Countryside Biogeography of Neotropical Mammals: Conservation Opportunities in Agricultural Landscapes of Costa Rica

GRETCHEN C. DAILY,* GERARDO CEBALLOS,† JESÚS PACHECO,† GERARDO SUZÁN,†§ AND ARTURO SÁNCHEZ-AZOFEIFA‡

*Center for Conservation Biology, Department of Biological Sciences, 371 Serra Mall, Stanford University, Stanford, CA 94305-5020, U.S.A.
†Instituto de Ecología, Universidad Nacional Autónoma de México, Apartado Postal 70-275, México D.F. 04510, Mexico
‡Earth Observation Systems Laboratory, Department of Earth and Atmospheric Sciences, University of Alberta, Edmonton, Alberta T6G 2E3, Canada

Abstract: *The future of mammalian diversity in the tropics depends largely on the conservation value of human-dominated lands. We investigated the distribution of non-flying mammals in five habitats of southern Costa Rica: relatively extensive forest (227 ha), coffee plantation, pasture, coffee with adjacent forest remnant (<35 ha), and pasture with adjacent forest remnant (<35 ha). Of the 26 native species recorded in our study plots, 9 (35%) were restricted to forest habitat, 14 (54%) occurred in both forest and agricultural habitats, and 3 (11%) were found only in agricultural habitats. Species richness and composition varied significantly with habitat type but not with distance from the extensive forest. Interestingly, small forest remnants (<35 ha) contiguous with coffee plantations did not differ from more extensive forest in species richness and were richer than other agricultural habitat types. Small remnants contiguous with pasture were species-poor. When clearing started, the study region likely supported about 60 species. Since then, at least 6 species (10%), one family (4%), and one order (11%) have gone extinct locally. The species that disappeared were the largest in their families and included carnivorous (e.g., jaguar* [Panthera onca]), *herbivorous (e.g., Baird's tapir*, [Tapirus bairdii]), *and arboreal (e.g., mantled howler monkey* [Alouatta palliata]) *species. Although there is no substitute for native forest habitat, the majority of native, nonflying mammal species use countryside habitats. The populations of many persist even >5 km from relatively extensive forest, at least over the 40 years since forest clearance. Moreover, if hunting ceased, we expect that at least one of the locally extinct species could be reestablished in the existing landscape. Thus, there is an important opportunity to maintain and restore the diversity, abundance, and ecosystem roles of mammals in at least some human-dominated regions of the Neotropics.*

Biogeografía del Campo de Mamíferos Neotropicales: Oportunidades de Conservación en Paisajes Agrícolas de Costa Rica

Resumen: *El futuro de la diversidad de mamíferos en los trópicos depende principalmente del valor de la conservación de tierras dominadas por actividades humanos. Investigamos la distribución de mamíferos no voladores en cinco hábitats del sur de Costa Rica: selva relativamente extensa (227 ha), plantaciones de café, pastizal, café con remanente de selva adyacente (<35 ha) y pastizal con remanente de bosque adyacente (<35 ha). De las 26 especies nativas registradas en nuestras parcelas de estudio, 9 (35%) estaban restringidas al hábitat de bosque, 14 (54%) ocurrieron tanto en hábitats de bosque como agrícolas, y 3 (11%) solo se encontraron en hábitats agrícolas. La riqueza y composición de especies varió significativamente con el tipo de hábitat pero no con la distancia al bosque extenso. Lo interesante es que las, los remanentes pequeños de*

§*Current address: Department of Biology, University of New Mexico, Albuquerque, NM 87131, U.S.A., email gdaily@stanford.edu*
Paper submitted July 9, 2002; revised manuscript accepted March 19, 2003.

bosque (<35 ha) contiguos a plantaciones de café no difirieron del bosque extenso en riqueza de especies y fueron más ricos que otros tipos de hábitat agrícolas. Los remanentes pequeños contiguos a pastizales fueron pobres en especies. Cuando comenzó la deforestación, la zona de estudio probablemente mantenía unas 60 especies. Desde entonces, por lo menos 6 especies (10%), una familia (4%) y un orden (11%) se han extinguido localmente. Las especies que desaparecieron fueron las mayores en sus familias e incluyeron especies carnívoras (por ejemplo, jaguar [Panthera onca]), *herbívoras (por ejemplo, tapir,* [Tapirus bairdii]) *y árboricolas (por ejemplo, mono aullador* [Alouatta palliata]). *Aunque no hay sustituto para el hábitat de bosque nativo, la mayoría de las especies de mamíferos no voladores nativos utilizan hábitats rurales. Las poblaciones de muchas especies persisten aun a >5 km de bosque relativamente extenso, por lo menos en los 40 años desde la deforestación. Más aun, si cesara la cacería, esperamos que por lo menos una de las especies localmente extintas se reestablezca en el paisaje existente. Por lo tanto, hay una importante oportunidad para mantener y restaurar la diversidad, abundancia y papeles ecológicos de mamíferos en por lo menos algunas regiones dominadas por humanos en los neotrópicos.*

Introduction

The future of biodiversity depends profoundly on the future of human food and fiber production. Agricultural, pastoral, and silvicultural activities are the leading proximate drivers of biodiversity loss (Heywood 1995; Sala 2000) and are projected to expand greatly over coming decades (e.g., Tilman et al. 2001). The threat embodied in this expansion could be mitigated, in part, through efforts to conserve—in human-dominated countryside—species whose native habitats are rapidly disappearing (Wilkie & Finn 1990; Pain et al. 1997; Medellín et al. 2000; Daily 2001; McNeely & Scherr 2002). *Countryside* refers to the growing fraction of Earth's unbuilt land surface whose ecosystem qualities are strongly influenced by humanity (Daily 2001). Countryside habitats include agricultural plots, plantation or managed forest, fallow land, gardens, and remnants of native habitat embedded in landscapes devoted primarily to human activities (Daily et al. 2001).

Yet there is little scientific basis for assessing the relative biodiversity-conservation value of alternative production regimes and landscape configurations. Such a basis is urgently needed to inform conservation investments, especially in regions under intensive or rapidly intensifying production. The lack of scientific understanding is evident even in the European Union, where extensive human-dominated countryside was created long ago, where its associated biodiversity has been the subject of detailed inquiry, where farmland is the land cover upon which many threatened species depend most (e.g., Tucker 1997), and where roughly 20% of farmland is presently under environmentally sensitive management (e.g., Pienkowski 1998; Kleijn et al. 2001).

In The Netherlands, for instance, over 20 years of biodiversity management schemes on farmland have yielded little perceptible benefit. The diversity of plants and abundance of target bird species is no higher on fields under management agreements than on those under conventional management (Kleijn et al. 2001). Although farmers abided by their agreements, conservation goals were not achieved because of poorly understood constraints on the conservation and restoration of biodiversity at both landscape and local scales, constraints such as atmospheric deposition of nitrogenous and sulphuric compounds, dispersal and seed-bank dynamics of plants, and possible decoupling of nesting cues used by birds (Bakker & Berendse 1999; Kleijn et al. 2001; D. Kleijn, personal communication).

Assessing the conservation potential of human-dominated landscapes requires investigating the activities, movements, and persistence of species not only in remnants of native habitat but also in the full array of countryside habitats (Saunders et al. 1993; Craig et al. 1999; Daily 2001; Hughes et al. 2002). The composition and configuration of countryside habitats strongly influences the diversity and composition of native plant and animal communities (e.g., Soulé et al. 1988; Robinson et al. 1992; Laurance 1999; Laurance & Laurance 1999; Lindenmayer et al. 1999; Daily et al. 2001). Although understanding of these influences on mammals is increasing (e.g., Laurance 1999; Chiarello 2000; Cuarón 2000; Lopes & Ferrari 2000), few large-scale studies have evaluated the conservation potential of countrysides for mammal communities. Undertaking such studies is particularly important in the Neotropics, where a major fraction of global biodiversity is threatened by habitat loss and fragmentation.

