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# Passive sampling effects and landscape location alter associations between species traits and response to fragmentation

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*Abstract.* As tropical reserves become smaller and more isolated, the ability of species to utilize fragmented landscapes will be a key determinant of species survival. Although several ecological and life history traits commonly are associated with vulnerability to fragmentation, the combination of traits that are most highly influential and the effectiveness of those traits in predicting vulnerability across distinct landscapes, remains poorly understood. We studied use of forest fragments by 25 mid- and large-sized neotropical mammals in Guatemala to determine how seven species traits influence vulnerability to fragmentation. We measured vulnerability in two ways: one measure that did not remove passive sampling effects (proportion of fragments occupied), and one that did (difference in occupancy rates within continuous and fragmented sites). We also examined the influence of species traits on patch occupancy rates of the same set of mammals on two landscapes in Mexico. When not accounting for passive sampling effects, body size, home range size, and vulnerability to hunting influenced how species responded to fragmentation. However, after controlling for passive sampling effects, only vulnerability to hunting strongly influenced sensitivity to fragmentation. Species that were heavily hunted were much less common in forest patches than in continuous forest sites of the same sampling size. The cross-landscape comparison revealed both similarities and differences in the species traits that influenced patch occupancy patterns on each landscape. Given the ubiquity of hunting in tropical environments, our findings indicate that management efforts in fragmented landscapes that do not account for hunting pressure may be ineffective in conserving heavily hunted tropical species. Our study also indicates that species traits may be useful in predicting relative patch occupancy rates and/or vulnerability to fragmentation across distinct landscapes, but that caution must be used as certain traits can become more or less influential on different landscapes, even when considering the same set of species.

*Key words: detectability; fragmentation; hunting; landscape; occupancy; passive sampling; species traits; tropical mammals; vulnerability.*

## INTRODUCTION

Preserving biodiversity in the tropics requires integration of conservation efforts both within and outside of reserves. Protected areas in the tropics only cover 5–10% of remaining tropical forest (Myers 2002) and are inadequate for the protection of a large number of species (Rodrigues et al. 2004, Ceballos 2007, Jenkins and Giri 2007). Moreover, tropical reserves are becoming smaller and more isolated over time because of forest loss within park borders and in the surrounding landscape (deFries et al. 2005). Human-modified landscapes outside of tropical reserves therefore will serve an increasingly important role in preserving species diversity (Chazdon et al. 2009). These landscapes typically consist of remnant forest patches embedded in a matrix of agriculture, cattle pasture, and secondary forest regrowth. Although recent studies have shown that a subset of forest species use agricultural and pastural habitats (e.g., Daily et al. 2003, Harvey et al. 2006), remnant forest patches are probably the most important components to conservation of biodiversity within fragmented landscapes. These patches provide critical habitat for many forest-dependent tropical species living outside of protected areas (Turner and Corlett 1996, Laurance and Bierregaard 1997).

Substantial interspecies variation exists in the ability of species to occupy or use forest fragments (Laurance 1991, Gascon et al. 1999, Laurance et al. 2002). Survival of species within forest patches is determined by a combination of patch and landscape attributes and the life history or ecological traits of species (Henle et al. 2004). An understanding of how species traits influence distribution or abundance in forest patches is important for identifying generalities in response to habitat loss and fragmentation (Henle et al. 2004, Ewers and Didham 2006). Such knowledge is beneficial to predicting and mitigating species loss in human-dominated landscapes (Laurance 1991, Davies et al. 2000).

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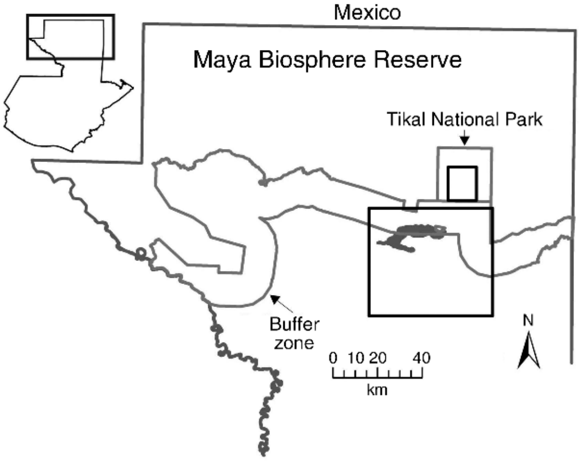

FIG. 1. The inset map shows the location of the Maya Biosphere Reserve in northern Guatemala. The enlarged portion shows the location of our study sites in relation to the Maya Biosphere Reserve. Continuous forest sites (upper black box) were located in the south-central portion of Tikal National Park, and forest patches (lower black box) were located in the buffer zone of the Maya Biosphere Reserve and private lands farther to the south.

Several species traits are commonly associated with vulnerability to fragmentation (hereafter we use the term "fragmentation" to denote both loss and fragmentation of habitat). However, the combination of traits that are most highly influential, and the degree to which those traits determine vulnerability on distinct landscapes, remains poorly understood for most taxa (Henle et al. 2004). Three factors confound analyses of how species traits influence vulnerability to fragmentation. First, studies do not always separate "passive sampling effects" from actual effects of habitat fragmentation (Johnson 2001, Haila 2002). Passive sampling effects are apparent patterns in the relative distribution or abundance of organisms among habitat fragments that are merely artifacts of sampling. Such effects occur because less abundant or patchily distributed species would be expected by chance alone to be present in fewer fragments than more abundant or evenly distributed species (Bolger et al. 1991, Johnson 2001, Haila 2002). These species are not necessarily more vulnerable to habitat fragmentation, but will be categorized that way if passive sampling effects are not taken into account in the analysis. A second common problem is that issues of detectability often are not considered in analyses. Species that appear to be vulnerable could merely be those that are harder to detect (Fleishman and Mac Nally 2007). Inclusion of these elusive species in the analysis without accounting for detectability will underestimate the actual number of patches occupied by such species (MacKenzie et al. 2002) and make identification of the real relationships between vulnerability of a species and ecological or life history traits more difficult. Finally, the ability to identify influential ecological and life history traits is hindered by a lack of cross-landscape comparisons. The opportunity rarely is available to examine how the same set of species respond to habitat fragmentation in different landscapes. This limits our ability to identify generalities in how species traits influence response to habitat patchiness and to evaluate the relative role of context-specific environmental factors vs. more intrinsic biological factors in controlling response patterns.

