rice, P.D. & McLean, J.R. (1999). *Sustainable coffee at the crossroads*. White paper, Consumer's Choice Council.
- Robertson, G.P. & Swinton, S.M. (2005). Reconciling agricultural productivity and environmental integrity: a grand challenge for agriculture. *Front. Ecol. Environ.* **3**, 38–46.
- Rolim, S.G. & Chiarello, A.G. (2004). Slow death of Atlantic forest trees in cocoa agroforestry in southeastern Brazil. *Biodiv. Conserv.* **13**, 2679–2694.
- Salas, J.B. (1993). *Arboles de Nicaragua*. Instituto Nicaragüense de Recursos Naturales y del Ambiente, Managua, Nicaragua.
- Somarriba, E., Harvey, C.A., Samper, M., Anthony, F., González, J., Staver, C. & Rice, R.A. (2004). Biodiversity conservation in neotropical coffee (*Coffea arabica*) plantations. In *Agroforestry and biodiversity conservation in tropical landscapes*: 198–226. Schroth, G., da Fonseca, G.A.B., Harvey, C.A., Gascon, C., Vasconcelos, H.L. & Izac, A.-M.N. (Eds). Washington, DC: Island Press.
- Sorensen, T.C. & Fedigan, L.M. (2000). Distribution of three monkey species along a gradient of regenerating tropical dry forest. *Biol. Conserv.* **92**, 227–240.
- Stoner, K.E. (1996). Habitat selection and seasonal patterns of activity and foraging of mantled howling monkeys (*Alouatta palliata*) in northeastern Costa Rica. *Int. J. Primatol.* **17**, 1–30.
- Tejeda-Cruz, C. & Sutherland, W.J. (2004). Bird responses to shade coffee production. *Anim. Conserv.* **7**, 169–179.
- Vandermeer, J., van Noordwijk, M., Anderson, J., Ong, C. & Perfecto, I. (1998). Global change and multi-species agroecosystems: concepts and issues. *Agric. Ecosys. Environ.* **67**, 1–22.
- Vandermeer, J. & Perfecto, I. (1997). The agroecosystem: a need for the conservation biologist's lens. *Conserv. Biol.* **11**, 591–592.
- Williams, H.E. & Vaughan, C. (1998). White-faced monkey (*Cebus capucinus*) ecology and management in neotropical agricultural landscapes during the dry season. *Rev. Biol. Trop.* **49**, 1199–1208.
- Williams-Guillén, K. (2003). *The behavioral ecology of mantled howling monkeys (Alouatta palliata) living in a Nicaraguan shade coffee plantation*. PhD thesis, New York University, New York.
- Wunderle, J.M.J. & Latta, S.C. (1996). Avian abundance in sun and shade coffee plantations and remnant pine forest in the Cordillera Central, Dominican Republic. *Ornitol. Neotrop.* **7**, 19–34.

## Supplementary material

The following material is available for this article online:

**Table S1** Tree species composition of shade trees with DBH  $\geq$  20 cm in Finca La Luz.

This material is available as part of the online article from <http://www.blackwell-synergy.com>