A possible counterargument is that "countryside" is what the world will have in the absence of conservation activity, so that understanding more about such landscapes is, at best, trivial because it would not inform conservation action and, at worst, damaging because it might foster inaction. This argument overlooks several critical factors. First, over the long run, a reserve network alone is unlikely to save more than a tiny fraction of Earth's biodiversity. The areas involved are (and are likely to remain) simply too small, too isolated, and too dynamic (undergoing both natural and accelerating anthropogenic change) to protect more (Rosenzweig 2003). The conservation value of nonreserve countryside is thus critical to augmenting the habitat area, connectivity, and range of conditions represented in reserves. Second, countryside is not uniform, but appears rather to range in conservation value from very low (supporting <10% of the native biota; e.g., extensive monocultures of annual crops) to very high (supporting > 90% of the native biota; e.g., diverse landscapes with significant native vegetation cover and little hunting) (e.g., Medellín & Equihua 1998; McNeely & Scherr 2002; G.D., unpublished data). Third, the delivery of locally supplied ecosystem services—including pollination, pest control, renewal of soil fertility, flood control, and water purification—often depends on the capacity of countryside species to generate them (Daily 1997). Fourth, motivated by the first three points, investments are being made worldwide in the conservation of countryside (Daily & Ellison 2002). Thus, a critical opportunity for conservation not only exists but is being acted upon, and countryside biogeography (and much other work) is needed to inform such action (Balvanera et al. 2001; Daily et al. 2001). There is a need to expand the focus of conservation, not to shift it away from extensive native habitats (Rosenzweig 2003).

We investigated the countryside biogeography of nonflying mammals in southern Costa Rica. Our objectives were to (1) compare the species richness, composition, and abundance of the mammalian fauna in the principal habitats of the countryside, coffee, pasture, and native forest; (2) assess the conservation value of small (<35-ha) forest remnants surrounded by coffee and pasture; (3) investigate the forest dependence of the fauna in open habitats by comparing the fauna at different distances (<1 km vs. 5–7 km) from relatively extensive forest; (4) characterize the faunal change that has occurred since large-scale deforestation; and (5) provide a baseline for future comparison.

Methods

Study Area and Design

Our work was based in a circle with a 15-km radius, centered on the Las Cruces Biological Field Station of the Organization for Tropical Studies (OTS/OET), Coto Brus, Costa Rica (elevation 1100 m). The station is between the agricultural lands of the Valle de Coto Brus (700–1240 m) and a partially forested and relatively inaccessible ridge (up to 1600 m). The area was originally covered by premontane wet forest but was converted to agriculture and cattle ranching in the 1950s and 1960s (Fig. 1). Since then, forest cover (now about 25%) has been relatively static, although some net deforestation continues. Approximately 20% of the cleared land is dedicated to coffee production, 30% to pasture, and the remainder to banana, yucca, mixed garden, fallow land, and seminatural habitat. Remnant forest occurs in small patches (mostly <35 ha) and riparian strips scattered across the landscape (Fig. 1). Mean annual temperature and rainfall are 22°C and 3420 mm, respectively, and the dry season runs from late January to early May.

We surveyed the mammalian fauna at 27 sites in five habitat types: forest, pasture, coffee, pasture-forest-remnant, and coffee-forest-remnant (Table 1). We sampled the forest-dwelling fauna in the Las Cruces Forest Reserve (227 ha), the largest mid-elevation remnant of native forest in the area, at three sites. These sites were as widely spaced as possible, with a minimum separation of 600 m. To characterize the fauna occurring on human-dominated land, we sampled the two principal open habitats, pasture and coffee, at six sites each. Pasture sites were actively grazed and had widely scattered trees, such as citrus or remnant forest specimens. Coffee sites had coffee shrubs 2–3 m high and sparsely planted, short-statured banana trees. To determine the influence of small remnants of forest, we sampled similar pasture and coffee habitats that were contiguous with a small remnant (<35 ha), also at six sites each. Forest remnants typically covered steep, often riparian terrain. Although lightly logged, they retained mature trees and had largely closed canopies with relatively open understories. Each forest-remnant site sampled a different remnant (this is not entirely apparent from the course-scale map in Fig. 1).

We tested the influence of proximity to relatively extensive forest by situating half of the four human-dominated site types near (<1 km) and half far (5–7 km) from the Las Cruces reserve (Table 1). This distance range captures the extremes of the local gradient. Beyond 7 km one approaches other relatively large remnant forests. It also is greater than the home range (diameter) of most species of mammals in the region. We situated all sites in as widely dispersed a manner as possible to minimize the influence of possible confounding factors.

In an attempt to control for other factors in this varied landscape, we selected sites 880–1200 m in elevation; no elevational replacement of species occurs within this range (Reid 1997; J. Pacheco, G. Ceballos, G. C. Daily, P. Ehrlich, G. Suzán, B. Rodríguez, and E. Marcé, unpublished data). Pasture sites had similar levels of grazing, and coffee sites were of roughly the same maturity, so vegetation cover was similar within site types. Wherever possible, we situated the human-dominated habitat sites in parts of the landscape with 20% forest cover remaining, as calculated at a 1-km^2 scale. All sites were in areas with 10–40% forest remaining. To quantify patterns of forest clearance and proximity of sites to the Las Cruces reserve, we used Landsat thematic mapper images acquired in 1997 and 2000 and a geographic information system (GIS). All forest units within a minimum mapping unit of 1.2 ha were extracted by means of a supervised classification (Janzen 1986). The shape of forest remnants was verified with aerial photographs (1:40,000) taken in 1992

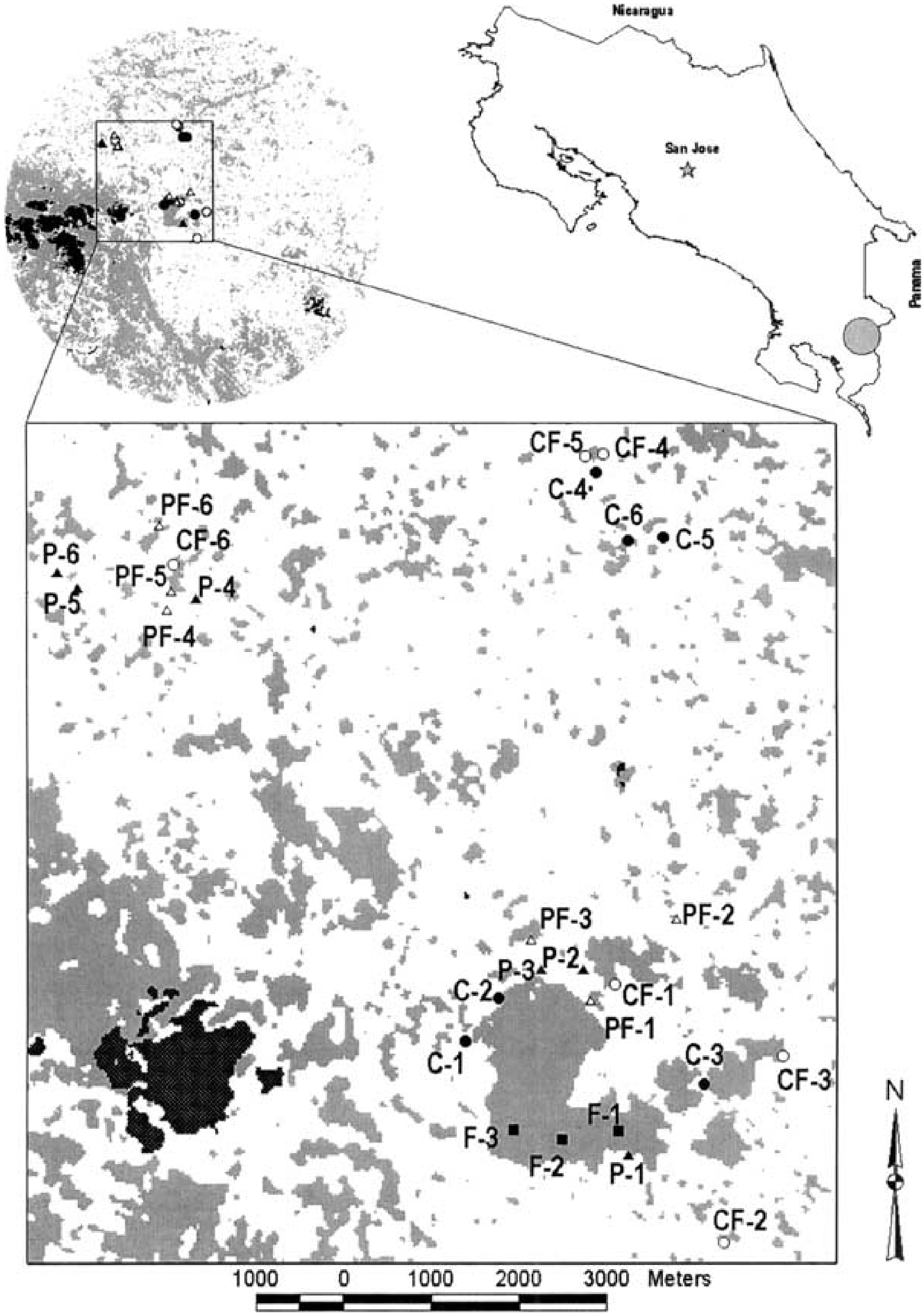

Figure 1. Map of the Las Cruces region (Coto Brus, Costa Rica), showing the distribution of forest remnants (grey), cloud cover (black), and locations of mammal sampling sites in the 15-km-radius study circle. Site codes are as in Table 1 and are associated with different symbols for easy reference between the fine- and coarse-scale maps.

by Costa Rica's National Geographic Institute (IGN) and with ground truthing.

