

ARE FOREST STRIPS CUT OUT FOR THE JOB OF CONSERVING BIODIVERSITY?
EVALUATING THE CASE FOR MAMMALS WITH HIERARCHICAL BAYESIAN
OCCUPANCY MODELS IN THE CHACO FOREST

By

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To the mammals of the Chaco forest

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Deforestation is a major cause of biodiversity loss, and the largest factor driving deforestation is expansion of agriculture. A key step toward successful conservation in agricultural areas is maximizing the biodiversity value of remaining forest. In subtropical and tropical regions, forest often is left in strips between agricultural fields under the assumption that biodiversity is sustained. In this thesis I examined how medium and large-sized mammals in the Argentine Chaco responded to forest strips retained along agricultural fields and how that response related to ecological traits of species.

Presence/absence data from camera traps in continuous forest and forest strips showed that almost half of the total mammal assemblage that occurs in my study site was impacted by conversion of forest to strips. Five species found in forest were completely absent from strips. Hierarchical Bayesian occupancy models also demonstrated that occurrence of mammals decreased in forest strips with increasing distance from continuous forest. Species that occupied a variety of habitats and had broader diets tended to exhibit higher occupancy in strips than species that specialized on primary forest habitat or a more narrow range of foods. Almost 70% of the species cited for my

area either were not detected or occurred in less than 10% of my sampling units. This low occurrence of mammals in strips and in continuous forest raises mayor concerns related to the long term survival of mammals in the Chaco.

CHAPTER 1 INTRODUCTION

Understanding and predicting distribution of animals in human modified landscapes is fundamental to much of ecological science, and lies at the heart of conservation and management of many species. This issue is particularly important in areas comprised of a mosaic of forest and human land uses. Globally, forest area has decreased by some 13 million ha each year in the last decade (FAO 2010). 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 by a wealthier and larger global population (Sachs et al. 2009; Tilman et al. 2001). Clarifying how wildlife species respond to different configurations of forest in agricultural landscapes will be essential for development of effective conservation policy to sustain wildlife in agriculturally dominated landscapes.

As a result of massive loss and fragmentation of habitat, remnant forest strips are a common feature of agricultural landscapes throughout the world (Boughey et al. 2011; Hawes et al. 2008; Seaman and Schulze 2010). In agricultural landscapes these strips of forest (also termed 'linear forest remnants' or 'hedgerows'; Boughey et al. 2011; Laurance and Laurance 1999) often extend from continuous primary forest into the agricultural matrix, but unlike 'wildlife corridors' do not necessarily connect habitat patches (Diamond 1975). Historically, strips of forest have been used to separate agricultural blocks to help prevent soil and wind erosion and spread of fire (Zanuncio et al. 1998). Some authors suggest that forest strips also can represent a valuable conservation asset to some small vertebrates and insects like dung-beetles, birds and small mammals by providing suitable habitat (Barlow et al. 2010a; Boughey et al. 2011;

de Lima and Gascon 1999; Lees and Peres 2008; Seaman and Schulze 2010).

However, understanding of the conservation value of forest strips in production landscapes is still poor (Hawes et al. 2008), especially for wide ranging animals and in sub-tropical ecosystems.

If current deforestation rates continue, forest strips will be among the most common features of agricultural landscapes in tropical and subtropical systems, and significant amounts of remaining forest will occur in strips. In South America, this conversion process is particularly acute in the dry subtropical Chaco, which is the second largest forest area after the Amazonia. Argentina contains 60% of the Chaco forest. This region has a deforestation rate that is 12 times larger than the world mean and 5 times larger than the continental mean deforestation rate (Seghezzo et al. 2011). In northern Argentina current environmental norms require that for every 100 ha of deforested land ~23-37 ha of forest must be left in strips surrounding agricultural plots (Adamoli et al. 2011). If the remaining Chaco forest is converted to agricultural land, in Salta province (NW Argentina) alone 1.6-2.6 million ha will be in forest strips, which is equivalent to 8-13% of the total national protected area of Argentina. This situation is not an isolated case. Strips of forest are widely accepted by large landowners and mandated by law throughout many tropical and subtropical areas of South America (Hawes et al. 2008, M Nuñez-Regueiro Pers Obs; Seghezzo et al. 2011).

Although a large amount of evidence points to the negative effects of habitat reduction and fragmentation on species diversity (Fahrig 2003), not all species are equally sensitive (Thornton et al. 2011b). Vulnerability of species to conversion of forest into strips of forests remnants may be related to the way in which species exploit habitat

and other resources. Loss of habitat area, and particularly interior forest habitat, may reduce the availability of optimum conditions and resources for some species, lowering the quality of their habitat (Fahrig 2003). Such changes may strongly affect forest specialists (i.e., species with smaller dietary and habitat breadth; Cagnolo et al. 2009). Species with large body mass also may be impacted by fragmentation because of their large space requirements (Carbone et al. 2005; Crooks 2002). Also, exposure of hunted species often increases in fragmented landscapes which could, in turn, exacerbate the effects of hunting (Peres 2001). Hunting is a significant threat throughout the tropics and also for subtropical systems (Altrichter et al. 2006). Species with lower reproductive rates have been shown to be the most vulnerable to hunting (Altrichter 2005). Incorporating species traits into analyses of species occurrence ultimately will help understand how species react to conversion of forest to forest strips.

Here, I examine how medium and large-sized mammals (body weight > 1 kg, hereafter referred to as mammals) respond to forest strips retained along agricultural fields in the Argentine Chaco, and how that response relates to ecological traits of species. Particularly, I expected the community composition of mammals to be different in strips of forest and in 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 large body mass, narrower dietary and habitat breadth, and species that are severely hunted. This work will contribute to conservation by providing insights into the response of medium to large mammals to conversion of forest to strips. Previous work has primarily focused on smaller vertebrates, insects and plants (Barlow et al. 2010b; Boughey et al. 2011; de Lima and Gascon 1999; Hawes et al. 2008; Laurance and Laurance 1999;

Lees and Peres 2008; Wehling and Diekmann 2009). Understanding this response is important both for evaluating impacts of landscape change on mammals and because medium to large mammals play key ecological roles in forest (Noss et al. 1996; Rozylowicz et al. 2011). Also, my work provides the first critical evaluation of biodiversity implications of current environmental norms in the endangered Chaco eco-region that result in forest being confined to thin strips around agricultural fields.

CHAPTER 2 METHODS

Research Design

To evaluate the response of mammals to conversion of forest to strips and to assess how that response changed with increasing distance from forest interior, I designed a comparative study in which I compared occurrence of mammals in forest and in strips along a transect (Figure 2-1). This comparison was carried out by creating mathematical models that accounted for variation in detection probability (as a function of vegetation structure) and modeled occurrence (collected from presence/ absence data from camera traps) as a function of distance along the transect. These hierarchical Bayesian occupancy models were constructed for all species that were present in more than 10 different camera traps.

To understand which life history traits were most closely associated with vulnerability of species to conversion of forest to strips, I analyzed the relationship between occurrence of mammals and species traits (i.e., trophic level, body mass, dietary and habitat breadth, litter size, age to first reproduction, and hunting pressure). This relationship was analyzed using two methods. First, I conducted a classification tree analysis to group the entire assemblage of species according to their site of occurrence (i.e., strips + forest, forest only, or not detected) and their ecological traits. Second, I graphically represented the relationship between vulnerability of species (obtained from occupancy models) and their ecological traits.

Study Site

This study was conducted in Chaco forest of Salta Province, NW Argentina, a subtropical region with high biodiversity and one of the world's highest deforestation

rates (Figure 2-2). In this region, annual deforestation rates have more than tripled in the last 10 years with expansion of the agricultural frontier as a result of increased international demand for soybeans (Gasparri and Grau 2009). The new National Forestry Law of Argentina, which requires classification of forested areas for different land uses, potentially could result in deforestation of an additional 1.6 million ha in Salta in the next 6-9 years and leaves open the option of subsequent deforestation of additional 5.4 million ha. If deforestation continues, the entire Chaco forest of Salta will be reduced to network of remnant forest strips embedded in an agricultural landscape.

The extent of my study area is ~9,000 km² and the geographical center is located at 24°29'31"S, 63°52'23"W. The study area is characterized by a central region dominated by soy and pasture in which strips of forest occur between all agricultural plots throughout the entire landscape. Large blocks of continuous forest surround this central agricultural area (Figure 2-2). The native vegetation is representative of dry Chaco forests, dominated by quebrachos (*Schinopsis lorentzei* and *Aspidosperma quebrachoblanco*) and accompanied by *Bulnesia sarmientoi*, *Prosopis alba*, *Prosopis nigra*, *Ziziphus mistol*, *Anadenanthera macrocarpa*, *Phyllostyllum rhamnoides*, and *Callicophyllum multiflorum* (Grau et al. 2008). Published accounts of terrestrial mammals for this area document 29 species >1 kg (Canevari and Vaccaro 2007; Mares et al. 1989; Wallace et al. 2010). I did not include in this list species associated with bodies of water (e.g., capybara, *Hydrochoerus hydrochaeris*) or primarily arboreal species (e.g., margay, *Leopardus wiedii*) because I did not adequately sample these species.

Site Location and Sampling Sites

From May 2010 to January 2011, I sampled occurrence of mammals in 12 transects placed in strips of primary forest between agricultural fields and extending into adjacent continuous primary forest (Figure 2-2). Using Google Earth I identified all strips of forest in my study area that ranged from 50 m to 100 m in width and were at least 16-km long in the study area. Most of these strips were created between 1995 and 2004. For my study, I only considered strips at least 8 km from the adjacent strip to assure biological and statistical independence. This distance is larger than the home range diameter of all but the largest carnivores (puma, jaguar; Canevari and Vaccaro 2007; Wallace et al. 2010). Therefore, the probability of sampling the same animal in different strip was low. I only sampled strips not severely degraded by fire (i.e., < 15% of the area of the forest strips affected by fire). To avoid biased results from nearby roads, transects were no closer than 3 km to any mayor road or highway. Sixteen forest strips met the requirements described above. From that pool, 12 strips were selected randomly for sampling. Samples were collected along transects that incorporated 8 km of the forest strip and 8 km of the adjacent contiguous forest (Figure 2-2). Each 16-km transect was treated as a block in occupancy models and each camera within a transect was considered a sampling unit.