We addressed these issues with a study of mammal distribution patterns in a fragmented tropical landscape in northern Guatemala. We studied use of forest fragments and continuous forest sites by 25 mid- and large-sized mammals to determine how species traits influence vulnerability to habitat fragmentation. We tested the generality of these results with a comparison of patch occupancy patterns of all 25 mammal species across three distinct fragmented landscapes and addressed several specific questions related to the influence of species traits on vulnerability:

1) What are the most important species traits influencing vulnerability to habitat fragmentation of mammals in Guatemala?
2) Does accounting for passive sampling effects alter the relative importance of species traits in determining vulnerability to habitat fragmentation? We predicted that traits influencing distribution of species in an unaltered landscape (i.e., body size, home-range size, reproductive rate, trophic level) would be less important in determining vulnerability to fragmentation once sampling effects were taken into account in the analysis.
3) Do the same set of ecological and life history traits explain interspecific variation in vulnerability to fragmentation on different landscapes? We predicted that the same species traits would explain vulnerability across landscapes. To address this question, we re-analyzed data from two studies conducted in nearby Mexican landscapes with the same species (Estrada et al. 1994, Urquiza-Haas et al. 2009) so that the results were comparable with our Guatemalan study. To our knowledge, this is the first attempt to look at whether or not similar suites of ecological and life history traits determine response to fragmentation for the same set of species inhabiting different landscapes.

## METHODS

### *Study area*

We conducted this study in a 300 000-ha area in the Petén region of northern Guatemala (Fig. 1). The northernmost part of the study area is an intact landscape of humid subtropical forest located within Tikal National Park, which itself is situated within the larger Maya Biosphere Reserve (an UNESCO world heritage site and the central section of the largest contiguous tropical forest in Central America; V. H. Ramos, *personal communication*). The southern part of

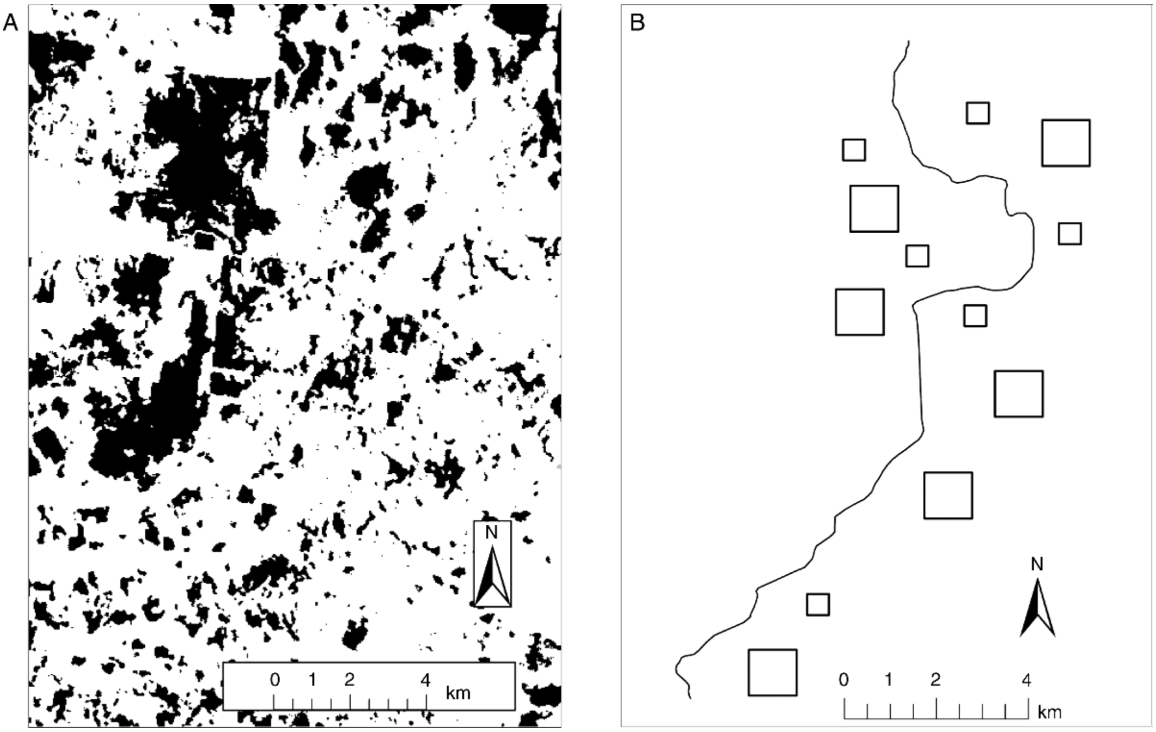

FIG. 2. (A) Map showing a small portion of our fragmented study area, with forest cover in black, and matrix habitat (agriculture/pasture and regenerating forest) in white. (B) Map showing our continuous forest study area, with black boxes indicating the position of 20- and 100-ha study sites in Tikal National Park. The central park road is also shown in black. These study sites were embedded within completely continuous forest cover.

the study area is a highly fragmented landscape located within the buffer zone of the Maya Biosphere Reserve and on private lands farther to the south. This area was formerly contiguous forest, but now consists of a diverse collection of primary rainforest patches embedded in a matrix of secondary and regenerating forest, cattle pasture and agricultural land (Fig. 2A). Forest destruction and fragmentation began in the late 1970s. Forest patches are thus no more than 30 years old. Forest cover in this area consists of subtropical humid rainforest with scattered patches of seasonally inundated bajo forest and a fringe of savannah forest in the south. Altitudinal variation is minimal (130 to 400 m above sea level). Annual average temperature of this region is 21–24°C, and annual average precipitation is 1350 mm with a marked dry season from December to May when the average monthly rainfall is only 60 mm.

We selected 50 primary rainforest patches that ranged in size from 2.9 to 445.5 ha and 12 sites in continuous forest (six sites each of 20 ha and 100 ha; Fig. 2B) as our study sites. Rainforest patches contained a diverse collection of tree species, but were often dominated by some combination of *Brosimum alicastrum, Manilkara zapota, Ficus* sp., *Vitex gaumeri, Pouteria* sp., *Sebastiana longicuspis*, *Terminalia amazonia*, *Alseis yucatánensis*, *Bursera simaruba*, *Spondias mombin*, *Aspidosperma megalocarpon*, *Dendropanax arboreus*, *Protium copal*, *Pimenta dioica*, and *Cedrela odorata*. We did not sample rainforest patches that were severely degraded by logging or fire, but we sampled a number of lightly degraded sites. Lightly degraded sites were those that still had a largely intact overstory of trees and where the effects of past fires were limited to less than 25% of the patch area. We did not sample patches of bajo forest, savannah forest, or secondary forest. Almost all forest patches in our study were used to some degree by local inhabitants for collection of non-timber forest products, hunting, or cattle grazing. Study sites in continuous forest were similar in tree composition and density to rainforest patches, but were surrounded by uninterrupted forest cover. Based on these characteristics, we made the assumption that these sites in continuous forest were analogous to pre-fragmentation conditions in the fragmented part of the study area. Continuous forest sites were situated greater than 500 m, but less than 3 km from the main road in Tikal National Park (Fig. 2B). This distance restriction was established to take advantage of the decreased hunting pressure on mammals close to the main road and archaeological ruins (which are patrolled more heavily by park guards), while minimizing disturbance related to traffic and human visitors to the park.

