

**ASSESSMENT OF MOVEMENT CORRIDORS FOR JAGUARS
IN EASTERN GUATEMALA**

by
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I want to dedicate this work to my beautiful country, Guatemala, and its people, in the hopes that it can contribute to further efforts that shape a brighter future for all forms of life in our country.



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ABSTRACT

Guatemala represents a constriction point in connectivity for jaguar populations in Mesoamerica. A thin and potentially threatened movement corridor for jaguar in eastern Guatemala has been projected based on least cost modeling, yet little is known about either the status of jaguar populations in eastern Guatemala or their likely use of the delineated corridor. Using a focal interview approach, I assessed occurrence of both jaguar and their prey within 6x6 km² cells in a 5,580 km² region of eastern Guatemala. Probability of detection of jaguar was estimated to be constant ($\hat{p} = 0.45$, SE= 0.03) throughout the study region. Site occupancy of jaguar was related to the amount of mature forest and wetland and prey diversity, while proximity to Protected Areas was a major predictor of prey occurrence. The analysis delimited a semi-continuous corridor for jaguar that connected with the termini of validated jaguar corridors in southern Belize and western Honduras, but that had little overlap with a previously hypothesized corridor in the region. Only one third of the potential Guatemala-Honduras connection remains functional for jaguar movement, and there are several current and impending threats to continued corridor viability for jaguars in eastern Guatemala.

Key Words: jaguar, *Panthera onca*, conservation, dispersal, corridor, Guatemala, habitat use, local interviews, occupancy modeling.

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INTRODUCTION

Mammalian carnivores influence the structure, health, and integrity of ecological systems (Terborgh *et al.* 1999); notwithstanding they face severe declines across their geographical range (Woodroffe 2000). Extirpation of large carnivores can lead to the simplification of ecosystems, subsequent loss of several species (Terborgh *et al.* 1999), and alterations in the herbivore and plant trophic level dynamics due to the release of mid-size predators and consumers (Crooks and Soule 1999). Extirpation and catastrophic declines of large carnivores have been attributed to human persecution along with habitat loss and fragmentation (Gittleman *et al.* 2001, Prugh *et al.* 2009), with the latter being the most imminent threat for long-term species' persistence. Large carnivores may be particularly vulnerable to extinction in fragmented landscapes due to their large body sizes, large home ranges, high ecological sensitivity (Noss *et al.* 1996, Woodroffe 2000, Crooks 2002, Conde *et al.* 2010), low abundance, and high potential for conflicts with humans (Woodroffe and Ginsberg 1998).

Persistence of large carnivores in the long-term requires the conservation of interconnected habitats (Miller and Rabinowitz 2002) throughout a species' geographic ranges (Sanderson *et al.* 2002a). Given the large area needs and vagility of large carnivores, it is unlikely that protecting single areas would provide enough resources for maintaining viable populations over time (Miller and Rabinowitz 2002). Moreover, jaguar populations in similar types of habitats but different geographical areas play different ecological functions (i.e. tropical lowland rain forest in Guatemala versus tropical lowland rain forests in Brazil), as a result of regional differences in species composition and geographical elements (Sanderson *et al.* 2002a). Therefore, long-term large carnivore conservation requires range-wide and international efforts

to target protection of jaguar populations with distinct ecological roles across political boundaries (Sanderson *et al.* 2002a).

Wildlife corridors have been advocated for both connecting animal populations (Noss 1983, Saunders and Hobbs 1991) and maintaining their viability across large spatial and temporal scales (Miller and Rabinowitz 2002). Despite the potential of corridors for sustaining large carnivores in fragmented landscapes there are several challenges in their implementation. Corridor design requires knowledge about the target species that may not be available, such as habitat and food requirements, spatial scale of their movements, size and placement of home ranges, dispersal patterns, and behavioral responses to different landscape features (Bennett 2003). Assessing a corridor's functionality for a target species fundamentally requires field-based evaluations (Colchero *et al.* 2010, Zeller *et al.* 2011) that help redefine corridor boundaries and confirm species use (Hilty *et al.* 2006, Noss and Daly 2006). Furthermore, effective management of corridors requires monitoring the maintenance of the corridor's ecological values and the achievement of the proposed goals; as well as considering the socio-political context of the corridor: people's views, perspectives, and awareness; community support, land tenure systems, and the political and economic climate of the region (Bennett 2003).

