



Spatial patterns of mammal occurrence in forest strips surrounded by agricultural crops of the Chaco region, Argentina



Mauricio M. Núñez-Regueiro^{a,*}, Lyn Branch^a, Robert J. Fletcher Jr.^a, Gustavo A. Marás^b, Enrique Derlindati^b, Andrés Tálamo^c

^a University of Florida, Department of Wildlife Ecology and Conservation, 110 Newins-Ziegler Hall, Gainesville, FL 32611-0430, United States

^b Universidad Nacional de Salta, Facultad de Ciencias Naturales, Av. Bolivia 5150, Salta 4400, Argentina

^c Universidad Nacional de Salta, Facultad de Ciencias Naturales, Consejo Nacional de Investigaciones Científicas y Técnicas, Av. Bolivia 5150, Salta 4400, Argentina

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ABSTRACT

Deforestation is a major cause of biodiversity loss, and the predominant factor driving deforestation is expansion of agriculture. A key step toward successful conservation in agricultural areas is maximizing biodiversity value of remaining forest. In subtropical and tropical regions, forest often is left in narrow strips between agricultural fields under the assumption that biodiversity is sustained. We examined use of forest strips and continuous forest by medium and large-sized mammals in Argentine Chaco with camera trapping and hierarchical Bayesian zero-inflated occupancy models and assessed how use related to ecological traits of species. Almost 70% of the species cited for our study area were not detected or were detected in less than 10% of the sampling units. Ten of the 23 species that occurred in the area were absent from strips or were detected most frequently in continuous forest, including all large-bodied species and forest interior specialists. Low occurrence of mammals in strips and in continuous forest raises major concerns related to long-term persistence of mammals in Chaco. Under current development policies, agriculture will continue to expand in this region, further threatening the second largest forest in South America. Alternative configurations for the forest-agriculture landscape, as well as synergism between landscape configuration and other threats, need to be evaluated and incorporated into policy if the rich mammalian fauna of this region is to be conserved.

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1. Introduction

Because of massive conversion of forested habitats to agriculture, many previously forested landscapes comprise large expanses of crops interspersed with forest patches and strips (Hawes et al., 2008). Understanding and predicting how wildlife responds to different configurations of forest in agricultural landscapes is essential for development of effective conservation policy. Deforestation is a major cause of loss of biological diversity, and the largest factor driving deforestation is expansion of agriculture to supply an increasing demand for food, biofuels, and other agricultural products (FAO, 2012). Forest buffers are often left along rivers and streams to reduce agricultural run-off and protect water quality (Naiman and Descamps, 1997), and upland forest strips are frequently retained around agricultural fields as windbreaks and to prevent soil erosion and spread of pests and fire (Eriksson et al.,

2001). Although upland forest strips likely are not as widespread as riparian buffers, these forest strips occur in agricultural landscapes in tropical and subtropical regions across the planet [e.g., Argentina (Seghezzo et al., 2011), Bolivia (L. Branch, pers. obs.), India (Sreekar et al., 2013), and Paraguay (Eriksson et al., 2001)]. Forest strips and their configuration (e.g., width) historically have been dictated by government policy to benefit agriculture and, more recently, with the additional assumption that these strips maintain biodiversity (Eriksson et al., 2001; Seghezzo et al., 2011). This pattern of land conversion thus represents a deliberate landscape design, albeit often a design with little consideration of conservation outcomes (Fig. 1).

Despite the widespread distribution of forest strips in production landscapes, the assumption that maintaining forest strips around crops allows forest biodiversity to persist in agricultural landscapes remains largely untested (Laurance and Laurance, 1999; Baudry et al., 2000). Forest strips have been evaluated in a limited range of ecological systems, principally temperate systems and to a lesser degree in wet tropical forests, and most studies have focused on small vertebrates, particularly birds (Hawes et al., 2008;

* Corresponding author at: University of Florida, School of Natural Resources and Environment, 110 Newins-Ziegler Hall, Gainesville, FL 32611-0430, United States.

E-mail address: mnureg@yahoo.com (M.M. Núñez-Regueiro).