Mammal Sampling

At each site we established one 70 × 70 m (0.49-ha) trapping grid containing 50 Sherman traps (8 × 8 × 23 cm), 9 Tomahawk traps (14 × 14 × 40 cm), and 9 baited track stations (1 × 1 m; e.g., Linhart & Knowlton 1975). At pasture-forest-remnant and coffee-forest-remnant sites, half the grid was in pasture or coffee and the other half in forest. We baited the Sherman traps with a mixture of peanut butter, oats, and vanilla and used sardines and bananas in Tomahawk traps and on track stations.

We conducted our surveys in the dry season from early March to May 1999. Each site was sampled on 2 consecutive nights in each of three evenly spaced sampling periods (8100 trap nights for Sherman traps and 1458 trap-nights each for Tomahawk traps and track stations). All individuals captured were marked and released after species and standard measurements were recorded. All tracks in track stations were identified to species with

Table 1. Total species richness by treatment in countryside habitats of the Las Cruces region, Coto Brus, Costa Rica.[a]

	Species richness		
Treatment (site code)	*near (<1 km)*[b]	*far (5–7 km)*[b]	*total*
Coffee (C)	9	6	9
Coffee-forest-remnant (CF)	13	16	22
Pasture (P)	8	8	12
Pasture-forest-remnant (PF)	8	9	12
Las Cruces Forest Reserve (LC)	—	—	17

[a] *The Las Cruces Reserve was sampled at three sites; all other treatments were replicated three times, both near and far, for a total of 27 sites.*
[b] *Distance is measured from the nearest edge of the Las Cruces reserve.*

field guides (Aranda 1991; Reid 1997). We followed Wilson and Reeder (1993) for nomenclature and Ceballos and Miranda (2000) and Reid (1997) for identification of species in the field. A few individuals of rodent species were collected as voucher specimens.

We complemented our trap data with systematic visual searches for mammals and their tracks. We made visual observations just before setting, checking, and picking up traps, from 0600 to 1200 hours and from 1600 to 1900 hours. Each site was evaluated six times.

Analysis

We excluded from the entire analysis four exotic species associated principally with homes and other human-made structures: the domestic dog (*Canis familiaris*) and cat (*Felis catus*), the black rat (*Rattus rattus*), and the house mouse (*Mus musculus*). Although we had 106 sightings and track-station records of dogs, this measure of dog abundance was not correlated with native species richness across site types (Pearson's $r = -0.017$, not significant). In total, we had only four records of cats, two of black rats, and one of a house mouse.

We assessed the effects of habitat and distance class on mammalian species richness with a two-way analysis of variance (ANOVA). To test these effects on the abundance of small mammals, we repeated the ANOVA with only numbers of animals captured in Sherman and Tomahawk traps, which offers more reliable measures of abundance than track stations.

We used the Jaccard similarity coefficient to quantify the similarity of species composition among sites. This index is the number of species shared by two sites divided by the total number of species from the two sites (Magurran 1988). To explore clustering of sites by species composition, we used a multidimensional scaling (MDS) algorithm (SYSTAT 7.0) to plot sites in two dimensions, with proximity of sites proportional to their similarity. We then used a randomization program (analysis of similarities [ANOSIM], Plymouth Routines in Multivariate Ecological Research, Carr 1997) to calculate the probability of acquiring a given level of clustering by chance.

To estimate the degree of faunal change that has occurred in the study region, we assembled a list of mammals that probably occurred in the area prior to deforestation. The historical species list was based on the literature (Rodríguez & Chinchilla 1996), museum records, local oral knowledge (collected in informal interviews with farmers), trophies (e.g., skulls, skins, and photos), and our own records. Those species judged locally extinct had no validated records for the past 15 years. Those judged extant or presumably extant were observed by us during the course of the study or had a record recently validated by another scientist. Finally, we evaluated the relative vulnerability of all species to extinction and classified species into four categories—low, moderate, high, and invasive—based on published studies of their requirements for habitat and other resources and their sensitivity to hunting and other human impacts.

Results

Species Composition

We made 158 captures (of 154 individuals) and 116 track-station records and visual sightings, sampling a total of 26 species over the course of the study. These species represented six orders, 12 families, and 26 genera (Appendix 1). Six additional species (Hoffmann's two-toed sloth, blackish small-eared shrew, red-backed squirrel monkey, Alfaro's pygmy squirrel, vesper rat, and Neotropical river otter) were recorded within 300 m from the forest sites during the sampling period (Appendix 1); four more (woolly opossum, Northern tamandua, red brocket deer, and white-tailed deer) were recorded in the 15-km-radius study region during the same period; and one more (silky anteater) was recorded in the region after the study period. (Scientific names are provided in Appendix 1.) All together, we observed eight orders and 16 families, represented by 37 species, of nonflying mammals in the region.

Hereafter, we exclusively refer to the species recorded in our sites, during the study period, except when otherwise noted. Interestingly, carnivores (11 spp.) were the most diverse order, followed by rodents, marsupials, primates, xenarthrans, and lagomorphs (Appendix 1). All recorded species were either small (<500 g) or medium (<20 kg) in size.

Effects of Habitat Type and Isolation

Species richness varied significantly with habitat type but not with distance from the Las Cruces reserve (Fig. 2). As expected, the Las Cruces reserve sites had the most recorded species of any site type (Table 1). Coffee-forest-remnant sites did not differ from the Las Cruces reserve

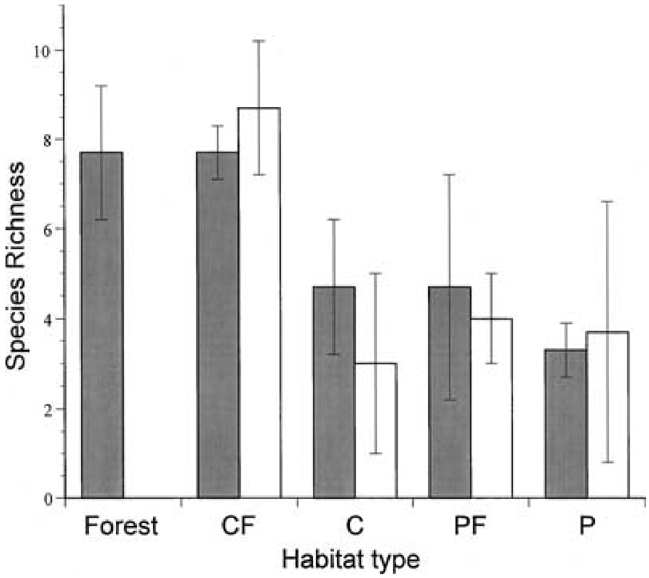

Figure 2. Mean (± 1 SE) mammal species richness by habitat type and distance class. Shaded bars represent sites in and near (<1 km) the Las Cruces reserve; open bars represent sites far from (5–7 km) the reserve. Results of two-way analysis of variance: habitat type: F = *9.838*, *df* = 3, p = *0.001*; *distance* : F = *0.216*, *df* = *1*, p = *0.648*; *interaction:* F = *0.541*, df = *3*, p = *0.661*. *The Las Cruces reserve and coffee-forest-remnant (CF) sites are similar* (p = *1.000*) *as a group, as are coffee (C), pasture (P), and pasture-forest-remnant (PF) sites* (p = *1.000*). *These two groups are significantly different from each other* (p < *0.007*), *however*.

