CHAPTER EIGHTEEN

Primates in Agroecosystems: Conservation Value of Some Agricultural Practices in Mesoamerican Landscapes

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INTRODUCTION

While there is a general perception that agricultural activities are the principal threat to biodiversity in the tropics (Donald, 2004; Henle *et al.*, 2004a,b), recent assessments suggest that some agroecosystems in fragmented landscapes may favor the persistence of diverse assemblages of animal species

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(Vandermeer, 2003; Schroth *et al.*, 2004). Agroecosystems, covering more than one-quarter of the global land area, or almost 5 billion hectares, are ecosystems in which people have deliberately selected crop plants and livestock animals to replace the natural flora and fauna (Altieri, 2004). There are highly simplified agroecosystems (e.g., pasturelands, intensive cereal cropping, and monocultures), and there are also others that support high biodiversity in the form of polycultures and/or agroforestry patterns (Pimentel *et al.*, 1992; Moguel and Toledo, 1999; Vandermeer, 2003; Henle *et al.*, 2004a,b; Melbourne *et al.*, 2004; Schroth *et al.*, 2004).

Recent evidence suggests that some agroecosystems may be important in sustaining vertebrate biodiversity in human modified tropical landscapes, as they may provide temporary habitat, may function as stepping stones, and may increase area of vegetation and availability of potential resources, among other benefits, for isolated segments of populations of a broad spectrum of animal species (Estrada *et al.*, 1993, 1994; Villaseñor and Hutto, 1995; Rice and Greenberg, 2000; Estrada and Coates-Estrada, 2000, 2002a,b; Perfecto and Armbrecht, 2003; Daily *et al.*, 2003; Greenberg, 2004; Harvey *et al.*, 2004). In the case of primates, there are a few reports indicating presence of primates in agroecosystems. For example, cabruca cacao in Brazil has attracted attention because of its ability to harbor primates such as the golden-headed lion tamarin (*Leontopithecus chrysonelis*), an endangered species (Rice and Greenberg, 2000). Similarly in Gulung Palung National Park in Kalimantan, primates such as leaf monkeys (*Presbytis rubicunda*) and gibbons (*Hylobates agilis*) are found in agroforests (Salafsky, 1993). Michon and de Foresta (1995) report the presence of seven primate species: macaques, leaf monkeys, gibbons, and siamangs (*Hylobates syndactylus*) in rubber (*Hevea brasiliensis*) and dammar (*Shorea javanica*) agroforests, and five species in durian (*Durio zibethinus*) agroforests in Sumatra and noted that their density was similar to that in primary forest. In Costa Rica, howler monkeys (*Alouatta palliata*) have been found in shaded coffee plantations (Somarriba *et al.*, 2004), and in Los Tuxtlas, Mexico, howler (*A. palliata*) and spider (*Ateles geoffroyi*) monkeys have been observed to be present in forest-shaded cacao and coffee plantations (Estrada *et al.*, 1994; Estrada and Coates-Estrada, 1996).

Extending from southern tropical Mexico to the Colombian border of Panama, Mesoamerica harbors the northernmost representatives of the primate order in the American continent. Primate species diversity is represented by 22 taxa. These belong to three families (Callithrichidae, Cebidae, and Atelidae), six genera (*Sanguinus, Aotus, Alouatta, Ateles, Saimiri,* and *Cebus*), and eight major species (see Rylands *et al.*, this volume; Rodriguez-Luna *et al.*, 1996; Rowe, 1996; Nowak, 1999). Major proximate threats to primate habitats in the region are agricultural activities aimed at building up pasturelands for cattle-raising and at expanding crop-land to raise food crops. General deforestation rate in the region is exceedingly high, estimated at 440,000 ha per year (Sader *et al.*, 1999; FAO, 2000), and current estimates (see Estrada *et al.*, this volume) indicate that about 70% of the original forest cover present in the region has been lost as a result of human activity.

While extensive pastureland for cattle grazing dominates fragmented landscapes in Mesoamerica, many of these also harbor various types of arboreal and non arboreal agroecosystems such as forest-shaded and tree-shaded (trees planted by man) coffee (*Coffea arabica*), cacao (*Theobroma cacao*), and cardamom (*Eletteria cardamomum*; Zingiberaceae), unshaded arboreal crops (e.g., allspice, *Pimienta dioica*, citrus, *Citrus* spp.), and non arboreal cultivars such as bananas, *Musa* spp., and corn, among others (FAO, 1999, 2001). Many of these landscapes also harbor thousands of meters of linear strips of live fences (single or double rows of trees) planted by local people to delimit pastures and agricultural lots (Harvey *et al.*, 2004). In Central American landscapes dominated by cattle production, live fences occur between 49% and 89% of all farms, with a mean density of 0.14 km of live fence per ha of farmland (Harvey *et al.*, submitted). These land-use practices have resulted in varied and highly heterogeneous landscapes in which natural, semi-natural, and introduced patches of vegetation coexist.

In this paper, we explore the value of some agricultural practices for the persistence of primate population in human-modified landscapes in Mesoamerica. We present results from surveys of primate populations in agroecosystems in fragmented landscapes in Los Tuxtlas, Mexico, in Lachuá, Guatemala, and in three localities (Central Pacific, Cañas, and Rio Frio) in Costa Rica. Data were used to determine the types of agroecosystems in which primate populations are present and the species involved, to assess how primate population parameters such as density, group size, and immature to adult female ratios vary among agroecosystems and with respect to those of populations of the same species in extensive and in isolated forest remnants. We also examined data from an ongoing study of the feeding ecology of howler monkeys (*A. palliata*) living in a cacao plantation in the lowlands of the Tabasco, Mexico, with the aim of assessing how primates sustain themselves in such agroecosystems.

METHODS

Los Tuxtlas, Veracruz, Mexico

In the region of Los Tuxtlas, in southern Veracruz, Mexico, we focused our investigation on a 300 km^2 fragmented landscape by the Gulf of Mexico coast (95°00′W, 18°25′N; mean annual precipitation 4900 mm; altitudinal gradient sea level to 550 m.a.s.l.) (Figure 1). In this landscape, forest fragments coexist in a mosaic of vegetation consisting of pastures lands (the dominant vegetation) with interdispersed seasonal non arboreal (corn, jalapeño chili pepper, beans, tobacco, and bananas) and perennial arboreal (cacao, coffee, oranges, and allspice—*P. dioica*, Myrtaceae) crops. Both cacao and coffee, and mixed crops of these two plants, are grown under the shade of rain forest arboreal vegetation or less commonly under the shade of coconut palms and other plants, or under the shade of banana shrubs and planted trees. In this landscape, pasturelands harbor extensive networks of live fences, which consist of live posts of *Bursera simaruba* (Burseraceae) and *Gliricidia sepium* (Fabaceae), among other species, planted by the local inhabitants to hold barbed wire to delimit boundaries of properties.

Presence or absence of howler (*A. palliata*) and spider monkeys (*A. geoffroyi*) was investigated in 132 agricultural sites representing 12 types of agroecosystems: cacao shaded by rain forest vegetation (10 sites), cacao shaded by legume trees (6 sites), and cacao shaded by coconut and other trees and banana (5 sites), coffee shaded by forest vegetation (10 sites), mixed cacao/coffee under the shade of forest vegetation (8 sites), citrus (10 sites), allspice (*P. dioica*) (10 sites), mango (*Mangifera indica*; 8 sites), bananas (10 sites), mixed mango/citrus/banana (5 sites), and young live fences (DBH of posts <30 cm; 25 sites of 5 km in length each) and old (DBH >30 cm; 25 sites of 5 km in length each) present in this landscape (tree species: *B. simaruba*, *G. sepium*, *Ficus* spp.). Data on population parameters were gathered following standardized sampling protocols (National Research Council, 1992; Wilson *et al.*, 1996) in some of the forest-shaded cacao, coffee, and mixed cacao/coffee plantations in which primates were present. Population data were also collected for primates found in forest fragments in the same countryside, and in a natural