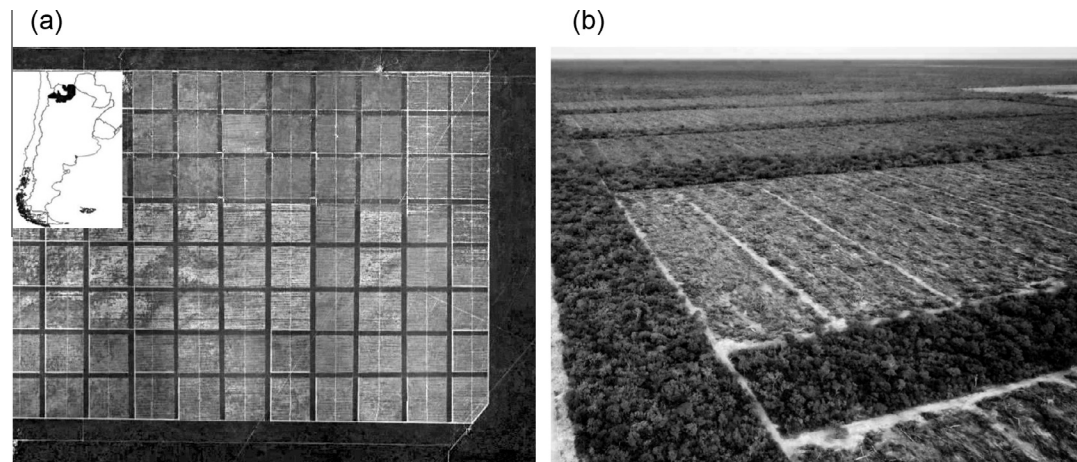


Fig. 1. (a) Province of Salta, Argentina, and satellite image of modified Chaco forest including remnant forest strips (dark strips) imbedded in ~34,000 ha of agricultural land (light squares, each ~200 ha), and adjacent continuous Chaco forest in Salta, Argentina. Satellite image downloaded from Google Earth. (b) Aerial photograph of forest strips in a recently deforested area in the Chaco region. Aerial photograph courtesy of Greenpeace Argentina.

Wehling and Diekmann, 2009). Conclusions to date are mixed. For example, studies in Amazonia have found greater activity of large terrestrial mammals in strips than in adjacent forest (Barlow et al., 2010), similar abundances of frogs and small mammals in remnant forest strips and adjacent continuous forest (de Lima and Gascon, 1999), and depauperate communities of birds and primates in strips as compared to continuous forest (Lees and Peres, 2008). To inform policy and design agricultural landscapes that incorporate conservation goals, understanding of conservation value of strips needs to be expanded to a greater range of geographic regions/ecological systems and a broader set of taxa.

Research on forest strips, and forest fragmentation in general, suggests that species responses to the forest strips may be diverse and possibly idiosyncratic (Henle et al., 2004). Understanding of how species traits (e.g., life history attributes and dietary and habitat requirements) influence the ability of species to use forest strips may improve prediction of impacts of forest conversion to croplands surrounded by forest strips and facilitate design of landscapes that promote species persistence. Such trait-based approaches have provided insights into vulnerability of species to climate change, habitat fragmentation, and hunting (Devictor et al., 2008; Diamond et al., 2011; Thornton et al., 2011; Chessman, 2013). Reproductive rate, determined by traits such as age at first reproduction and litter size, influences ability of species to persist in the face of human-induced mortality factors such as hunting, as well as population recovery following a decline (Altrichter, 2005). Body size often correlates negatively with reproductive rate, but also can contribute to vulnerability because species with large body size require large quantities of food and space that may be not available in human-dominated landscapes (Thornton and Fletcher, 2014). Also, these species often are preferred as game (Peres, 2001). Hunting is a significant threat throughout tropics and subtropics, and exposure of species to hunting often increases where forests are fragmented (Peres, 2001). Vulnerability of species to conversion of continuous forest into remnant forest strips also may be inversely related to ability of species to exploit multiple habitats and food resources. A general pattern emerging from many studies is that specialist species are more likely to respond adversely to a variety of global changes than are generalist species (Devictor et al., 2008). Reduction in abundance or total loss of specialist species can result in a shift to communities dominated by generalist species, resulting in a decrease in functional diversity and biotic impoverishment in the

form of functional homogenization of the community (Olden, 2006).

We examine the conservation value of forest strips for medium and large mammals in Argentine Chaco with the goal of informing on-going land use planning that will largely determine the future of forests in this region (Seghezzo et al., 2011; Piquer-Rodríguez et al., 2015). Tropical dry forests and savannas, such as Chaco, are a high conservation priority worldwide, because these regions have suffered extensive habitat conversion (Hoekstra et al., 2005). The Chaco forest of Argentina, Bolivia, and Paraguay is the second largest forest in South America after the Amazon forest, and 60 percent of this forest occurs in Argentina (Piquer-Rodríguez et al., 2015). Diversity of medium and large mammals in Chaco rivals that of tropical forests in South America, and endemism is high (Mares, 1992; Redford et al., 1990). Forest cover in Chaco remained relatively intact until recently with extensive land uses focused on cattle ranching, charcoal extraction, and selective logging (Gasparri and Grau, 2009). In the last two decades, expansion of modern agribusiness has rapidly accelerated forest conversion in this region (Hansen et al., 2013). In northern Argentina current environmental norms require that forest strips at least 100 m wide be left surrounding agricultural plots when forest is cut (~23–37 ha of forest strips for every 100 ha of deforested land), resulting in huge expanses of commercial crops, particularly soybeans (*Glycine max*), divided by a grid of forest strips (Fig. 1, Ginzburg et al., 2012). An increasing number of studies document patterns of land-cover change in Argentine Chaco, but field studies are scarce and very little is known about impacts of this process on biodiversity or, more specifically, the value of these modified landscapes for wildlife (Piquer-Rodríguez et al., 2015; Periago et al., 2015).

We evaluated use of forest strips in Argentine Chaco by medium and large mammals (body weight > 1 kg) and assessed how this use relates to their ecological traits. We expected composition of mammals to differ in forest strips and continuous forest, and that the most vulnerable species (i.e., species that are more likely to be absent from forest strips) would be those with low reproductive rate, large body mass, narrower habitat and dietary breadth, and species that are severely hunted. This work not only supports a broader understanding of effects of habitat loss and creation of forest strips, but also documents the critical situation for wildlife in Chaco, which has the world's highest deforestation rate (Hansen et al., 2013).

