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Research Article

Effects of hunting and fragmentation on terrestrial mammals in the Chiquitano forests of Bolivia

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Abstract

In recently fragmented landscapes, hunting pressure increases because hunters can access previously remote habitats. Yet fewer than 0.5% of fragmentation studies with mammals have also assessed the impacts of hunting. Herein, by means of camera-traps and track-plots, we analyzed the impact of hunting and forest fragmentation on species richness and relative abundances of twelve species of large and medium-sized mammals. With both methods we found fewer species in hunted sites than in control sites, but the effect was inconsistent in fragmented habitats with hunting. Hunting negatively affected the indices of abundance for five of the 12 species and never had a positive effect. Contrary to the hypothesis that the combination of fragmentation and hunting would lead to the largest decrease in abundance, we found that the addition of fragmentation in hunted landscapes negatively affected only two species (red brocket deer [*Mazama americana*] and margay cat [*Leopardus wiedii*]) and positively affected three smaller species (crab-eating foxes [*Cerdocyon thous*], coaties [*Nasua nasua*], and agoutis [*Dasyprocta* spp.]). We also found a significant relationship between body mass and the effects of fragmentation (smaller species positively affected), but no relationship between body mass and the effect of hunting. Had we only compared results from the control with fragmented sites, we would have found a negative effect of fragmentation on five species abundance indices, a negative effect on species richness, and a positive effect on three species abundance indices. These results indicate that a failure to explicitly incorporate the effects of hunting into the design of fragmentation experiments can lead to widely different conclusions.

Keywords: camera-trap, track-plot, multimodel inference, relative abundance, species richness

Resumen

En paisajes recientemente fragmentados, la presión de cacería aumenta porque los cazadores pueden acceder a hábitats antes remotos. Sin embargo, menos del 0,5% de los estudios de fragmentación sobre mamíferos ha evaluado también el impacto de la cacería. Por medio de trampas-cámara y parcelas de huellas analizamos los impactos de la cacería y la fragmentación sobre la riqueza y abundancia relativa de doce especies de mamíferos medianos y grandes. Con ambos métodos encontramos menos especies en el sitio bajo cacería, pero el efecto fue inconsistente cuando sumamos la fragmentación. La cacería afectó negativamente los índices de abundancia de 5 de las 12 especies, y nunca tuvo un efecto positivo. Contrario a la hipótesis de que la fragmentación y cacería combinadas llevarían a la mayor disminución de la abundancia, encontramos que la adición de la fragmentación sólo afectó negativamente a dos especies (un venado [*Mazama americana*] y el gato margay [*Leopardus wiedii*]) y positivamente a tres especies (zorro cangrejero [*Cerdocyon thous*], coatíes [*Nasua nasua*], y agutíes [*Dasyprocta* spp.]). Encontramos una relación significativa entre masa corporal y efecto de fragmentación (especies menores afectadas positivamente), pero no entre masa corporal y efecto de la caza. Si hubiéramos comparado sólo los resultados del control y sitios fragmentados, habríamos encontrado un efecto negativo de la fragmentación sobre la abundancia de cinco especies, uno negativo sobre la riqueza de especies, y uno positivo sobre la abundancia de tres especies. Estos resultados indican que el no incorporar los efectos de la cacería en el diseño de experimentos de fragmentación puede llevar a conclusiones diferentes.

Palabras clave: abundancia relativa, inferencia multimodelo, parcelas de huellas, riqueza de especies, trampas-cámara

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Introduction

Habitat fragmentation is one of the leading causes of wildlife declines and extinctions [1-4]. In many ecosystems, fragmentation and hunting increase at the same time [5] because fragmentation allows hunters access to previously remote habitats [6]. Given that habitat fragmentation rarely occurs in isolation from hunting, most studies of fragmentation either ignore hunting pressure or consider hunting a given consequence of fragmentation [7].

Assessing the effects of hunting and fragmentation allows managers to target conservation appropriately, as each of these pressures requires different management practices for the conservation of threatened species [8]. Curbing fragmentation often requires working with land owners and securing conservation easements, whereas controlling hunting often involves education programs and enforcement of no-hunting covenants [6]. The conflation of these two anthropogenic disturbances could lead to ineffective management because we have not correctly identified the mechanism(s) driving population declines.

Failure to study the impacts of hunting can lead to a systematic bias in the results of fragmentation studies [5,9]. If hunting has already caused local extinction, the addition of fragmentation may have little or no discernible effect. Alternatively, the addition of fragmentation to a landscape that has been hunted may drive down the abundances of species that are not the targets of hunting pressure [5,7,10].

At least 1,220 published studies have analyzed the effects of habitat fragmentation on mammals (Web of Science search 29 January 2012 with words “habitat fragment” and “mammal” in topic). Yet only five of these studies have assessed the impact of both fragmentation and hunting [5,8,11-13]. The vast majority of fragmentation research ignores the effects of hunting.

We examined the relative impact of hunting on medium and large mammals in both contiguous and fragmented Chiquitano forests of southeastern Bolivia. Due to the geographical location between the Chaco (xeric forest), the Amazon (rainforest), and the Pantanal (seasonally flooded savanna), the Chiquitano forests possess a wide diversity of rare mammals [14-15]. The Chiquitano forests are also fragmented by the pattern of habitat loss [16-18]. As of 1998, the forests near Santa Cruz had lost 48% of their original area in a patchwork pattern due to the rapid expansion of farms and ranches [19], and these areas continue to lose forest (see methods below, also Hansen et al. [20]).

Within this eco-region, we evaluated an index of relative abundances for 18 species of terrestrial mammals in three landscape conditions: fragmented forests with hunting; contiguous forests with hunting; and contiguous forests without hunting. With this design we can assess the impact of hunting and we can assess the impact of fragmentation in hunted landscapes. We cannot accurately assess their interaction because landscapes that are fragmented and free from hunting pressure are simply not present. We used body mass as a potential predictor of the effects of first hunting, and second fragmentation in hunted forests, as previous work has shown that both of these pressures disproportionately impact larger mammals [5,12,21-24]. We therefore asked the following questions: 1) How does hunting impact mammalian abundances and species richness? 2) How does fragmentation affect the abundance and species richness of mammals in hunted forests? 3) Can body mass predict the effect of hunting or the effects of fragmentation in hunted forests?

To answer these questions, we used track-plots and camera-traps to estimate an index of relative abundance and species richness among treatments. Track-plots and camera-traps are complementary [25], and the combination of these methods ensures that differences in abundance indices are accurately identified [26]. Each of these methods may provide a biased estimate of abundance (for example, some species may be trap-shy); however, as long as these biases are similar among treatments, any such bias will not alter the interpretation.