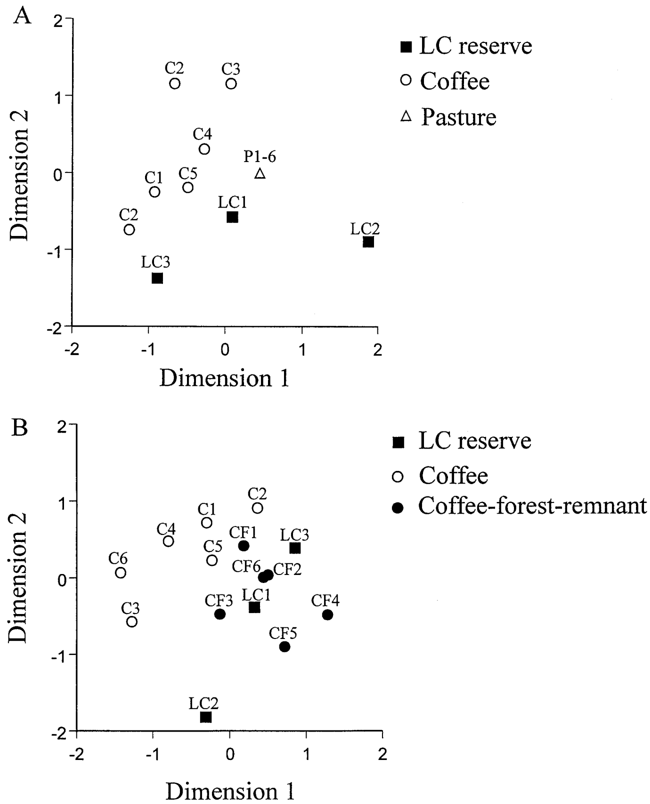

Figure 3. Multidimensional scaling (MDS) plots based on Jaccard coefficients of similarity: (a) Las Cruces (LC) reserve, coffee (C), and pasture (P) sites (R^2 = *0.962*, *stress level* = *0.086*; *ANOSIM: global* R = *0.142*, p = *0.097*); *(b) Las Cruces reserve, coffee, and coffee-forest-remnant (CF) sites* (R^2 = *0.876*, *stress level* = *0.150*; *ANOSIM: global* R = *0.256*, p = *0.023*). *(In a all pasture sites are sufficiently similar as to collapse to one point with the monotonic Kruskall loss function in the MDS).*

in species richness ($p > 0.95$, post hoc pairwise tests) but were significantly different from the other agricultural habitat types ($p < 0.01$ for each comparison, Bonferonni adjustment). Coffee, pasture, and pasture-forest-remnant sites were not significantly different from one another ($p > 0.95$, Bonferonni adjustment). Thus, coffee-forest-remnant sites were significantly richer than coffee sites (ANOVA: $F = 23.803$, df = 1, $p = 0.001$), but there was no significant difference in the richness of pasture sites with and without a forest remnant ($F = 0.635$, df = 1, $p = 0.444$).

The multidimensional scaling (MDS) analysis, based on the Jaccard index of similarity in species composition, yielded a result consistent with the ANOVA: sites clustered by habitat type (ANOSIM: global $R = 0.166$, $p = 0.011$) but not by distance class (ANOSIM: global $R = 0.018$, $p = 0.318$). The MDS plots are shown for some site types to highlight interesting clusterings and separations in the clearest possible way (Fig. 3a & 3b). (Projecting the multidimensional relationships between all site types onto one two-dimensional plot produces a confusing picture that is not shown. The statistical significance of the clustering is tested independently of the MDS plots, directly from the matrix of Jaccard similarity coefficients [Carr 1997].)

Nine (35%) species were restricted to forest habitat (e.g., the kinkajou); 14 (54%) were found in both forest and agricultural habitats (e.g., the common opossum), and 3 (11%) were found only in agricultural habitats (e.g., the hispid cotton rat). Of those species restricted to forest habitats, 2 were found only in the Las Cruces reserve, 6 in both the reserve and small remnants, and 1, the jaguarundi, was sampled only in small remnants, although we observed it at other times in the Las Cruces reserve.

To test for effects on abundance, we pooled data for the two most abundant taxa, rodents and (separately) marsupials. Habitat type exerted a significant effect on rodent abundance, but distance class did not (two-way ANOVA: habitat type: $F = 4.749$, df = 3, $p = 0.015$; distance: $F = 1.639$, df = 1, $p = 0.219$; interaction: $F = 0.842$, df = 3, $p = 0.491$). Neither factor was significant for marsupials

Table 2. The status of nonflying mammal taxa of the Las Cruces region, Coto Brus, Costa Rica.*

	Total	*Locally extinct (%)*	*Locally extant (%)*	*Recorded in region during and after study period (%)*	*Recorded in study sites in study period (%)*
Orders	9	1 (11)	8 (89)	8 (89)	6 (67)
Families	23	1 (4)	22 (96)	16 (70)	12 (52)
Genera	56	5 (9)	51 (91)	37 (66)	26 (46)
Species	60	6 (10)	54 (90)	37 (62)	26 (43)

**See Appendix 1 for the list of taxa.*

(two-way ANOVA: habitat type: $F = 1.473$, df $= 3$, $p = 0.260$; distance: $F = 2.200$, df $= 1$, $p = 0.157$; interaction: $F = 0.600$, df $= 3$, $p = 0.624$).

Faunal Change

Our compilation of records of non-flying mammal species suggests that the Las Cruces region historically supported approximately 60 species (Appendix 1). In the last four decades, at least 6 species (10%), five genera, one family, and one order have gone extinct locally (Table 2). These species—the giant anteater, mantled howler monkey, Central American spider monkey, jaguar, white-lipped peccary, and tapir—accounted for 15–100% of the original local species richness in their respective families. They were also the largest species in their families. A knowledgable local informant believes that at least one additional species, the water opossum, may have also disappeared. Records of this typically rare species were scarce and more difficult to verify than the six others named above. Depending on the status of the water opossum, it appears that, of the 23 families on the historical list, 17–18 have not yet experienced local extinctions.

Discussion

Clearly there is no substitute for native forest habitat: at least six species with important ecological roles (Robinson 1996; Terborgh 1988) have been extirpated from the study region, and others have doubtless experienced great reductions in size and density of populations. If forest cover declines further or if the remaining large forest tracts are fragmented into small patches, further population declines and extinctions will likely result. Moreover, the occurrence of a diverse mammalian fauna in the approximately 40-year-old landscape does not guarantee its long-term persistence; rather, it suggests a window of opportunity for assessing and maintaining or augmenting the conservation value of the countryside (Daily 2001).

We were encouraged to find that such a rich mammal community has persisted, at least over the short term, in a region with relatively high levels of forest clearance and human population density. Our study, although providing only lower bound estimates of the diversity and abundance of mammals, shows that the majority of native, nonflying mammal species utilize countryside habitats. We attribute their continued survival in the region to several factors: the substantial proportion of countryside remaining in forest remnants, the apparent conservation value of coffee plots contiguous with remnants, and the significant decline in hunting since the 1980s reported by locals. Further sampling would increase the species richness associated with countryside habitats, making our records and interpretation conservative.

Landscape Structure and Conservation Value

Both the amount of remaining forest and its spatial distribution among other countryside habitats appear to influence the conservation value of the region. The importance of the amount of remaining forest is suggested by the way species richness varied with habitat type but not with distance from relatively extensive forest (see contrasting results for moths in Ricketts et al. 2001). The largest forest tract (the Las Cruces reserve) was key to maintaining the regional diversity of mammals because it was the sole locus of some of the most specialized species (see also Andren 1994; McGarigal & McComb 1995; Trzcinski et al. 1999).