2. Materials and methods

2.1. Study area

Our study was conducted in Chaco forest of Salta Province, Argentina. The study area (~9000 km²; center, 24°29'31"S, 63°52'23"W) is dominated by soybeans and pasture with strips of forest 50–100 m wide between all agricultural plots, surrounded by large blocks (>1000 km²) of continuous forest (Fig. 1a). Within the forest, traditional land-use practices of cattle ranching, charcoal extraction, and selective logging continue around small homesteads (one or two families) scattered throughout the forest (Altrichter, 2005). Subsistence hunting is common, occurring opportunistically during other activities and during targeted hunts into the forest every one-two weeks. People from neighboring towns also occasionally hunt in the area.

Native vegetation in our study area is representative of dry Chaco forests, dominated by quebrachos [*Schinopsis lorentzii* (Anacardiaceae) and *Aspidosperma quebrachoblanco* (Apocynaceae)] and accompanied by *Bulnesia sarmientoi* (Zygophyllaceae), *Prosopis alba*, *Prosopis nigra*, *Anadenanthera macrocarpa* (Fabaceae), *Ziziphus mistol* (Rhamnaceae), *Phyllostyllum rhamnoides* (Ulmaceae), and *Callicophyllum multiflorum* (Rubiaceae) (Morello and Adamoli, 1974). Based on published accounts of terrestrial mammals, 30 species > 1 kg should occur in our study area (Mares et al., 1989; Canevari and Vaccaro, 2007; Wallace et al., 2010).

2.2. Sampling design

From May 2010 to January 2011, we sampled occurrence of mammals in 12 transects placed in strips of remnant forest between agricultural fields and extending into adjacent continuous forest. Sampling occurred during dry season because roads are largely impassable during wet season. Using Google Earth, we identified all strips of forest in our study area that were at least 16-km long. Most of these strips were created between 1995 and 2004. We only considered strips at least 8-km apart to assure biological and statistical independence. This distance is larger than home range diameters of all but the largest carnivores (puma, jaguar; Wallace et al., 2010). We only sampled strips not severely degraded by fire (i.e., <15% of strip area affected by fire). All strips were 100 m wide. To avoid biases from nearby roads, transects were no closer than 3 km to any major road. Sixteen forest strips met the requirements described above, and 12 strips were selected randomly for sampling. Species occurrence data were collected with cameras along transects that incorporated 8 km of the forest strip and 8 km of adjacent contiguous forest. Each 16-km transect was treated as a block in occupancy models, and each camera within a transect was considered a sampling unit (see below).

Five cameras (Bushnell TrophyCam, Bushnell Corporation, Overland Park, KS, USA) were placed in each strip of forest, and 5 cameras were placed in continuous forest along each transect. In continuous forest, the first camera was placed at the limit with the forest strip and then cameras were placed at intervals of 1.6 km. In forest strips, a camera was placed every 1.6 km beginning 1.6 km from the edge of continuous forest. Cameras were placed in the nearest appropriate location to designated points (always < 5 m away), including game trails, den sites, and other areas containing animal sign. We placed the camera sensor approximately 10–20 cm off the ground so that smaller species could not avoid detection by walking under the sensor. Cameras remained at each sampling point for 16 days following Thornton et al. (2011), who studied similar species. Logistics of sampling over our entire study area during the dry season precluded a longer sample period. All cameras on a transect were sampled

simultaneously. We recorded presence/absence for each species over every 4-day interval to create a series of repeat detection/non-detection data for modeling detection probabilities (MacKenzie et al., 2002). Generally, 6–7 days occurred between deployments at different transects.

2.3. Species traits for vulnerability analyses

For the 30 mammal species cited for our study area, we determined trophic level, body mass, dietary and habitat breadth, litter size, and age at first reproduction from field guides and recently published studies. Vulnerability to hunting was assessed by interviewing 27 residents from homesteads in forest surrounding our transects. Informants grouped species as: 1 = rarely/never hunted or killed; 2 = occasionally hunted or killed, but not a preferred game species or actively persecuted species; 3 = often hunted or killed. Detailed procedures for deriving species traits and correlations among traits are in Appendix A1. Body size and age at first reproduction were the only highly correlated traits ($r > 0.60$). Consequently, age at first reproduction was omitted from models.

2.4. Assessment of environmental covariates

Understorey density and total canopy cover (i.e., shrubs and trees) were included in models as potential factors influencing probability of detection and occupancy. Camera sensitivity can be affected by solar radiation, which varies with total canopy cover (see Bushnell TrophyCam 2009 manual). We estimated understorey density and canopy cover from standardized digital photographs centered at each camera site (Halchak et al., 2011). Both variables were highly variable and did not differ significantly between continuous forest and strips (Appendix A2). An index of local hunting pressure also was included in initial models of occupancy. To obtain this index, we calculated density of homesteads around each camera within an 8-km radius using ArcGIS10. This distance is the average maximum distance traveled per day on foot by hunters in Chaco forest in Salta (Leake, 2009), and falls within the range of other values reported for Chaco (Altrichter, 2005; Hill et al., 1997).