Methods

Study Area

Study sites were located approximately 140 to 160 km NE of Santa Cruz, Bolivia, on a ranch with large natural habitats and a neighboring farm devoted to mechanized agriculture (Fig. 1). Vegetation was similar in all sites and consisted of a transitional Chaco-Chiquitano forest dominated by deciduous trees, with cacti in well drained soils and palms in seasonally flooded depressions [27]. To reduce biotic and abiotic differences, all study sites were in the same general area (29 km between the most distant sites).



Fig. 1. Map of study sites and treatments in southeastern Bolivia. Track-plots were sampled at the marked locations during the years listed in the legend, and camera-traps were established in 2008 at the locations marked with a camera icon.

We used a random number generator to select study sites within three landscape “treatments.” Our control sites (no hunting or fragmentation) were located on the eastern side of this ranch, which was protected from hunting as part of a long-term conservation easement (at approximately 17°7'S and 61°49'W). The control sites were protected from hunting by active monitoring of the one possible access point, the extreme difficulty to impossibility of motorized access, and the large distance from the nearest public road (>24 km and at least four hours round trip to the nearest site). Our hunted-only sites (no fragmentation) were on the western side of the ranch and near a public road, along which hunting by locals, farm and ranch employees, and sport hunters from Santa Cruz was concentrated, but fragmentation was minimal (at approximately 17°7'S and 61°57'W). Our fragmented-plus-hunted sites were established in forest fragments (92 ha, 105 ha, 117 ha, 128 ha, 137 ha, 215 ha, 220 ha, 228 ha, and 231 ha in size) in the neighboring agricultural farm (at approximately 17°5'S and 62°2'W). These fragments (as defined in Collinge and Forman [18]) were isolated from contiguous forests between 1992 and 2004 by a matrix of mechanized agriculture, and also suffered heavy hunting pressure. Typical of research at this spatial scale, we were unable to intersperse the three treatments of study sites [28-29].

Hunting in this region targeted all 18 species, occurred both day and night on or near roads, and predominately entailed the use of guns, spotlights, or dogs [30] (personal observation). Certainly not all species are equally preferred by nor vulnerable to hunters, and this difference in hunting impacts was predicted to influence the abundance indices.

Each year and within each treatment, we established five study sites located at least 1 km apart and at least 100 meters from the nearest forest edge. One of the five study sites was a grid 180 m in length by 180 m in width. However, preliminary analysis revealed that our questions could be answered more efficiently with transects; thus the remaining four study sites consisted of one transect each, 500 m in length. Not all study sites were necessarily in the same location for both 2007 and 2008. Due to spacing of our study sites, we could not assess the abundance indices of species that have home ranges greater than 25 km² [31].

Flooding during January of 2008 prevented mechanized access to all the original control sites, and therefore we established five new study sites within the control area in that year. In April of 2008, land owners deforested sections of their land in both the hunted treatment and the fragmented-plus-hunted treatment. We therefore established one new study site in the hunted treatment, and four new study sites in the fragmented-plus-hunted treatment (Fig. 1). The deforestation of land in close proximity to the hunted treatment and fragmented-plus-hunted treatment could influence the results by causing a temporary crowding effect in 2008 [29]. We controlled for this possibility by including year as a covariate in the statistical models (see analysis below and see Table 1 for an example).

Track-Plots

We set up track-plots approximately every 60 m within each transect ($n = 9$ / transect) and systematically along the borders of each grid ($n = 8$ / grid). Although no bait was used, where possible we established track-plots in locations with mammal signs. We created 1 m by 1 m track-plots on the ground by cleaning and leveling the surface, then layering the surface with fine, sieved soil. The track-plots were not covered, and as a result rain occasionally rendered a track-plot ineffective for a night. Twice during the early dry season (April to June) and late dry season (August to October) of both 2007 and 2008, we inspected track-plots once a day consecutively for four days and recorded species presence in the hunted treatment (total trap-nights = 1,081) and the fragmented-plus-hunted treatment (total trap-nights = 1,156). We inspected track-plots located in the control during both seasons of 2007, but only during the late dry season of 2008 (total trap-nights = 874). We followed

established methods for species identification with track-plots in the Chiquitano forest [32-33], and validated the accuracy of our species identification with camera-traps (see below). On a few occasions we could not differentiate between sympatric species of the same family and we recorded the observation as such.

Camera-Traps

In June of 2008 we placed camera-traps at five sites in the fragmented-plus-hunted treatment (total trap-nights = 1,344), six sites in the hunted treatment (total trap-nights = 1,496), and four sites in the control (total trap-nights = 1,279). Despite flooding and difficulty of access, we successfully placed the camera-traps within the four transects of the control treatment that were originally established in 2007. Within each study site, we selected two track-plots that were at least 200 m apart and installed two camera-traps on opposite sides of each track-plot ($n = 4$ / site). We used an equal mixture of MC2-GV, Stealth Cams, or TrailMaster 35-1 cameras at all locations. We positioned camera-traps facing one another such that photographs would expose each lateral side of a passing mammal, thus improving the chance of a photograph and permitting individual identification of species that have spots or marks [34-37]. We placed cameras 30-40 cm above ground and checked cameras at least once a week through September 2008.

Analysis: indices of relative abundances and species richness

Previous research with track-plots has demonstrated a clear correlation between the number of tracks and population abundance [38-40]. However, the propensity for an individual mammal to walk across more than one track-plot within the same study site was high due to the short distance between track-plots. To mitigate auto-correlation of tracks within the same study site, we reduced all track plot data to presence-absence for each species in each site in each season [31,38,40]. Thus the number of detections for each species could be a minimum of zero and a maximum of 15 for the control treatment (5 sites * 3 seasons), 20 for the hunted treatment (5 sites * 4 seasons), and 20 for the fragmented-plus-hunted treatment (5 sites * 4 seasons).

Camera-traps photographed 21 identifiable species. With two genera (*Didelphis* spp. and *Dasyprocta* spp.) we were unable to differentiate between sympatric species. Using published techniques for identifying unique marks and patterns [34,36-37], we counted the number of unique individuals in six of these species: tapirs (*Tapirus terrestris*), ocelots (*Leopardus pardalis*), margays (*Leopardus wiedii*), jaguars (*Panthera onca*), giant armadillos (*Priodontes maximus*), and coatis (*Nasua nasua*). The remaining 15 species lacked distinctive marks, thus instead of individual identification we counted the number of photographs per site. To mitigate the effects of auto-correlation, we only counted one photo per day [41]. Previous research with camera-traps has demonstrated that the number of photographs closely correlates with population abundance [41-45] (but see Jennelle et al. [46]). We address the lack of independence between trapping rates and abundance estimates [46] by having trapping efforts of greater than 250 camera-days [47] and by confirming the results with track-plot indices of abundance.