The importance of spatial patterning is shown by the way coffee plantations enhance the conservation value of small forest remnants. The coffee-forest-remnant sites, whether near or far from the Las Cruces reserve, were very similar to the Las Cruces reserve sites in both species composition and abundance. Because sites were quite widely dispersed (Fig. 1), this is unlikely to be a result of local site effects. Pasture-forest-remnant sites, by contrast, were depauperate. Mature coffee shrubs appear to provide cover and facilitate movement, connecting mammal populations into larger metapopulations and reducing the likelihood of local extinction. Some species, such as agoutis and squirrels, captured in coffee may have been foraging and not simply in transit between forest remnants. Although coffee plantations in the Las Cruces region are typically shaded only by sparsely planted, short-statured trees (e.g., bananas) that are not used by arboreal species, the coffee itself is densely planted. Local coffee on its own, however, is clearly not suitable as habitat for most species, unlike complex coffee plantations elsewhere that grow under a well-developed canopy (e.g., Moguel & Toledo 1999).

Like pure coffee sites, pasture and pasture-forest-remnant sites appear to hold little conservation value for most mammals. We found, as expected, higher densities of both invasive and generalist species of rodents in pastures (see also Laurance 1994; Adler et al. 1997; Stevens & Husband 1998).

Distance from relatively extensive forest had no effect over the 0–7 km range available for testing in the region. It is possible that the majority of the mammal species we observed far from extensive forest are maintaining populations in those countryside habitats. On the basis of information on home range and vagility, it is very unlikely that individuals of many species routinely traverse the countryside from the Las Cruces Forest to sites many kilometers away (Nowak 1999). At the same time, some of the larger, more vagile species found at far sites may depend on relatively extensive forest. This dependence may simply not have been revealed in our study because of the linear measure of distance we used or because of insufficiently large sample sizes.

Distance is difficult to measure in a way that reflects the likelihood or frequency of movement between points on a landscape. On the Olympic Peninsula (Washington, U.S.), for instance, Perault and Lomolino (2000) found that linear distance to nearest old-growth forest does not correlate with the species richness of forest-dependent mammals in a forest corridor. Species richness, however, relates positively to the amount of old-growth forest in the landscape adjacent to forest corridor sites. The "corridors" in this study were >1 km wide in places (and >8 km long) and served as breeding habitat for many species. By Las Cruces standards, they constitute relatively extensive habitat themselves. Our study did not test the conservation value of much narrower riparian strips of forest, but incidental observations suggest their possible importance. We recorded tracks or specimens of at least 18 species of mammals in riparian strips in the study region, including several species that were not recorded in our sampling plots (e.g., brocket deer and river otter). Other researchers have found similar positive effects of riparian strips (Robinson 1996; Laurance & Laurance 1999).

Species' Vulnerability to Human Impacts

Although forest clearance and fragmentation are most likely the overriding causes of population declines in the countryside, dogs, pesticides, and especially hunting are probably also important factors (e.g., Redford 1992; Robinson 1996; Carrillo et al. 2000; Escamilla et al. 2000). Giant anteaters, for instance, are susceptible to fire and dogs, and usually do not survive in fragmented habitats (Nowak 1999).

In the Las Cruces region, local people say they kill wild mammals perceived to endanger domestic animals (e.g., Treves et al. 2002). During our research we recorded a river otter, several common opossums, and a tayra killed for that reason. Jaguars are widely considered a pest because they prey on cattle and are systematically destroyed with traps and guns (Swank & Teer 1989; Quigley & Crawshaw 1992; Ceballos et al. 2002). The last record of a jaguar in the Las Cruces region is from 1973. Tapirs are prime food and intensively hunted virtually everywhere they occur (Terwilliger 1978; Ayres et al. 1991). Baird's tapirs have disappeared from Ecuador, El Salvador, and large regions in Mexico and Central America and are considered in danger of global extinction (Fragoso 1991; World Conservation Union 2000). We have evidence that the last tapir in the Las Cruces forest area was killed in 1970.

Finally, monkeys are usually very vulnerable to hunting, especially in fragmented forests (Rylands & Keuroghlian 1988; Mittermeier 1991; Nowak 1999; Peres 2001). Spider monkeys are considered a delicacy and are now locally extinct in many areas, from Mexico to South America (Leopold 1959; Mittermeier 1991). Local people attributed their extirpation in the Las Cruces region to intensive hunting, similar to their fate in other regions in Costa Rica (Wilson et al. 2002). The disappearance of the howler monkey is somewhat surprising because they survive elsewhere in intensively managed countryside; local people attributed their disappearance to hunting as well.

Our study supports the hypothesis that large species are in general more prone to extinction than small species (Simberloff 1986; Caughley 1994). The six locally extinct species were either the largest mammals originally found in the Las Cruces region or the largest mammals in their order and family, or both. All are considered rare, threatened, or endangered worldwide (World Conservation Union 2000). Most of them require large tracts of native habitat to survive (Leopold 1959; Robinson 1996) and may have become locally extinct even in the absence of hunting. White-lipped peccaries, for instance, live in large herds with a complex social structure (Sowls 1984) and require extensive tracts of native forest. In contrast, the collared peccary, still surviving in the region, usually occur in smaller groups and are relatively tolerant of human disturbance; indeed, they can sometimes become crop pests.

Our research also supports recent conclusions that extinction risk resulting from habitat modification and persecution varies in a complex way with body size and life-history traits (Glanz 1991; Robinson 1996; Beissinger 2000; Owens & Bennett 2000), although, in the absence of hunting, occurrence in open countryside habitats may prove a good predictor of vulnerability (e.g., Laurance 1991). We classified mammal species of the Las Cruces region in four broad categories, according to our best judgment of their vulnerability to both land-use change and associated human impacts, such as hunting (Fig. 4, Appendix 1). We could not estimate the relative effects of land-use change and hunting independently (for such estimates see, for example, Peres [2001] and Purvis [2001]). Our classification applies to Costa Rica. Interestingly, personal observations suggest that some of the same species may respond to habitat change differently in other regions, such as in Brazil, Mexico, and Venezuela (e.g., Medellín & Redford 1992; Ceballos 1995).

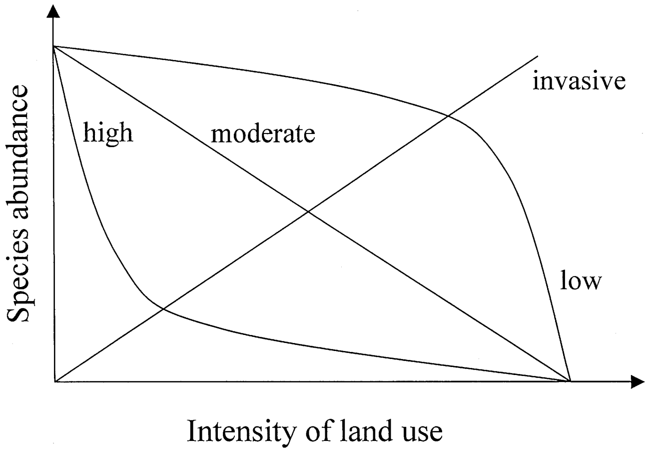

Figure 4. Varied species responses to changing land-use intensity and associated human impacts. Sensitivity levels (high, moderate, low) are explained in the text.

The 18 (30%) species classified as highly sensitive require specific macro- or microhabitats for refuge sites and food supply (Wilson & Janzen 1983; Robinson 1996; Reid 1997) and/or are hunted. Many of these have already disappeared, and we expect the remaining species to also disappear if the Las Cruces reserve is destroyed. On the other hand, if hunting ceased, we would expect the howler monkey and possibly others to persist in the existing landscape.

The 19 (31%) species designated moderately sensitive require forest (Robinson 1996; Reid 1997; Ceballos & Miranda 2000) but frequently range outside forest and do not depend on specific forest habitats. The continued survival of the larger of such species will likely depend on the area of forest habitat within their dispersal range (Robinson 1996). Ocelots, for example, expand their home ranges in fragmented landscapes to encompass sufficient forest habitat (Bisbal 1989; Sunquist et al. 1989; Andren 1994).

The 19 (31%) relatively insensitive species use both natural and human-created habitats and, in general, are able to maintain or increase their abundance in countryside (e.g., Fonseca & Robinson 1990; Robinson 1996; Ceballos & Miranda 2000). We assumed that invasive species (five spp., 8% in the region) were absent from the area prior to forest clearance. Although they generally contribute little to maintaining original ecosystem functions, some (e.g., coyotes) can play an important role by controlling smaller mammalian predators (e.g., opossums) that otherwise are released in the absence of the original top carnivores (Crooks & Soulé 1999).