### *Species ecological and life history traits*

We determined values of seven life history and ecological traits for each species using field guides and

TABLE 1. Life history and ecological traits of mammals studied in northern Guatemala.

| Species | Common name | Body mass (kg) | Home range (ha) | Trophic level† | Repro. rate (young/year) | Dietary breadth‡ | Habitat breadth‡ | Hunting vuln.§ |
|---|---|---|---|---|---|---|---|---|
| *Didelphis marsupialis* | common opossum | 1.5 | 12 | 2 | 12 | 7 | 7 | 1 |
| *Didelphis virginianus* | Virginia opossum | 1.8 | 12 | 2 | 12 | 7 | 7 | 1 |
| *Dasypus novemcinctus* | nine-banded armadillo | 3.0 | 6 | 2 | 4 | 5 | 6 | 3 |
| *Tamandua mexicana* | northern tamandua | 6.2 | 25 | 3 | 1 | 1 | 5 | 1 |
| *Alouatta pigra* | Yucatán black howler | 6.9 | 17 | 1 | 0.5 | 2 | 2 | 2 |
| *Ateles geoffroyi* | Central American spider monkey | 7.0 | 250 | 1 | 0.3 | 1 | 1 | 2 |
| *Leopardus pardalis* | ocelot | 9.7 | 1695 | 3 | 0.5 | 6 | 3 | 2 |
| *Leopardus wiedii* | margay | 3.6 | 1095 | 3 | 0.5 | 6 | 3 | 2 |
| *Panthera onca* | jaguar | 65.9 | 5600 | 3 | 1 | 3 | 3 | 3 |
| *Puma concolor* | puma | 45.0 | 6500 | 3 | 1.3 | 3 | 4 | 3 |
| *Puma yagouaroundi* | jaguarundi | 5.2 | 1065 | 3 | 2.5 | 7 | 5 | 2 |
| *Urocyon cinereoargenteus* | gray fox | 2.7 | 95 | 2 | 4 | 7 | 6 | 1 |
| *Conepatus semistriatus* | striped hog-nosed skunk | 2.5 | 103 | 2 | 4 | 4 | 4 | 1 |
| *Eira barbara* | tayra | 4.5 | 1375 | 2 | 2.5 | 5 | 4 | 1 |
| *Nasua narica* | white-nosed coati | 4.6 | 60 | 2 | 3.5 | 4 | 3 | 2 |
| *Potos flavus* | kinkajou | 3.3 | 23 | 1 | 1 | 4 | 2 | 1 |
| *Procyon lotor* | northern raccoon | 5.6 | 50 | 2 | 3.5 | 8 | 6 | 2 |
| *Tapirus bairdii* | Baird's Tapir | 240 | 125 | 1 | 0.5 | 3 | 3 | 3 |
| *Pecari tajacu* | collared peccary | 19.0 | 249 | 2 | 2 | 6 | 3 | 3 |
| *Tayassu pecari* | white-lipped peccary | 33.5 | 2387 | 2 | 2 | 5 | 1 | 3 |
| *Mazama americana* | red brocket deer | 22.0 | 52 | 1 | 1 | 3 | 2 | 3 |
| *Odocoileus virginianus* | white-tailed deer | 34.0 | 284 | 1 | 1.5 | 3 | 5 | 3 |
| *Coendou mexicanus* | Mexican porcupine | 2.0 | 19 | 1 | 1 | 3 | 2 | 1 |
| *Agouti paca* | paca | 8.5 | 2 | 1 | 1.5 | 4 | 4 | 3 |
| *Dasyprocta punctata* | Central American agouti | 3.5 | 2 | 1 | 1.5 | 4 | 3 | 3 |

† Key to trophic levels: 1, primarily browser/grazer or frugivore; 2, omnivore; 3, primarily carnivore/myrmecophage.

‡ Values for dietary and habitat breadth based on number of food or habitat categories used. Higher values indicate more generalized diets or habitats. See Appendix A for full description of trait categories.

§ Key to hunting vulnerability: 1, rarely/never hunted or killed; 2, occasionally hunted; 3, often hunted (e.g., a preferred game species).

published literature (Table 1). The procedure and literature used to determine values for each trait category are described in Appendix A. These traits were chosen because they commonly are hypothesized to influence vulnerability to fragmentation in mammals based on empirical and theoretical evidence (Laurance 1991, Peres 2001, Henle et al. 2004, Ewers and Didham 2006). Ecological and life history variables used in our study were correlated. Consequently, we performed a principal-components analysis (PCA) using proc FACTOR in SAS (SAS Institute 2008) to reduce the number of variables and remove correlations. We log-transformed body mass and home-range size prior to input in the PCA analysis. Results from the PCA indicate that 83% of the variation in the seven traits is explained by just three axes. Based on factor loadings, these three axes each represent a distinct aspect of mammalian biology and ecology (Table 2). PCA axis 1 (reproduction/niche specialization axis) represents a gradient from species with low reproductive rates and specialized diets and habitats, to species with high reproductive rates and generalized diets and habitats. PCA axis 2 (body size/hunting vulnerability axis) represents a gradient from species with small body size and low vulnerability to hunting (i.e., are rarely or never hunted) to species with large body size and high vulnerability to hunting (i.e., heavily hunted/persecuted species). PCA axis 3 (home range/trophic level axis) represents a gradient from species with small home ranges and lower trophic levels to species with large home ranges and higher trophic levels.

### *Mammal surveys*

We determined mammal presence/absence within forest patches and continuous sites from January 2006 to August of 2008 using camera traps and visual censuses. This combination of techniques gave us the best chance to detect the presence of elusive arboreal and terrestrial species. We avoided sampling during mid-late wet season (mid-September to mid-December) because of problems with camera performance in very wet conditions. We surveyed approximately half of the forest patches and continuous forest sites in the dry season, and half in the early wet season. This eliminated the potential for bias in our results in fragmented vs. continuous forest sites because of season of sampling.

We deployed camera traps for a 16-day period in each site. A photograph of a species at any camera within a site was considered an indication of presence. We recorded presence/absence for each species within each site after every 4-day interval. By breaking up the 16-day period into 4-day sessions, we created a series of repeat detection/non-detection data (i.e., a detection history) for use in modeling detection probabilities for each

Table 2. Factor loadings from principal-components analysis of ecological and life history traits.

| Variable | PCA axis 1 | PCA axis 2 | PCA axis 3 |
|---|---|---|---|
| Body mass | −0.32† | 0.84 | 0.23 |
| Home range | −0.21 | 0.24 | 0.89 |
| Trophic level | 0.29 | −0.09 | 0.87 |
| Reproductive rate | 0.82 | −0.30 | −0.15 |
| Dietary breadth | 0.80 | −0.12 | 0.23 |
| Habitat breadth | 0.89 | −0.15 | 0.00 |
| Hunting vulnerability | −0.13 | 0.94 | −0.05 |
| Eigenvalues | 3.07 | 1.79 | 0.98 |
| Variation explained (%)‡ | 43.82 | 25.50 | 14.04 |

*Note:* See *Methods: Species ecological and life history traits* for interpretation of axes.