We used generalized linear models [48] and multimodel inference [49-50] to assess the relative effects of hunting and fragmentation-plus-hunting on the probability of track detection, photo detection, or species richness. The use of multimodel inference (MMI) relies on individual interpretation without absolute statements of significance [51].

With track-plots, we used a binomial distribution to regress the presence or absence of tracks against the predictors of hunting, fragmentation, season, year, and number of trap-nights. With the camera-traps, we used a Poisson distribution to regress the number of individuals or number of photographs

against the predictors of hunting, fragmentation, and number of trap-nights. For all mammal families with more than one species detected, we also performed an additional analysis at the family level in order to evaluate whether trends found at the species level were likewise found throughout a taxonomic group. With the two measures of species richness (one generated from tracks and the second from photos), we used a Poisson distribution to regress the number of species per site against the same predictors associated with either track-plots or camera-traps listed above, and in equations (1) and (2) below. We defined hunting and fragmentation as absent or present, season as early dry or late dry, and year as 2007 or 2008. Season is a fixed effect, as it is well-defined and means the same thing regardless of year. Because the number of years was small ($n = 2$), we decided to treat years as a fixed effect and thereby limit the scope of the analysis to these two years. To have treated 2007 and 2008 as a random sample of two years would have severely decreased statistical power [52]. Since number of trap-nights was not nominal, but rather a count, this variable appeared in the model as a covariate [48]. The full main effects generalized linear models (GLM) were thus:

$$(1) \text{ presence/absence (tracks) or } n \text{ (species)} \sim \beta_0 + \beta_1 * \text{hunting} + \beta_2 * \text{fragmentation} \\ + \beta_3 * \text{trap-nights} + \beta_4 * \text{year} + \beta_5 * \text{season}$$

and

$$(2) n \text{ (photos, individuals, or species)} \sim \beta_0 + \beta_1 * \text{hunting} + \beta_2 * \text{fragmentation} + \beta_3 * \text{trap-nights}$$

To assess relative abundances or species richness, we used multimodel inference through serial exclusion of hunting, fragmentation, season, and year as well as all possible combinations of these variables (see Table 1 and 2 for detailed examples). Since careful evaluation of pseudo- R^2 values can be of interpretive merit [53], we calculated the McFadden and the Nagelkerke / Cragg and Uhler pseudo- R^2 values associated with the full models from the analyses of track-plots and camera-traps (Table 3). We always included either hunting or fragmentation or both in each regression, because the goal of the research is to assess their relative effects on mammalian abundances. By including hunting and fragmentation in an equal number of models, we avoided biasing our results based upon the number of times a predictor was in the model [54]. We did not examine interactions between hunting and fragmentation because a fragmented forest without hunting did not exist.

Since we calculated two different abundance indices for each species (track-plots and camera-traps), requiring a typical criteria of 95% confidence interval with both estimates would result in a highly conservative type I error rate ($\alpha = 0.05 * 0.05 = 0.0025$) [55-57]. An alternative approach was therefore needed. Effects of hunting or fragmentation were considered indicative of a negative or positive impact on the population only when two criteria were met. First, both indices of abundance must agree in sign (track-plots and camera-traps). Second, if an abundance index was calculated, then at least one coefficient (β) must exceed 1.4 times the unconditional standard error, equivalent to an 84% confidence interval for a single species [56]. If an abundance index could not be calculated, then a Wilcoxon rank sum test must be significant ($P < 0.05$). Although the resulting type I error rate for a single species is higher than typical, the overall type I error for the set of species quickly diminishes to low values if at least five of the 12 species ($\alpha = 0.023$) or six of the 17 populations ($\alpha = 0.028$) satisfy the criteria. To aid the interpretation of the results, we calculated the type I error rate (α) associated with a two-sided (negative or positive) evaluation of hunting or fragmentation.

Due to unpredictable weather and logistical constraints, the number of trap-nights varied from site to site during each trapping session with both the track-plots (21 to 102) and the camera-traps (32 to 363). We therefore included trap-nights as a predictor in every regression. Since study site shape (grid or transect) might affect the number of tracks or photos, we evaluated the addition of this factor. We

found that the effect of study site shape on coefficients or standard errors of any other predictor variable was less than 0.01, and therefore we excluded this predictor from the analysis. Investigation of the residual deviance and degrees of freedom indicated that the data were not over-dispersed, except in one of the three regressions evaluating species richness with number of photographs. However, based upon AICc values this regression had effectively no weight ($\Delta = 14$, $w_{\beta_2} < 0.001$), and including or excluding this regression did not change the reported model averaged coefficients nor standard errors.

Table 1. An example of model averaging for estimating an index of *Tapirus terrestris* relative abundances with track-plots. Mathematical equations for calculating AICc, Δ_i , and w_i are as in Anderson et al. [49]:

$$\Delta_i = \text{AIC}_i - \text{minAIC} \quad w_i = \exp(-1/2 \Delta_i) / \sum \exp(-1/2 \Delta_i)$$

The same model combinations ($n = 12$) were used in order to generate the index of abundance for each species and family ($n = 21$), and the **model averaged** results are given in figures 2 and 3. The parameters used in model averaging are from the following generalized linear model:

$$\text{presence/absence} \sim \beta_0 + \beta_1 \cdot \text{hunting} + \beta_2 \cdot \text{fragmentation} + \beta_3 \cdot \text{season} + \beta_4 \cdot \text{trap-nights} + \beta_5 \cdot \text{year}$$

Model	AICc _i	Δ_i	$w_i \beta_1$	β_1	$w_i \beta_2$	β_2
{ $\beta_2 \beta_3 \beta_4$ }	41.72	0			0.34	-2.3
{ $\beta_2 \beta_3 \beta_4 \beta_5$ }	42.53	0.8			0.23	-2.39
{ $\beta_1 \beta_2 \beta_3 \beta_4$ }	43.65	1.93	0.22	-0.29	0.13	-2.1
{ $\beta_1 \beta_4$ }	44.23	2.5	0.16	-1.72		
{ $\beta_1 \beta_3 \beta_4$ }	44.34	2.61	0.16	-1.36		
{ $\beta_1 \beta_2 \beta_3 \beta_4 \beta_5$ }	44.53	2.8	0.14	0.01	0.08	-2.4
{ $\beta_2 \beta_4 \beta_5$ }	44.9	3.18			0.07	-1.9
{ $\beta_2 \beta_4$ }	45.15	3.42			0.06	-1.79
{ $\beta_1 \beta_2 \beta_4$ }	45.32	3.59	0.1	-1.23	0.06	-1.14
{ $\beta_1 \beta_4 \beta_5$ }	45.49	3.76	0.09	-1.53		
{ $\beta_1 \beta_3 \beta_4 \beta_5$ }	45.84	4.11	0.07	-1.27		
{ $\beta_1 \beta_2 \beta_4 \beta_5$ }	46.15	4.43	0.06	-0.87	0.04	-1.41
model averaged				-0.96		-2.15