Sampling Protocol for Camera Traps

Five camera traps (Bushnell TrophyCam, Bushnell Corporation, Overland Park, KS, USA) were placed in each strip of forest and 5 cameras in the continuous forest (i.e., 10 cameras in each transect; Figure 2-2). 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 strips of forest, a camera was placed every 1.6 km beginning 1.6 km from the

edge of the forest. Cameras were placed in the nearest appropriate location to the designated points. These locations included small and large game trails, water holes, den sites, and other areas containing substantial signs of animal use such as tracks, digging, or scraping. I placed the camera sensor approximately 10 – 20 cm off the ground so that smaller species could not avoid detection by walking under the sensor. Camera traps remained at each sampling point along the transect for 16 days. I broke up the 16-day period into 4-day sessions to create a series of repeat detection/non-detection data (i.e., a detection history) for use in modeling detection probabilities for each species (MacKenzie et al. 2002a).

Assessment of Environmental Covariates

I included covariates in hierarchical occupancy models that represented distance categories for the 1.6-km spacing of cameras along each transect (i.e., categories 1-5 for continuous forest and 6-10 for strips of forest; Figure 2-2) and also measured forest structure. Covariates for forest structure (understory density and canopy cover) were included in probability of detection models. Detection of an animal likely varies as a function of density of understory vegetation. Also camera sensitivity can be affected by solar radiation which varies with canopy cover (see Bushnell TrphiCam, 2009 manual for more details). To evaluate forest structure in strips of forest and continuous forest, I took standardized digital photographs centered at each camera trap site (Halchak et al. 2011; Lees and Peres 2008). For understory density estimations, I took 4 photographs in each cardinal direction parallel to the ground at 15 cm from the ground. For canopy cover analyses, I took a single photograph perpendicular to the ground. Images then were analyzed using ImageJ free-ware (Java-based image processing program developed at the National Institute of Health), which counted the number of forest (dark)

pixels across the image and calculated a mean and SD for each image (Halchak et al. 2011). Data from the 4 photographs of the understory were averaged for each site. To analyze differences in canopy cover and understory density of sites located in continuous forest versus. strips, I first calculated a mean value for each vegetation covariate from samples within the forest or strip portion of the transect. Then, using these transect-level mean values, I conducted a paired t-test to compare vegetation structure in forest versus. strips.

Species Traits for Vulnerability Analyses

For the 29 mammal species cited for my study area, I determined trophic level, body mass, dietary and habitat breadth, litter size, and age to first reproduction from field guides and recently published studies (Canevari and Vaccaro 2007; Mares et al. 1989; Wallace et al. 2010). Trophic level was categorized as follows: 1 = primarily browser/grazer or frugivore, 2 = omnivore, 3 = primarily carnivore/myrmecophage. I calculated body mass as the average of male and female body mass. When only a range was given, I took the midpoint of the range. I estimated dietary and habitat breadth as the number of habitat or dietary categories a species uses based on published information (Canevari and Vaccaro 2007; Mares et al. 1989; Wallace et al. 2010). Dietary breadth was calculated as the number of categories of different prey types eaten by each species. Categories included in the analysis were: grass, browse, crustacean/fish, insects/arthropods, hard mast, soft mast, small mammals, large mammals, reptiles/amphibians, birds, carrion, and domestic crops. Habitat breadth was calculated by counting the number of habitat categories used by a species, including only those habitats commonly encountered in Chaco: primary dry forest, secondary/regenerating forest, savanna/pasture or cropland, and near-urban

environments. Litter size was the average number of young produced per year. Age to first reproduction was recorded as the average number of months from birth to first reproduction. Other reproductive parameters, such as number of litters per year, were not available for many of the species in my study area.

Prior to analysis correlations among species traits were examined with Spearman's rank correlation to determine if these traits were supplying redundant information. Most species traits examined in this study were not correlated (Appendix A). Exceptions were as follows: a) Species with small body size also tended to have an early first reproduction and exploit many habitat types ($R^2 = 0.61$ and 0.46 , respectively; Appendix A); b) In general, species that had many young per litter also consumed many dietary categories ($R^2 = 0.54$).

Vulnerability to hunting was assessed by interviewing 27 informants distributed evenly across my study area. Informants were local, long-term (> 6 years) resident hunters and agricultural workers who are regular visitors to the sample area and are thoroughly familiar with the medium to large-bodied vertebrate fauna. To assure that interviewees knew the species, I asked them to identify species present in the sample area from a selection of color plates of mammals and birds, including 10 species known to be absent from the study region. Informants recognized that the 10 species did not occur in the region >90% of the time. Informants grouped species into the following categories: 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.

Hierarchical Bayesian Occupancy Models

Species occupancy was analyzed with hierarchical occupancy mixed models using Bayesian inference and the history of detections collected from camera trap sampling.

These models can incorporate detection probabilities to overcome sampling biases related to differences in species detection and can include sampling designs that incorporate random block effects. If imperfect detection is not taken into account, some species may appear to be vulnerable than other species merely because these species are harder to detect (Dorazio and Royle 2005; MacKenzie 2006; Thornton et al. 2011a). Underestimation of the relationship between species occurrence and habitat covariates in logistic regression type of models has been documented when imperfect detection was not taken into account (Kery 2010; Royle and Dorazio 2009). This modeling approach also was appropriate for my study because of the nested study design (i.e., cameras were located within transects).

Interpretation of modeled occupancy differs in my study from traditional patch occupancy studies (MacKenzie et al. 2002b) because my study likely does not comply with the closure assumption for occupancy models (i.e., many of the mammal species in my study were capable of moving in and out of sites during sampling; MacKenzie 2006; MacKenzie et al. 2002b). The occupancy estimator is best interpreted as “probability of use” of a site, rather than probability of occupancy. However, for ease of presentation, I will continue to use traditional occupancy terminology in this thesis.

I modeled occupancy for species that had a naïve estimate of occupancy of >10% (n=9). These occupancy models had two components: probability of detection (p) and probability of occupancy (ψ_i). I modeled p as a linear function of two environmental covariates, canopy cover and understory density. The full model included both environmental covariates. The final model for each species only included environmental covariates that had a strong association with probability of detection (i.e., I discarded

covariates in which credible intervals overlapped zero.). I modeled ψ_i as a function of a fixed effect (distance along the transect where the species was detected) and a random effect (transect). The magnitude of the parameter estimate “distance” signals the strength of association between distance categories along a transect and occupancy. Negative values indicate that a species was more likely to occupy a given site as distance from the strip into the forest interior increased and less likely to occupy the strip as distance from continuous forest into the strip increased (i.e., as occupancy increased from d10 to d1 (Figure 2-1), the “distance” parameter became more negative). Positive values indicate the opposite pattern (i.e., occupancy decreased from d10 to d1). Transect was included as a random effect because sampling units within a transect may not be biologically independent. I did not include canopy cover and understory density because the model behaved better (i.e., achieved convergence at fewer number of iterations) with few parameters. I chose to include distance along the transect instead of canopy cover or understory density because I was interested in understanding the overall pattern of species response to strips per se. Both components of the hierarchical model were analyzed simultaneously using program Winbugs (Gilks et al. 1994), which was called remotely from program R with the package R2Winbugs (Sturtz et al. 2005). For details on modeling approaches for occupancy and detection probability and for code details, see Appendix B.

Relationship Between Vulnerability and Species Traits

To better understand links between species traits of mammals and their response to conversion of forest to strips, I used two approaches. First, I divided all species of mammals that were detected in the study area or should occur in the study area into three categories. Category 1 comprised all species not detected in my study that should

occur in the area based on the known distribution of these species (Canevari and Vaccaro 2007; Mares et al. 1989; Wallace et al. 2010). Local forest residents also confirmed that these species have occurred in the area in the near past (i.e., less than 5 years). The second category corresponded to species that were detected only in continuous forest. Last category included species that were either detected in strips of forest and in continuous forest or only in strips of forest (one species). I used classification tree analysis to group species into homogeneous sets using species ecological traits as independent variables (Andersen et al. 2000). I used CRT growing method for classification tree with a Gini impurity measure that maximized the homogeneity of child node with respect to the value of the target variable. Second, for species that were modeled for occupancy (n=9), I graphically represented the relationship between the model parameter “distance” and species ecological traits. I did not analyze this relationship statistically (e.g., with a linear regression) because of 1) the asymmetric nature of the posterior distribution around the mean values of parameter “distance” and 2) some variables were categorical (e.g., habitat/dietary breadth and hunting). Methods like linear regression assume equivalent distances between categories, which is not likely to occur in case of categorical variables (i.e., species with habitat breadth value of 2 are not twice as broad, in terms of diet, than a species with a value of 1).

CHAPTER 3 RESULTS

Vegetation Structure

Forest structure in continuous forest differed from forest strips only for understory density (understory density, $F= 4.07$, $df=10$, $p=0.07$; canopy cover, $F=2.4$, $df=10$, $p=0.15$). On average understory in continuous forest was denser than in forest strips (mean \pm SD, continuous forest, 236 ± 3.1 ; strip, 227 ± 8.9 ; units are expressed in number of forest pixels in the image. See methods for more details.). Also, understory density was more heterogeneous with increasing distance away from the forest edge into the strip of forest (Figure 3-1). Canopy cover was highly variable among sites in both continuous forest and strips, and exhibited no obvious trends comparable to those of understory density (mean \pm SD, continuous forest, 174 ± 18.6 ; strip, 201 ± 19.4 ; Figure 3-2).