2.5. Hierarchical Bayesian occupancy models

Species occupancy was analyzed with hierarchical occupancy mixed models with zero inflation accounting for overdispersion using Bayesian inference and history of detections collected from camera traps (Royle and Dorazio, 2008). These models incorporate detection probabilities to overcome sampling biases related to differences in species detection that can result in biased estimation of the relationship between species occurrence and habitat covariates (Royle and Dorazio, 2008). Hierarchical Bayesian models also can incorporate random block effects and, thus, were appropriate for our nested study design (e.g., cameras located within transects, Royle and Dorazio, 2008; Rota et al., 2011).

We modeled occupancy for all species with a naïve estimate of occupancy >10% of sampling units ($N = 9$ species, Table 1). These occupancy models had two components: probability of detection (p) and probability of occupancy (ψ_i). In final models presented here, we modeled p as a linear function of two environmental covariates, canopy cover and understorey density. We modeled ψ_i as a function of distance along the transect where the species was detected (fixed effect, distance hereafter) and transect (random effect) because sampling units within transects likely are not biologically independent. The magnitude of the parameter estimate for distance signals strength of association between distance categories along a transect and occupancy. Negative values indicate that a species was less likely to occupy a given site as distance

Table 1
Number of sites with detections of mammals in continuous forest and forest strips, and life history and ecological traits of these mammals in Chaco forest. The maximum number of sites where a species could be detected was 5 sampling units in forest and 5 sites in strips on each of 12 transects (120 sites total).

Species name ^a		Species traits ^b							Number of sites with detections	
Scientific name	Common name	Body	Hab	Hunt	Diet	Trophic	Litter	FRep	Forest	Strip
<i>Tapirus terrestris</i>	South American Tapir	207.7	5	3	3	1	1	36	2	0
<i>Panthera onca</i>	Jaguar	83.9	5	3	3	3	2	30	0	0
<i>Puma concolor</i>	Puma	54	6	3	4	3	2.8	27	5	1
<i>Catagonus wagneri</i>	Chacoan Peccary	35.6	2	3	3	1	2.7	30	3	0
<i>Mazama americana</i>	Red brocket Deer	33.1	3	3	2	1	1	15	1	0
<i>Myrmecophaga tridactyla</i>	Giant Anteater	30.9	3	2	1	3	1	39	12	2
<i>Tayassu pecari</i>	White-lipped Peccary	28.9	3	3	5	1	1	18	0	0
<i>Priodontes maximus</i>	Giant Armadillo	27.7	3	3	2	2	1.5	10.5	0	0
<i>Pecari tajacu</i>	Collared Peccary	24.9	5	3	5	1	2	18	9	3
<i>Mazama gouazoubira</i>	Gray Brocket Deer	20.4	7	3	2	1	1	13.5	20	17
<i>Leopardus pardalis</i>	Ocelot	7.8	4	1	4	3	1.7	23	1	0
<i>Procyon cancrivorus</i>	Crab-eating Raccoon	7.3	5	1	6	2	3.4	18	1	1
<i>Cerdocyon thous</i>	Crab-eating Fox	5.2	7	2	6	2	4	11	5	7
<i>Eira barbara</i>	Tayra	5.1	6	1	5	2	2	20	1	0
<i>Lycalopex gymnocercus</i>	Pampas Fox	4.9	7	2	6	2	4	12	11	16
<i>Nasua nasua</i>	South American Coati	4.6	6	1	5	2	3.7	24	1	1
<i>Euphractus sexinctus</i>	Six-banded Armadillo	4.4	3	3	5	2	1.5	9	2	1
<i>Herpailurus yagouaroundi</i>	Jaguarundi	4.3	4	2	5	3	2.5	18	0	0
<i>Lagostomus maximus</i>	Plains Vizcacha	4.2	3	3	2	1	1.9	11	0	0
<i>Dasyops novemcinctus</i>	Nine-banded Armadillo	4	8	3	4	2	4	24	0	3
<i>Leopardus geoffroyi</i>	Geoffroy's Cat	3.4	6	2	5	3	2	21	7	11
<i>Dasyprocta punctata</i>	Central American Agouti	3	3	1	3	1	1.3	16	1	1
<i>Conepatus chinga</i>	Molina's Hog-nosed Skunk	2.3	6	1	6	2	3.5	10.5	11	10
<i>ChaetophRACTUS villosus</i>	Large Hairy Armadillo	2.3	5	3	3	2	1.6	9	4	2
<i>Dolichotis salinicola</i>	Chacoan Cavy	2.1	4	2	3	1	1.5	2.8	8	5
<i>Galictis cuja</i>	Lesser Grison	1.9	4	1	4	3	3	20	1	2
<i>Tolypeutes matacus</i>	Southern Three-banded Armadillo	1.2	3	3	4	2	1	9	8	3
<i>Didelphis albiventris</i>	White-eared Opossum	1	8	2	6	2	6.9	10	1	2
<i>ChaetophRACTUS vellerosus</i>	Screaming Hairy Armadillo	1	4	3	5	2	2	9	1	1
<i>Sylvilagus brasiliensis</i>	Tapeti	1	4	3	3	1	1.2	24	0	0

^a List includes species that either were present at our site or should occur there based on published literature and interviews.