Table 2. An example of model averaging for estimating an index of *Tapirus terrestris* relative abundances with camera-traps. Mathematical equations for calculating AICc, Δ_i , and w_i are as in Anderson et al. [49]:

$$\Delta_i = \text{AIC}_i - \text{minAIC} \quad w_i = \exp(-1/2 \Delta_i) / \sum \exp(-1/2 \Delta_i)$$

The same model combinations ($n = 3$) were used in order to generate the index of abundance for each species and family ($n = 16$), and the **model averaged** results are given in figures 2 and 3. The parameters used in model averaging are from the following generalized linear model:

$$n(\text{photos or individuals}) \sim \beta_0 + \beta_1 \cdot \text{hunting} + \beta_2 \cdot \text{fragmentation} + \beta_3 \cdot \text{trap-nights}$$

Model	AICc _i	Δ_i	$w_i \beta_1$	β_1	$w_i \beta_2$	β_2
{ $\beta_1 \beta_3$ }	45.81	0	0.73	-3.20		
{ $\beta_1 \beta_2 \beta_3$ }	47.80	1.98	0.27	-3.29	1.00	0.18
{ $\beta_2 \beta_3$ }	70.39	24.57			<0.01	-2.19
model averaged				3.22		0.18

Table 3. The McFadden and the Nagelkerke / Cragg and Uhler (N/CU) pseudo-R² values* associated with the full models from the analyses of abundance indices with track-plots (equation 1) and camera-traps (equation 2). Pseudo-R² values need careful interpretation as low values are typical [70], as values for different models of equally good or poor fit can vary [70], as values cannot be interpreted independently, and as values cannot be compared across datasets. However, pseudo-R² values can be informative when considered in addition to AIC values [53].

Family Species (common name)	Track-Plots		Camera-Traps	
	McFadden	N/CU	McFadden	N/CU
Tapiridae				
<i>Tapirus terrestris</i> (tapir)	0.34	0.44	0.47	0.91
Cervidae (deer)	0.20	0.32	0.55	0.99
<i>Mazama americana</i> (red brocket)	0.25	0.34	0.46	0.92
<i>Mazama gouazoubira</i> (gray brocket)	0.15	0.25	0.48	0.94
Tayassuidae (peccaries)	0.11	0.17	0.21	0.51
<i>Pecari tajacu</i> (collared peccary)			0.15	0.29
Myrmecophagidae (anteaters)	0.06	0.09	0.11	0.24
<i>Myrmecophaga tridactyla</i> (giant anteater)			0.10	0.22
<i>Tamandua tetradactyla</i> (tamandua)	0.07	0.10		
Felidae (felids)	0.26	0.40	0.20	0.54
<i>Leopardus pardalis</i> (ocelot)	0.10	0.14	0.22	0.50
<i>Leopardus wiedii</i> (margay)	0.24	0.34	0.06	0.10
Cuniculidae				
<i>Cuniculus paca</i> (paca)	0.11	0.19		
Dasypodidae (armadillos)	0.12	0.20	0.25	0.62
<i>Dasypus novemcinctus</i> (nine-banded)	0.20	0.30		
<i>Euphractus sexcinctus</i> (six-banded)	0.10	0.17		
<i>Tolypeutes matacus</i> (three-banded)	0.27	0.37		
Canidae (canids)				
<i>Cerdocyon thous</i> (crab-eating fox)	0.09	0.15		
Procyonidae				
<i>Nasua nasua</i> (coati)	0.12	0.19	0.58	0.96
Mustelidae (weasels)				
<i>Eira Barbara</i> (tayra)	0.39	0.54	0.09	0.15
Dasyproctidae				
<i>Dasyprocta</i> spp. (agouti)	0.20	0.32	0.30	0.63
Didelphidae				
<i>Didelphis</i> spp. (opossum)	0.30	0.41		
Leporidae (lagomorphs)				
<i>Sylvilagus brasiliensis</i> (tapeti)	0.14	0.22	0.22	0.60

*McFadden Pseudo-R² = $1 - \ln(L(M_{full.model}))/\ln(L(M_0))$

N/CU Pseudo-R² = $(1 - (L(M_0)/L(M_{full.model}))^{(2/n)}) / (1 - L(M_0)^{(2/n)})$, where

$L(M_0)$ = likelihood of the null model (intercept only)

$L(M_{full.model})$ = likelihood of the full main effects model

Three species (giant anteaters [*Myrmecophaga tridactyla*], jaguarundis [*Puma yaguarondi*], giant armadillos) had only one track observed in all treatments and thus were excluded from the abundance analysis (Table 4). We had no track observations of collared peccaries (*Pecari tajacu*) in 2008, and as a result the GLM did not converge.

Eight species and the opossums (*Didelphis* spp.) had a total of fewer than four photographs in all treatments, and thus were excluded from the abundance analysis due to small sample size (Table 5). Only one species with a home range greater than 25 km² (white-lipped peccaries [*Tayassu pecari*]) had more than four photographs, but was likewise excluded from the abundance analysis to avoid violations of sampling independence among treatments [31].

Two species, pacas (*Cuniculus paca*) and nine-banded armadillos (*Dasypus novemcinctus*), had more than four photographs but were not photographed in all three treatments. As a result, the GLM did not converge with these species. As an alternative, we used a Wilcoxon rank sum test to compare the number of photographs per 100 trap-nights from treatments with and without fragmentation, and to compare treatments with and without hunting. Although this technique prevented us from determining how much hunting and fragmentation-plus-hunting affected abundance indices, the test allowed us to investigate whether abundance indices from the compared treatments were different.

Table 4. Number of tracks recorded by species per 100 trap-nights across treatments as ordered by mass. The numbers below do not control for auto-correlation within sites and in some cases may be inflated due to one individual repeatedly frequenting a given track-plot.