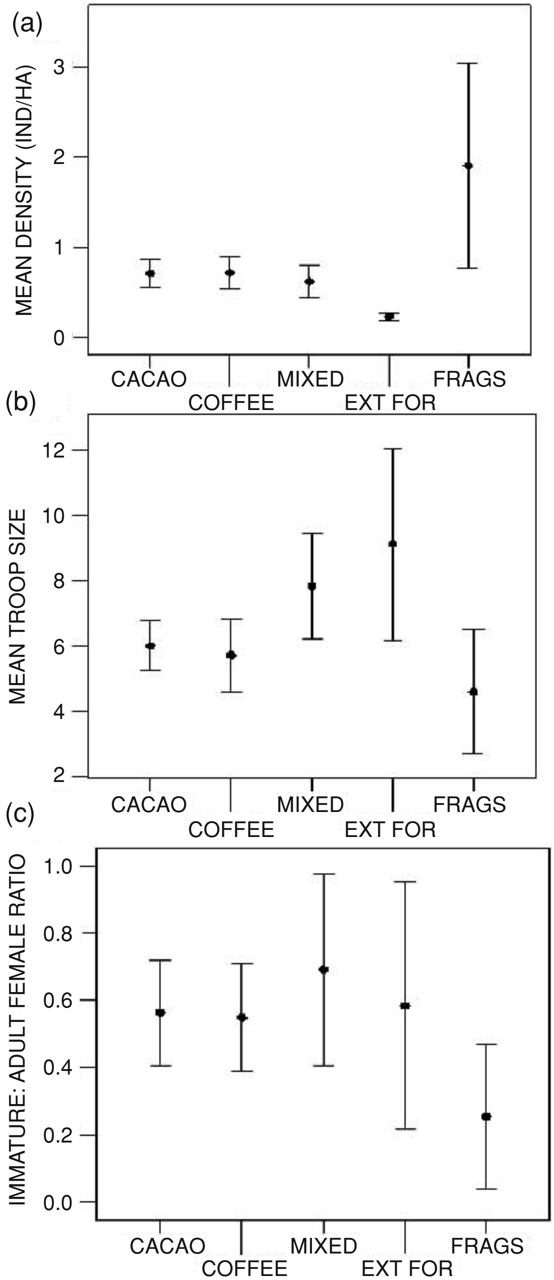

Figure 1. Mean (±SD) population density (a), mean troop size (b), and mean immature to adult female ratio (c), in populations of mantled howler monkeys (*Alouatta palliata*) residing in shaded (rain forest vegetation) cacao, coffee and mixed (cacao and coffee) agroecosystems, in extensive forests (>100 km^2; "EXT FOR") and in forest fragments (<10 km^2; "FRAGS") in Los Tuxtlas, Mexico.

protected area (15,000 ha) abutting the landscape. Interviews with the owners of the farms provided general information on whether the presence of the primates in the plantations had a neutral (no damage) or negative (damage) impact upon the cultivated fruit trees (e.g., cacao, coffee, bananas, and citrus).

Lachuá, Guatemala

In Guatemala, surveys of black howler monkeys (*Alouatta pigra*) were conducted, during 2002–2003 in cardamom plantations (*E. cardamomum*; Zingiberaceae) growing both under the shade of rain forest vegetation and in forest fragments not being used for agricultural purposes in a 230 km^2 fragmented landscape in the ecoregion of Lachuá (15°59′N, 90°36′W; mean annual precipitation 2252 ± 328 mm; altitudinal gradient 150–300 m.a.s.l.). Mean values for the demographic parameters of interest were compared with the overall means of eight populations of *A. pigra* existing in extensive forest tracts (>1000 ha; see Van Belle, this volume).

Costa Rica

Squirrel, howler, and capuchin monkeys were surveyed in agroecosystems present in fragmented landscapes in three distinct geographic locations. Population parameters for these primates were estimated in these habitats and in forest fragments. In the Central Pacific region of Costa Rica, one study area was a 540 km^2 landscape where the national park Manuel Antonio is located (9°59′N, 84°5′W and 9°43′N, 84°12′W; mean annual precipitation 3860 mm; altitudinal gradient sea level to 500 m.a.s.l.). In this landscape, forest fragments are surrounded by pastures and interdispersed with patches of second growth are forestry (*Tectona grandis* and *Gmelina arborea*) and African palm plantations (*Eliaeis guinneensis*), and other arboreal monocultures (e.g., bananas and mangos). Squirrel (*Saimiri oerstedii citrinellus*) and capuchin (*Cebus capucinus*) monkeys were found in some of these plantations.

Another study area was located in Cañas, province of Guanacaste (10°22′N and 85°08′W; annual precipitation varies from 1000 to 2500 mm; altitude 100–250 m.a.s.l.). The study site was a 100 km^2 fragmented landscape (original forest cover was tropical dry forest) which along with pastures also harbored patches of forestry (*Albizia saman* and *T. grandis*) and fruit plantations (e.g., banana—*Musa* spp., mango—*M. indica*, guayaba—*Psidum guajava*, guaba—*Inga* spp., among others), as well as networks of live fences (primarily live posts of *Bursera simarouba* (54.2% of the trees), *Pachiraquinat* (27.6% of the trees, *Ficus* spp. (3.8% of the trees), *G. sepium* (1.9% of trees), and *Tabebuia rosea* (1.9%), among others). The landscape is dominated by cattle production, with pastures covering 48.4% of the landscape and the remaining forest patches and riparian forests covering 23.3% of the landscape; the remaining area is under crop production (principally sugarcane) or small forest plantations. Howler monkeys (*A. palliata*) were present in this landscape and were observed opportunistically during an in-depth study of other taxa (birds, bats, dung beetles, and butterflies in this area).

A third study area consisted of another 100 km^2 fragmented landscape located in Rio Frio, Saraquipí, province of Heredia (10°22′N and 83°54′W; mean annual precipitation 3962 mm; altitude 80–250 m.a.s.l.) whose original vegetation was tropical wet forest. Pastures dominated the landscape (accounting for 45% of the landscape), but also present were forest fragments, riparian forests, fruit-tree groves (mainly *Citrus* sp.) palmito plantations, live fences (principally *Erythrina costarricensis* and *G. sepium*), and forestry plantations. Forest fragments and riparian forests together account for 20.7% of the landscape, but most of these are small ($<$10 ha).

Comalcalco, Tabasco, Mexico

The feeding ecology of a small population of mantled howler monkeys (*A. palliata*) was investigated for a 9-month-long period in 2003, in a 12 ha cacao plantation located in Comalcalco (18°26′N, 93°32′W; mean annual precipitation 2700 mm, altitude 10 m.a.s.l.), Tabasco, Mexico. Cacao trees in this plantation were mainly shaded by trees of *Pithecelobium saman* (Fabaceae) and *G. sepium* (Fabaceae) planted by the owners of the plantation about 50 years earlier. Individuals of another 28 tree species (e.g., *Ficus* spp., *M. indica*, *Cedrela odorata*, etc.) providing shade to the cacao trees were present in the plantation and these became established by planting by humans or via seed dispersal by birds, bats, and/or the primates that exist there. Observations of the feeding behavior of the howler monkey troop were conducted following standardized procedures (see Estrada *et al.*, 1999; Garcia del Valle *et al.*, 2003; Fuentes *et al.*, 2003; Muñoz, 2004 for details).

RESULTS

Los Tuxtlas, Mexico

In Los Tuxtlas, the presence of primates was detected in 8 of the 12 types of agroecosystems investigated. In these, we counted 184 monkeys, of which 73% were howler monkeys and 27% were spider monkeys. Howler and spider monkeys were present in 38% and in 16% of the agroecosystem sites we surveyed ($N = 82$; excluding live fences), respectively (Table 1). Both howler and spider monkeys were detected in the shaded cacao, coffee, and mixed plantations, in the mango/citrus/banana plantations and in old live fences. In addition, howler monkeys were detected in cacao plantations shaded by coconut palms or shaded by other trees and bananas, and in banana plantations (Table 1). No primates were found residing in the citrus, allspice, and mango groves we surveyed, but in a few instances we observed some individuals moving through sections of these groves that were adjacent to the forest where they resided. Presence of howler and of spider monkeys was observed only in old live fences (Table 1). According to the information provided to us by the owners of the farms, the howler and spider monkeys cause no damage to the cacao and coffee plants. However, crop damage was reported in the banana, mango, citrus, and allspice plantations (Table 1).