Species Detection

I detected 23 species of mammals in my study site (Table 3-1). Seventeen species were detected in continuous forest and strips. One species was found exclusively in forest strips (nine-banded armadillo). Five species (ocelot, tapir, red brocket deer, tayra, chacoan peccary) were found only in continuous forest. Six species that should occur in my study area (based on published literature and interviews) were not detected (plains vizcacha, jaguar, giant armadillo, jaguarondi, tapeti, white-lipped peccary). Most species were detected in less than 10 sampling units (Table 3-1).

Accounting for detectability in the analysis resulted in considerable increase in occupancy estimates, especially for species that were difficult to detect (Table 3-2). On average, estimates of occupancy corrected for detectability increased by 27% from the

naïve estimate of occupancy. For species that were easy to detect when present (i.e., many detection records at a given site), such as the chacoan cavy, modeled occupancy estimates were similar to naïve estimates. Modeled occupancy estimates for the species recorded in at least 10 samples units ranged from 0.14 (chacoan cavy) to 0.56 (giant anteater).

Relationship Between Species Occurrence and Location Along Transects

Species also varied in their response to distance from forest edge (Table 3-2). Parameter “distance” estimates for 5 species were negative, indicating that the species was more likely to occupy a given site as distance of the sample location from the forest interior decreased (i.e., from d10 to d1; Table 3-2, Figures 3-3A and 3-3B). In some cases species’ occurrence decreased gradually along the transect from forest into strips (e.g., Molina’s skunk, gray brocket deer; Figure 3-3B), and in other cases a more abrupt decrease occurred in occurrence near the forest boundary (e.g., giant anteater, Figure 3-3A). Credible intervals for the distance parameter were wide and overlapped zero, except in the case of the giant anteater and the collared peccary. These two species were most clearly associated with forest interior. Four species exhibited positive parameter estimates for distance, indicating that occurrence increased with distance from the forest interior into the strip (i.e., from d1 to d10, Table 3-2, Figures 3-3C and 3-3D). However confidence limits for the distance parameter also overlapped zero for these species, except in the case of the pampas fox. Occurrence of this species strongly increased with distance from forest (Figure 3-3C).

Relationship Between Site of Occurrence and Species Traits

Habitat breadth was the most important variable for classifying all species recorded for my study area in the classification tree by the environments in which these

species were detected (i.e., not detected in study area but cited in the literature), detected in forest only, or detected in strips and forest; Figure 3-4). About half of the species that were detected only in forest or were not detected in my study area even though they were cited for the area (n=6) were primary forest specialists and about half (n=5) were generalist species (i.e., they used other habitats as well as primary forest). In contrast, 94% of the species that occurred in strips as well as forest were categorized as generalist species. Other species traits (i.e., trophic level, body mass, dietary breadth, litter size, first reproduction, and hunting) were not used by the classification tree to group species. Although I could not statistically test for relationships between species traits and occurrence of these mammals (n=9 modeled species) along transects (as represented by the “distance” parameter), some trends were apparent from graphical representation. Species with narrow dietary and habitat breadth tended to be more likely to occupy forest interior sites (Figures 3-5A and 3-5B). Also, species that had small litter sizes were more likely to occupy forest interior sites (Figure 3-5C), but this trait was correlated with diet breadth (Appendix A). Other ecological traits (i.e., age to first reproduction, body size, hunting pressure, and trophic level) did not show a linear relationship with the distance parameter (Appendix C).

CHAPTER 4 DISCUSSION

Patterns of Occurrence and Distance Along Transects

My study indicate that at least 44% of the medium to large mammals currently present in my study area responded negatively to conversion of forest to strips. Five species found in forest were completely absent from strips, and five other species tended to decrease in occupancy along the strips as distance from the forest increased and exhibited highest occupancy in interior forest. In contrast, three species appeared to benefit from strips. The proportion of sites occupied by pampas fox, Geoffrey's cat and the crab eating fox increased in strips as distance from the forest increased, though this pattern was significant only for the pampas fox. In other parts of their geographical range, all three of these species occupy a variety of open habitats (e.g., savannas, grasslands, and scrublands), as well as forest (Wallace et al. 2010). The nine-banded armadillo was the only species that I detected in strips, but not in forest. This species is widely distributed throughout tropical forest, as well as savannas (Wallace et al. 2010), but only was detected in three cameras in my study and thus may not have been sampled adequately.

Results of my study both support and contrast with studies of species use of forest strips in other regions. In studies of birds and medium to large mammals in riparian forest in tropical regions, species richness has been found to be either similar or lower in forest strips compared to more continuous forest (Hawes et al. 2008; Lees and Peres 2008; Seaman and Schulze 2010), and in upland (terra firme) forest, fewer bird species occupied strips than continuous forest (Hawes et al. 2008). Forest strips in both habitats

supported fewer forest specialist birds than habitat generalists (Hawes et al. 2008; Seaman and Schulze 2010).

In contrast to my study, a study of use of forest strips by medium to large mammals in the Amazon reports that these mammals use strips more than continuous forest (Barlow et al. 2010a). Some of the mammals in the Amazon study were the same species found in my study area (e.g., collared peccary, grey brocket deer, giant armadillo, and others). Differences between this study and mine in patterns of occurrence may relate to the landscape matrix, which was comprised of *Eucalyptus* plantations in the Amazonian study and pasture or soybean in the Chaco. Medium to large mammals apparently forage in the understory of the *Eucalyptus* matrix (Barlow et al. 2010a). Soybeans and pasture may provide less suitable habitat and may be less permeable to movement of forest species in my area. Barlow et al. (2010) do not provide information on patterns of occurrence of individual species or forest specialists versus generalists so I cannot compare the results of our studies in detail.

Declines in richness and abundance of species in forest strips has been documented for plants, dung-beetles, birds and arboreal mammals as distance from continuous forest increases (Barlow et al. 2010a; Hawes et al. 2008; Laurance and Laurance 1999; Lees and Peres 2008; Wehling and Diekmann 2009). In demonstrating a loss of forest interior species with increasing distance from continuous forest, my results further strengthens these patterns and adds support to the notion that this may be wide spread across taxa. Structural changes in the vegetation may explain at least part of the patterns I documented. In my study understory became more open with distance from forest along the strips, and this may have provided more appropriate

conditions for species that use non-forested habitats and poorer habitat for forest specialists.

Patterns of Occurrence and Species Traits

Species response to conversion of forest to strips should relate to how species use space and exploit resources as well as their vulnerability to direct human impacts such as hunting (Cagnolo et al. 2009; Fahrig 2003; Peres 2001). Studies of forest fragmentation have demonstrated that forest specialist species often are most affected by fragmentation (Cagnolo et al. 2009). Species that use large areas also often disappear from fragments because their area requirements are not met (Shahabuddin and Ponte 2005). Moreover, conversion of forest to fragments or strips can increase hunting pressure by increasing access (Altrichter 2006; Peres 2001).

In my study area, species that occupied a variety of habitats and had broader diets tended to exhibit higher occupancy in strips than species that specialized on primary forest habitat or a more narrow range of foods. Similarly, other studies of mammals have found that species with smaller dietary and habitat breadth are most affected by fragmentation (Cagnolo et al. 2009). Also responses of arboreal mammals to linear corridors are determined by traits such as diet, denning requirements, and degree of arboreality (Laurance and Laurance 1999). Assuming the quality of habitat and dietary elements remains constant from forest to strips, as area in strips decreases (compared to forest), the quantity of habitat and dietary elements required by forest species could decrease. The patterns that I detected in vegetation structure also may indicate that abundance or quality of resources decrease with distance from the forest into the strips as a function of changes in habitat quality rather than solely area.

However, habitat and dietary breadth clearly do not explain all the patterns of mammal occurrence observed in my study. Almost half the species that were absent from the study area or were found only in forest (n=5) were not habitat specialists and these species varied widely in diet breadth. I did not analyze the relationship between occurrence and area requirements of species because home range data were missing for some mammals, instead, I examined body size, which generally correlates with area requirements. In my study area, body size was not a strong predictor of use of forest strips by mammals or of species that were absent from the study area. For example, small armadillos such as the three banded armadillos were more common in forest than in strips, and the larger nine-banded armadillo was only recorded in strips. Both large (e.g., jaguar and white-lipped peccary) and small species (e.g., plains vizcacha and tapeti rabbit) were absent from the study area. All of these species, as well as many others such as the collared and Chacoan peccaries and tapirs, are heavily hunted in Chaco (Altrichter 2005; 2006, Núñez-Regueiro Pers. Obs.; Altrichter and Almeida 2002). For this reason, I expected to find a strong relationship between occurrence of species and hunting pressure, and the lack of effect of hunting in species occurrence was a surprise. One possible explanation for lack of evidence of impacts of hunting on mammal occurrence is that my estimate of hunting pressure (how frequently a species was killed) was imprecise (e.g., 16 of the 29 species are listed as heavily hunted, though hunting pressure certainly varies among these species). Also this measure confounds animal abundance and preference of hunters. For example, species may be killed infrequently because their populations already have declined from hunting, not because hunters would not kill the species if they had the opportunity. Mammal species

that have a faster reproductive rate often may be better able to cope with decrease in population size better than species with slower reproductive rates. In areas with high hunting pressure, like my study site, reproductive traits might give an idea of how resilient a species is to hunting. The fact that my data showed that forest interior species also tended to have a lower reproductive rate (as seen by the low number of young in a litter) could support the idea that species less resilient to hunting are more vulnerable to conversion of forest into strips. However, the number of young also was correlated with diet breadth, so these factors are confounded. Separating the contributions of naturally low densities and hunting pressure on observed occurrence of mammals is difficult, but more attention needs to be paid to evaluating effects of hunting in Chaco.