Species (common name)	Mass (kg)	Control	Hunted	Hunted & Fragmented
<i>Sylvilagus brasiliensis</i> (tapeti)	0.83	4.81	7.86	4.81
<i>Didelphis</i> spp. (opossums)	1.27	0.11	3.33	1.47
<i>Tolypeutes matacus</i> (three-banded armadillo)	1.5	1.14	0.28	0.52
<i>Dasypus</i> spp. (agouti)	4	2.06	2.78	1.56
<i>Eira barbara</i> (tayra)	4.85	0.92	0.83	1.90
<i>Euphractus sexcinctus</i> (six-banded armadillo)	4.85	1.03	0.74	1.12
<i>Nasua nasua</i> (coati)	5.1	0.57	0.83	1.56
<i>Cerdocyon thous</i> (crab-eating fox)	5.75	1.26	1.48	1.64
<i>Leopardus wiedii</i> (margay)	6	0.69	0.83	0.09
<i>Tamandua tetradactyla</i> (tamandua)	6	0.46	0.37	0.26
<i>Dasypus novemcinctus</i> (nine-banded armadillo)	6.3	0.69	0.46	1.12
<i>Puma yagouaroundi</i> ^a (jaguarundi)	6.75	0.11	0	0
<i>Cuniculus paca</i> (paca)	9	1.03	0.83	0.61
<i>Leopardus pardalis</i> (ocelot)	10	0.57	0.28	0.17
<i>Mazama gouazoubira</i> ^b (gray brocket)	18	1.49	1.02	1.21
<i>Pecari tajacu</i> (collared peccary)	26	0.69	0.93	0.52
<i>Priodontes maximus</i> ^a (giant armadillo)	30	0	0	0.17
<i>Myrmecophaga tridactyla</i> ^a (giant anteater)	30.5	0	0.09	0
<i>Tayassu pecari</i> ^a (white-lipped peccary)	35	0	0	0
<i>Mazama americana</i> ^b (red brocket)	36	0.92	0.28	0.09
<i>Puma concolor</i> ^a (puma)	74.5	0.11	0.09	0
<i>Panthera onca</i> ^a (jaguar)	94.5	0	0.19	0
<i>Tapirus terrestris</i> (tapir)	238.5	1.49	0.46	0.09

^a Species excluded from the regression of abundance as predicted by weight in figure 4.

^b Not all *Mazama* tracks could be identified at the species level ($n = 8$) and thus these observations are not included in this table. Sympatric *Mazama* species were differentiated based upon size and spacing of the cloven hoof [27,32-33] and verified photographically where possible.

Analysis: body mass

As in Chiarello [58], we used body mass for each species (recorded in Emmons and Feer [59]) to determine if hunting or fragmentation-plus-hunting had a predictably greater impact on larger species. For this analysis, we performed a linear regression of the coefficient values from both the track-plot ($n = 16$) and camera-trap ($n = 11$) analyses against body mass, trapping method (either track-plot or camera-trap), and their interaction. We assessed the response of coefficients from hunting or

fragmentation-plus-hunting separately. Investigation of Cook's distance revealed fitted values with an influence greater than the 20th percentile, thus we log-transformed body mass [60]. We dropped the interaction term from the model because this predictor variable had little support ($P > 0.2$ for both models) and did not alter other predictor variables or their associated standard error more than 0.01. The two linear regressions were given as:

$$(3) \text{ coefficient (hunting or fragmentation-plus-hunting)} \sim \beta_0 + \beta_1 * \ln(\text{body mass}) + \beta_2 * \text{method (track-plot or camera)}$$

Results from the above regression indicated that the strength of the fragmented-plus-hunting treatment decreased with increasing body mass. Investigation of the coefficients revealed a discernible break point at 6 kg where positively and negatively affected species naturally separated. To assess whether fragmentation-plus-hunting affected mammals with body masses of at least 6 kg differently from mammals with less than 6 kg, we performed a Wilcoxon rank sum test to compare the coefficients from both groups.

Table 5. Number of photographs recorded by species per 100 trap-nights across treatments as ordered by mass. The numbers below do not control for auto-correlation within sites and in some cases may be inflated due to one individual repeatedly being photographed.

Species (common name)	Mass (kg)	Control	Hunted	Hunted & Fragmented
<i>Sylvilagus brasiliensis</i> (tapeti)	0.83	0.55	0.07	0.82
<i>Didelphis</i> spp. ^a (opossums)	1.27	0.00	0.07	0.15
<i>Tolypeutes matacus</i> ^a (three-banded armadillo)	1.5	0.08	0.00	0.22
<i>Dasyprocta</i> spp. (agouti)	4	0.39	0.13	0.45
<i>Eira barbara</i> ^a (tayra)	4.85	0.08	0.07	0.15
<i>Euphractus sexcinctus</i> ^a (six-banded armadillo)	4.85	0.00	0.00	0.07
<i>Nasua nasua</i> (coati)	5.1	0.16	0.07	1.71
<i>Cerdocyon thous</i> (crab-eating fox)	5.75	0.47	0.07	0.37
<i>Leopardus wiedii</i> (margay)	6	0.16	0.07	0.15
<i>Tamandua tetradactyla</i> ^a (tamandua)	6	0.00	0.00	0.07
<i>Dasyurus novemcinctus</i> ^a (nine-banded armadillo)	6.3	0.16	0.00	0.52
<i>Puma yagouaroundi</i> ^a (jaguarundi)	6.75	0.08	0.00	0.00
<i>Cuniculus paca</i> ^a (paca)	9	0.47	0.00	0.00
<i>Leopardus pardalis</i> (ocelot)	10	1.25	0.13	0.52
<i>Mazama gouazoubira</i> (gray brocket)	18	1.88	0.20	0.22
<i>Pecari tajacu</i> (collared peccary)	26	0.23	0.13	0.22
<i>Priodontes maximus</i> ^a (giant armadillo)	30	0.16	0.07	0.07
<i>Myrmecophaga tridactyla</i> (giant anteater)	30.5	0.08	0.13	0.30
<i>Tayassu pecari</i> ^a (white-lipped peccary)	35	0.47	0.00	0.00
<i>Mazama americana</i> (red brocket)	36	1.56	0.20	0.07
<i>Puma concolor</i> ^a (puma)	74.5	0.08	0.07	0.07
<i>Panthera onca</i> ^a (jaguar)	94.5	0.23	0.00	0.00
<i>Tapirus terrestris</i> (tapir)	238.5	1.80	0.07	0.07

^a Species excluded the regression of abundance as predicted by weight in figure 4.

Results

We found evidence of 23 different species in the control, 21 species in the hunted treatment, and 20 species in the fragmented-plus-hunting treatment. Twenty species were positively identified in all three treatments, but three species were not. Two species (jaguarundis and white-lipped peccaries) were only recorded in the control, while jaguars were recorded in both the control and the hunted treatment (Tables 4 and 5).

Hunting correlated with a decrease in species richness (n species per site) according to both track-plots (model averaged coefficient $[\beta_1] = -0.20$, unconditional standard error $[SE] = \pm 0.13$, predictor importance $[\sum w_i] = 0.73$) and camera-traps ($\beta_1 = -1.01$, $SE = \pm 0.32$, $\sum w_i = 1.00$). The addition of fragmentation yielded a mixed result, with species richness estimates unchanged according to track-plot results ($\beta_2 = -0.11$, $SE = \pm 0.14$, $\sum w_i = 0.45$) but then estimated to increase according to camera-trap results ($\beta_2 = 0.77$, $SE = \pm 0.34$, $\sum w_i = 0.83$). For the sake of consistency, we calculated the Nagelkerke/Cragg and Uhler's pseudo- R^2 values for the full model using both track-plots (pseudo- $R^2 = 0.22$) and camera-traps (pseudo- $R^2 = 0.89$).