Comparison of Demographic Traits

A. palliata

Mean howler monkey population densities in the forest-shaded cacao (0.71 ± 0.15 individuals/ha), coffee (0.71 ± 0.18 individuals/ha), and mixed cacao/coffee (0.64 ± 0.21 individuals/ha) plantations, were significantly higher than in extensive forests (0.23 + 0.05 individuals/ha) (t-test, $p < 0.01$ in all cases; Figure 1), but significantly lower than in forest fragments (1.9 ± 1.13 individuals/ha; t-test, $p < 0.01$ in all cases; Figure 1a). Mean troop size was higher in the howler populations living in extensive forests (9.1 ± 2.93 individuals; $N = 20$ troops) than in cacao (6.0 ± 0.75 individuals; $N = 8$ troops) and coffee (6.0 ± 0.82 individuals; $N = 7$ troops) agroecosystems (t-test, $p < 0.01$). This mean value did not differ with respect to that in mixed cacao/coffee plantations (8.3 ± 8.68 individuals; $N = 6$ troops) (Figure 1), but

Table 1. Agroecosystems surveyed for presence of primates in Los Tuxtlas, Mexico. Impact (0) = neutral, (M) = minor, (−) = negative (e.g., crop/plant damage)

Agroecosystem	Condition	Number of sites surveyed	*Alouatta palliata* sites present	*Ateles geoffroyi* sites present	Impact
Los Tuxtlas, Mexico					
Cacao	Forest shade	10	6	4	(0)
Cacao	Legume trees shade	6	3	1	(0)
Coffee	Forest shade	10	6	2	(0)
Mixed (cacao/coffee)	Forest shade	8	6	3	(0)
Cacao	Coconut/banana shade	5	3	0	(0)
Citrus	Not shaded	10	0	0	(M)
Allspice	Not shaded	10	0	0	(M)
Mango	Not shaded	8	0	0	(M)
Mango/citrus/bananas	Not shaded	5	3	1	(−)
Bananas	Not shaded	10	4	2	(−)
Total		82	31	13	
Percentage of sites with presence			38	16	
Young live fences (mean DBH <25 cm)		25	0	0	(0)
Old live fences (mean DBH >25 cm)		25	12	3	(0)
Total sites with presence		132	43	16	
Total agroecosystems with presence			8	7	

mean howler monkey troop size was significantly higher in the agroecosystems and in the extensive forest than in the fragments (4.6 ± 1.92 individuals; $N = 37$ troops; t-test, $p < 0.01$ in all cases) (Figure 1b). Mean immature to adult female ratios were 0.56 ± 0.15 in cacao, 0.55 ± 0.16 in coffee, and 0.58 ± 0.24 in mixed cacao/coffee. While these values did not differ from that in extensive forests (0.52 ± 0.37; Figure 1c), they were significantly higher (t-test, $p < 0.01$ in all cases) than the mean value in forest fragments (0.25 ± 0.21) (Figure 1).

A. geoffroyi

Spider monkeys live in small temporary subgroups of unstable composition, which are part of larger groups or communities. Because of the fusion–fission nature of their social organization, it is rare to see all members of the community in the same location, suggesting that it is not easy to make generalizations on density and/or subgroup size for this primate species (Kinzey, 1997). Bearing this in mind, the mean values we present next for population density, subgroup size, and immature to adult female ratios are gross estimates. Mean population density estimates for spider monkeys in agroecosystems (0.36 ± 0.35 individuals/ha in cacao, 0.45 ± 0.07 individuals/ha in coffee, and 0.68 ± 0.02 individuals/ha in mixed cacao/coffee) did not differ from those in extensive forests (0.37 ± 0.28 individuals/ha), but were significantly higher than those in forest fragments (0.04 ± 0.03 individuals/ha; t-test, $p < 0.01$ in all cases; Figure 2a). Mean spider monkey subgroup size (5.3 ± 1.52 individuals in cacao, $N = 6$ subgroups; 5.0 ± 1.41 individuals in coffee, $N = 5$ subgroups; 6.6 ± 1.52 individuals in mixed cacao/coffee, $N = 5$ subgroups; 6.0 ± 1.54 individuals in extensive forests, $N = 30$ subgroups; 5.0 ± 2.62 individuals in fragmented forests, $N = 10$ subgroups) did not differ statistically among habitats, and the only noticeable feature was the large variations in spider monkey mean subgroup size in the forest fragments compared to the smaller variation found in agroecosystems and extensive forests (Figure 2b). Mean immature to adult female ratios (0.72 ± 0.25 in cacao, 0.67 ± 0.29 in coffee, and 0.72 ± 0.25 in mixed cacao/coffee) did not differ from the mean value in extensive forests (0.88 ± 0.27), but they were significantly higher (t-test, $p < 0.05$ in all cases) than in forest fragments (0.19 ± 0.07) (Figure 2c).

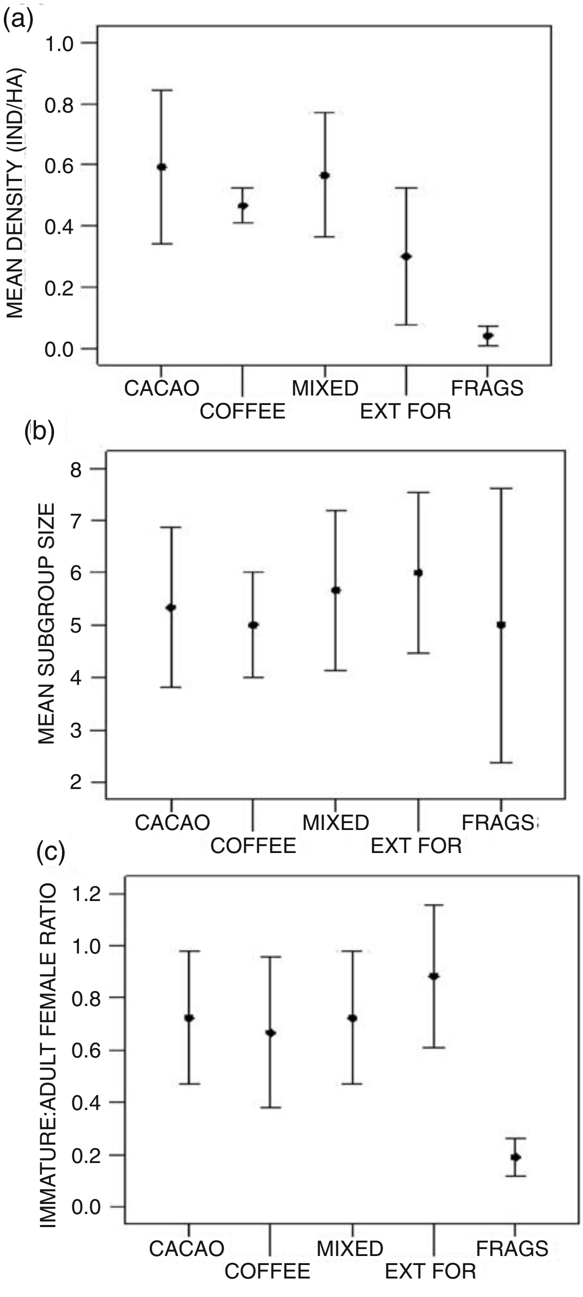

Figure 2. Mean (±SD) population density (a), mean troop size (b), and mean immature to adult female ratio (c), in populations of spider monkeys (*Ateles geoffroyi*) residing in shaded (rain forest vegetation) cacao, coffee and mixed (cacao and coffee) agroecosystems, in extensive forests (>100 km^2; "EXT FOR") and in forest fragments (<10 km^2; "FRAGS") in Los Tuxtlas, Mexico.

Lachuá, Guatemala

A. pigra

In Lachuá, Guatemala, howler monkey presence was recorded in forest-shaded cardamom and in coffee agroecosystems, but demographic data were collected only in the former habitat. Mean population density for black howler monkeys in cardamom agroecosystems was significantly smaller (0.59 ± 0.86 individuals/ha) than in forest fragments (2.48 ± 3.76 individuals/ha) (*t*-test, $p < 0.01$), but did not differ from mean values in extensive forests (0.21 ± 0.10 individuals/ha) (Figure 3a). Mean troop size in the cardamom plantations (5.36 ± 1.75 individuals; $N = 11$ troops) did not differ from mean values in forest fragments (5.00 ± 1.73 individuals; $N = 9$ troops), but it was significantly smaller (*t*-test, $p = 0.01$) than in extensive forests (6.54 ± 1.20 individuals; $N = 120$ troops) (Figure 3b). On average, mean immature to adult female ratios were higher in the cardamom (1.08 ± 0.55) and extensive forests (1.09 ± 1.40) than in forest fragments (0.85 ± 0.65), but the values in the cardamom plantations did not differ statistically from those in extensive and in fragmented forests (Figure 3c).