General Patterns of Occurrence

Almost 70% of species cited for my area were either not detected (n=6) or occurred in less than 10 sampling units (n=14) after 1920 camera/nights. All species that IUCN (2011) categorizes as threatened in my study area fall within this group (e.g., Chacoan peccary, endangered; giant armadillo, vulnerable; and tapir, vulnerable), with the exception of the giant anteater (vulnerable), which occupied >10% of the sites but was significantly more likely to occupy continuous forest sites. This low rate of occurrence may occur because medium to large mammals naturally occur at very low densities in my study area and thus were not detected (i.e., sampling effect), or because this fauna has suffered from human impacts even in continuous forest. For some large bodied species that naturally occur at low densities throughout their range (e.g., jaguar and giant armadillo), lack of detection of these species may be related to sampling effect. However the puma, which is a large bodied wide-ranging species that also

generally occurs at low densities throughout its range (most of north and South America), was detected in 6 sampling units. For many mammals that the 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, tapir; IUCN 2011). At the limits of species distributions, optimal environment conditions and resources may occur with less frequency than in the center of their distribution (Guisan and Thuiller 2005; Stearns 1976), resulting in lower population densities and thus limited detection in my sampling. However studies in protected area of the Bolivian Chaco demonstrate large mammals densities equal to or larger than many tropical forests to the north (Maffei et al. 2004). Thus if low densities of mammals are related to the geographic boundaries of distributions, this phenomena is limited to the southernmost Chaco and not the entire Chaco region. Although the low rate of occurrence that I documented for many mammal species may be partially explained by sampling effect, this low occurrence also likely relates to human impacts on the Argentine Chaco. Throughout the Argentine Chaco, forest has been highly modified and degraded as a consequence of grazing and logging (Torrella et al. 2011). The few studies of medium to large mammals that have been conducted in this region primarily focus on harvest of peccaries and conclude that hunting of Chacoan peccaries and white-lipped peccaries is not sustainable (Altrichter 2005; Altrichter and Almeida 2002). Likewise serious declines have occurred in jaguar populations (Rabinowitz and Zeller 2010). These studies in conjunction with my data, point to the need to understand the complex factors that impact the Chaco fauna. For example, the effects of hunting likely are vastly underestimated in my study. I could not analyze the relationship

between species occurrence and hunting, or other ecological traits, for a large set of the species that should occur in my area because the species were absent or the number of records in camera traps was too low.

Assessment of the fauna of the Chaco is important because of the rich biodiversity and the enormous threat imposed by rapid loss of forest. The diversity and level of endemism of the medium and large terrestrial mammals of the Chaco is at least comparable to other forests recognized as highly important for conservation such as the Amazon (Mares 1992; Ojeda et al. 2003; Redford et al. 1990). For example, particular attention needs to be paid to Chacoan peccary, known only from fossil records (and was found still to exist in 1974), which is an endemic and endangered species detected in my study site only in continuous forest. Other species, such as the Chacoan naked-tailed armadillo (*Cabassous chacoensis*), that occurs east of my sampling area, are also endemic to this region (Redford et al. 1990). Furthermore, deforestation rates have increased in recent years and are expected to continue (Gasparri 2009, Seghezzo 2011, Torrella et al. 2011), threatening the long term existence of the Chaco and its biodiversity. The magnitude of the problem, which has only continued to grow, was captured more than 20 years ago by Redford et al. (1990), who referred to the Argentine Chaco forest as “one of the greatest, yet least known, ecological catastrophes in South America”.

CHAPTER 5 CONSERVATION IMPLICATIONS

According to my findings, if forest continues to be converted to strips in agricultural landscapes, forest specialist will disappear from the Chaco forest. Furthermore, the decrease in occurrence of numerous mammals with increasing distance from the forest interior highlights the importance of keeping primary forest strips short to help maintain biodiversity and functional connectivity for forest species in agricultural landscapes. Moreover, the observed response of mammals (i.e., >44% of species impacted by conversion of forest to strips) could be an underestimate of the long-term effect of forest transformation. Strips in my study area were relatively recent (i.e., < 10 years old) and extinction debts may occur (Tilman et al. 1994). Strips of forest will become much more common if deforestation continues as expected and therefore the total impact of strips on biodiversity likely will increase with time because of the predominance of this landscape configuration.

I do not advocate however that strips of forest should be eliminated. Forest strips retain (at least in the short term) some mammals and are preferable to complete deforestation. However, alternative configurations for retaining forest remnants need to be examined urgently in the mammalian fauna of the Chaco is to retained (e.g., conserving same area but in large interconnected blocks).

CHAPTER 6 CONCLUSIONS

Conversion of continuous forest to forest strip clearly has significant negative impacts on medium to large mammals. Occurrence of mammals in my study area decreased in forest strips with increasing distance from continuous forest, as reported for a variety of other taxa. In my study area species that occupied a multiple habitats and had broader diets tended to exhibit higher occupancy in strips than species that specialized on primary forest habitat or a more narrow range of foods. However, these two factors do not explain all the patterns that I observed. Almost 70% of the species cited for my area either were not detected or occurred in less than 10% of my sampling units, and thus I could not evaluate the relationship between occurrence of these species and species traits. The low occurrence of these species could be related, in part, to naturally low abundance of these species because Argentine Chaco represents the southern-most range limit of a variety of these species. However, other factors such as habitat degradation and hunting also likely influence occurrence of mammals. Finally, low occurrence of mammals in strips and in continuous forest raises major concerns related to the long term survival of mammals in the Chaco, and points to the urgent need for conservation measures to preserve this rich fauna.

Table 3-1. Number of detections, life history and ecological traits of mammals in the Chaco forest that either are present at my site or should occur based on published literature and interviews. Key to abbreviations: Site indicates the location where a species was detected (F, Continuous forest; S, Strip of forest; F+S, Continuous forest and strips of forest; A, Absent from study area). Cf is the total number of cameras where detection occurred in continuous forest; Cs is the total number of cameras where detection occurred in strips of forest; Tf is the total number of transects where a species was detected in forest; Ts is the total number of transects where a species was detected in strips; Trophic is a species' trophic level; Body is adult body mass (kg); Diet, diet breadth (larger values indicate more diet categories); Hab, habitat breadth; Litter, litter size (number of young produced per litter); FRep, age at first reproduction; Hunt, hunting pressure (larger values show larger hunting pressure). See methods for full description of species traits.

Species	Common name	Site	Cf	Cs	Tf	Ts	Trophic	Body	Diet	Hab	Litter	FRep	Hunt
<i>Mazama gouazoubira</i>	Gray Brocket Deer	F+S	20	17	9	7	1	20.4	2	3	1.0	13.5	3
<i>Lycalopex gymnocercus</i>	Pampas Fox	F+S	11	16	5	9	2	4.6	6	4	4.0	12.0	2
<i>Leopardus geoffroyi</i>	Geoffroy's Cat	F+S	7	11	5	7	3	3.4	3	3	2.0	21.0	2
<i>Conepatus chinga</i>	Molina's Hog-nosed Skunk	F+S	10	6	4	3	2	2.3	6	3	3.5	10.5	1
<i>Myrmecophaga tridactyla</i>	Giant Anteater	F+S	12	2	7	2	3	30.9	1	2	1.0	39.0	2
<i>Dolichotis salinicola</i>	Chacoan Cavy	F+S	8	5	1	1	1	2.1	3	3	1.5	2.8	2
<i>Cerdocyon thous</i>	Crab-eating Fox	F+S	5	7	5	6	2	5.2	6	3	4.0	11.0	2
<i>Pecari tajacu</i>	Collared Peccary	F+S	9	3	6	2	1	24.9	3	1	2.0	18.0	3
<i>Tolypeutes matacus</i>	Southern Three-banded Armadillo	F+S	8	3	4	2	2	1.2	4	2	1.0	9.0	3
<i>Chaetophractus villosus</i>	Large Hairy Armadillo	F+S	4	2	3	2	2	2.3	3	3	1.6	9.0	3
<i>Puma concolor</i>	Puma	F+S	5	1	3	1	3	54.0	4	2	2.8	27.0	3

Table 3-1. Continued	Common name	Site	Cf	Cs	Tf	Ts	Trophic	Body	Diet	Hab	Litter	FRep	Hunt
<i>Dasyus novemcinctus</i>	Nine-banded Armadillo	S	0	3	0	2	2	4.0	4	2	4.0	2.0	3
<i>Didelphis albiventris</i>	White-eared Opossum	F+S	1	2	1	1	2	1.0	6	4	6.9	10.0	2
<i>Euphractus sexcinctus</i>	Six-Banded Armadillo	F+S	2	1	2	1	2	4.4	6	2	1.5	9.0	3
<i>Galictis cuja</i>	Lesser Grison	F+S	1	2	1	2	3	1.9	2	2	3.0	20.0	1
<i>Catagonus wagneri</i>	Chacoan Peccary	F	3	0	3	0	1	35.6	2	1	2.7	30.0	3
<i>Chaetophractus vellerosus</i>	Screaming Hairy Armadillo	F+S	1	1	1	1	2	1.0	6	2	2.0	9.0	3
<i>Dasyprocta punctata</i>	Central American Agouti	F+S	1	1	1	1	1	3.0	3	2	1.3	16.2	1
<i>Nasua nasua</i>	South American Coati	F+S	1	1	1	1	2	4.6	6	2	3.7	24.0	1
<i>Tapirus terrestris</i>	Tapir	F	2	0	2	0	1	207.7	3	1	1.0	36.0	3
<i>Eira barbara</i>	Tayra	F	1	0	1	0	2	5.1	5	3	2.0	20.0	1
<i>Leopardus pardalis</i>	Ocelot	F	1	0	1	0	3	11.9	5	1	1.7	23.0	1
<i>Mazama americana</i>	Red Brocket Deer	F	1	0	1	0	1	33.1	3	2	1.2	15.0	3
<i>Lagostomus maximus</i>	Plains Vizcacha	A	0	0			1	4.4	2	3	1.9	12.4	3
<i>Panthera onca</i>	Jaguar	A	0	0			3	83.9	3	2	2.0	30.0	3
<i>Priodontes maximus</i>	Giant Armadillo	A	0	0			2	27.7	2	1	1.5	10.5	3
<i>Puma yagouaroundi</i>	Jaguarundi	A	0	0			3	64.0	3	1	2.5	18.0	2
<i>Sylvilagus brasiliensis</i>	Tapeti	A	0	0			1	1.0	4	3	1.2	13.0	3
<i>Tayassu pecari</i>	White-lipped Peccary	A	0	0			1	27.7	3	1	1.0	18.0	3

Table 3-2. Results from hierarchical Bayesian models. Parameter estimates for occupancy and “distance” covariate are presented with 95% Bayesian credible intervals. Negative values indicate that a species was more likely to occupy a given site as distance from the strip into the forest interior increased and less likely to occupy the strip as distance from continuous forest into the strip increased (i.e., as occupancy increased from d10 to d1 (Figure. 2-1), the “distance” parameter became more negative). Positive values indicate the opposite pattern (i.e., Occupancy decreased from d10 to d1).