† Factor loadings indicate the correlation coefficients between the original variables and the "new" PCA variables.

‡ Total variance explained by the three axes = 84%.

species. Because absence of a species could be the result of either true absence or failure to detect a species, detectability must be included to avoid underestimating occupancy (MacKenzie et al. 2006).

We placed camera traps in a variety of locations in each study site to maximize the number of species photographed. These locations included roads, small and large game trails, water holes, den sites, and other areas containing substantial signs of animal use such as tracks, digging, or scraping. We placed camera traps at least 10 m from the edge of patches, with the sensor approximately 10–20 cm off the ground so that smaller species could not avoid detection by walking under the sensor. We used both passive (Leaf River model C-1BU; Leaf River Outdoor Products, Taylorsville, Mississippi, USA) and active (Trailmaster model 1500; Goodson and Associates, Inc., Lenexa, Kansas, USA) infrared camera traps in approximately equal proportions within each site. We placed more cameras in larger sites (Table 3) and spaced them farther apart in order to cover a larger area. We included patch size in assessments of detectability to account for potential biases related to unequal sampling per unit area in the patches

Camera-trapping was ineffective for sampling arboreal species, as well as two terrestrial species (white-tailed deer [*Odocoileus virginianus*] and collared peccaries [*Pecari tajacu*]). In order to document presence/absence of these species, we performed visual censuses of sites in the early morning (between sunrise and three hours after sunrise). Surveys were repeated five times within a two-week period for each site, resulting in a series of detection/non-detection data for use in modeling detection probabilities. In order to cover as much of the site as possible and to increase our chance of encountering species, we did not cut transects for walking within each site. We surveyed sites by walking along small roads, human foot paths, and game trails, and by walking through sections without any obvious trails. We walked approximately 1 km/h and recorded direct observations of animals, vocalizations, and well-defined tracks as indications of presence within the site. For small sites (less than 10 ha), we were able to walk through most or all of the site during each session. For sites too large to survey completely in one session, we divided the site into two to four sections and randomly chose a section to walk each session. We repeated this process until we had five surveys for the site.

For 17 forest patches and four continuous sites, we also conducted visual censuses two hours prior to sunrise to search for arboreal nocturnal mammals, particularly kinkajous (*Potos flavus*). We cut meter-wide transects within multiple sections of each site in order to move through the fragments during the night. We walked transects at a very slow pace (0.5 km/h) and used flashlights to search for mammals in the trees. We repeated nocturnal surveys five times, walking a different transect each night. For both daytime and nocturnal surveys, we walked greater distances in larger patches, but did not walk the same distance per unit area in small and large patches (Table 3). As with camera

Table 3. Sampling effort employed for camera trapping and visual censusing of mammals in forest patches and continuous forest sites.

| | Number of | | Distance walked per session (km)† | |
|---|---|---|---|---|
| Site size | Patches surveyed | Cameras placed in patch | Daytime surveys | Nighttime surveys |
| 2.9–10 | 12 | 7 | 0.8 | 0.5 |
| >10–20 | 13 | 10 | 1.0 | 0.8 |
| >20–40 | 12 | 14 | 1.2 | 1.0 |
| >40–80 | 5 | 17 | 1.5 | 1.0 |
| >80–160 | 13 | 20 | 1.8 | 1.2 |
| >160–320 | 4 | 25 | 2.0 | 1.5 |
| >320 | 3 | 28 | 2.0 | 1.5 |

† Distances listed were walked five times in each fragment.

traps, we included patch size in assessments of detectability to account for potential biases related to unequal sampling per unit area in the patches.

### *Measuring vulnerability to fragmentation*

We modeled patch occupancy and detection probabilities for each species using logistic regression in program PRESENCE (*available online*).[2] Because many species in our study were capable of moving in and out of patches during sampling, the occupancy estimator is best interpreted as "probability of use" of a patch, rather than probability of occupancy. The detection parameter is best interpreted as probability of being within the patch and detected during sampling (MacKenzie et al. 2006). For ease of presentation, we will use traditional occupancy terminology in this paper.

We used three measures of vulnerability: (1) overall proportion of forest patches occupied by each species, (2) difference between probability of occupancy in forest patches and continuous forest sites of 20-ha size, and (3) difference between probability of occupancy in forest patches and continuous forest sites of 100 ha in size. These two later measures account for passive sampling effects in the analysis by comparing expected patterns of occupancy in continuous forest sites with observed patterns in forest fragments of a similar sampling size. The two sizes (20 ha and 100 ha) were chosen to represent the size range of most patches in our study area (Table 3). Although the ideal way to account for passive sampling effects is to have pre- and post-fragmentation information on species distribution, such information is rarely available and our comparative approach is appropriate given similarities between study sites in continuous forest and fragmented areas.

To determine measures of vulnerability, we modeled occupancy and detection probabilities using detection/non-detection data collected from all 50 forest patches and 12 continuous forest sites for 24 species. For kinkajous, modeling was limited to the 17 forest patches and four continuous forest sites surveyed during predawn hours. In program PRESENCE, we first modeled detection as a function of size of the site (i.e., patch size or size of the site in continuous forest) and a categorical variable representing fragmented vs. continuous sites, keeping occupancy constant. We determined the best fit detection model for each species using $\text{AIC}_\text{c}$ (Burnham and Anderson 2002). Species with less than seven total detections in all sites combined were considered to have constant detection probabilities. We then took the best fit or constant detection model, and modeled probability of occupancy using size of the site and fragmented vs. continuous forest status. Based on this final model, we calculated the overall proportion of patches occupied by summing the individual occupancy estimates for each patch (excluding occupancy estimates from continuous sites) and dividing by the total number of patches. This was our first measure of vulnerability, with higher proportion of patches occupied indicating less vulnerable species. For our second measure of vulnerability, we used occupancy models for each species to estimate the probability of occupancy in a 20-ha forest site and a 20-ha patch and subtracted the two values. We repeated this process for 100-ha sites, which was our third measure of vulnerability. High positive values resulting from these two analyses indicate species that had high occupancy probabilities in continuous forest sites, but low occupancy probabilities in forest patches of the same size. These species are considered highly vulnerable to habitat fragmentation. Conversely, high negative values indicate species that benefit from habitat fragmentation, as they were more commonly encountered in forest patches than in continuous forest sites of the same size. For the analysis of vulnerability, we limited the number of covariates used in modeling detection and occupancy to two because of sparse data sets for several species (e.g., jaguars, tapir, puma [*Puma concolor*]).