^b Key to abbreviations: Body, adult body mass (kg); Hab, habitat breadth (larger values indicate more habitat categories); Hunt, hunting pressure (larger values show larger hunting pressure); Diet, diet breadth (larger values indicate more diet categories); Trophic, trophic level; Litter, litter size (number of young produced per litter); FRep, age at first reproduction; see Appendix A1 for full description of species traits.

from forest interior increased, and positive values indicate the opposite pattern. The full model for each species included additive effects of both environmental covariates on p , as well as distance and transect effects on ψ_i . We also initially considered other covariates (e.g., index of hunting) that were discarded because credible intervals associated with these models overlapped 0 (see Appendix A3).

Detection and occupancy components of the hierarchical model were analyzed simultaneously using program WinBUGS called remotely from program R with R2Winbugs (Gilks et al., 1994; Sturtz et al., 2005). For details on modeling and code, see Appendix A3.

2.6. Relationship between vulnerability and species traits

To understand links between species traits of mammals and their presence in forest and strips, we used two approaches. First, we divided species into three categories. The first category (ND) comprised all species not detected in our study area that should occur in the area based on the known distribution of these species (Mares et al., 1989; Canevari and Vaccaro, 2007; Wallace et al., 2010). Local forest residents confirmed that these species have occurred in the area in the near past. The second category (F) corresponded to species that were detected only in continuous forest. Last category (F + S) included species that were either detected in strips of forest and in continuous forest or only in forest strips (one species). We used classification tree analysis to examine variation in site occurrence as a function of species ecological traits (Andersen et al., 2000). We used percent correctly classified as a

measure of predictive success (Andersen et al., 2000) and Cohen's kappa statistic to determine overall significance of the optimal classification tree (R package "irr"; Gamer et al., 2010). Second, for species that were modeled for occupancy ($N = 9$), we conducted a series of weighted GLMs between measures of species' responses to distance along the transect from forested interior (i.e., estimates of distance parameter from individual-level occupancy models) and all ecological traits of species. The weight of each point in our analysis was the inverse of the standard deviation of the distance parameter (Bender et al., 1998). We fitted models in program R using "glm" function and "identity" link. Models were selected using Akaike Information Criterion with small sample size correction (AICc).

3. Results

3.1. Species detection

We recorded 23 species of mammals in our study area, but most species were detected in less than 10 sampling units (Table 1). Six species that should occur in our study area (based on published literature and interviews) were not detected (jaguar, white-lipped peccary, giant armadillo, jaguarundi, plains vizcacha, tapeti). Five species were found only in continuous forest (South American tapir, Chacoan peccary, red brocket deer, ocelot, tayra). Eighteen species were recorded in continuous forest and strips, and the nine-banded armadillo was found exclusively in forest strips. Modeled occupancy estimates for the 9 species recorded in at least

10 sampling units ranged from 0.19 (Chacoan cavy) to 0.57 (gray brocket deer) (Table A3).

3.2. Relationship between species occurrence and distance along transects

Species modeled for occupancy varied in use of continuous forest and forest strips (Fig. 2, A3). Occurrence of giant anteater and collared peccary decreased near the forest boundary (Fig. 2a and b). Occurrence of gray brocket deer and three-banded armadillo also appeared to decline gradually along the transect from forest into strips (Fig. 2c and d). However, credible intervals for the distance parameter were wide and overlapped zero except in the case of giant anteater and collared peccary, the two species most clearly associated with forest interior. Occurrence of pampas fox increased with distance from forest into the strip (Fig. 2f). Two other species appeared to exhibit similar trends (Fig. 2h and i), but detection rates were lower (Table 1) and credible intervals for the distance parameter overlapped zero.

3.3. Relationship between site of occurrence and species traits

Body size and habitat breadth were the species traits most closely associated with site occupancy. A classification tree with one split based on body size best fit the data and divided species into the following groups: (1) not detected in study area or in forest only, and (2) detected in forest and strips. Species with body size >25 kg (N = 8) were not recorded or only detected in continuous forest, with the exception of pumas and giant anteaters (Table 1). These two species were detected in forest sampling units more often than in strips. Of the 22 species with body size <25 kg recorded in the study area, 17 occurred in strips, and all these species except the nine-banded armadillo also were found in forest (Table 1). This tree correctly classified 78% of the cases, which

was more than expected by chance (Cohen's kappa = 0.48, z = 2.67, p < 0.001). For the 9 species modeled for occupancy, probability of species occurrence with distance (i.e., from forest interior and along the forest strip) was inversely related to body size and positively related to habitat breadth (body size, $\beta = -0.32$, SE = 0.06, t = -5.51, p < 0.01; habitat breadth, $\beta = 0.94$, SE = 0.24, t = 3.84, p < 0.01; best fit GLM model, Fig. 3, Table A4. Although local informants indicated that most of mammal species in our study were hunted, this variable, along with diet breadth, trophic level, and litter size, did not emerge in models as important for understanding the relationship between site of occurrence and species traits (Table A4).