Conservation Policy

Species classified as forest specialists and forest generalists (or as highly and moderately sensitive) should have high conservation priority because they are intrinsically more vulnerable to extinction and because habitat generalists may not assume their roles in ecosystem functioning. With the local extinction of white-lipped peccaries, for instance, forest wallows tend to dry up, and many species of frogs and toads that depend on those wallows for reproduction also disappear (Zimmerman & Bierregaard 1986). Similarly, the local extinction of large carnivores can have profound effects on the population densities of prey species, which in turn may affect populations of other animals and plants (Robinson 1996; Terborgh 1999). The decline or disappearance of small forest specialists such as bats and rodents can also significantly alter the structure and composition of plant communities (Wilson & Janzen 1983; Howe 1984; Terborgh 1988; Dirzo & Miranda 1990; Redford 1992). Additionally, the increase in abundance of some species, including rodents and opossums, can have a direct impact on human health because such mammals are important links for emerging or reemerging diseases (Daily & Ehrlich 1996).

Overall, we hope that our findings will help build a vision of more integrated conservation policies that include both expansive wilderness and countryside. Obviously, forest restoration in the Las Cruces region would contribute to securing the native mammal community, as would the establishment and protection of reserves. Short of this, our findings suggest that management of the countryside with a goal of maintaining the mammal community could enhance its chances of persistence even without increasing the total amount of forest cover. For instance, discouraging hunting (e.g., Plumptre et al. 2000; Treves et al. 2002) or placing of agriculture with significant vegetation height diversity and cover, such as coffee, next to remnant forest could enhance the conservation value of the landscape.

Synergistic interactions among diverse human impacts—such as land-use change, hunting, invasive species, emerging pathogens, climate change, fire, and soil degradation—will make integrated conservation a major challenge (Laurance & Cochrane 2001). Nonetheless, countryside is the most common habitat mosaic in the world today because of human activities. We must learn to maximize its usefulness as a biodiversity reservoir.

Acknowledgments

We thank J. Ilama, E. Marce, J. Mieren, and B. Stephens for superb field assistance; I. Moorthy for excellent assistance with the geographic information system; A. Herra for wonderful hospitality; L. D. Gómez, G. Hewson, and other station staff for general support; and the Winslow Foundation and P. and H. Bing for generously making this work possible. The work of G. Ceballos and J. Pacheco was partially supported by the Institute of Ecology of the

National Autonomous University of Mexico. We are also grateful for helpful comments on the manuscript from A. Cuarón, P. Ehrlich, J. Hellmann, W. Laurance, M. Lomolino, R. Medellín, T. Ricketts, and J. Robinson.

Literature Cited

Adler, G. H., J. J. Arboledo, and B. L. Travi. 1997. Diversity and abundance of small mammals in degraded tropical dry forests of northern Colombia. Mammalia **61**:361–370.

Andren, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. Oikos **71**:355–366.

Aranda, M. 1991. Rastros de los mamiferos silvetres de Mexico: manual de campo. INIREB, Xalapa, Veracruz.

Ayres, M. J., D. M. Lima, E. Souza, and J. L. K. Barreiros. 1991. On the track of the road: changes in subsistence hunting in a Brazilian Amazon village. Pages 82–92 in J. G. Robinson and K. H. Redford, editors. Neotropical wildlife use and conservation. Chicago University Press, Chicago.

Bakker, J. P., and F. Berendse. 1999. Constraints in the restoration of ecological diversity in grassland and heathland communities. Trends in Ecology & Evolution **14**:63–68.

Balvanera, P., G. C. Daily, P. R. Ehrlich, T. Ricketts, S. A. Bailey, S. Kark, C. Kremen, and H. Pereira. 2001. Conserving biodiversity and ecosystem services. Science **291:** 2047.

Beissinger, S. R. 2000. Ecological mechanisms of extinction. Proceedings of the National academy of Sciences of the United States of America **97**:11688–11689.

Bisbal, F. J. 1989. Distribution and habitat association of the carnivores in Venezuela. Pages 339–362 in K. Redford and J. F. Eisenberg, editors. Advances in Neotropical mammalogy. Smithsonian Institution Press, Washington, D.C.

Carr, M. R. 1997. PRIMER user manual. Plymouth routines in multivariate ecological research. Plymouth Marine Laboratory, Plymouth, United Kingdom.

Carrillo, E., G. Wong, and A. D. Cuarón. 2000. Monitoring mammal populations in Costa Rican protected areas under different hunting restrictions. Conservation Biology **14**:1580–1591.

Caughley, G. 1994. Directions in conservation biology. Journal of Animal Ecology **57**:771–785.

Ceballos, G. 1995. Vertebrate diversity, ecology, and conservation in Neotropical deciduous forests. Pages 195–220 in S. Bullock, E. Medina, and H. Mooney, editors. Seasonally dry tropical forests. Cambridge University Press, Cambridge, United Kingdom.

Ceballos, G., and A. Miranda. 2000. Guía de campo de los mamíferos de la costa de Jalisco: a field guide to the mammals of the Jalisco coast. Fundación Ecológica de Cuixmala A.C., México, D.F.

Ceballos, G., C. Chávez, C. Materola, A. Rivera, and W. Wall. 2002. Tamaño poblacional y conservación del jaguar (*Panthera onca*) en la Reserva de la Biosfera Calakmul, Campeche, Mexico. Pages 403–417 in, R. A. Medellín C. Chetkiewicz, A. Rabinowitz K. H. Redford, J. G. Robinson E. Sanderson, and A. Taber, editors. Jaguares en el nuevo milenio: una evaluación de su estado, detección de prioridades y recomendaciones para la conservación de los jaguares en américa. Universidad Nacional Autónoma de México and Wildlife Conservation Society, Mexico.

Craig, J., N. Mitchell, and A. D. Saunders, editors. 1999. Nature conservation in production environments: managing the matrix. Surrey Beatty and Sons, Sydney.

Crooks, K. R., and M. E. Soulé. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. Nature **400**:563–566.

Chiarello, A. G. 2000. Density and population size of mammals in remnants of Brazilian Atlantic Forest. Conservation Biology **14**:1649–1657.

Cuarón, A. D. 2000. A global perspective on habitat disturbance and tropical rainforest mammals. Conservation Biology **14**:1574–1579.

Daily, G. C. editor. 1997. Nature's services: societal dependence on natural ecosystems. Island Press, Washington, D.C.

Daily, G. C. 2001. Ecological forecasts. Nature **411:** 245.

Daily, G. C., and P. R. Ehrlich. 1996. Global change and human susceptibilty to disease. Annual Review of Energy and the Environment **21**:125–144.

Daily, G. C., and K. Ellison. 2002. The new economy of nature: the quest to make conservation profitable. Island Press, Washington, D.C.

Daily, G. C., P. R. Ehrlich, and A. Sánchez-Azofelia. 2001. Countryside biogeography: use of human dominated habitats by the avifauna of southern Costa Rica. Ecological Applications. **11**:1–13.

Dirzo, R., and A. Miranda. 1990. Contemporary Neotropical defaunation and forest structure, function, and diversity: a sequel to John Terborgh. Conservation Biology **4**:444–447.

Escamilla, A., M. Sanvicente, M. Sosa, and C. Galindo-Leal. 2000. Habitat mosaic, wildlife availability, and hunting in the tropical forest of Calakmul, Mexico. Conservation Biology **14**:1592–1601.

Fonseca, G. A. B., and J. G. Robinson. 1990. Forest size and structure: competitive and predatory effects on small mammal community. Biological Conservation **53**:265–294.

Fragoso, J. M. V. 1991. The effects of hunting on tapirs in Belize. Pages 154–162 in J. G. Robinson and K. H. Redford, editors. Neotropical wildlife use and conservation. Chicago University Press, Chicago.

Glanz, W. E. 1991. Mammalian densities at protected versus hunted sites in Central Panama. Pages 163–173 in J. G. Robinson and K. H. Redford, editors. Neotropical wildlife use and conservation. Chicago University Press, Chicago.

Heywood, V. H., editor. 1995. Global biodiversity assessment. Cambridge University Press, Cambridge, United Kingdom.