We were able to evaluate the effects of hunting and fragmentation-plus-hunting on a total of 18 species in 13 families with either track-plots or camera-traps. For 12 of these species, we were able to use both methods, allowing us to assess the consistency of the estimates between methodologies (Fig. 2 and 3). In addition, we conducted family level analyses on the five families with multiple species (Fig. 2 and 3).

Using the criteria that both methods must agree in sign and at least one must exceed 1.4 times the unconditional standard error or pass a Wilcoxon rank sum test, we found negative effects of hunting on five of the 12 species ($\alpha = 0.023$) and on nine of the 17 populations evaluated ($\alpha < 0.001$). The coefficients exceeded the standard error with both indices of abundance for two species (red brocket deer [*Mazama americana*] and ocelots) and both were negatively impacted by hunting (Fig. 2). At higher taxonomic levels, peccaries (Tayassuidae), felids (Felidae) and armadillos (Dasypodidae) all showed negative responses to hunting using both methodologies; brocket deer (Cervidae) showed negative responses according to camera-trap results; and anteaters (Myrmecophagidae) showed no strong responses (Fig. 2). Using the same criteria, six of the 17 populations evaluated were impacted by the addition of fragmentation ($\alpha = 0.028$). Fragmentation in the presence of hunting resulted in further negative effects on the abundance indices of two species (red brocket deer and margays) and positive effects on the abundance indices of three different species ($\alpha = 0.023$; Fig. 3). Strong positive effects of fragmentation-plus-hunting were detected for armadillos, with the model averaged coefficients exceeding the unconditional standard errors with both methods.

Three species had home ranges too large to assess the indices of relative abundances with these methods [31], including pumas (*Puma concolor*), jaguars, and white-lipped peccaries. Of these, only white-lipped peccaries had more than four photographs in all treatments, and all photographs were in control sites (Table 5).

Pacas were photographed an average of 0.45 photographs per 100 trap-nights in sites without hunting (6 photos in total). This was significantly different from sites with hunting, where no paca photos were detected (Wilcoxon rank sum, $W = 38.5$, $P = 0.0028$). Sites with and without fragmentation did not show a difference in the number of photographs (Wilcoxon rank sum, $W = 32.5$, $P = 0.2203$).

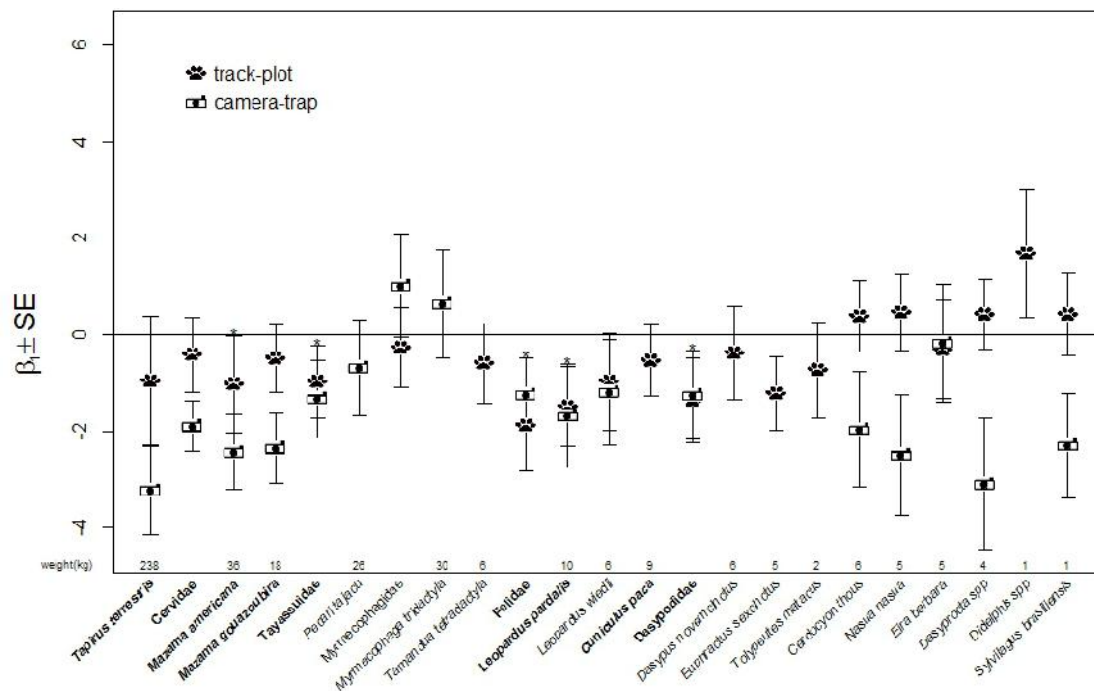


Fig. 2. Model averaged coefficients (β_1) and unconditional standard errors (SE) for species and families in hunted sites relative to non-hunted sites using track-plots and camera-traps. The asterisk (*) indicates that both methods of estimation (tracks and photos) agree in sign and that both estimates exceed the SE. Bold font indicates that both methods agree in sign and that at least one abundance estimate exceeds 1.4*SE or that a Wilcoxon sign test is significant ($P < 0.05$). All photographs of *Dasyprocta* spp. in the fragmented-plus-hunted treatment occurred within one site.