	Naïve Occupancy	Estimates of Occupancy	95% Credible intervals		“distance”	95% Credible intervals	
Giant Anteater	0.15	0.56	0.39	0.76	-5.73	14.58	-0.52
Collared Peccary	0.13	0.38	0.18	0.60	-2.91	-7.50	-0.15
Southern Three- banded Armadillo	0.12	0.48	0.28	0.70	-2.14	-9.60	3.07
Gray Brocket Deer	0.40	0.60	0.48	0.73	-0.58	-2.27	0.44
Molina's Hog- nosed Skunk	0.17	0.41	0.27	0.61	-0.42	-4.61	3.19
Chacoan Cavy	0.14	0.14	0.14	0.15	1.02	-0.89	3.54
Pampas Fox	0.29	0.51	0.36	0.70	1.86	0.14	7.52
Geoffroy's Cat	0.20	0.54	0.27	0.76	2.35	-0.14	3.50
Crab-eating Fox	0.13	0.57	0.37	0.77	5.47	-0.14	13.79

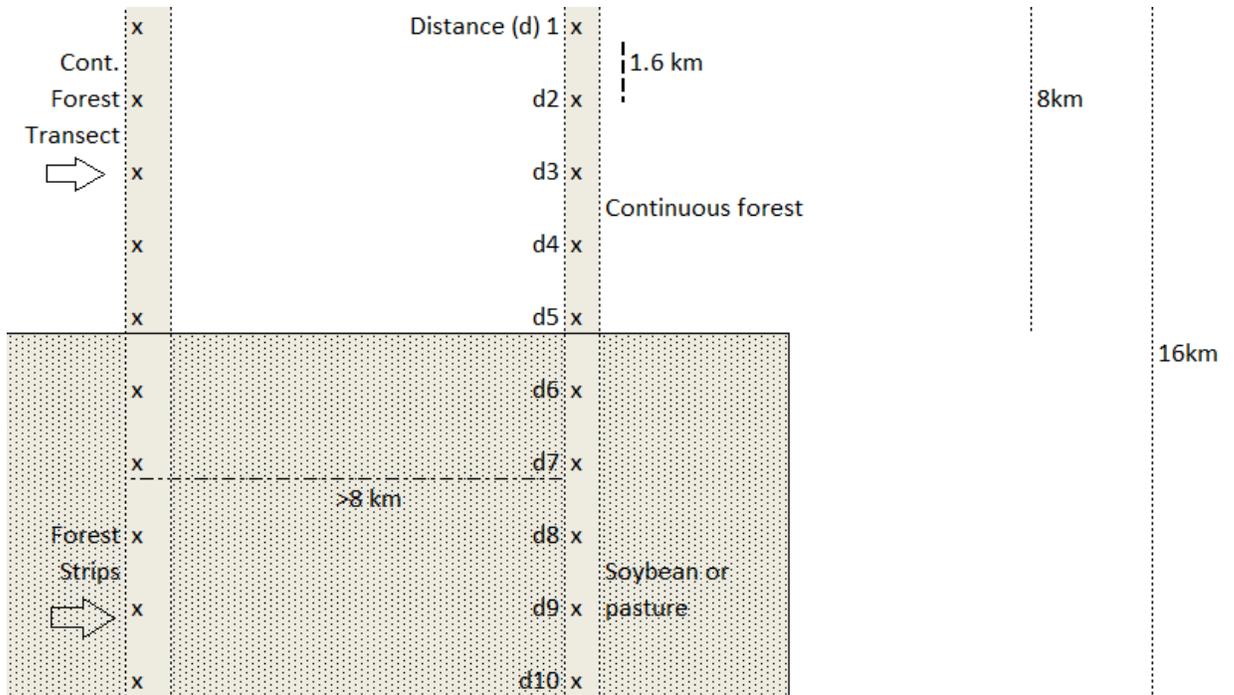


Figure 2-1. Diagram of sampling design. X marks the specific locations of camera traps. Diagram also shows distance categories along a transect. Distance categories 1-5 correspond to continuous forest and distance categories 6-10 to strips of forest. Strips are 50-100 m wide. Diagram not to scale.

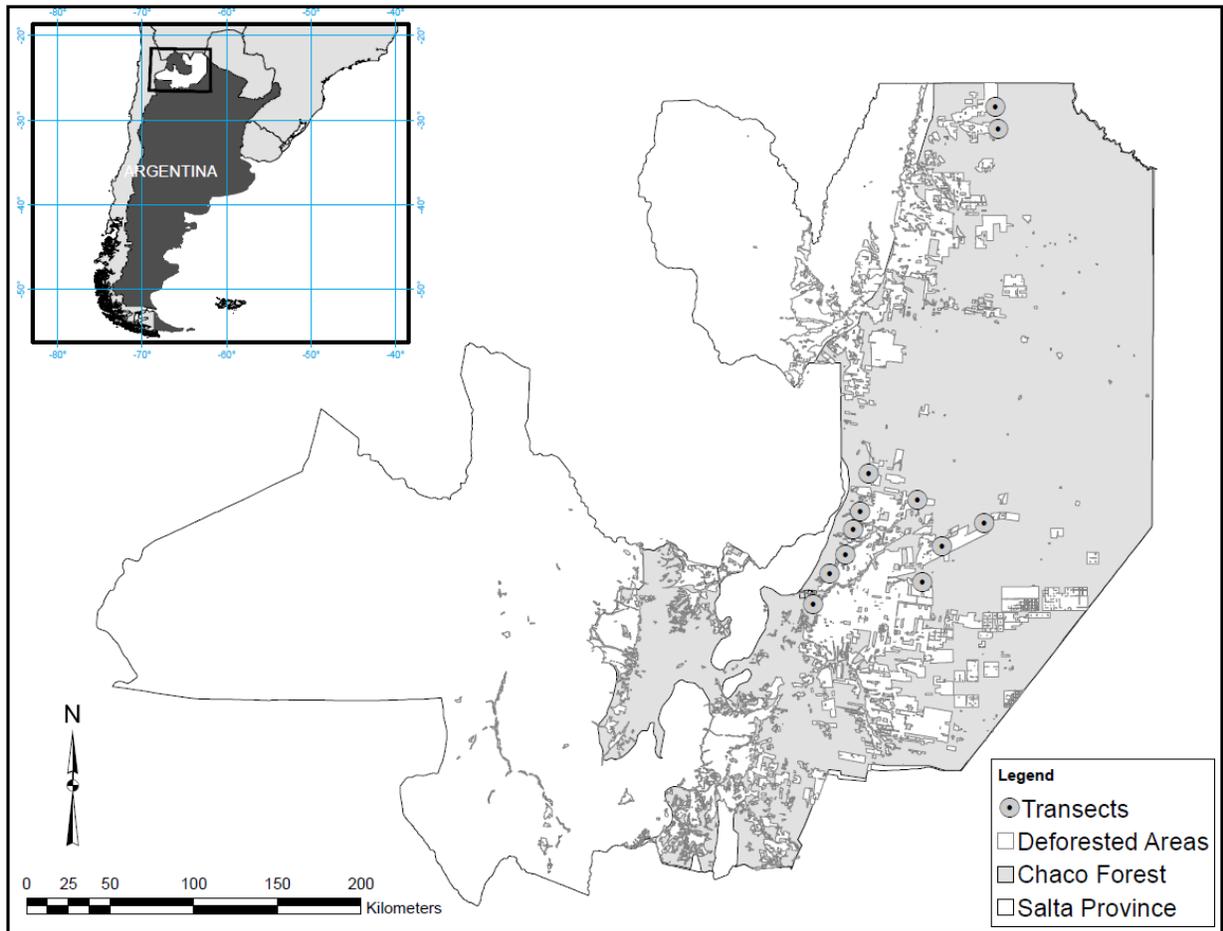


Figure 2-2. Map of study area in the province of Salta, Argentina.