Costa Rica

In the fragmented landscape of the Central Pacific region, surveys showed the presence of squirrel and capuchin monkeys in fruiting-tree groves and in African palm plantations. Estimated mean densities for squirrel monkeys in the former habitat were 0.42 ± 0.14 individuals/ha, while in the latter was 0.14 ± 0.08 individuals/ha. These values did not differ from those in forest fragments (0.35 ± 0.24 individuals/ha) (Kruskal–Wallis test, $p = 0.17$) (Figure 4a). Mean troop size in the fruit and palm plantations was 19.0 ± 1.41 and 22.6 ± 9.87 individuals, respectively. These values were within the range of those in forest fragments (29.14 ± 13.9 individuals; Kruskal–Wallis test, $p = 0.35$) (Figure 4b). Mean immature to adult female ratios were 0.18 ± 0.03 in the fruit and 0.14 ± 0.05 in the palm plantation. These values did not differ from those in forest fragments (0.16 ± 0.06; Kruskal–Wallis test, $p = 0.44$) (Figure 4c).

In the case of capuchin monkeys, mean density was 0.63 + 0.11 individuals/ha in the fruit and 0.10 ± 0.01 in the palm plantations, but values did not differ from those in forest fragments (0.31 ± 0.26) (Figure 5a). Mean troop size in the fruit and palm plantations was 12.5 ± 2.12 and 7.6 ± 1.53 individuals, respectively. The values in the fruit plantations fell within the range of those

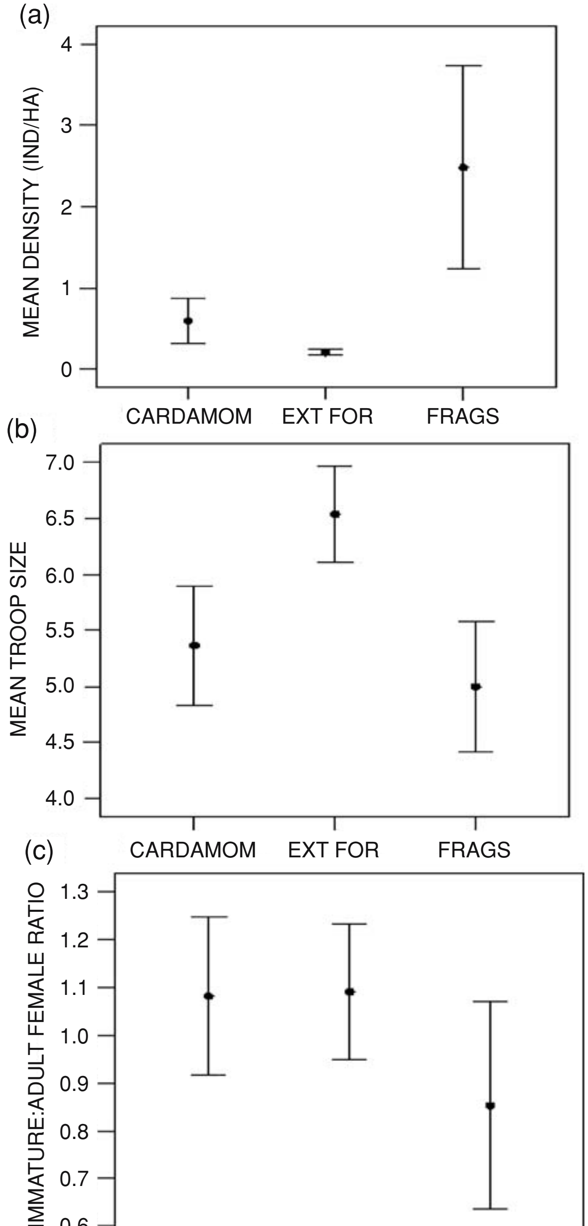

Figure 3. Mean (±SD) population density (a), mean troop size (b), and mean immature to adult female ratio (c), in populations of black howler monkeys (*Alouatta pigra*) living in cardamom agroecosystems shaded by rain forest vegetation, in extensive forests (>100 km^2; "EXT FOR") and in forest fragments (<10 km^2; "FRAGS") in Lachuá, Guatemala.

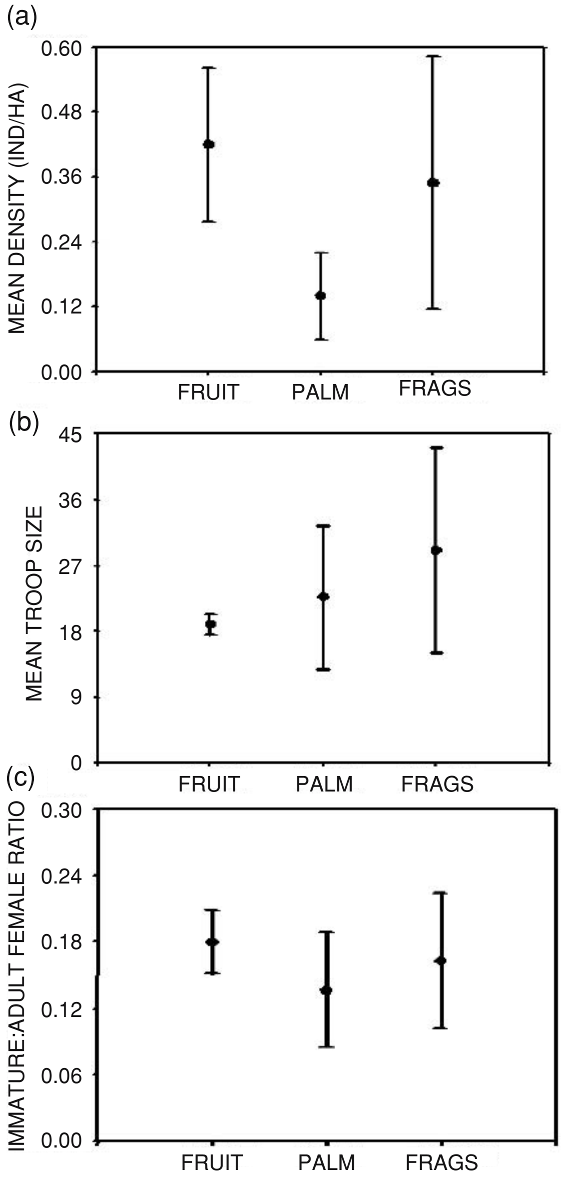

Figure 4. Mean (±SD) population density (a), mean troop size (b), and mean immature to adult female ratio (c), in populations of squirrel monkeys (*Saimiri oerstedii*) in fruit (FRUIT) and palm (PALM) agroecosystems and in forest fragments (FRAGS <10 km^2) in Central Pacific Costa Rica.

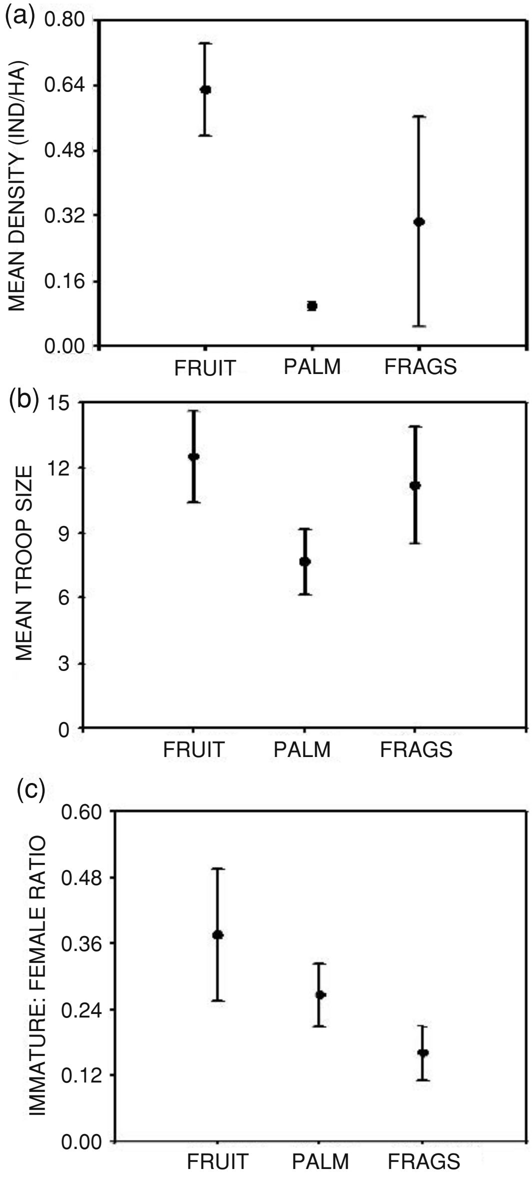

Figure 5. Mean (±SD) population density (a), mean troop size (b), and mean immature to adult female ratio (c), in populations of capuchin monkeys (*Cebus capucinus*) in fruit (FRUIT) and palm (PALM) agroecosystems and in forest fragments (FRAGS <10 km^2) in Central Pacific Costa Rica.

in forest fragments (11.1 ± 2.70 individuals; Kruskal–Wallis test, $p = 0.7$), but those in the palm plantations were significantly lower ($p < 0.05$) (Figure 5b). Mean immature to adult female ratios were 0.38 ± 0.12 in the fruit and 0.27 ± 0.06 in the palm plantation. In the forest fragments, mean values were 0.16 ± 0.05. The three habitats differed significantly in this measure (Kruskal–Wallis test, $p = 0.005$) (Figure 5c).