### *Influence of species traits on vulnerability*

We evaluated the influence of ecological and life history traits on vulnerability to fragmentation with multiple regression and hierarchical partitioning. We used two approaches to account for correlations between the species traits: (1) we used the uncorrelated PCA axes of species traits as predictor variables in a multiple regression, and (2) we used hierarchical partitioning analysis (Chevan and Sutherland 1991) to tease apart the independent contribution of each individual species trait. For the first approach, we ran three separate regressions with proc REG in SAS (SAS Institute 2008) using the three PCA axes as predictor variables and our three measures of vulnerability as dependent variables. Because the PCA axes are orthogonal, partial $R^2$ values of each axis can be used to evaluate the relative influence of each axis on the response variable. For the second approach, we employed hierarchical partitioning analysis with the original seven species traits as predictor variables using the "hierpart" macro in SAS (Murray and Conner 2009). Hierarchical partitioning analysis calculates the increase in model fit associated with each predictor variable by averaging the goodness of fit increase across the hierarchy of models in which the variable appears (see [Chevan and Sutherland 1991] for additional explanation). This analysis estimates the independent explanatory power of a variable (i.e., effect on a response variable attributable solely to that particular predictor) and joint explanatory power (i.e., effect on a response variable attributable to joint action with other predictors) of each predictor variable. The independent explanatory power serves as the appropriate measure of the influence of a predictor variable on a response (Chevan and Sutherland 1991, Mac Nally 2000). The key advantage of hierarchical partitioning analysis is

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[2] ⟨http://www.mbr-pwrc.usgs.gov/software/presence.html⟩

that this method can provide an accurate assessment of the independent effect of a predictor variable, even in the presence of multicollinearity (Murray and Conner 2009; but see Smith et al. [2009] for a criticism of this approach).

### *Cross-landscape comparison of vulnerability*

We compared results of our analysis to two other studies that involved the same species (Estrada et al. 1994, Urquiza-Haas et al. 2009). Estrada et al. (1994) studied patch occupancy of small and large mammals in 35 lowland rainforest fragments of Los Tuxtlas, Mexico, and Urquiza-Haas et al. (2009) studied patch occupancy of mid- and large-sized mammals in 147 fragments of tropical dry forest in Yucatán Peninsula, Mexico (hereafter referred to as Yucatán). As in our study, the overall proportion of fragments occupied was determined for each species, although the methodology of the two studies differed from our own. Estrada et al. (1994) used live traps and diurnal/nocturnal visual surveys to determine presence/absence of mammals within patches, and Urquiza-Haas et al. (2009) used interviews with landowners to determine patch occupancy. Patch occupancy estimates were not listed in the original paper for the Los Tuxtlas data, but were obtained from the author (A. Estrada, *personal communication*). Results of these two studies were not corrected for passive sampling effects, and thus are comparable only to our vulnerability measure of "overall proportion of fragments occupied."

All species were included in our comparison ($n = 25$) because these species or closely related species were found in all three landscapes. Patch occupancy patterns of common and Virginia opossums (*Didelphis marsupialis* and *Didelphis virginianus*) were evaluated at the genus level in the Yucatán landscape, but were treated as separate species for the Los Tuxtlas and Guatemalan landscapes. We therefore treated them as separate species for the Yucatán landscape, and assigned each species the same patch occupancy as was recorded for the two species combined (i.e., 100%). Whether or not we combine data for these two species did not alter results of the subsequent analysis. For the Los Tuxtlas landscape, data were collected on *Alouatta palliata* and *Dasyprocta mexicana* instead of *Alouatta pigra* and *Dasyprocta punctata* as in our study and the Yucatán study. However, because of similarities in morphology and ecology of these species (Reid 1997), we included them in the analysis and treated them as equivalent species.

We tested for general correlations between the rankings of species vulnerability in our study and the two Mexican studies using Spearman's correlation coefficients. This analysis tested whether or not species that tended to be ranked lower in terms of overall patch occupancy in our study also tended to rank lower in the other two landscapes. We also performed multiple regression and hierarchical partitioning analysis to determine which combination of species traits were most important in influencing patch occupancy on each landscape. We made the assumption that the values used in our study for the ecological and life history traits of species could be applied to those same species in the Mexican landscapes. This assumption is likely to hold for some traits such as body size and trophic level, but may not hold for other traits such as home-range size. However, given the lack of region specific information for many of these traits and the geographic proximity of the three study areas, we believe our approach is appropriate as a first assessment of cross-landscape generalities in species response to fragmentation.

## Results

We detected 25 species of mid- and large-sized mammals within our study sites in 12 960 camera-trap nights and 400 km of visual surveys. All species detected in continuous forest sites also were detected in one or more fragments, except for white-lipped peccaries (*Tayassu pecari*), which only were detected in continuous forest. The number of species detected in forest patches varied between 3 and 19, with significantly more species detected in larger patches ($P < 0.01$). We detected between 7 and 16 species in continuous forest sites, with marginally more species detected in the larger 100-ha sites ($P < 0.10$).

### *Vulnerability to fragmentation*

Relative vulnerability of species to fragmentation as measured by proportion of patches occupied varied greatly among species. Occupancy of forest patches in our study area ranged from 0 (e.g., white-lipped peccaries) to nearly 100% (e.g., kinkajous; Table 4). Best-fit models and parameter estimates for each species are presented in Appendix B. Inclusion of detectability in the analysis resulted in substantial increases in overall patch occupancy for species that were difficult to detect (Table 4). For example, the estimated percentage of patches occupied increased 20.8% and 19.2% from the naive estimate that did not include detectability for the Mexican porcupine (*Coendou mexicanus*) and tayra (*Eira barbara*), respectively.

Relative vulnerability as measured by differences in occupation of continuous and fragmented forest sites of the same size also varied greatly between species (Table 4). Some species were much more common in continuous forest, such as white-tailed deer, red brocket deer (*Mazama americana*), and puma, whereas others were much more commonly encountered in forest patches, including northern tamandua (*Tamandua mexicana*) and northern raccoon (*Procyon lotor*). Results of the vulnerability analysis using 20-ha and 100-ha sites were similar for all species.

### *Influence of species traits on vulnerability*

Our measure of vulnerability that was uncorrected for sampling effects (overall proportion of patches occu-

TABLE 4. Three measures of vulnerability to habitat fragmentation for the Guatemalan study site, and patch occupancy estimates for Yucatan and Los Tuxtlas landscapes based on data in Estrada et al. (1994) and Urquiza-Haas et al. (2009).