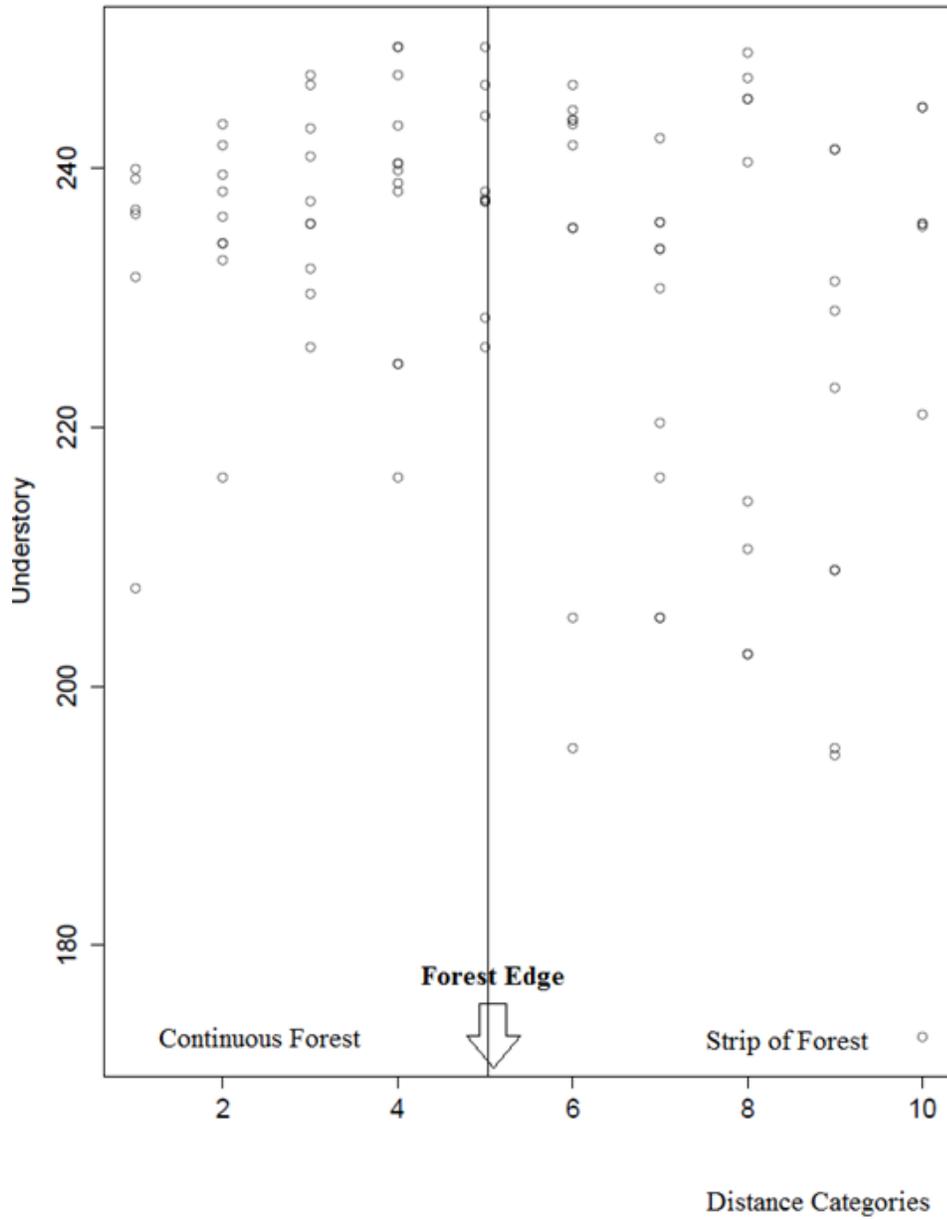


Figure 3-1. Understory density (number of dark pixels) by distance categories (at 1.6-km increments) along the transect. Higher values of understory density represent more dense vegetation.

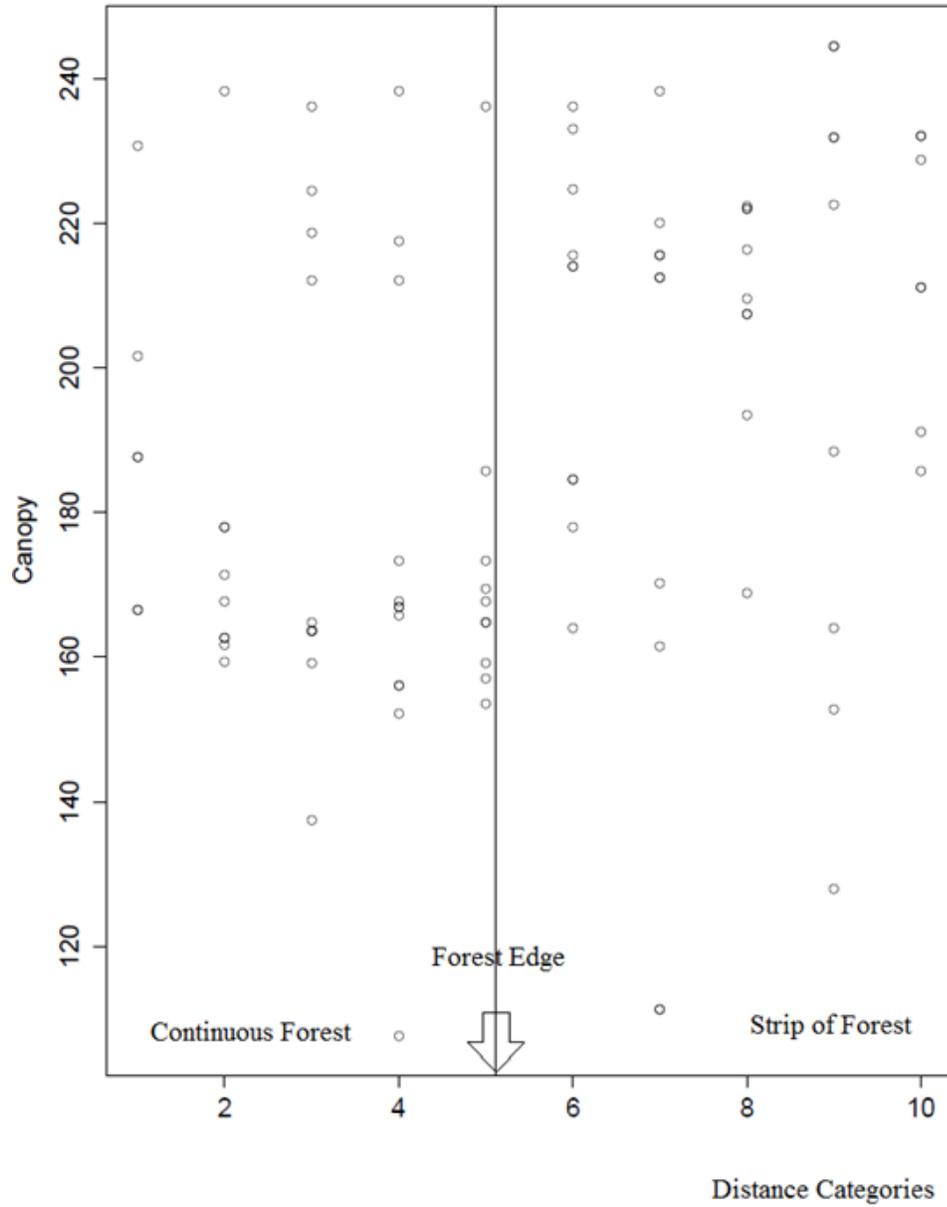


Figure 3-2. Canopy cover (number of dark pixels) by distance categories along the transect. Higher values of canopy cover represent more dense vegetation.

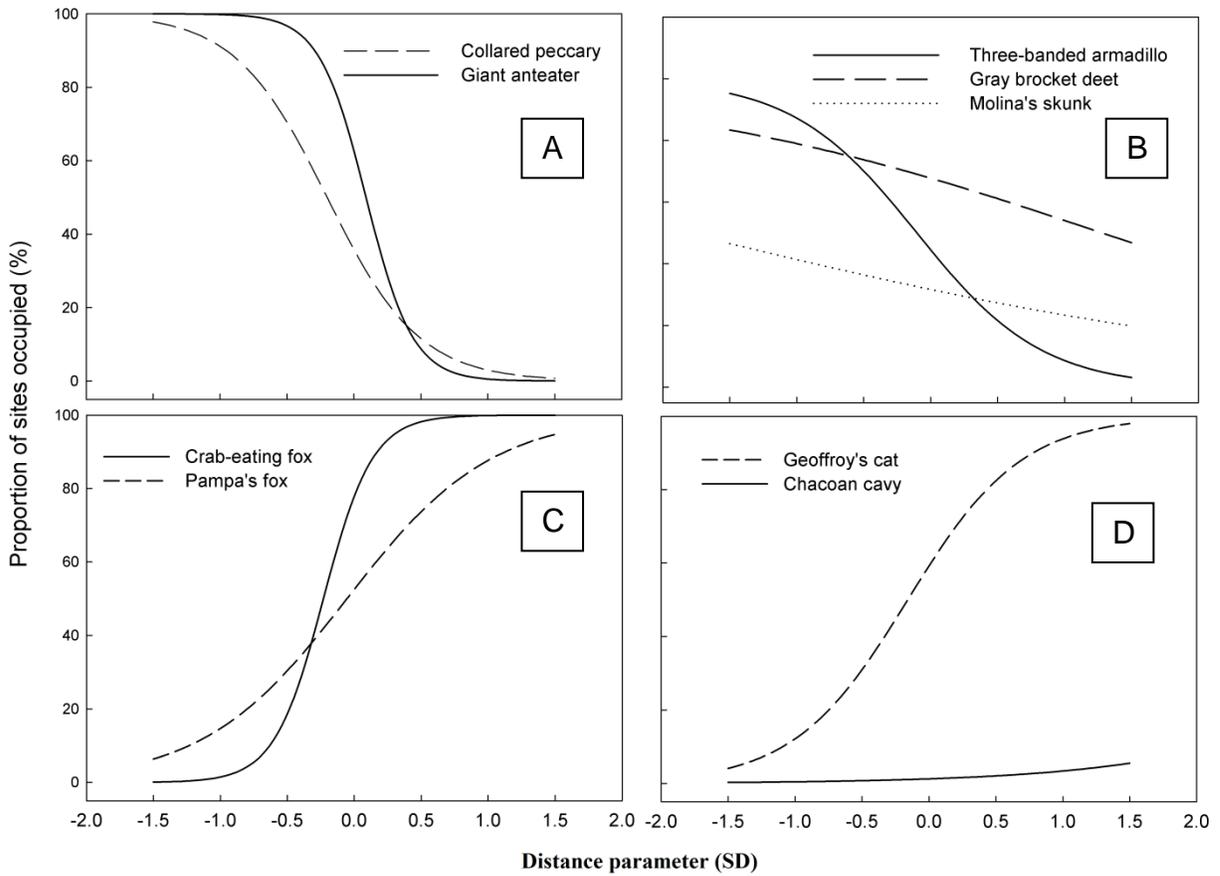


Figure 3-3. Results of hierarchical occupancy models for modeled species. Distance categories are presented in standard deviation units. Negative values of the distance parameter indicate that a species was more likely to occupy a given site as distance from the strip into the forest interior increased and less likely to occupy the strip as distance from continuous forest into the strip increased (i.e., As occupancy increased from d10 to d1 (Figure. 2-1), the “distance” parameter became more negative). Positive values indicate the opposite pattern (i.e., occupancy decreased from d10 to d1).