In Cañas, howler monkeys were found not only in forest fragments, but also in fruiting tree groves, forestry plantations, and in live fences. Mean density values in the first two agroecosystems were 0.55 ± 0.07 and 0.39 ± 0.16 individuals/ha, respectively, whereas in forest fragments the mean density was 0.48 ± 0.14 individuals/ha; habitats did not differ in this measure (Kruskal–Wallis test, $p = 0.09$) (Figure 6a). Mean troop size was 5.5 ± 0.71 and 8.5 ± 0.71 individuals at the fruit and at the forestry plantations, respectively. In the forest fragments, mean troop size was 7.8 ± 2.1 individuals. These values did not differ among habitats (Kruskal–Wallis test, $p = 0.21$) (Figure 6b). Mean immature to adult female ratios were 0.37 ± 0.05 and 0.41 ± 0.04 in the fruit and forestry plantation, respectively, and these were higher than in forest fragments (0.28 ± 0.08; Kruskal–Wallis test, $p = 0.03$) (Figure 6c). In Rio Frio, howler monkeys were observed in live fences and forest fragments; capuchins, on the other hand, were only found in forest fragments.

Howler Monkey Feeding Ecology in a Cacao Plantation, Comalcalco, Mexico

The howler population living in the 12-ha cacao plantation consisted of a single troop of 24 individuals (5 adult males, 11 adult females, 6 juveniles, and 2 infants; estimated population density was 2.0 individuals/ha). This troop (part of a larger howler monkey population once existing in the area when it was forested) has been living in the cacao plantation for as long as the plantation has been in existence (about 50 years; owners, pers. comm.). The 9-month-long investigation of the feeding ecology of the howler monkey troop in the cacao plantation revealed that howler monkeys did not use the *T. cacao* leaves, fruit or flowers as food. Instead they concentrated their foraging on the leaves, fruits, and flowers of 16 plant species (11 plant families), that together with other tree species, provided the shade to the cacao trees. Thirteen of the plant species used by the howlers as source of food were trees (nine botanical families), and the others were a liana and two epiphytes (Table 2). Three tree species, *Ficus*

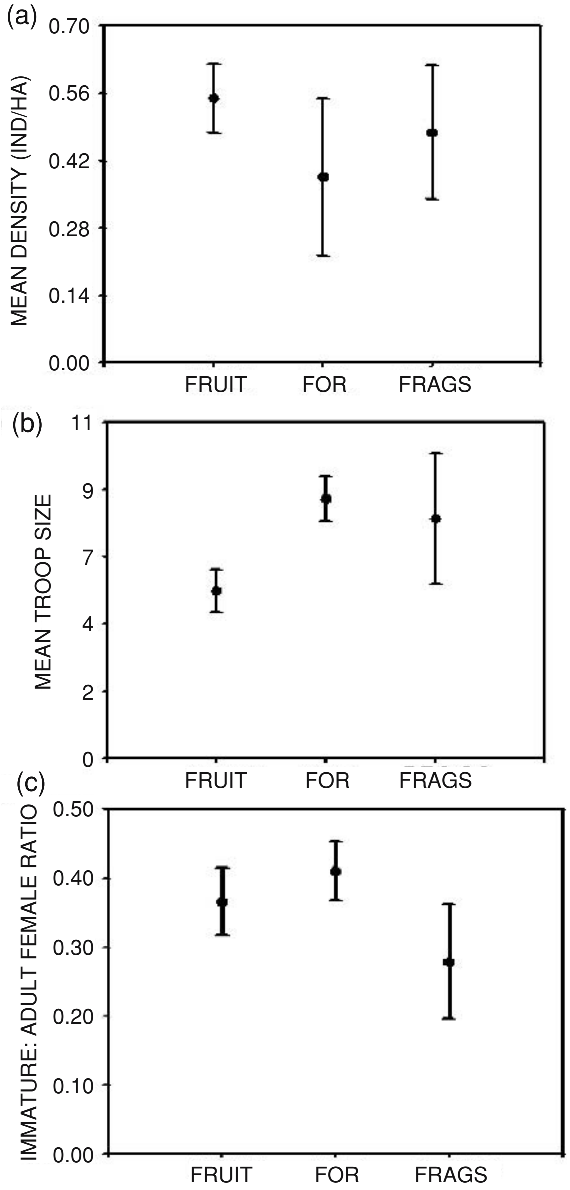

Figure 6. Mean (±SD) population density (a), mean troop size (b), and mean immature to adult female ratio (c), in populations of howler monkeys (*Alouatta palliata*) in fruit (FRUIT) and forestry (FOR) plantations and in forest fragments (FRAGS <10 km^2) in Cañas, Costa Rica.

Table 2. Plant species used as a source of food by a troop of howler monkeys ($N = 24$) living in a cacao plantation in Comalcalco, Tabasco, Mexico. Species with no code in parenthesis are trees. (E) = epiphyte, (V) = vine. Species are ranked by percent of feeding time

Species	Family	Trees used	Months used	Trees in site	Percent of feeding time
Ficus cotinifolia	Moraceae	22	9	36	41.6
Pithecellobium saman	Fabaceae	41	9	99	15.6
Gliricidia sepium	Fabaceae	30	9	103	12.7
Ficus sp.	Moraceae	4	6	6	8.7
Ficus obtusifolia	Moraceae	11	8	18	7.1
Spondias mombin	Anacardiaceae	6	3	13	5.3
Diphysa robinioides	Fabaceae	13	8	35	3.5
Manilkara zapota	Sapotaceae	1	2	1	2.1
Mangifira indica	Anacardiaceae	2	3	7	0.9
Busera simaruba	Burseraceae	1	1	6	0.7
Eritrina americana	Fabaceae	6	3	55	0.5
Cecropia obtusifolia	Cecropiaceae	1	1	14	0.4
Selenicereus sp. (E)	Cactaceae	1	4	–	0.4
Terminalia amazonia	Combretaceae	1	2	3	0.3
Paullinia pinata (V)	Sapindaceae	1	1	–	0.2
Syngonium podophyllum (E)	Araceae	1	1	–	0.03

cotinifolia, *P. saman*, and *G. sepium*, accounted for 70% of total feeding time recorded, and three additional tree species contributed to 21%; the rest of the tree species accounted for another 8% (Table 2).

The number of species used per month as a source of food by the howler monkeys in the cacao plantation ranged from 5 to 11 (mean 8.0 ± 1.63), and Sorensen's index of species overlap between adjacent months ranged from 0.57 to 0.84 (mean 0.76 ± 0.09) (Figure 7). Consumption of young leaves (50.7%; range 23.0–69.9% of feeding time per month) and of mature fruits (29.1%; range 11.9–63.6% of feeding time per month) predominated in the howlers' diet (Figure 8). Three important correlations were detected in patterns of resource use. First, use of tree species was positively associated to their relative abundance in the plantation. Second, percent of feeding time per species was found positively associated to the number of months species were used as a source of food by the howlers. Third, the number of plant parts used per species was found to be positively associated to percent of feeding time per species (Figure 9).