Several approaches to delineating wildlife corridors have been implemented around the world (Bennett 1990, Zeller *et al.* 2001, LaRue and Nielsen, 2008), but the most ambitious initiatives focus on corridors for jaguar (*Panthera onca*, Linnaeus 1758; Rabinowitz and Zeller 2010) and tiger (*Panthera tigris*, Linnaeus 1758; Wikramanayake *et al.* 2004). Both initiatives were based on expert opinion to designate distinct ecological conservation units (core populations) as well as connections among them across the geographical distribution of the species, considering factors such as habitat integrity, poaching pressure, and current population

status and future trends. Furthermore, in the framework of the jaguar corridor initiative, a field method for validating corridors across large study areas and diverse levels of protection and land ownership has been established (Zeller *et al.* 2011). This validation method uses systematic and objective interview-derived data collected from people living in a given region to study habitat use of jaguars and prey under an occupancy framework (MacKenzie *et al.* 2006). The advantage of this method is that it provides a credible and cost-effective technique to validate wildlife corridors for jaguars given the cryptic ecology and low abundance of the species (Ceballos *et al.* 2002, Nuñez *et al.* 2002), as well as the large spatial scale for which data is required to be collected, which make it impractical to use conventional detection techniques (Msoffe *et al.* 2007, Zeller *et al.* 2011).

Herein, I applied the Zeller *et al.* (2011) occupancy modeling approach with interview-derived data to validate the putative jaguar corridor in eastern Guatemala as delineated by Rabinowitz and Zeller (2010). The jaguar is an important carnivore in the Neotropics (Núñez *et al.* 2002, Chávez *et al.* 2006, Foster *et al.* 2010b) whose geographic range has declined by 54% since 1900 (Sanderson *et al.* 2002b). The eastern Guatemala region holds two stable jaguar conservation units in the Biosphere Reserve of Sierra de las Minas and the Area of Special Protection Sierra Santa Cruz. The region is of high geographical priority for jaguar conservation because it provides a critical linkage among populations in Guatemala, Mexico, Belize and Honduras (Rabinowitz and Zeller 2010, Sanderson *et al.* 2002b). Despite the strategic importance of eastern Guatemala for long-term jaguar conservation, the corridor may be severed due to its limited width combined with high rates of development and land use change in the region (McNab and Polisar 2002, Sanderson *et al.* 2002a), including the construction of a high magnitude project, the Interoceanic Corridor of Guatemala –ICG- (*Corredor Interoceánico de*

Guatemala). Given the ecological importance of eastern Guatemala for jaguar, this study focused on jaguar habitat use as a means of validating the functionality of the hypothesized jaguar corridor in the region. The objectives of this study were to (1) assess patterns of spatial occurrence of jaguars in eastern Guatemala, (2) identify ecological variables that predict the occurrence of jaguar and its prey, and (3) provide a scientific basis for delineating a biologically functional corridor to facilitate jaguar movement in the region. The main contributions of this work for jaguar conservation are the further boundary refinement for the eastern Guatemalan corridor as well as greater insight into the ecology of the jaguar in the region, current status of the habitat quality in the corridor, and an overview of the socio-political context of the corridor.

METHODOLOGY

Study area

The putative jaguar corridor in eastern Guatemala was located in the province of Izabal and partially that of Zacapa. The 5688 km² region encompassing the corridor included several federal Protected Areas of mainly undisturbed forest located in mountainous terrain, private lands developed primarily for cattle ranching and agriculture mostly located in lowlands, and other lands including forest remnants and second growth patches of various ages on both private and public ownership. The study region encompasses seven Ecoregions within one Biome: Central American humid Atlantic forests, Central American pine-oak forests, Belizean coast mangrove, North Honduran mangroves, Peten-Campeche humid forests, Central American montane forests, and the Motagua valley thornscrub. The biome in the corridor region is the Tropical rain forest, characterized by high levels of rain and humidity (>200cm/year) and an

annual temperature higher than 24 °C (IARNA 2003). Human population density in the region is 46 habitants/km², with 67% of its people living in rural areas (PNUD 2010).