| Species | Naïve PFO† | Overall PFO‡ | Diff. occ. 20-ha sites§ | Diff. occ. 100-ha sites§ | PFO Yucatan¶ | PFO Los Tuxtlas# |
|---|---|---|---|---|---|---|
| *Didelphis marsupialis* | 66.0 | 76.5 | −33.5 | −33.9 | 100 | 54.3 |
| *Didelphis virginianus* | 31.9 | 36.0 | 15.3 | 16.8 | 100 | 40.0 |
| *Dasypus novemcinctus* | 70.0 | 70.4 | −0.9 | −0.8 | 100 | 14.3 |
| *Tamandua mexicana* | 62.0 | 86.9 | −77.4 | −77.5 | 95.9 | 17.1 |
| *Alouatta pigra*‖ | 80.0 | 80.7 | 23.9 | 13.0 | 32.0 | 45.7 |
| *Ateles geoffroyi* | 38.0 | 38.3 | 79.7 | 63.8 | 55.1 | 2.9 |
| *Leopardus pardalis* | 34.0 | 45.5 | 24.9 | 10.5 | 81.0 | 2.9 |
| *Leopardus wiedii* | 52.0 | 57.1 | −11.3 | −10.6 | 64.0 | 5.7 |
| *Panthera onca* | 6.0 | 9.0 | 14.5 | 28.0 | 55.1 | 0.0 |
| *Puma concolor* | 6.0 | 14.7 | 66.4 | 84.0 | 66.7 | 2.9 |
| *Puma yagouaroundi* | 24.0 | 36.1 | −17.5 | −28.1 | 79.6 | 14.3 |
| *Urocyon cinereoargenteus* | 42.0 | 45.7 | 17.8 | 17.8 | 100 | 0.0 |
| *Conepatus semistriatus* | 56.0 | 60.2 | 0.1 | 0.1 | 100 | 8.6 |
| *Eira Barbara* | 24.0 | 43.2 | −25.7 | −28.3 | 94.6 | 14.3 |
| *Nasua narica* | 60.0 | 62.4 | 7.3 | 7.4 | 98.0 | 20.0 |
| *Potos flavus* | 88.0 | 96.9 | −25.0 | −21.2 | 93.2 | 17.1 |
| *Procyon lotor* | 48.0 | 71.0 | −36.0 | −38.3 | 97.3 | 17.1 |
| *Tapirus bairdii* | 2.0 | 2.3 | 26.7 | 47.9 | 12.2 | 0.0 |
| *Pecari tajacu* | 14.0 | 16.2 | 50.2 | 38.6 | 91.2 | 14.3 |
| *Tayassu pecari* | 0.0 | 0.0 | 0.0 | 16.7 | 4.1 | 0.0 |
| *Mazama americana* | 30.0 | 31.1 | 50.2 | 46.3 | 84.4 | 2.9 |
| *Odocoileus virginianus* | 20.0 | 24.4 | 74.3 | 64.2 | 91.8 | 0.0 |
| *Coendou mexicanus* | 36.0 | 56.8 | −28.4 | −31.3 | 92.5 | 22.9 |
| *Agouti paca* | 66.0 | 66.4 | 30.3 | 20.5 | 98.0 | 40.0 |
| *Dasyprocta punctata*‖ | 44.0 | 44.3 | 52.5 | 45.2 | 98.0 | 28.6 |

† Percentage of fragments occupied (PFO): estimated percentage of patches occupied in Guatemala not corrected for detectability ([number of fragments where species was detected at least once/total number of fragments] × 100).

‡ Estimated percentage of patches occupied in Guatemala corrected for detectability ([sum of individual occupancy probabilities from each patch/total number of patches] × 100).

§ Occupancy probability (expressed as percentage) of continuous forest sites minus occupancy probability in forest patch of same size.

¶ Percentage of patches occupied in Yucatan based on interviews with landowners (Urquiza-Haas et al. 2009).

# Percentage of patches occupied in Los Tuxtlas based on live trapping and visual censuses (Estrada et al. 1994).

‖ For Los Tuxtlas data set, data were collected on *Alouatta palliata* and *Dasyprocta mexicana*.

pied) was influenced strongly by PCA axis 2 and 3 (Table 5). This indicates that species that are larger and more heavily hunted, and species that have larger home ranges and higher trophic levels, tended to occupy fewer fragments than those species that did not have those traits. Parameter estimates and partial $R^2$ values indicate that axis 2 (body size/hunting axis) was the most important predictor. Overall, the model with all three

TABLE 5. Results from regression analysis using PCA axes as predictor variables and three measures of vulnerability to fragmentation as response variables.

| Predictor variables | Parameter estimate | $P$ | Partial $R^2$ |
|---|---|---|---|
| Response variable = proportion of fragments occupied | | | |
| Axis 1 (reproduction/specialization) | 0.01 ± 0.04 | 0.76 | 0.01 |
| Axis 2 (body size/hunting) | −0.18 ± 0.04 | <0.01 | 0.45 |
| Axis 3 (home range/trophic level) | −0.09 ± 0.04 | 0.03 | 0.12 |
| Response variable = difference in occupancy of 20-ha continuous forest sites and 20-ha patches | | | |
| Axis 1 (reproduction/specialization) | −0.08 ± 0.06 | 0.24 | 0.04 |
| Axis 2 (body size/hunting) | 0.23 ± 0.06 | <0.01 | 0.34 |
| Axis 3 (home range/trophic level) | −0.07 ± 0.06 | 0.30 | 0.03 |
| Response variable = difference in occupancy of 100-ha continuous forest sites and 100-ha forest patches | | | |
| Axis 1 (reproduction/specialization) | −0.08 ± 0.06 | 0.22 | 0.04 |
| Axis 2 (body size/hunting) | 0.25 ± 0.06 | <0.01 | 0.44 |
| Axis 3 (home range/trophic level) | −0.04 ± 0.06 | 0.49 | 0.01 |

*Notes:* Parameter estimates are means ± SE.

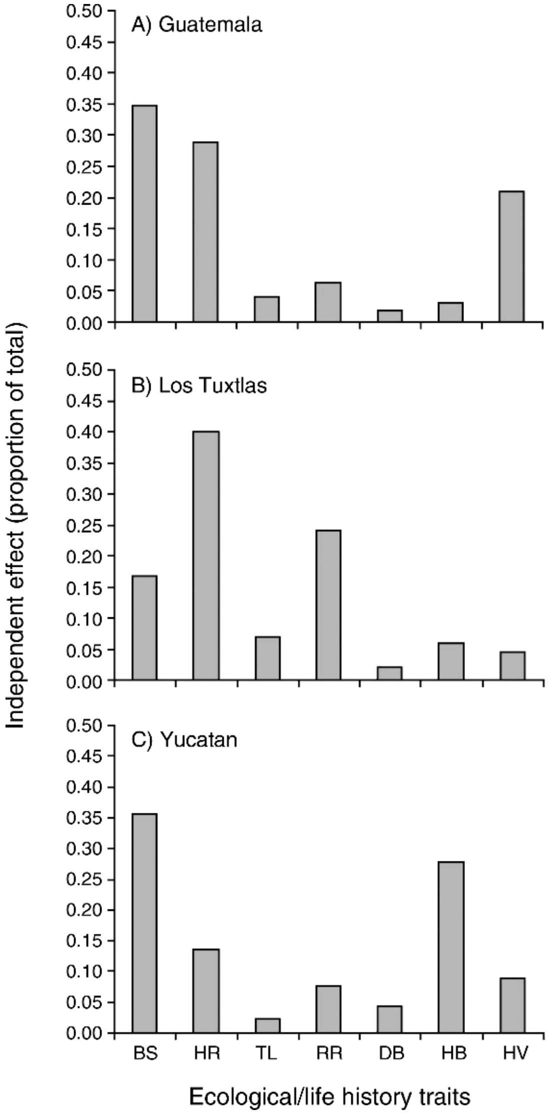

FIG. 3. Results of hierarchical portioning analysis for (A) proportion of patches occupied in Guatemala, (B) proportion of patches occupied in Los Tuxtlas, Mexico, based on data in Estrada et al. (1994), (C) proportion of patches occupied in Yucatán, Mexico, based on data in Urquiza-Haas et al. (2009). Key to abbreviations: BS, body size; HR, home range size; TL, tropic level; RR, reproductive rate; DB, dietary breadth; HB, habitat breadth; HV, hunting vulnerability.

predictors explained a large amount of variation in patch occupancy ($R^2 = 0.58$). Results from the hierarchical partitioning analysis generally confirm the results from the PCA regression analysis, but enabled us to look at the importance of individual predictors in more detail (Fig. 3A). The overall proportion of fragments occupied was influenced most strongly by body size, home range, and to a lesser extent by hunting vulnerability.