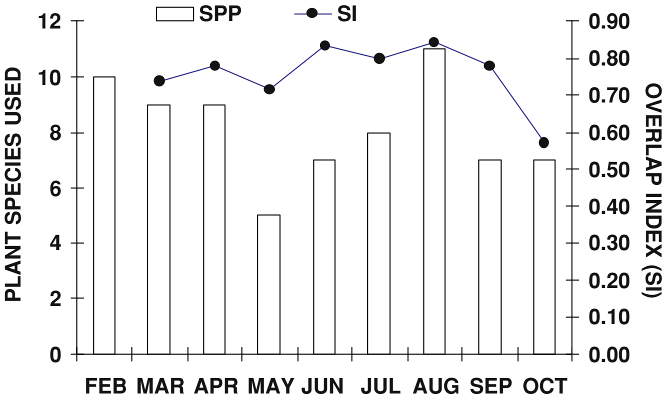

Figure 7. Monthly variation in use of plant species by a howler monkey troop living in a cacao plantation shaded by planted trees in Comalcalco, Tabasco, Mexico. Also shown are the values of Sorensen's index of species overlap between adjacent months (a value of 0 = no overlap, a value of 1 = 100% overlap).

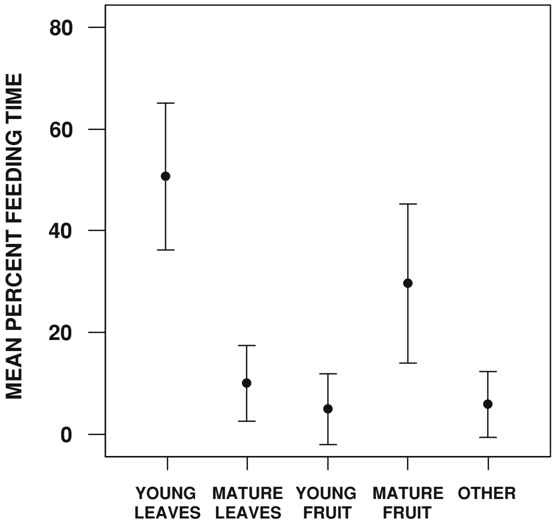

Figure 8. Mean monthly percent of feeding time spent by the howlers consuming the plant parts that were their major source of food in the cacao plantation in Comalcalco, Tabasco, Mexico.

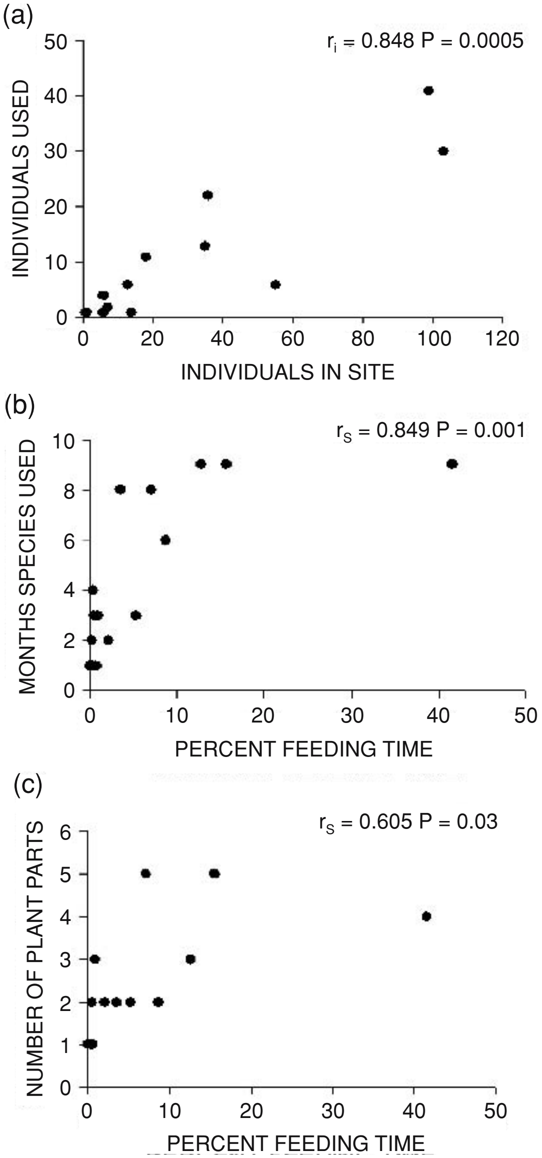

Figure 9. Associations between number of trees of species used by the howler monkeys as a source of food present in a cacao plantation and number of trees actually used by the monkeys for this purpose (a), number of month each species in the howlers' diet was used and percent of feeding time (b), and number of plant parts used (young leaves, mature leaves, young fruit, mature fruit, and others) per species and percent of feeding time (c).

DISCUSSION

General Aspects

The results of our study showed that, in fragmented Mesoamerican landscapes, primates use some agroecosystems as habitat for permanent and/or temporary residency. Some of these habitats seem also to facilitate the movements of primates in the fragmented landscape. For example, howler, spider, squirrel, and capuchin monkeys have been observed moving from forest patch to forest patch by making use of arboreal agroecosystems in the landscape, such as shaded coffee and cacao agroecosystems. Further, mature live fence trees (>25 cm DBH) with wide, intact canopies may be used by heavy primates such as howler and spider monkeys for the same purpose, while younger live fences may support smaller squirrel and capuchin monkeys, thus avoiding movement on the ground and through open areas. Live fences may also offer food to primates that visit these habitats. For example, howler, spider, squirrel, and capuchin monkeys have been observed consuming the leaves and fruits of *B. simaruba* and of *Ficus* spp., *G. sepium*, *Spondias* spp., *Cordia* spp., which in many localities in Mesoamerican are some of the most important tree species with which local people build live fences (Harvey *et al.*, submitted). These species have also been reported as top ranking tree species in the leaf and fruit diet of some of these primates (Milton, 1980; Estrada, 1984; Ramos-Fernández and Ayala-Orozco, 2003).

Data also showed that not all agroecosystems may be suitable for primate visitation and/or residency. For example, our surveys indicated that primates did not permanently or temporarily reside in citrus, allspice, and mango groves and only occasionally visited banana plantations. Usually, these plantations were bordering the forest patch in which the monkeys resided or they traveled to them by moving along a strip of forest or of old live fences, returning to their forest patch shortly afterwards. Several factors may mitigate against visitation and or residency by primates in these habitats. The wide inter-row space between the cultivated plants and their sparse vegetation mean lack of suitable structures for arboreal locomotion by large monkeys such as howler and spiders. Extreme climatic conditions in this habitats, as well as greater exposure to potential predators, including humans and dogs, may deter primates from visiting or establishing temporary or permanent residency in these agroecosystems. In the case of live fences, the narrow width of live fences (the average width of live fences is generally <8 m; Harvey *et al.*, submitted) means that these elements are only able to serve as passageways, rather than as true habitats.

In contrast, in agroecosystems such as cacao, coffee, mixed cacao/coffee, and cardamom, growing under the shade of rain forest trees, and in forestry plantations, the complexity of the mid and upper canopy, enhanced by the numerous epiphytes, vines, lianas, and other climbing plants, present on the trees, offer many potential food resources, shelter, resting sites, and cover from potential dangers for howler, spider, squirrel, and capuchin monkeys making use of these habitats (Estrada and Coates-Estrada, 1996; Greenberg, 2004). The presence in these agroecosystems of tall (>20 m) rain forest trees of plant families such as Moraceae (e.g., *Ficus* spp., *Poulsenia armata*, *Brosimum alicastrum*), Fabaceae (e.g., *Pterocarpus rorhii*, *Lonchocarpus guatemalensis*), Sapotaceae (e.g., *Manilkara zapota*, *Pouteria campechiana*), Anacardiaceae (*Spondias radlkoferi*), Lauraceae (e.g., *Nectandra ambigens*, *Ocotea* spp.), and Annonaceae (e.g., *Rollinia jimenezii*), among others, means the existence of a contiguous canopy cover for these arboreal primates. Further, some of these tree species are also known to be an important source of leaves and of fruit for the monkeys (Estrada, 1984; Estrada *et al.*, 1999; Ramos-Fernández and Ayala-Orozco, 2003). Data from Costa Rica suggest that squirrel and capuchin monkeys may also reside in large (>100 ha) African palm plantations because these contain small patches of other trees where the monkeys find shelter and a relatively high abundance of potential food represented by the palm fruit (they feed on the sugary pulp encasing the seed) and by insects found in the palm fronds and trunk.

Although there was some variability in the demographic parameters examined within and between populations of the primate species present in the agroecosystems investigated in Los Tuxtlas, population density, mean troop size, and immature to adult female ratios of these populations more closely resembled those in extensive forest tracts than in fragmented landscapes. While high population densities for *A. palliata* and *A. pigra* in forest fragments forests are suggestive of saturation of remnants (Estrada and Coates-Estrada, 1996; see Van Belle, this volume), in spider monkeys, the lower densities detected in forest fragments than in agroecosystems and extensive forests, may be the result of hunting and low fruit availability.