4. Discussion

4.1. General patterns of occurrence

Almost 70% of species cited in the literature for our study area were either not detected or occurred in less than 10 sampling units, including all species categorized by IUCN (2015) as threatened (white-lipped peccary, vulnerable; Chacoan peccary, endangered; giant armadillo, vulnerable; and South American tapir, vulnerable), with one exception. The giant anteater (vulnerable) occupied >10% of the sites but was significantly more likely to occupy continuous forest sites. Low rate of occurrence of mammals in both forest and strips could be explained because medium to large mammals naturally occur at very low densities in our study area and thus were not detected with our sampling effort (i.e., a sampling effect), or because this fauna has suffered from human impacts even in continuous forest. Another potential explanation is that cameras were not effective in detecting mammals, but this is unlikely because trigger speed and sensitivity of cameras were adequate for our species, and we followed camera-trapping protocols of other studies of these species (e.g., Maffei et al., 2004;

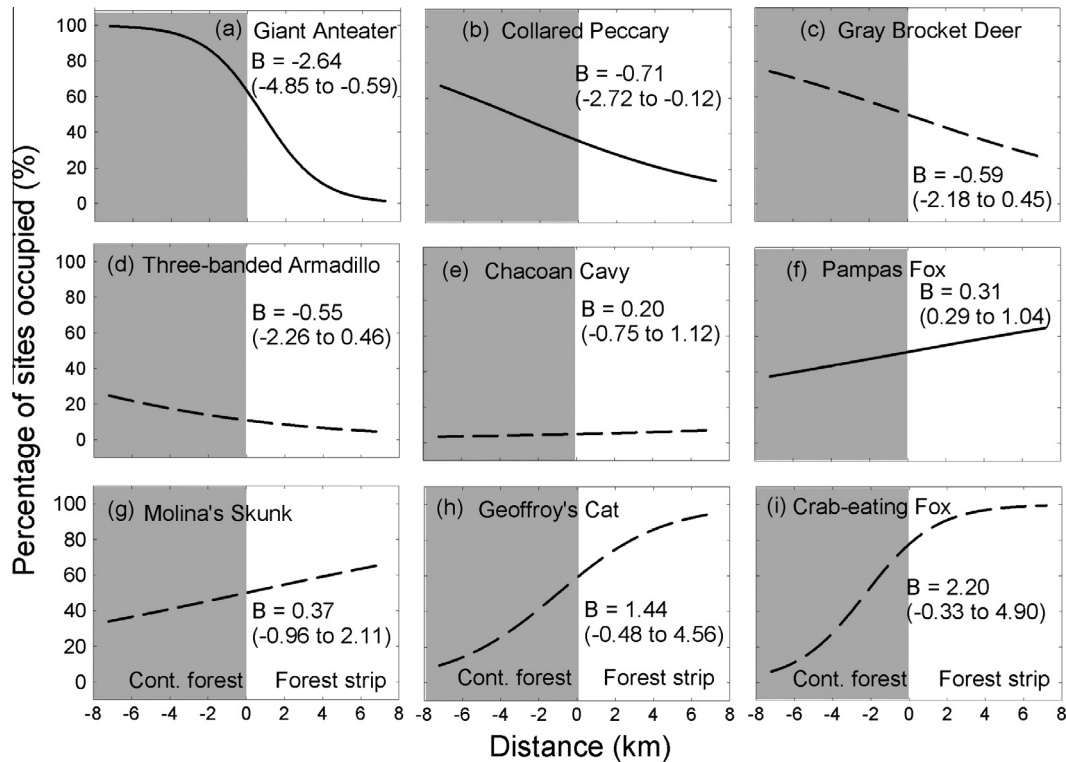


Fig. 2. Relationship between distance along the transect and occupancy of mammals as determined from hierarchical occupancy models. Distance values correspond to distance (km) from the forest edge (0) with negative values for continuous forest (gray area) and positive values for forest strips (white area). 95% Bayesian credible intervals for parameter estimates of distance covariate (β_{dist}) are shown in parentheses. Dashed lines correspond to models where credible intervals for β_{dist} overlapped zero.

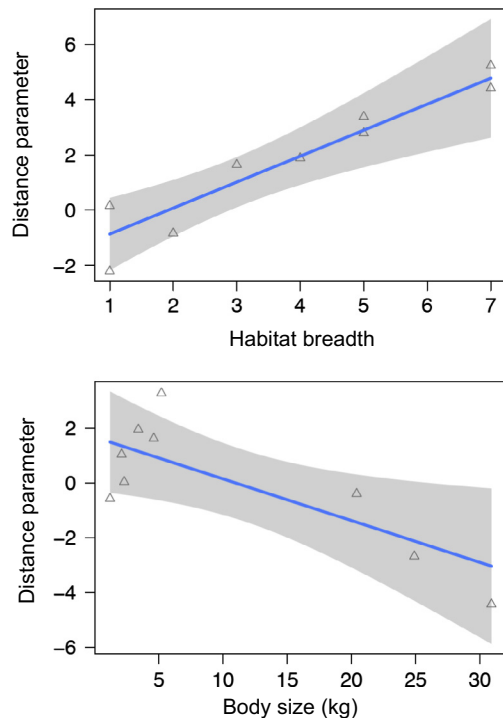


Fig. 3. Relationship between body size and habitat breadth and the distance parameter from occupancy models, as determined by the weighted regression analysis. The shaded areas represent 95% confidence intervals.