Howe, H. 1984. Implication of seed dispersal by animals for tropical reserve management. Biological Conservation **30**:261–281.

Hughes, J. B., G. C. Daily, and P. R. Ehrlich. 2002. Agricultural policy can help preserve tropical forest birds in countryside habitats. Ecology Letters **5**:121–129.

Janzen, J. R. 1986. Introductory digital image processing. Prentice-Hall, Englewood Cliffs, New Jersey.

Kleijn, D., F. Berendse, R. Smit, and N. Gilissen. 2001. Agri-environment schemes do not effectively protect biodiversity in Dutch agricultural landscapes. Nature **413**:723–725.

Laurance, W. F. 1991. Ecological correlates of extinction proneness in Australian tropical rainforest mammals. Conservation Biology **5**:79–89.

Laurance, W. F. 1994. Rainforest fragmentation and the structure of small mammal communities in tropical Queensland. Biological Conservation **69**:23–32.

Laurance, W. F. 1999. Introduction and synthesis. Biological Conservation **91**:101–107.

Laurance, W. F., and M. A. Cochrane. 2001. Synergistic effects in fragmented landscapes. Conservation Biology **15**:1488–1489.

Laurance, S. G., and W. F. Laurance. 1999. Tropical wildlife corridors: use of linear rainforest remnants by arboreal mammals. Biological Conservation **91**:231–239.

Leopold, A. S. 1959. Wildlife from Mexico. California University Press, Los Angeles.

Lindenmayer, D. B., R. B. Cunningham, M. L. Pope, and C. F. Donnelly. 1999. The response of arboreal marsupials to landscape context: a large-scale fragmentation study. Ecological Applications **9**:594–611.

Linhart, S. B., and F. F. Knowlton. 1975. Determining the relative abundance of coyotes by scent station lines. Wildlife Society Bulletin **3**:119–124.

Lopes, M. A., and S. F. Ferrari. 2000. Effects of human colonization on the abundance and diversity of mammals in Eastern Brazilian Amazon. Conservation Biology **14**:1658–1665.

Magurran, A. E. 1988. Ecological diversity and its measurement. Princeton University Press, Princeton, New Jersey.

McGarigal, K., and W. C. McComb. 1995. Relationship between landscape structure and breeding birds in the Oregon coast range. Ecological Monographs **65:**235–260.

McNeely, J. A., and S. J. Scherr. 2002. Ecoagriculture: strategies to feed the world and save wild biodiversity. Island Press, Washington, D.C.

Medellín, R. A., and M. Equihua. 1998. Mammal species richness and habitat use in rainforest and abandoned agricultural fields in Chiapas, Mexico. Journal of Applied Ecology **35:**13–23.

Medellín, R. A., and K. H. Redford. 1992. The role of mammals in Neotropical forest-savanna boundaries. Pages 519–548 in P. Furley, J. Ratter, and J. Proctor, editors. Nature and dynamics of forest-savanna boundaries. Chapman and Hall, London.

Medellín, R. A., M. Equihua, and M. A. Amin. 2000. Bat diversity and abundance as indicators of disturbance in Neotropical rainforests. Conservation Biology **14:**1666–1675.

Mittermeier, R. 1991. Hunting and its effects on wild primate populations in Suriname. Pages 93–107 in J. G. Robinson and K. H. Redford, editors. Neotropical wildlife use and conservation. Chicago University Press, Chicago.

Moguel, P., and V. M. Toledo. 1999. Biodiversity conservation in traditional coffee systems of Mexico. Conservation Biology **13:**11–21.

Nowak, R. N. 1999. Walker's mammals of the world. 6th edition. Johns Hopkins Press, Baltimore, Maryland.

Owens, I. P. F., and P. M. Bennett. 2000. Ecological basis of extinction risk in birds: habitat loss versus human persecution and introduced predators. Proceedings of the National Academy of Sciences of the United States of America **97:**12144–12148.

Pain, D. J., D. Hill, and D. I. McCracken. 1997. Impact of agricultural intensification of pastoral systems on bird distributions in Britain 1970–1990. Agriculture Ecosystems & Environment **64:**19–32.

Perault, D. R., and M. Lomolino. 2000. Corridors and mammal community structure across a fragmented, old-growth forest landscape. Ecological Monographs **70:**401–442.

Peres, C. A. 2001. Synergistic effects of subsistence hunting and habitat fragmentation on Amazonian forest vertebrates. Conservation Biology **15:**1490–1505.

Pienkowski, M. W. editor. 1998. Forum: biodiversity and high-nature-value farming systems. Journal of Applied Ecology **35:**948–990.

Plumptre, A., T. Hart, A. Vedder, and J. Robinson. 2000. Support for Congolese conservationists. Science **288:** 617.

Purvis, A. 2001. Mammalian life histories and responses of populations to exploitation. Pages 169–181 in J. Reynolds G. M. Mace, K. H. Redford, and J. G. Robinson, editors. Conservation of exploited species. Cambridge University Press, Cambridge, United Kingdom.

Quigley, H. B., and P. G. Crawshaw. 1992. A conservation plan for the Jaguar in the Pantanal region of Brazil. Conservation Biology **61:**149–157.

Redford, K. H. 1992. The empty forest. BioScience **42:**412–422.

Reid, F. A. 1997. A field guide to the mammals of Central America and Southeast Mexico. Oxford University Press, New York.

Ricketts, T. H., G. C. Daily, P. R. Ehrlich, and J. P. Fay. 2001. Countryside biogeography of moths in a fragmented landscape: biodiversity in native and agricultural habitats. Conservation Biology **15:**378–388.

Robinson, J. G. 1996. Hunting wildlife in forest patches: an ephemeral resource. Pages 111–130 in J. Schelhas and R. Greenberg, editors. Forest patches in tropical landscapes. Island Press, Washington, D.C.

Robinson, G. R., R. D. Holt, M. S. Gaines, S. P. Hamburg, M. L. Johnson, H. S. Fitch, and E. A. Martinko. 1992. Diverse and contrasting effects of habitat fragmentation. Science **257:**524–526.

Rodríguez, J., and F. Chinchilla. 1996. Lista de mamíferos de Costa Rica. Revista de Biología Tropical **44:**877–890.

Rosenzweig, M. 2003. Win-win ecology: how the Earth's species can survive in the midst of human enterprise. Oxford University Press, New York.

Rylands, A. B., and A. Keuroghlian. 1988. Primate populations in continuous and forest fragments in central Amazonia. Acta Amazonia **18:**291–307.

Sala, O., et al. 2000. Global biodiversity scenarios for the year 2100. Science **287:**1770–1774.

Saunders, D. A., R. J. Hobbs, and P. R. Ehrlich. 1993. Reconstruction of fragmented ecosystems: global and regional perspectives. Surrey Beatty & Sons, Chipping Norton, New South Wales, Australia.

Simberloff, D. 1986. The proximate causes of extinction. Pages 259–276 in D. M. Raup and D. Jablonski, editors. Patterns and processes in the history of life. Springer-Verlag, Berlin.

Soulé, M. E., D. T. Bolger, A. C. Alberts, R. Sauvajot, J. Wright, M. Sorice, and S. Hill. 1988. Reconstructed dynamics of rapid extinction of chaparral requiring birds in urban habitat islands. Conservation Biology **2:**75–92.

Sowls, L. K. 1984. The peccaries. University of Arizona Press, Tucson.

Stevens, S. M., and T. P. Husband. 1998. The influence of edge on small mammals: evidence from Brazilian Atlantic forest fragments. Biological Conservation **85:**1–8.

Sunquist, M. E., F. Sunquist, and D. E. Daneke. 1989. Ecological separation in a Venezuelan Llanos carnivore community. Pages 197–232 in K. Redford and J. F. Eisenberg, editors. Advance in Neotropical mammalogy. Smithsonian Institution Press, Washington, D.C.

Swank, W. G., and J. G. Teer. 1989. Status of the jaguar—1987. Oryx **23:**14–21.

Terborgh, J. 1988. The big things that run the world: a sequel to E. O. Wilson. Conservation Biology **2:**402–403.

Terborgh, J. 1999. Requiem for nature. Island Press, Covelo, California.