In Los Tuxtlas, the smaller mean group sizes and lower immature to adult female ratio of howler and of spider monkeys in forest fragments than in extensive forests and in agroecosystems suggest lower reproductive potential. Both howler and spider monkeys are subjected to hunting, illegal pet trade, and continued habitat degradation in small forest fragments, pressures with a higher impact upon spider monkey populations (Duarte and Estrada, 2003). In contrast, hunting of monkeys is practically non existent in the cacao and coffee plantations where howler and spider monkeys exist.

In general, population parameters such as mean group size and immature to adult female ratios of primates in agroecosystems were higher than in forest fragments and in some cases approached those in extensive forests. This suggests that primate populations living in the agroecosystems sustain reproductive potential. Permanent and semi-permanent residency in agroecosystems and use of these as stop-overs are the feature of the various ways in which primates use these habitats in the landscapes investigated. Howler monkeys have been observed to reside in several cacao, coffee, and cacao/coffee plantations in Los Tuxtlas for >15 years, but spider monkeys residency in these habitats is less permanent, 3, 6, and 12 months, after which they have moved to nearby patches of forest vegetation or to other shaded plantations. Here, the patchy nature of the resources preferred by spider monkeys (e.g., mature fruit) may exert important constraints upon the length of time they can reside in cacao or in coffee plantation, as these usually constitute small (4–15 ha) units of vegetation in the landscape. In contrast, howler monkeys can persist for several decades in these habitats, as our study in Comalcalco has shown, by exploiting the leaves, fruit, and flowers of individuals of major tree species (*F. cotinifolia, P. saman,* and *G. sepium*) providing shade to the cacao plants, trees which they consistently seek out in the plantation.

Impact of Primates in Agroecosystems

Long-term observations of primates in the cacao, coffee, and cacao/coffee agroecosystems and interviews with the farmers in Los Tuxtlas, indicate that the monkeys residing in these habitats do not feed on the economically important fruits; instead they concentrate their feeding on leaves and fruits of the tall rain forest trees providing the shade for the plantation. In Los Tuxtlas as well as in other sites in Mesoamerica, farmers may tolerate a certain amount of damage to fruit crops such as citrus, bananas, allspice, among others, especially when these crops constitute a minor source of income in their subsistence. However, when the plantations are a key source of income and excessive damage is produced by the monkeys, humans respond by shooting the monkeys or by aggressively chasing them away. Such reactions may deter primates from residing or regularly visiting these habitats.

Notwithstanding the above, the presence and activities of primates may be beneficial to the plantations. For example, the feeding activities of howlers at these habitats may favor primary productivity by accelerating the flow of nutrients and the conversion of matter and energy (Estrada and Coates-Estrada, 1993). The ingestion of fruits may favor the dispersal of seeds of species that are their sources of fruit, contributing to the persistence of trees of these species in the plantations (Estrada and Coates-Estrada, 1991).

Monkey defecation may also result in important additions and dispersal of nutrients to the soil of the plantation. It has been reported that the waste excretion of howlers tend to be very nutrient rich (Milton *et al.*, 1980; Nagy and Milton, 1979), producing dung that contains 1.8–2.1% N and 0.3–0.4% P (based on dry mass measurements; Milton *et al.*, 1980). In contrast, concentrations of nutrients in leaf litter are ~1% N and 0.04% P for tropical moist forests (Vitousek and Sanford, 1986, cited in Feeley, 2004). Using these data, Feeley (2004) reports that total soil nitrogen concentration under the trees in which howlers defecate in Venezuelan forests was 1.6–1.7 times greater than in control sites (test plots in surrounding soil), and that phosphorus concentration was 3.8–6 times greater under their resting or resting/feeding trees than in the surrounding soil, probably enriching the soil and nutrient uptake of these trees (Feeley, 2004). In the agroecosystems in which primates reside, this may benefit not only the trees use for resting and/or feeding, but also the cacao, coffee, cardamom, and other cultivated plants growing directly under these.

Conservation Implications

In spite of the preliminary nature of our investigation, it is evident that certain types of agroecosystems in Mesoamerican fragmented landscapes have an important potential in favoring the persistence of primate populations. These agroecosystems may be used as stepping-stones when primates move through the landscape or as foraging habitats or as habitats for temporary or permanent residency. Our surveys in Los Tuxtlas (Mexico), Lachuá (Guatemala), and in the three landscapes in Costa Rica, showed that 15 types of economically important agroecosystems are used by the Mesoamerican primate species investigated (Table 3). Seven of these are shaded either by rain forest vegetation or by arboreal vegetation planted by man, and monkeys were found temporarily

Table 3. Summary of agroecosystems in which primate populations were found in Mexico (Los Tuxtlas), Guatemala (Lachuá), and Costa Rica (Central Pacific, Cañas, and Rio Frío). The asterisk indicates the habitats in which monkeys were found permanently or temporarily residing. The other habitats are used as foraging stop-overs or as stepping stones when moving in the fragmented landscape

Agroecosystem	Condition	*Alouatta palliata*	*Alouatta pigra*	*Ateles geoffroyi*	*Saimiri oerstedii*	*Cebus capucinus*
Cacao*	Forest shade	×		×		
Cacao*	Legume trees shade	×				
Coffee*	Forest shade	×	×	×		
Mixed (cacao/coffee)*	Forest shade	×		×		
Cacao*	Coconut banana shade/	×				
Cardamom*	Forest shade		×			
Forestry plantations*	Shaded	×			×	×
Citrus	Not shaded	×				
Allspice	Not shaded	×				
Mango	Not shaded	×		×	×	×
Mango/citrus/bananas	Not shaded	×		×		
Bananas	Not shaded	×		×		
Fruit-tree groves	Not shaded	×		×	×	×
African Palm*	Not shaded				×	×
Live fences	Not shaded	×	×	×	×	×

or permanently residing in some of these. The others are basically used as stop-over habitats to forage or to move from one patch of vegetation to another (Table 3). The presence of extensive networks of live fences in many parts of Mesoamerican modified landscapes seems to enhance connectivity among isolated social units existing in native and anthropogenic patches of vegetation, and monkey may also find food resources in these linear habitats.

Habitat loss and fragmentation reduces the availability of adequate habitats and the effective size of primate populations, and results in isolation of remnant populations which are subjected to stochastic demographic events that put them at risk (Chapman and Ribic, 2002; Henle *et al.*, 2004a,b) (Figure 10a). But tolerance of species to habitat loss and fragmentation may be related to an ability to traverse open areas to reach other forest fragments or other vegetation types and use resources within the matrix (see Mandujano *et al.*, this volume; Law *et al.*, 1999; Schulze *et al.*, 2000). Such tolerance may be enhanced by the presence of patches of agroforests and of other arboreal agroecosystems (*sensu*