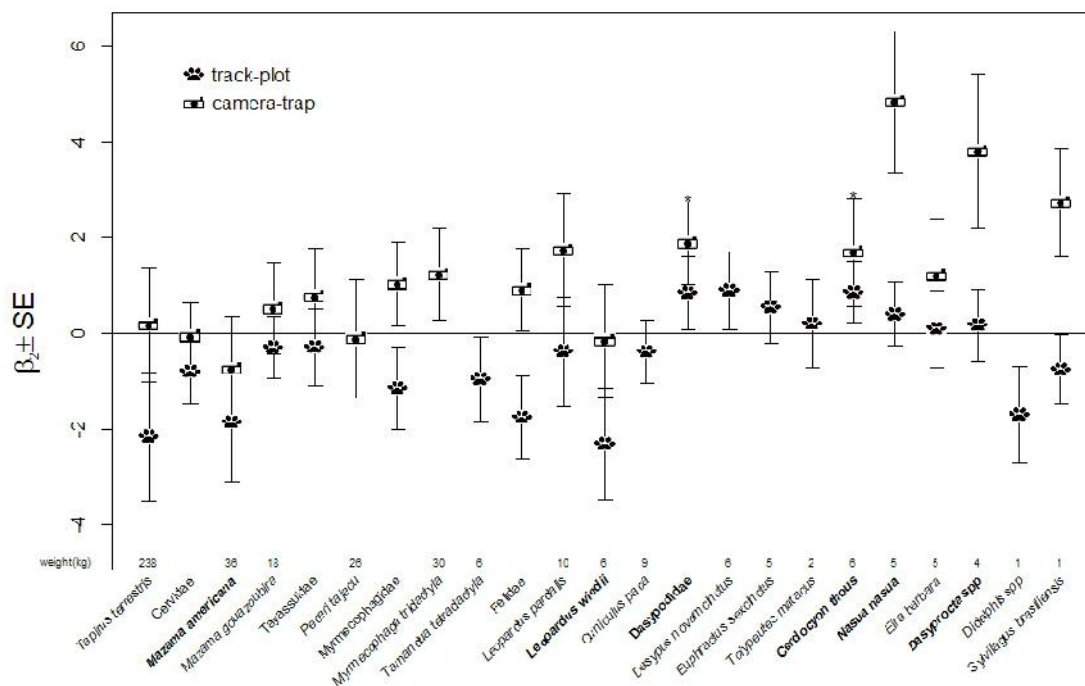


Fig. 3. Model averaged coefficients (β_2) and unconditional standard errors (SE) of species and families in fragmented-plus-hunted sites relative to contiguous sites using track-plots and camera-traps. The asterisk (*) indicates that both methods of estimation (tracks and photos) agree in sign and that both estimates exceed the SE. Bold font indicates that both methods agree in sign and that at least one abundance estimate exceeds 1.4*SE. All photographs of *Dasyprocta* spp. in the fragmented-plus-hunted treatment occurred within one site.

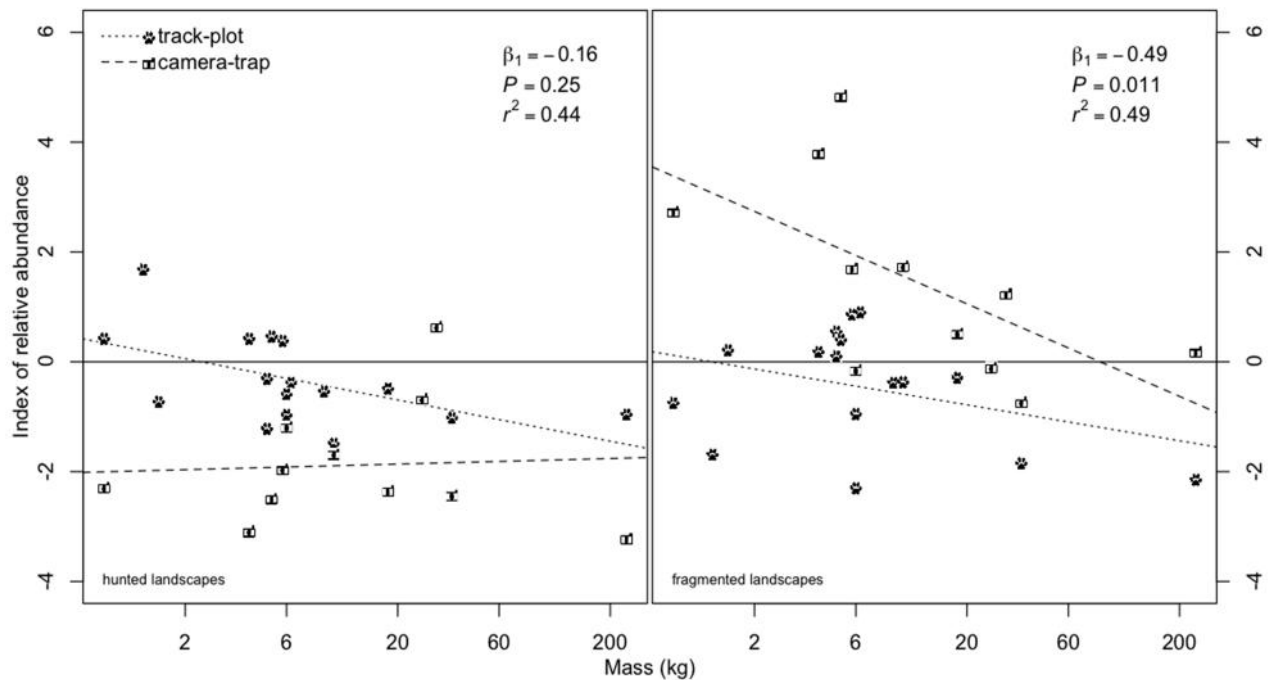


Fig. 4. Relationship between mammal index of abundances and body mass as estimated by two methods, track-plots and camera-traps. The left panel depicts a comparison of abundance indices from hunted relative to control landscapes, and the right panel depicts a comparison of abundance indices from fragmented relative to contiguous landscapes. Regression coefficient (β_1) is the slope of the fitted regression after controlling for methodology (eq. 3). The P -value is the probability that β_1 equals zero. The coefficient of correlation (r^2) compares the fitted regression to the actual values.

Nine-banded armadillos were photographed seven times in the fragmented-plus-hunted treatment, and twice in the control. Comparison of sites with and without fragmentation revealed no appreciable difference in the number of photographs per 100 trap-nights (Wilcoxon rank sum, $W = 13$, $P = 0.094$). Similarly, investigation of sites with and without hunting revealed no appreciable differences in the number of photographs per 100 trap-nights (Wilcoxon rank sum, $W = 25$, $P = 0.70$).

Body mass correlated with the effect of fragmentation in hunted landscapes. Smaller mammals tended to be more abundant in fragmented sites and larger species were less abundant as estimated by both camera-traps and track-plots (Fig. 4, right panel). By contrast, body mass did not correlate with the effect of hunting (Fig. 4, left panel). In both indices of abundance estimation (track-plots and camera-traps), all species with abundance indices negatively affected by fragmentation in hunted landscapes had a body mass of at least 6 kg, and conversely, all species that were positively affected by fragmentation in hunted landscapes had a body mass less than 6 kg (Fig. 3). Within the fragmented-plus-hunted sites, indices of relative abundance (model averaged coefficient [β_2] from eq. 1 and 2) were significantly different for species with a body mass of less than 6 kg (avg. $\beta_2 = 1.08$) compared to species with a body mass of at least 6 kg (avg. $\beta_2 = -0.32$; Wilcoxon rank sum, $W = 132.5$, $P = 0.0404$).

Discussion

Hunting had negative impacts on most abundance indices and on species richness, whereas the addition of fragmentation had mixed results. Hunting negatively impacted the abundance indices in 53% of the populations analyzed, and hunting reduced species richness estimates with track-plots by 18% and with camera-traps 64%. Conversely, the addition of fragmentation had a negative impact on

abundance indices with 12% of the populations analyzed, and had a positive impact on 18% of the populations. The addition of fragmentation was also estimated to both reduce species richness by 10% (track-plots) and increase species richness by 216% (camera-traps). These results contradict the hypothesis that the combination of fragmentation and hunting would lead to the largest decreases in abundance and species richness.