Accounting for passive sampling effects altered the relative influence of species traits on vulnerability to fragmentation. Our measure of vulnerability corrected for sampling effects (the difference in occupancy between fragmented and continuous forest sites of similar size) was influenced strongly only by axis 2 (Table 5). This result was similar for either 20-ha or 100-ha sites. This indicates that species that are larger and more heavily hunted tended to be much more likely to occupy continuous forest sites than forest patches of the same size. Overall fit of these models was slightly lower, with only 41.3% and 49.2% of the variation explained by the full models for 20-ha and 100-ha sites, respectively. Hierarchical partitioning demonstrated that this measure of vulnerability was driven largely by differences in hunting vulnerability, which accounted for almost half of the explained variance in both cases (Fig. 4A and B).

### *Cross-landscape comparison*

In general, species that had lower levels of patch occupancy in our study also had lower levels of patch occupancy in the Los Tuxtlas and Yucatán landscapes ($r = 0.66$ and 0.52, respectively). This agreement between studies only holds when comparing the rankings of species in terms of their *relative* vulnerability; absolute values of patch occupancy differed substantially between the studies (Table 4). All three PCA axes had a significant effect on vulnerability to fragmentation for species in Los Tuxtlas ($P = 0.022$, 0.026, and 0.002, respectively), and these axes explained 54.2% of the variation in the response. In Yucatán, the reproduction/niche breadth and body size/hunting axes were related to vulnerability ($P = 0.015$ and 0.011, respectively), and all three axes explained 44.0% of the variation in proportion of patches occupied. Hierarchical partitioning generally agreed with the PCA analyses but with some added detail on individual predictors. For the Los

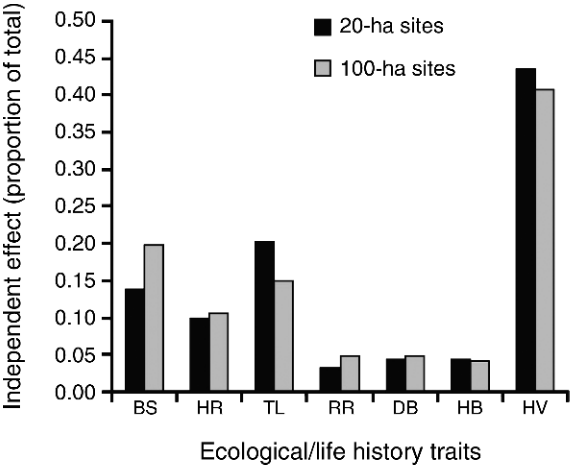

FIG. 4. Results of hierarchical portioning analysis for difference in occupancy of continuous sites and forest patches of 20-ha and 100-ha size. Key to abbreviations: BS, body size; HR, home range size; TL, tropic level; RR, reproductive rate; DB, dietary breadth; HB, habitat breadth; HV, hunting vulnerability.

Tuxtlas data set, home range and reproductive rate were most influential, accounting for a large amount of the explained variation in vulnerability (Fig. 3B). In Yucatán, body size and habitat breadth had the highest levels of independent explanatory power (Fig. 3C).

## Discussion

### *Influence of species traits on vulnerability*

After accounting for passive sampling effects and detectability differences between species, vulnerability to hunting was the single most important species trait influencing how species responded to fragmentation in our Guatemalan study site. Species that were more heavily hunted were more vulnerable to fragmentation. The negative impacts of hunting on densities and/or abundances of tropical mammals have been well documented in continuous forest across the Americas (Bodmer et al. 1997, Carillo et al. 2000, Hill et al. 2003). Many of the species included in our study respond negatively to hunting pressure in continuous forests of Guatemala and Mexico (Naranjo and Bodmer 2007, Reyna-Hurtado and Tanner 2007). However, the effect of hunting on mammal distribution and abundance has not been documented widely in fragmented habitats (but see Cullen et al. 2000), even though the lack of sufficient forest area and ease of access of hunters to forest patches may make species especially vulnerable to hunting within forest remnants (Peres 2001, Parry et al. 2009). Our data provide empirical support for a profound impact of hunting on tropical vertebrates in fragmented landscapes by showing that more heavily hunted and persecuted species were most likely to show a large reduction in their occupancy of forest patches when compared to their normal occupancy patterns in continuous forest.

The relative influence of particular species traits changed substantially depending on whether or not we accounted for sampling effects in our estimate of vulnerability to fragmentation. As predicted, two traits that are important in determining the density/distribution of mammals in continuous forest (body size and home-range size) were very important in driving vulnerability to fragmentation when sampling effects were not removed. Species that have these traits are expected to be present in a smaller proportion of patches just by virtue of their natural rarity. These traits declined substantially in importance when we accounted for sampling effects by comparing occupancy patterns in forest patches with expected occupancy patterns in continuous forest. Thus, body size and home range may not be as important in determining vulnerability to fragmentation as indicated by an examination of patch occupancy patterns alone.

Although some studies that correlate species traits with vulnerability to fragmentation account for sampling effects (e.g., Bolger et al. 1991, Davies et al. 2000, Meyer et al. 2008), a substantial number do not and employ measures such as overall patch occupancy or raw species–area curves to infer sensitivity to fragmentation (e.g., Onderdonk and Chapman 2000, Crooks 2002, Virgos et al. 2002, Viveiros de Castro and Fernandez 2004, Wang et al. 2009). Other authors have pointed out the pitfalls of using patch occupancy rates or raw species-area curves to infer vulnerability to fragmentation (Bolger et al. 1991, Johnson 2001, Haila 2002, Meyer et al. 2008). Our results demonstrate that, in some instances, non-removal of sampling effects could lead to incorrect conclusions regarding the importance of species traits. In particular, not accounting for passive sampling effects could lead to an increased emphasis on the importance of traits associated with natural abundance or widespread distribution such as body size, home range size, or potentially niche breadth that may not be warranted. However, in some systems, these traits exert a heavy influence on regional extinction proneness (Woodroffe and Ginsberg 1998, Purvis et al. 2000, Kamilar and Paciulli 2008) and correlate with vulnerability to fragmentation even after the removal of sampling effects (Davies et al. 2000, Shahabuddin and Ponte 2005). The importance of these traits cannot be discounted. However, removal of sampling effects will promote a better understanding of the influence of these types of traits on species' vulnerability to fragmentation (sensu Meyer et al. 2008).