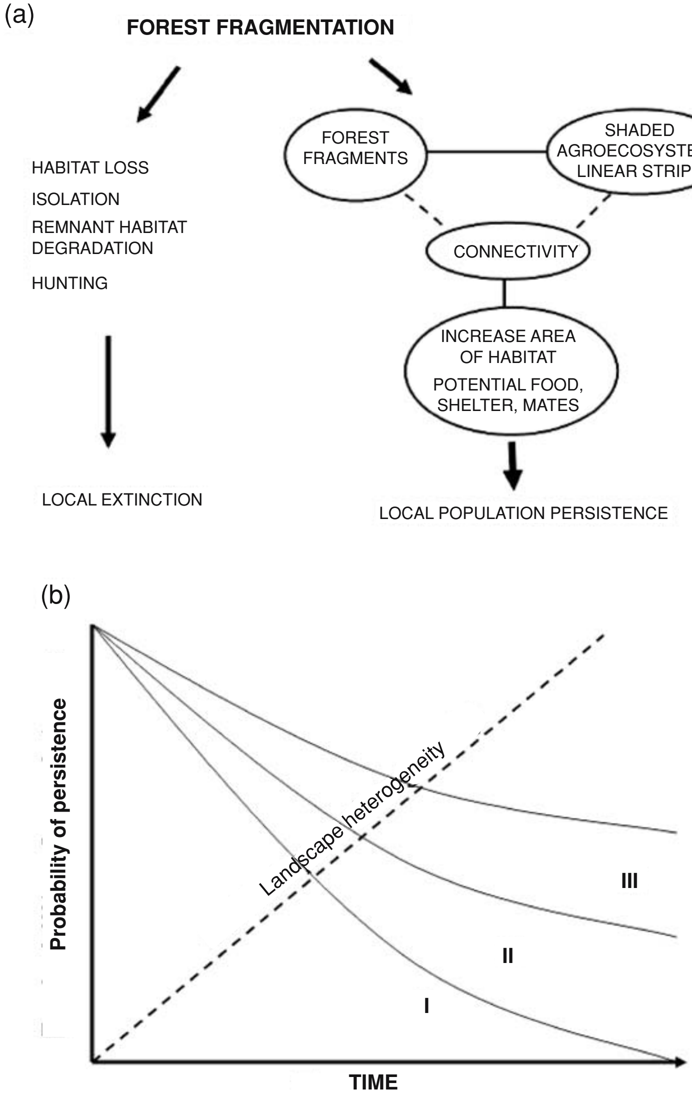

Figure 10. (a) Paths in landscape changes resulting from habitat fragmentation by human activity. The route on the left leads to extensive habitat loss and fragmentation/isolation of remnant primate populations, with a rapid decline toward extinction. In this scenario, the landscape is mainly dominated by pasturelands. The route on the right, consists of landuse patterns in which forest fragments are sourrrounded by a heterogenous matrix consisting of pastures and different types of agroecosystems. Such conditions may allow primate populations to persist in the human modified landscape. (b) Three scenarios of land management with varying effects upon primate population persistence. (I) A few forest fragments and pasturelands (low landscape heterogeneity), (II) forest fragments, a few arboreal agroecosystems and networks of live fences, (III) forest fragments and a complex and diverse assemblage of arboreal agroecosystems and agroforests, and complex networks of linear strips of vegetation (high landscape heterogeneity).

Schroth *et al.*, 2004) in intermediate positions (Figure 10a). Heterogeneity of the landscape, involving various types of arboreal agroecosystems, including live fences, may be an important general feature of some landscapes favoring dispersal and possibly connectivity between isolated segments of primate populations (see Mandujano *et al.*, this volume; Laurance *et al.*, 2002; Harvey *et al.*, 2004). The presence of agroecosystems in fragmented landscapes may represent, for remnant primate fauna, increased area of vegetation available, increased diversity of resources and habitats potentially available, increased stop-over points in the matrix, and possibly reduced isolation of populations in forest fragments. The net medium and long-term effect of the interaction among these factors may be persistence of primate populations/species in the landscape (Figure 10a).

Depending on the complexity of the landscape, we could contemplate three conservations scenarios. In one, continuous forest is reduced to a collection of a few forest fragments, with primate populations undergoing fragmentation and isolation and rapid decline in population sizes (I, Figure 10b). In a second scenario, the landscape may contain forest fragments and patches of one or two (e.g., forest-shaded cacao and coffee) types of agroecosystems, including live fences. Under this scenario (II, Figure 10b), the enhanced structural and functional connectivity may allow primate populations to persist for a longer time than in the first scenario. A third, and more complex scenario, may be one in which the fragmented landscape is highly heterogeneous. Here, in addition to forest fragments, the landscape has more patches of more types of arboreal shaded agroecosystems (e.g., cacao, coffee, cacao/coffee, and cardamom) and of sun-loving arboreal plantations (e.g., citrus, allspice, etc.) located at distances not far from one another and from forest patches. Interdispersed in the landscape are also linear strips of forest vegetation along rivers and streams and a complex network of live fences that interconnect the various patches of forest and man-made arboreal vegetation in the landscape. Under this scenario, the likelihood of primate population persistence (assuming no other pressures) may be at its highest (III, Figure 10b).

Caveats to Consider

Adjacency and/or proximity of agroforests and of other types of arboreal agroecosystems to forest fragments, as well as the presence of networks of live fences may favor dispersal of primates in fragmented landscapes. However, we also need to consider to what extent such movements may place individuals and/or groups in a perilous matrix where they are more exposed to the elements, to humans, to dogs, and to other dangers. Moreover, in fragmented landscapes forest fragments and agroecosystems may also act as ecological sinks and traps for primate populations (Kristan, 2003; Murphy and Lovett-Doust, 2004; Laurance and Vasconcelos, 2004). For example, our records for Los Tuxtlas showed that not all plantations surveyed were occupied by howler and/or spider monkeys. Thus, howlers and spider monkeys were absent in 62% and in 84% of the plantation sites surveyed, respectively. This suggests that in many cases resources may not be sufficient to support primate populations, structural connectivity of landscape vegetation units may be insufficient to facilitate dispersal or that people or other stochastic events may have eradicated the primates from these habitats. It is also not clear about the threshold level of landscape tree cover below which primates would be lost from an agroecosystem. Is there an overall level of tree cover and connectivity that must be maintained or is a threshold level of forest cover that is more important? Another thing that is often not known is the degree to which primates in agroecosystems are actively moving to other forested areas and depend on these other areas.

Changes in regional and world market demands may result in the disappearance of or in change in the local and regional distribution of agroforests and of other agroecosystems where primate populations can exist. For example, the current trend to switch from forest-shade coffee to sun-loving coffee in many Mesoamerican countries may mean an important loss of habitats where primate populations could persist (Perfecto and Armbrecht, 2003). Similarly, the trend to expand cultivation of sun-loving coffee at the expense of areas dedicated to the cultivation of forest-shaded cacao has similar consequences (Rice and Greenberg, 2000; FAO, 2004). In many areas of Mesoamerica, forest-shaded cacao and cacao agroforestry systems have been abandoned due to disease problems, and converted to other land uses (such as pastures, banana or plantain production), which have lower value for biodiversity conservation.

In conclusion, our investigation suggests that further research is needed to document the value of certain types of agroecosystems for the persistence of primate populations in fragmented landscapes in Mesoamerica and also to work with farmers to seek ways in which agricultural landscapes can be managed sustainably for both productive and conservation goals. Such research needs to assess how the primate species present in such landscapes respond to the presence of different types of agroecosystems and to their spatial configuration, to determine threshold levels of tree and forest cover within agroecosystems for primate habitation, to determine the medium and long-term conservation value of specific agroecosystems, and to evaluate how primate populations can be managed in those cases where they may become agricultural pests. Such research is of relevance in light of the proposed Mesoamerican Biological Corridor project (UNDP, 1999; World Bank, 2004; http://www.biomeso.net/), in which a major objective is to sustain local biodiversity and diminish isolation of animal and plant populations in natural protected areas. To achieve this, the MBC project contemplates the sustainable use of fragmented landscapes in intermediate locations among natural protected areas in the region.

SUMMARY

While there is a general perception that agricultural activities are the principal threat to primate biodiversity in the tropics, empirical evidence was presented in this paper to investigate the value of certain types of agroecosystems for sustaining primate populations in fragmented landscapes in Mesoamerica. Presence of primates was investigated in Los Tuxtlas, Mexico, in Lachuá, Guatemala, and in three landscapes in Costa Rica. We also compared the similarity in population parameters (density, group size, and immature to adult female ratios) of five primate species (*A. palliata*, *A. pigra*, *A. geoffroyi*, *S. oerstedii*, and *C. capucinus*) living in agroecosystems with those of the same species living in extensive and/or in fragmented forests. Primates were found in 15 agroecosystems. Some species were found residing in shaded agroecosystems (e.g., cacao, coffee), but not in unshaded plantations (e.g., citrus, allspice), which were used as foraging or stop-over habitats. For howler and spider monkeys in Mexico, mean values of primate demographic parameters in agroecosystems more closely resembled those in extensive than in fragmented forests. Those for squirrel and capuchin monkeys fell within the range of populations in forest fragments. Farmers reported crop damage by primates in banana, mango, citrus, and allspice plantations, but responses toward the monkeys' activities ranged from tolerance to expulsion. No damage was reported by howler and spider monkeys to the shaded cacao, coffee, and cardamom plants or in forestry plantations. Some primate species can persist in cacao plantation by exploiting the leaves and fruits of tree species providing shade for the cultivated plants, while others can do so by visiting various agroecosystems on a regular basis. Our study suggests that certain types of agroecosystems, specifically those grown under the shade of forest or of planted trees, favor the persistence of primate populations in

fragmented landscapes. At these habitats, the presence and feeding activities of primates may benefit the plantations by accelerating primary productivity, by dispersing the seeds of their fruit sources, and by adding important amounts of nutrients, via their defecation, to the soil of the plantation.

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