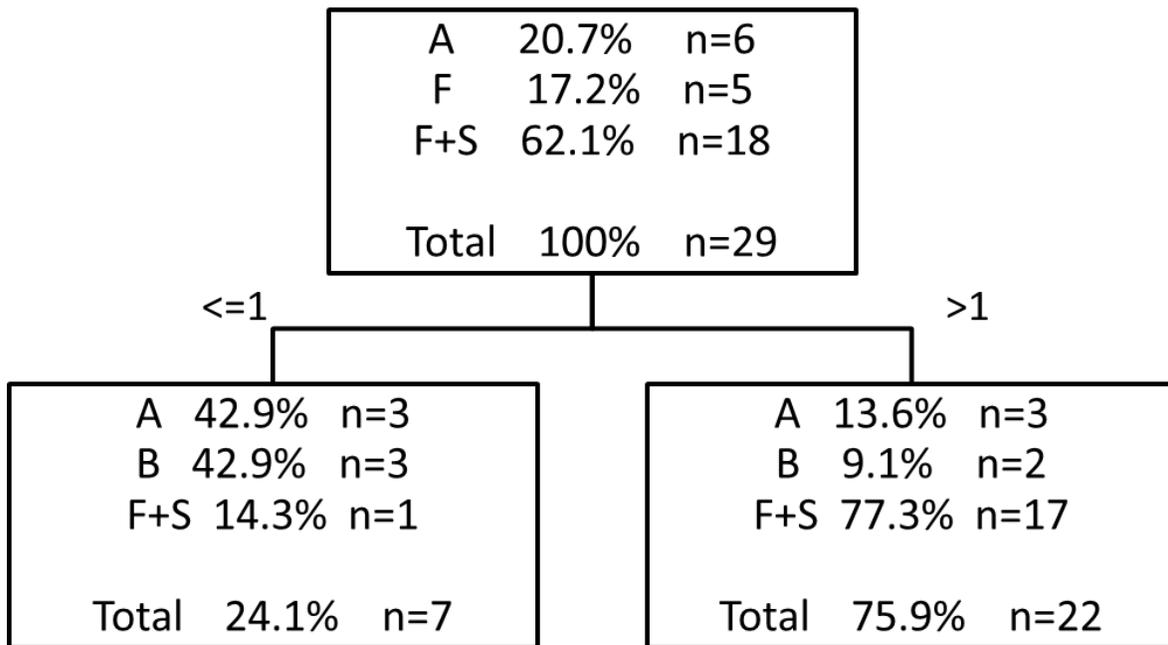


Figure 3-4. Results of classification tree. The splitting variable in the classification tree is habitat breadth. Species with habitat breadth ≤ 1 correspond to forest specialists. Similarly, species with habitat breadth > 1 correspond to generalist species. Species that were detected in forest strips and in continuous forest are represented by F+S ($n=18$). Category A ($n=6$) corresponds to species that were not detected in the study area but have been reported in published literature for the area, and category F represents species that were only found in continuous forest ($n=5$).

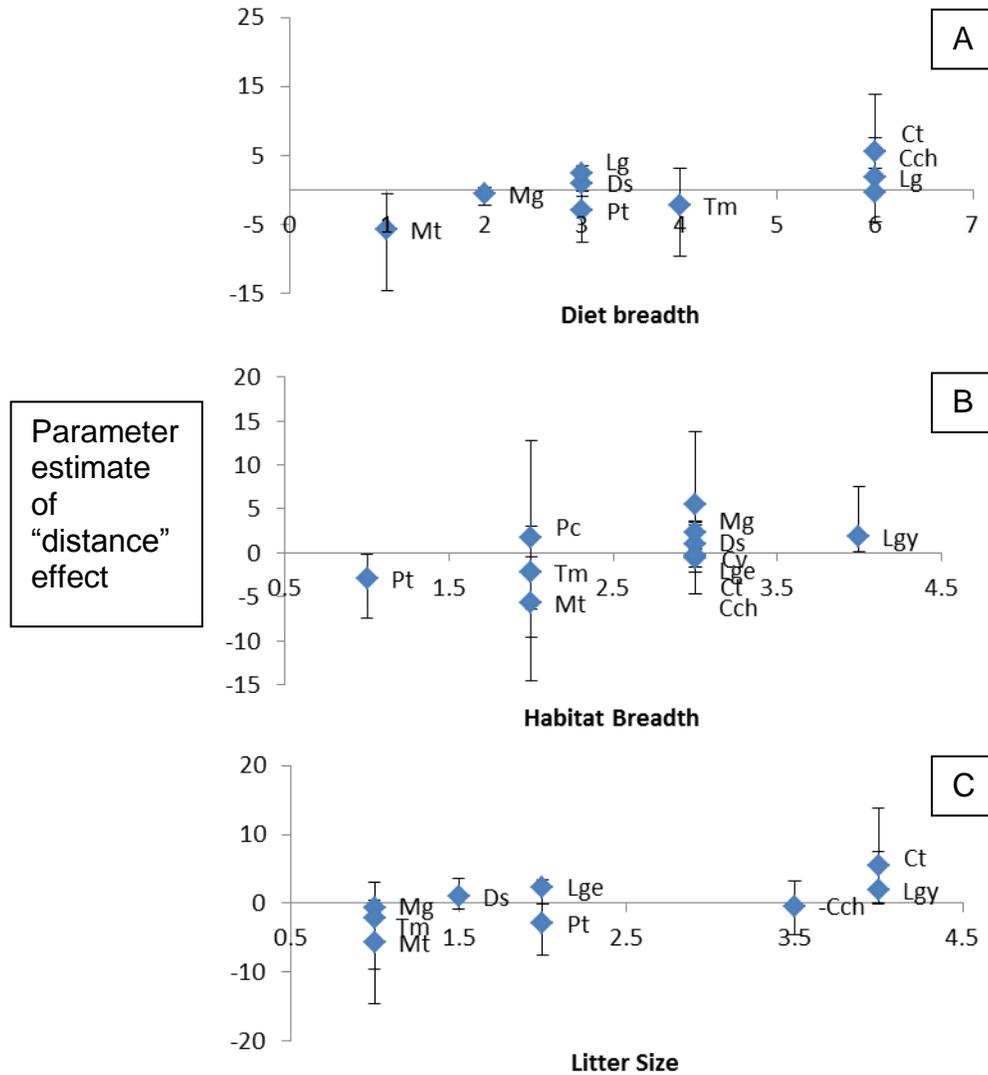


Figure 3-5. Relationship between parameter estimate of "distance" (see Table 2 for explanation of distance parameter) with, Dietary (A), Habitat (B) breadth, and Litter Size (C). Key to abbreviation: Pt, *Pecary tajacu*; Mt, *Myrmecophaga tridactyla*; Tm, *Tolypeutes matacus*; Ds, *Dolichotis salinicola*; Mg, *Mazama gouazoubira*; Cch, *Coenopatus chinga*; Lge, *Leopardus geoffroyi*; Ct, *Cerdocyon thous*; Lgy, *Lycalopex gymnocercus*. Error bars represent Bayesian credible intervals.

APPENDIX A
CORRELATION MATRIX

Spearman's rank correlation between species ecological traits. Values presented in the matrix are "r". Key to abbreviations: Trophic, trophic level; Body, body mass; Diet, diet breadth; Hab, habitat breadth; Litter, litter size; FRep, age to first reproduction; Hunt, hunting pressure.

	Trophic	Body	Diet	Hab	Litter	FRep	Hunt
Trophic	1.00	-0.05	0.13	-0.02	0.24	0.27	-0.34
Body	-0.05	1.00	-0.28	-0.46	-0.24	0.61	0.29
Diet	0.13	-0.28	1.00	0.37	0.54	-0.36	-0.30
Hab	-0.02	-0.46	0.37	1.00	0.44	-0.42	-0.20
Litter	0.24	-0.24	0.54	0.44	1.00	-0.21	-0.31
FRep	0.27	0.61	-0.36	-0.42	-0.21	1.00	-0.10
Hunt	-0.34	0.29	-0.30	-0.20	-0.31	-0.10	1.00

APPENDIX B HIERARCHICAL OCCUPANCY BAYESIAN MODELS

To formalize the distinction between variation in detectability and variation in occurrence, I introduced a distinction between observation (i.e., the observed occupancy state, y) and the underlying state variable (i.e., the true occupancy state, z) which is only observed imperfectly (Royle and Dorazio 2009).