Thornton et al., 2011). For some large-bodied species that naturally occur at low densities throughout their range (e.g., jaguar and giant armadillo), lack of detection may be related to sampling effect. However, the puma, a large-bodied, wide-ranging species that also occurs at low densities throughout its range (most of North and South America), was detected in 6 sampling units. For many mammals that Chaco shares with tropical forest in Central and South America, Chaco forest (particularly in Argentina and Paraguay) corresponds to the southernmost part of their distributions (e.g., jaguar, ocelot, peccaries, South American tapir; IUCN, 2015). At limits of species distributions, optimal environmental conditions and resources may occur with less frequency than in the center of their distributions (Case et al., 2005), resulting in lower population densities and, thus, potentially limiting detection in our study area. However, in protected areas in Bolivian Chaco, large mammal densities are equal to or larger than in many tropical forests to the north (Maffei et al., 2004). Thus, if low densities of mammals are related to geographic boundaries of distributions, this phenomenon is likely limited to southernmost Chaco and not the entire Chaco region. Although the low occurrence that we documented for many species may be partially explained by sampling effect or geography, this low occurrence also likely relates to human impacts on Argentine Chaco. Throughout the region, forest has been highly modified and degraded as a consequence of grazing and logging, and hunting is severe though poorly documented for most species (Altrichter, 2005).

4.2. Use of forest strips

Although the mammal species most vulnerable to conversion of continuous forest to forest strips already may have been lost from our study area, 14 of the 24 species remaining were absent from strips or were recorded most frequently in continuous forest. In contrast, only 3 medium-sized carnivores and possibly the nine-banded armadillo may benefit from conversion of forest to a

landscape characterized by forest strips around agricultural fields based on our occurrence data. Our study is consistent with other research that documents lower use of strips than continuous forest by dung-beetles, birds and arboreal mammals (Barlow et al., 2010; Hawes et al., 2008; Laurance and Laurance, 1999; Lees and Peres, 2008; Wehling and Diekmann, 2009). However, in contrast to our results, medium to large mammals in the Amazon have been reported to use strips more than continuous forest (Barlow et al., 2010). Some mammals were shared between the Amazon study and our study (e.g., collared peccary, giant armadillo, and others), and strip widths were comparable (~100 m). Differences in results of the two studies may relate to the landscape matrix surrounding forest strips, which comprised *Eucalyptus* plantations in the Amazonian study and pasture or soybeans in Chaco. Forest mammals foraged in understory of *Eucalyptus* (Barlow et al., 2010). Local landowners at our study site reported seeing mammals in strips or at the edge of strips, but rarely in the agricultural matrix. Soybean and pasture matrix of Chaco may provide less suitable habitat and may be less permeable to movement of forest species, as observed for birds in Chaco forest (Mastrangelo and Gaving, 2014). Alternatively, discrepancies between the two studies could be related to hunting pressure if hunting of mammals is higher in strips as compared to forest in Chaco, and the reverse occurs in Amazonia. Hunting takes place at both sites (Barlow et al., 2010), but relative hunting pressure in forest versus strips is unknown.

4.3. Patterns of occurrence and species traits

Studies of forest fragmentation have demonstrated that forest specialists often are more impacted by forest loss and fragmentation than generalist species particularly because of insufficient resources and sensitivity to edge effects (Henle et al., 2004; Peres, 2001). Large-bodied species that range widely (e.g., large carnivores) often disappear from fragments because their area requirements are not met, and also forest fragmentation increases their vulnerability to other threats such as hunting. Although large blocks of continuous forest remain in our study area, for some wide-ranging species such as white-lipped peccaries and jaguars, this forest already may be too fragmented to sustain populations (Quiroga et al., 2013). Large-bodied species and species that specialize on forest habitat either were not recorded in our study area or occupied forest sites more often than strips. This group included herbivores (browsers/grazers and frugivores), omnivores, myrmecophages, and carnivores. All species recorded more frequently in strips than in continuous forest had body mass less than 10 kg and were habitat generalists, occupying a variety of open habitats (e.g., grasslands and scrublands) as well as forest across their ranges (Mares et al., 1989; Canevari and Vaccaro, 2007; Wallace et al., 2010).

The degree to which occupancy of mammals in our study area is influenced by quantity versus quality of habitat, or other factors such as vulnerability to hunting, is unknown, but multiple factors likely are important. In this region, conversion of forest to agricultural fields with forest strips results in immediate loss of ~78% of forest area (depending on local regulations; Ginzburg et al., 2012), drastically reducing habitat for forest specialists. Yet, understanding of habitat quality for mammals in Chaco forest and strips is limited. Research on vegetation has focused primarily on forest structure. Forest strips, as well as edges of continuous forest, have higher density of shrubs and small trees and lower abundance of large trees than in forest interior (Ginzburg et al., 2012). These habitat changes should produce more browse, and possibly higher quality browse, in strips for species such as tapirs and deer. However, we detected tapirs and red brocket deer only in continuous forest, and occupancy of grey brocket deer was similar or slightly lower in strips than forest. Many mammals in this forest

eat seeds and fruits (Wallace et al., 2010), and 55% of the woody flora of Chaco is dependent on mammalian dispersal (Periogo et al., 2015). If mammal density is low in strips, either because important food trees are less abundant in strips or for other reasons, this could reduce recruitment of food trees leading to further negative feedback on mammal populations. During our study, zoochoric fruits appeared to be less abundant in the forest strips than in forest interior, but more detailed studies are needed to understand links between conversion of forest to strips and habitat quality for mammals (Periogo et al., 2015).