Conflating hunting and fragmentation can lead to inaccurate findings. Within the Chiquitano forests of Bolivia, hunting reduced the abundance indices of five species of mammals, reduced estimates of species richness, and never had a positive impact. Three of these species had similarly low abundance indices in fragmented-plus-hunted treatment, but two had even lower abundances. Conversely, the addition of fragmentation positively impacted three smaller species and inconsistently impacted species richness estimates. If we had only compared the abundance indices from the control with fragmented sites, we would have found a negative effect of fragmentation on abundance indices of five species, a negative effect on species richness, and a positive effect on abundance indices of three species. These results indicate that a failure to explicitly incorporate the effects of hunting into the design of fragmentation experiments can lead to widely different conclusions.

Although we can address the effects of fragmentation in addition to hunting, we must be cautious because we are unable to examine fragmentation in isolation from hunting. The lack of a strong effect of fragmentation on most mammalian abundance indices might change with time since the forests we studied were fragmented between 1992 and 2004, and fragmentation effects can take over two decades to materialize [61]. The effects of fragmentation might have been reduced for larger mammals that can potentially disperse the 2.8 km to 7.2 km separating the fragmented sites from the contiguous forests. Hunting may have swamped any effect from fragmentation. Hunting pressure in the fragmented sites may have been lower than in the contiguous forests with hunting. However, our happenstance recordings of hunting during 2007 and 2008 indicate a small difference between hunted ($n = 9$) and fragmented-plus-hunted ($n = 6$) treatments, and both treatments had more observations of hunting than the control ($n = 1$).

Previous research with ungulates (tapirs, peccaries, and brocket deer) and felids found a negative effect of both hunting [8,11,22-23,62] and fragmentation [12]. However, we found that when both anthropogenic disturbances are assessed in tandem, hunting reduces ungulate and felid abundance indices, while the addition of fragmentation negatively affects the abundance index of two species (red brocket deer and margays) which are known to depend more on closed forest [59].

Even in contiguous forests, hunting appeared to result in lower species richness and lower abundance indices of hunted species. However, the impacts were not uniform, with some species more susceptible (e.g. ungulates, armadillos, felids) and others generally unaffected (e.g. anteaters, mustelids, lagomorphs). Hunting pressure may have partially contributed to this difference. Previous work with ungulates and armadillos in this region (in the Chiquitano forests surrounding San Antonio de Lomerío, approximately 40 km northeast of our sites) found that these species represented 68% of harvested biomass and 58% capture frequency [30]. Thus hunter preference likely contributed to varied responses of mammals to the presence of hunting.

Fragmentation was the primary cause of higher relative abundance indices for agoutis (*Dasyprocta* spp.), coatis, armadillos, and crab-eating foxes (*Cerdocyon thous*) in the fragmented-plus-hunted forests. Diet and predation likely contributed to these findings. Coatis, crab-eating foxes, and armadillos are omnivores and agoutis are herbivores, and all of these species likely consume crops within the matrix. The increase in these species may also have been a result of decreased predation

and competition from larger predators such as jaguars, ocelots, and margays. Both ocelots and margays had far lower abundance indices in fragments relative to the control, and although in total we only recorded three photographs and one track in contiguous forests, we found no evidence of jaguars within the fragments. Hence the increase in abundance indices of crab-eating foxes and coatis may have been a result of mesopredator release [63], the increase in agoutis and armadillos a result of release from predation (see also Michalski and Peres [12] for more data on increases in armadillos in fragmented habitats), and the increase in all four a result of crop consumption.

Body mass clearly delineated how fragmentation-plus-hunting affected abundance indices (Fig. 4, right panel). Increasing body mass correlated with decreasing abundance indices. Mammals less than 6 kg in body mass had much higher abundance indices (model averaged coefficient [β] from eq. 1 and 2) in the fragmented treatment (avg. $\beta_2 = 1.08$). Conversely, mammals with 6 kg or greater body mass had slightly lower abundance indices in the fragmented treatment (avg. $\beta_2 = -0.32$). In other words, this trend is largely fueled by the positive effects of fragmentation-plus-hunting on mammals with a body mass between 1 kg and 6 kg.

Conversely, the effects of hunting on abundance indices were not significantly related to body mass (Fig. 4, left panel). Previous research and field observations in the Chiquitano forest indicated that most hunting is opportunistic, with hunters taking both small and large mammals, and that all 18 of the species we studied are hunted [30]. We also found no evidence of a positive effect of hunting on abundance indices for any species or family. Thus in the Chiquitano forest, hunting appears to have uniformly negative effects on mammal abundance indices.

Implications for conservation

Previous research has focused on either hunting or fragmentation, and in each case, one subsumed the other. This approach works if we assume that hunting always comes with fragmentation, but may lead us to ignore the negative impacts of hunting alone. Our research suggests that negative impacts on species richness and abundances that might be ascribed to fragmentation, could instead be due to hunting.

The implications with fragmentation are mixed. The addition of fragmentation to a hunted landscape can have a negative effect for larger species (>6 kg) and a positive effect for smaller species (<6 kg). Thus if a larger mammal is threatened, then protection from fragmentation is needed. But if a smaller mammal is threatened in a hunted landscape, it might be tempting to conclude that fragmenting the environment could lead to increases in abundance. However, the positive effects found in this study might have been due to the addition of crops as food supplies or mesopredator release, and reproducing such positive impacts with the same species in a different landscape might prove elusive. In addition, such a strategy would have negative effects on other species that may be of concern or interest.

With regard to hunting, the conservation implications are simple, as the effects were consistently negative. If a species is threatened and known to be targeted and harvested, then regardless of body size the mammal needs protection from hunting. Failure to adequately protect hunted species can lead to empty forests [64]. Given that mammals are hunted, legally or illegally, in environments where roads are present [65-66], protected areas need to be contiguous and without roads [67].

In these Chiquitano forests of Bolivia, protecting mammals from hunting entails tailoring management strategies to address the different types of hunters and to protect listed species [30]. Sport and

recreational hunting should be controlled as hunting is only authorized for abundant eared doves and picazuro pigeons. With subsistence hunters, management measures within indigenous lands should promote not-hunted reserve areas, protect watering holes, prevent forest fires, and limit the harvest of threatened species. Importantly, the protection of threatened mammals listed in the national red data book [68], such as tapirs (VU), giant armadillos (VU), jaguars (VU), and peccaries (NT), needs to be enforced.

In conclusion, this research demonstrates the need to assess the potential effects of hunting when analyzing the impacts of fragmentation. Since protection of threatened species from hunting and fragmentation entails widely different management practices [8], failure to consider hunting might lead to false conclusions and ineffective management recommendations.

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