Terwilliger, V. J. 1978. Natural history of Baird's tapir on Barro Colorado island, Panama Canal Zone. Biotropica **10:**211–220.

Tilman, D., J. Fargione, B. Wolff, C. D'Antonio, A. Dobson, R. Howarth, D. Schindler, W. H. Schlesinger, D. Simberloff, and D. Swackhamer. 2001. Forecasting agriculturally driven global environmental change. Science **292:**281–284.

Treves, A., R. R. Jurewicz, L. Naughton-Treves, R. A. Rose, R. C. Willging, and A. P. Wydeven. 2002. Wolf depredation on domestic animals in Wisconsin, 1976–2000. Wildlife Society Bulletin **30:**231–241.

Trzcinski, M. K., L. Fahring, and G. Merriam. 1999. Independent effects of forest cover and fragmentation on the distribution of forest breeding birds. Ecological Applications **9:**586–593.

Tucker, G. M. 1997. Priorities for bird conservation in Europe: the importance of the farmed landscape. Pages 79–116 in D. J. Pain and M. W. Pienkowski, editors. Farming and birds in Europe: the common agricultural policy and its implications for bird conservation. Academic Press, San Diego, California.

Wilkie, D. S., and J. T. Finn. 1990. Slash-burn cultivation and mammal abundance in the Ituri Forest, Zaïre. Biotropica **22:**90–99.

Wilson, D. E., and D. H. Janzen. 1983. Mammals. Pages 426–442 in D. H. Janzen, editor. Costa Rican Natural history. Chicago University Press, Chicago.

Wilson, D. E., and D. M. Reeder (eds). 1993. Mammal species of the world: a taxonomic and geographic reference. 2nd edition. Smithsonian Institution Press, Washington, D.C.

Wilson, D. E., R. M. Timm, and F. Chinchilla. 2002. Mamíferos de Costa Rica. Pages 215–240 in G. Ceballos and J. A. Simonetti, editors. Diversidad y conservación de los mamíferos Neotropicales. Fondo de Cultura Económica, Mexico.

World Conservation Union (ICUN). 2000. 2000 IUCN red list of threatened animals. IUCN, Gland, Switzerland.

Zimmerman, B. L., and R. O. Bierregaard. 1986. Relevance of the equilibrium theory of island biogeography and species-area relations to conservation with a case from Amazonia. Journal of Biogeography **13:**133–143.

Appendix 1. Status of nonflying mammal species of the Las Cruces region, Coto Brus, Costa Rica.

Taxonomy (order, family, and species)	*English name*	*Vulnerability class*	*Locally extinct[a]*	*Locally extant[a]*	*Recorded in this study*		
					LC[b]	*FR[c]*	*OH[d]*
Didelphimorphia							
Didelphidae							
Didelphis marsupialis	common opossum	low		X	X	X	X
Philander opossum	gray four-eyed opossum	low		X	X	X	X
Chironectes minimus	water opossum	high	X*				
Marmosa mexicana	Mexican mouse opossum	low		X	X	X	X
Caluromys derbianus	Central American woolly opossum	low		X†			
Xenarthra							
Myrmecophagidae							
Myrmecophaga tridactyla	giant anteater	high	X*‡				
Tamandua mexicana	northern tamandua	moderate		X*†‡			
Cyclopes didactylus	silky anteater	high?		X§			
Megalonychidae							
Choloepus hoffmanni	Hoffmann's two-toed sloth	moderate		X	X**		
Bradypodidae							
Bradypus variegatus	brown-throated three-toed sloth	moderate		X*‡			
Dasypodidae							
Dasypus novemcinctus	nine-banded armadillo	low		X			X
Insectivora							
Soricidae							
Cryptotis nigriscens	blackish small-eared shrew	low		X	X**		
Primates							
Cebidae							
Saimiri oerstedii	red-backed squirrel monkey	high		X	X**		
Cebus capucinus	white-faced capuchin	moderate		X	X		
Alouatta palliata	mantled howler	high	X*‡				
Ateles geoffroyi	Central American spider monkey	high	X*‡				
Rodentia							
Sciuridae							
Sciurus granatensis	red-tailed squirrel	low		X	X	X	
Microsciurus alfari	Alfaro's pygmy squirrel	moderate		X	X**		
Geomyidae							
Orthogeomys cavator	Chiriqui pocket gopher	low		X*‡			
Heteromyidae							
Heteromys desmarestianus	forest spiny pocket gopher	low		X‡			
Muridae							
Melanomys caliginosus	dusky rice rat	low		X		X	X
Nyctomys sumichrasti	vesper rat	high		X	X**		
Oryzomys alfaroi	Alfaro's rice rat	low		X	X	X	X
Oryzomys couesi	Coue's rice rat	invasive		X‡			
Oligoryzomys fulvescens	northern pygmy rice rat	invasive		X	X	X	X
Peromyscus mexicanus	Mexican deer mouse	low		X‡			
Reithrodontomys mexicanus	Mexican harvest mouse	low		X‡			
Rheomys raptor	Goldman's water mouse	high		X‡			
Sigmodon hispidus	hispid cotton rat	invasive		X			X
Tylomys watsoni	Watson's climbing rat	high		X	X		
Zygodontomys brevicauda	common cane rat	invasive		X		X	X
Erethizontidae							
Coendou mexicanus	Mexican porcupine	moderate		X*‡			
Agoutidae							
Agouti paca	paca	moderate		X	X	X	X
Dasyproctidae							
Dasyprocta punctata	Central American agouti	moderate		X	X	X	
Echimydae							
Hoplomys gymnurus	armored rat	moderate?		X*‡			
Proechimys semispinosus	Tomes' spiny rat	moderate		X‡			
Carnivora							
Canidae							
Canis latrans	coyote	invasive		X*‡			
Urocyon cinereoargenteus	gray fox	low		X			X
Mustelidae							
Mustela frenata	long-tailed weasel	low		X	X	X	X
Eira barbara	tayra	moderate		X	X	X**	X
Galictis vittata	greater grison	high		X‡			
Conepatus semistriatus	common hog-nosed skunk	low		X	X		X
Spilogale putorius	spotted skunk	low		X		X	X
Lontra longicaudis	Neotropical river otter	high		X	X**	X**	

Appendix 1. (continued)

Taxonomy (order, family, and species)	*English name*	*Vulnerability class*	*Locally extinct*[a]	*Locally extant*[a]	*Recorded in this study*		
					LC[b]	*FR*[c]	*OH*[d]
Procyonidae							
Procyon lotor	northern raccoon	low		X	X	X	X
Nasua narica	white-nosed coati	moderate		X	X	X	X
Potos flavus	kinkajou	moderate		X	X	X	
Bassaricyon gabbii	olingo	high		X	X	X	
Bassariscus sumichrasti	cacomistle	moderate		X‡			
Felidae							
Pantera onca	jaguar	high	X*‡				
Puma concolor	puma	moderate		X*‡			
Leopardus pardalis	ocelot	moderate		X	X	X	X
Leopardus tigrinus	oncilla	high		X*‡			
Leopardus wiedii	margay	high		X*‡			
Herpailurus yaguarondi	jaguarundi	moderate		X		X	
Artiodactyla							
Tayassuidae							
Tayassu pecari	white-lipped peccary	high	X*‡				
Tayassu tajacu	collared peccary	moderate		X*‡			
Cervidae							
Mazama americana	red brocket	moderate		X*†‡			
Odocoileus virginianus	white-tailed deer	high		X*†‡			
Perissodactyla							
Tapiridae							
Tapirus bairdii	Baird's tapir	high	X*‡				
Lagomorpha							
Leporidae							
Sylvilagus dicei	forest rabbit	low		X	X*		X
Totals	61		7	54	25	20	19

[a] *For species not recorded in the study sites during the study period:* **local knowledge, including records supported by photos, skins, or skulls;* †*visual record during the study period, in the general region;* ‡*literature and other records by other scientists in recent years;* §*visual record after the end of the study period, in the general region;* ***visual record during the study period within 300 m from study sites.*
[b] *Records from the Las Cruces Forest Reserve.*
[c] *Records from within forest remnants, at coffee-forest-remnant and pasture-forest-remnant sites.*
[d] *Records from open habitats (in coffee and pasture at coffee, pasture, coffee-forest-remnant and pasture-forest-remnant sites).*