Prior studies conducted on medium-large mammals in Argentine Chaco point to hunting as a significant factor in population declines (Altrichter, 2005; Quiroga et al., 2013). Thus, lack of statistical support for hunting as a predictor of species occurrence in our study was unexpected. This may have occurred for several reasons. First, with only three categories, our index of hunting based on interviews may have been too simple to fully represent differences in hunting pressure among species. Second, a significant part of the hunting pressure may come from hunters living in urban areas, which is very difficult to quantify and not included in our models. Third, and perhaps most important, many species were detected by few or no cameras, precluding analyses of occupancy. These species may be locally extinct or at low densities as a result of hunting, or because of combined effects of hunting, forest loss and fragmentation. Hunting is a major driver of occupancy patterns for mammals in fragmented tropical forest, and body size and vulnerability to hunting often are positively correlated (Thornton et al., 2011; Peres, 2001). In our study area many small-bodied species also are heavily hunted, potentially because larger game species have been depleted, but also because some of these species such as three-banded armadillo are highly preferred by hunters (Altrichter, 2006). Overall, 77% of the mammals that occurred, or should occur, in our study area are hunted; 53% of these species are heavily hunted in our study area and throughout Chaco, including all large-bodied species (>25 kg) except the anteater (Altrichter, 2005, 2006; Quiroga et al., 2013). The only heavily hunted species that commonly occurs in strips and continuous forest in our study area is the gray brocket deer, which is a habitat generalist that uses agricultural areas as well as forest (Wallace et al., 2010).

4.4. Conservation implications

Given that strips of forest are mandated by law in many tropical and subtropical areas and widely accepted by large landowners (Hawes et al., 2008; Seghezzo et al., 2011), forest strips likely will comprise an increasingly large portion of remaining forest, not only in Chaco, but also in other regions undergoing rapid forest conversion for agriculture (FAO, 2012). Evidence from our studies and others (Lees and Peres, 2008) demonstrates that these strips contain only a subset of the original fauna in these forests. In the case of Chaco, as forest is converted to forest strips embedded in agricultural fields, loss of forest specialists and persistence of generalists lead to functional homogenization of biodiversity, which may be accompanied by loss of vital ecosystem services such as seed dispersal by forest mammals (Devictor et al., 2008; Puechagut et al., 2013). Our study likely underestimates long-term effects of forest transformation. Strips in our study area are relatively recent (i.e., <10 years old) and undoubtedly harbor extinction debts (Tilman et al., 1994). As agriculture continues to expand in Chaco, alternative landscape configurations urgently need to be designed, evaluated, and incorporated into policy if the mammalian fauna of Chaco is to be retained. Ample evidence points to the importance of large fragments and aggregated habitat to prevent local extinctions of wildlife (Rybicki and Hanski, 2013). Retention of forest strips may have detrimental impacts on

agricultural production because, for example, trees shade crops and compete with crop plants for water (Ginzburg et al., 2012). Conserving the same total forest area that is destined for strips, but in large interconnected blocks, may receive support from private landowners, who control most of the forested areas in northern Argentina. In our study area, landowners have shown interest in increasing biodiversity value of their land, and a conservation payment program associated with the 2009 Argentine National Forestry Law provides an opportunity to explore, and potentially finance, multi-sectorial conservation/production schemes.

An important point that emerges from our study is the critical situation of the fauna of Chaco. This fauna is poorly studied, diverse, and subject to multiple interacting threats. Diversity of medium and large terrestrial mammals of Chaco is comparable to tropical forests such as the Amazon (Mares, 1992; Redford et al., 1990). Armadillos reach their peak diversity in Argentine Chaco (Zuleta and Bolkovic, 1994). The endemic Chacoan peccary was known only from fossil records until 1974 (Wetzel et al., 1975). The few studies of medium to large mammals that have been conducted in this region primarily focus on jaguars and hunting of peccaries (Altrichter, 2005, 2006; Quiroga et al., 2013). These studies conclude that hunting of Chacoan peccaries and white-lipped peccaries is not sustainable and that local extinction of jaguars may be imminent in Argentine Chaco (Altrichter, 2005; Quiroga et al., 2013). Sustainable harvest management strategies have been widely implemented in tropical regions of South America (e.g., Bodmer et al., 1988), but are lacking, and particularly challenging, in Chaco (Altrichter, 2008). Conservation challenges of Chaco were captured more than two decades ago by Redford et al. (1990), who referred to Argentine Chaco forest as “one of the greatest, yet least known, ecological catastrophes in South America”. The 2009 Argentine National Forestry Law, which requires that all provinces produce land use plans to conserve forest (Seghezzo et al., 2011), provides an unprecedented opportunity to address these challenges and design a more functional forest-agriculture landscape. However, recent analyses project that forest area in Chaco will decline substantially under the current implementation plan for this law, and that ecoregional planning across Chaco is required to maintain forest cover and connectivity (Piquer-Rodríguez et al., 2015). In addition to designing alternative landscapes, synergisms between the configuration of the Chaco landscape and threats such as hunting need to be addressed as part of the planning process if the “empty forest” syndrome is to be avoided (Altrichter, 2005; Redford, 1992; Periogo et al., 2015).

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocon.2015.04.001>.

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