I distinguished between detection probability, the probability of observing the species given that it is present, i.e.,

$$p = \Pr(y_i = 1 | z_i = 1)$$

and occurrence probability, which is

$$\psi = \Pr(z_i = 1)$$

In particular, I described the relationship between y and z , in terms of p and ψ , by the compound Bernoulli model which, for the observation model is:

$$y_i | z_i \sim \text{Bernoulli}(z_i \times p)$$

and, for the process or state model,

$$z_i \sim \text{Bernoulli}(\psi_i); (z_i \in \{0, 1\}); \text{site } i \text{ is occupied if } z_i = 1, \text{ site is unoccupied if } z_i = 0).$$

I modeled ψ_i as a function of both fixed and random effects:

$$\text{logit}(\psi_i) = \beta_0 + \beta_{\text{cov}} \times x_i + \gamma_t$$

β_0 is an intercept term, β_0 is a vector of regression parameters associated with covariates, x_i is a vector of distance covariates at sampling unit i , and γ_t is a random effect of transect t .

The magnitude of the covariate “distance” signals the strength of association between distance categories along a transect and occupancy. Negative values indicate that a species was more likely to occupy a given site as distance from the strip into the

forest interior increased and less likely to occupy the strip as distance from continuous forest into the strip increased (i.e., As occupancy increased from d_{10} to d_1 (Figure. 2-1), the “distance” parameter became more negative). Positive values indicate the opposite pattern (i.e., Occupancy decreased from d_{10} to d_1). I effectively blocked each site by transect by including a random transect effect in the model, which can be a useful way to deal with potential spatial autocorrelation.

I included the additional observation model that accounts for imperfect detection.

I modeled detection or non-detection of a species as a Bernoulli random variable:

$$y_i \sim \text{Bernoulli}(p)$$

I modeled p_i as a linear function of covariates likely to influence detection probability as:

$$\text{logit}(p_i) = a_0 + a_{\text{cov}} \times \delta_i$$

Where a_0 is an intercept term, a_{cov} is a vector of regression parameter associated with environmental covariates, δ_i is a vector of detection covariates at site i .

I included two environmental covariates: canopy cover and understory density.

Prior distribution

For all fixed effects in Bayesian models, I specified vague normal prior distribution with a mean 0 and variance 1000 (Royle and Dorazio 2009).

I used a non-informative Uniform (0, 1) prior distribution on the intercept parameters α_0 and β_0 , which we transformed to the logit scale (Rota et al. 2011). I specified all random effects to have a mean zero and a non-informative Uniform (0, 10) prior distribution for each standard deviation parameter.

```

#Code for a hierarchical occupancy model

dist.mean = mean(mazama$dstance) #variables are centered
dist.sd = sd(mazama$dstance)
under.mean = mean(mazama$und_dens)
under.sd = sd(mazama$und_dens)
canopy.mean = mean(mazama$cnp_cvr)
canopy.sd = sd(mazama$cnp_cvr)

trans <- as.numeric(factor(mazama$trans))

data <- list(
  n=length(mazama$Site), #l specify the length so it can reiterate
  j=mazama$count,#number of detections/camara
  y=mazama$total,
  distance=((mazama$dstance-dist.mean)/dist.sd),
  canopy=((mazama$cnp_cvr-canopy.mean)/canopy.sd),
  understory=((mazama$und_dens - under.mean)/under.sd),
  trans=trans,
  ntrans=max(trans)
)

inits <- function(){ #load inits for WinBugs
  list(
    bMean=runif(1),
    b1=rnorm(1),
    aMean=runif(1),
    a1=rnorm(1),
    a2=rnorm(1),
    z=as.integer(mazama$total>0),
    transect.effect=rnorm(max(trans)),
    sd.transect=runif(1,0,5)
  )
}

params <- list(
  'b0',
  'b1',
  'a0',
  'a1',

```

```

'a2',
'bMean',
'occ.fs'
)

# Define model
cat("
  model{

#Prior distributions for fixed effects (B&A)

bMean ~ dunif(0,1)
b0 <- log(bMean) - log(1-bMean)    #log transform parameter
b1 ~ dnorm(0,.001)                 #set priors for b
aMean ~ dunif(0,1)
a0 <- log(aMean) - log(1-aMean)
a1 ~ dnorm(0,.001)
a2 ~ dnorm(0,.001)

#Prior distributions for random effect variance parameters
sd.transect ~ dunif(0,10)
tau.transect <- pow(sd.transect,-2)

#Prior distributions for random effects
for(r in 1:ntrans){
transect.effect[r] ~ dnorm(b0, tau.transect)}

for (i in 1:n) { #start initial loop over the n sites
  # True state model for the partially observed true state
  z[i] ~ dbern(psi[i])    # True occupancy z at site i
  psi[i] <- 1/(1+exp(-fu[i]))
  fu[i]<- b1*distance[i] + transect.effect[trans[i]]

  #observation model
  mu.y[i] <- z[i] * p[i]
  p[i]<- 1/(1+exp(-cu[i]))
  cu[i] <- a0 + a1*understory[i] + a2*canopy[i]
  y[i] ~ dbin(mu.y[i],j[i])
}

```

```
    }##for loop

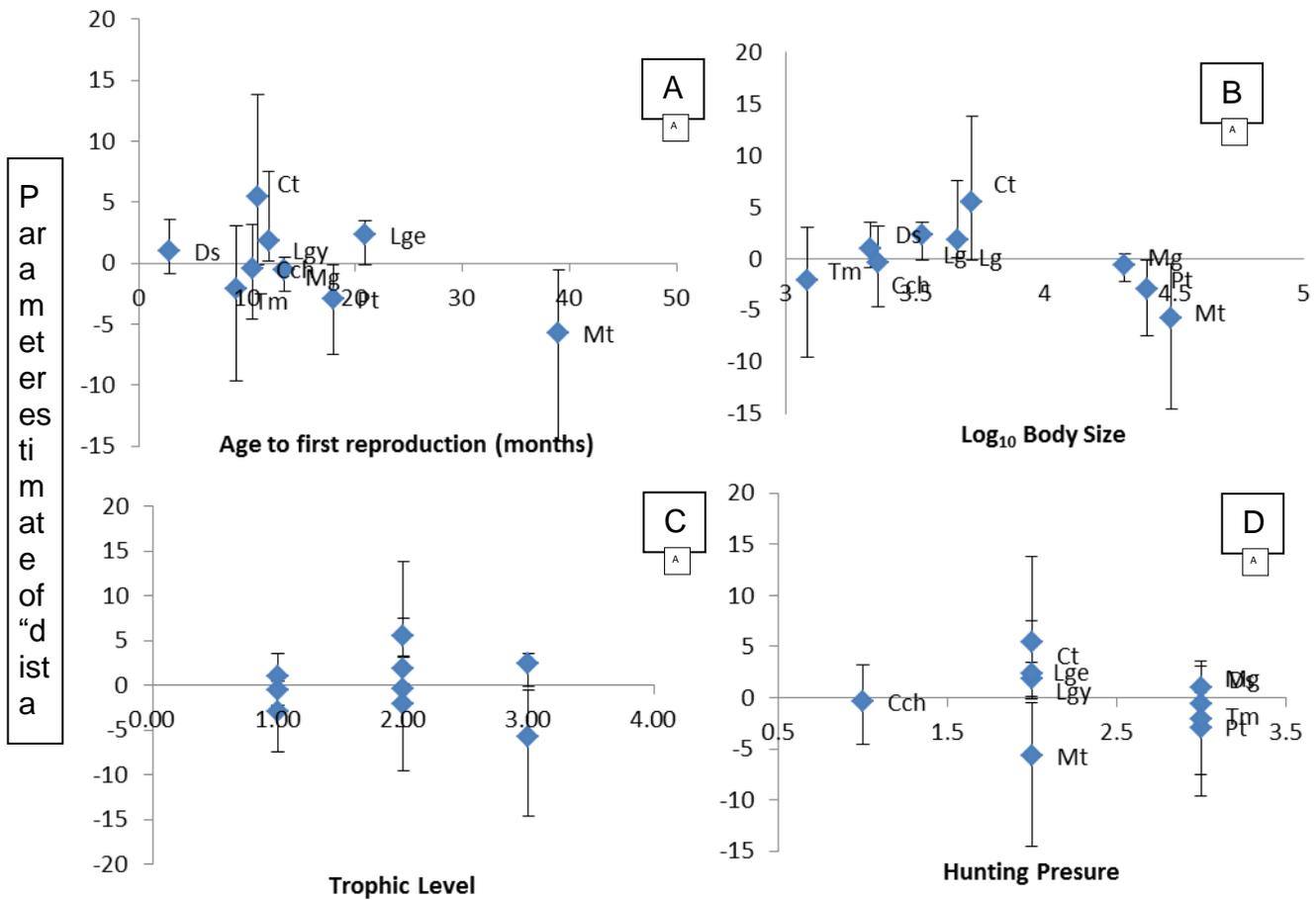
    occ.fs <- (sum(z[]))/n # Number of occupied sites

  } #model

  ",fill=TRUE, file="trainingmodel.txt")

out = bugs(data, inits, params,
model.file='trainingmodel.txt',
debug=T, n.chains=3, n.iter=100000, n.burnin=20000, n.thin=3, DIC=F,
working.directory=getwd())
```

APPENDIX C
PARAMETER DISTANCE AND SPECIES TRAITS



Relation between parameter estimate of Distance with Age to first reproduction (A), Log₁₀ of Body Size (B), Hunting Pressure (C), and Trophic Breadth (D). Interpretation of "distance" is the same as in Table 2. Key to abbreviations: Pt, Pecary tajacu; Mt, Myrmecophaga tridactyla; Tm, Tolypeutes matacus; Ds, Dolichotis salinicola; Mg, Mazama gouazoubira; Cch, Coenopatus chinga; Lge, Leopardus geoffroyi; Ct, Cerdocyon thous; Lgy, Lycalopex gymnocercus.

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