### *Cross-landscape comparison*

Similar to the results from Guatemala, species traits strongly influenced variation in overall patch occupancy patterns of mid- and large-sized mammals in both Mexican landscapes. Averaged across all three landscapes, species traits examined in this study explained approximately 52% of the variation in overall patch occupancy for this set of mid- and large-sized mammals. Thus, intrinsic biological and ecological traits are extremely important in determining patch occupancy rates for the species considered here.

Relative rankings of species with respect to patch occupancy were in general agreement among the three study landscapes, although correlations were far from perfect. Overall, species that were ranked lower in terms of patch occupancy on one landscape tended to be ranked lower on the other landscapes, and vice versa. These correlations among study landscapes were apparent only when considering relative rankings of species. Absolute levels of patch occupancy for the same species differed drastically among the study sites. In general, species had the lowest levels of patch occupancy in Los Tuxtlas and highest levels in Yucatán. For example, coatis occupied 20% of the patches in Los Tuxtlas, 63% of the patches in Guatemala, and 98% of the patches in Yucatán.

Although there was some degree of correlation in rankings of species according to patch occupancy, the relative importance of species traits in determining patch occupancy patterns differed among the three landscapes. In particular, the influence of reproductive rate, habitat breadth, and hunting vulnerability on patch occupancy patterns changed substantially across landscapes. This was true even though we limited our comparison to the same set of species in each landscape. Because our cross-landscape analysis used a measure of fragmentation sensitivity that did not account for passive sampling effects, our comparison is perhaps best viewed as an analysis of how species traits influence patch occupancy, rather than vulnerability to habitat fragmentation *per se*. However, our general finding that different traits can emerge as important on different landscapes for the same set of species is applicable to studies of species' vulnerability to habitat fragmentation.

Although difficult to assess based on only three study sites, variation in the influence of species traits on patch occupancy may be affected by context-specific differences between the landscapes. For example, the relatively large influence of hunting vulnerability on patch occupancy in our Guatemalan landscape compared to the Mexican landscapes could be related to differences in hunting pressure among the three areas. Patches in our study area were heavily impacted by hunting pressure whereas this was not the case in Los Tuxtlas at the time of the study (A. Estrada, *personal communication*). Subsistence and commercial hunting occurs in Yucatán (T. Urquiza-Haas, *personal communication*), but hunting pressure may be less intense than in northern Guatemala where a rapidly increasing and extremely poor rural population creates a large demand for wild game. Also, different cultural hunting norms may have contributed to the disparity among the three landscapes (between Mexico and Guatemala) in the role of hunting vulnerability in determining species response to fragmentation. However, many of the species denoted in this study as highly preferred game species or highly persecuted species are the same in Mexico (Escamilla et al. 2000, Urquiza-Haas et al. 2009). The importance of habitat breadth in the Yucatán compared to the other landscapes may be related to differences in the type of patches studied in each area. Patches in the Yucatán were a mixture of primary, secondary, and disturbed habitats, whereas patches in Guatemala and Los Tuxtlas were largely undisturbed primary forest sites. Because habitat breadth is important in determining use of disturbed or secondary forest habitats, this trait could be a more important influence on patch occupancy patterns in Yucatán.

Similarly, context-specific differences in the physical characteristics of patches (e.g., patch quality, distance of patches from sources) could explain, in part, the large descrepancies in absolute levels of patch occupancy seen across the three landscapes. Other differences among the three landscapes in climate, seasonality, and human population densities also may be important. Alternatively, the variation in absolute patch occupancy rates could be explained by differences in methodology. Interviews used in Yucatán may have resulted in higher estimates of patch occupancy for species because they measured both past and present use of patches by mammals. Mammals were recorded as present if they had been observed within the patch in the last five years (Urquiza-Haas et al. 2009). The generally lower estimates of patch occupancy in Los Tuxtlas may have been influenced by the use of live traps instead of camera traps or lower levels of trapping effort. Also, the Los Tuxtlas study was done before techniques existed for incorporation of detectability in patch occupancy estimates. A failure to incorporate dectectability may have biased estimates of occupancy lower for some species.

Collectively, results from the cross-landscape comparison indicate both similarities and differences in how the same species responded to habitat patchiness on distinct landscapes. The strong influence of both body size and home-range size in determining patch occupancy on all three landscapes probably accounts for the correlation between the studies in terms of the relative rankings of species according to patch occupancy rates. This suggests that it may be possible to predict with some degree of accuracy relative patch occupancy patterns of these species on novel landscapes, which is one of the major goals of analyzing the relationship between species traits and response to landscape change (Mac Nally and Bennett 1997). However, the influence of other variables, particularly reproductive rate, habitat breadth, and hunting vulnerability on patch occupancy patterns changed substantially across landscapes and likely accounts for the less than perfect nature of the correlations. The search for generalities in species response to habitat patchiness, and potentially to habitat fragmentation per se, based on shared ecological and life history characteristics therefore will be made more difficult because of variability in the importance of traits among landscapes.

### *Conclusions*

Our results indicate that vulnerability to hunting drives many of the interspecies differences in sensitivity to habitat fragmentation in northern Guatemala. Because we were able to incorporate detectability in our analysis, our findings do not reflect detection differences between species but instead real patterns in vulnerability. Hunting pressure on mid- and large-sized mammals is common in many fragmented tropical environment (Peres 2001). Reduction of hunting pressure may have a marked positive effect on the ability of species to use and persist within fragmented landscapes of the tropics and thus should be a primary focus of management efforts in human-dominated environments with high levels of hunting. Our work also shows that the way in which vulnerability to fragmentation is measured, and in particular whether or not passive sampling effects are accounted for in the analysis, can alter conclusions regarding the relative influence of species traits on sensitivity to fragmentation. Finally, our cross-landscape comparison found correlations among mammals on three distinct landscapes when comparing the relative ranking of species in terms of patch occupancy, which suggests some degree of similarity in response that could be used to predict how the same species will react on novel landscapes. However, our comparison also demonstrates that the relative influence of certain species traits on patch occupancy patterns (and likely to some extent on vulnerability to fragmentation) changes across landscapes, perhaps because of context-specific differences between landscapes. Moreover, absolute values of patch occupancy were markedly different on the three landscapes. We found these results even though we were considering almost the exact same set of species in all three landscapes. These findings therefore suggest some limitations in the use of species ecological and life history traits to predict variation in patch occupancy and/or sensitivity to fragmentation across diverse landscapes, at least until we are able to better incorporate extrinsic factors such as context-specific differences among landscapes into the analysis.

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## APPENDIX A

Details of compilation of ecological and life history traits (*Ecological Archives* A021-040-A1).

## APPENDIX B

Parameter estimates for best-fit occupancy models (*Ecological Archives* A021-040-A2).