Documenting species occurrence through structured interviews

For this study, I divided the putative jaguar corridor and adjacent landscapes into 156 cells, each 6x6 km in size (Fig. 1), within which jaguar and key jaguar prey species' occurrence was documented based on sightings recalled by residents knowledgeable of wildlife in the region. Sightings of animals or their sign were documented using a structured focal interview approach following Zeller *et al.* (2011), with interviews conducted over a 6-month period (May-Oct 2012). When possible, potential interviewees were previously identified by local guides and leaders, as well as by snowball sampling (Johnson 2005), otherwise, all men seen during the field visits were approached until the required number of interviews were performed for each sampling site. Each interviewee identified their Area of Knowledge (AOK) as one or more 6 x 6 km grid cells in which they had visited the forest at least twice per month over the past year or was an area they hunted in. Additional records of jaguar sign noted by interviewees over the past 20 years were recorded separately. I recorded species presence over the past year within a grid cell when an interviewee reported seeing an individual of a given species either alive or recently killed (direct sighting) or reported sign of the animal such as tracks (indirect sighting). The credibility of species sightings was assessed by asking interviewee's for a detailed description of the animal or sign observed as well as having them identify the species or its tracks from a set of pictures. In addition to jaguar sightings, interviewees were queried about the presence of white-lipped peccary (*Tayassu pecari*), collared peccary (*Pecari tajacu*), white-tailed deer (*Odocoileus virginianus*), red brocket deer (*Mazama temama*), Central American agouti (*Dasyprocta*

punctata), paca (*Cuniculus paca*), and nine-banded armadillo (*Dasypus novemcinctus*). For these prey species the frequency with which interviewees had observed them was recorded as the number of visits per month in which the interviewee found the target species or its tracks in their AOK's.

To overcome false reports, which may arise from interviewees perceiving a need to provide a specific answer regardless of their knowledge, seemingly dubious information prompted a series of additional questions designed to corroborate sightings (Gros 1998, McNab and Polisar 2002, Zeller *et al.* 2011), and only evidence gathered personally by each interviewee was retained for analysis. To avoid double counting jaguars, I attempted to identify multiple sightings of a given animal by different interviewees that traveled or worked together. Lastly, a set of questions related to the interviewees' views on jaguars (e.g., whether they thought the species was beneficial, harmful, or neutral to them) were posed to better understand perceptions of jaguars as well as education needs for jaguar conservation.

A two-tiered sampling approach was undertaken to balance the effort needed to obtain unbiased and precise estimates of jaguar detection and probability of occurrence with the logistical constraints of sampling such a large study region (Zeller *et al.* 2011). Grid cells were randomly assigned to those requiring 6 or more interviews (n=85) versus those requiring only 1-2 interviews (n=73; Fig. 1).

Occupancy modeling for jaguars and their prey

Detectability and habitat use of jaguar and their prey were analyzed as single-state, single-season occupancy models (Mackenzie *et al.* 2006) using program PRESENCE version 5.3 (Hines 2006). I used single-state prey models instead of multi-state models because there is a

straight-forward method for assessing the fit of single-state models, through a simple Pearson chi-square statistic and parametric bootstrapping (MacKenzie and Bailey 2004), and due to potential uncertainty of abundance data derived from interviews. However, the parameter Ψ (probability of occupancy) was interpreted as a parameter of “habitat use” because I was unable to meet the assumption of population closure using my survey approach (Zeller *et al.* 2011).

Habitat use by jaguars was modeled as a function of site and survey covariates (Table 1, Appendix I). My expectations for both jaguar and their prey were that the probability of detection (\hat{p}) would correlate positively with effort (Zeller *et al.* 2011) and site covariates. Detection covariates included 1) survey effort (the number of visits to the interviewee’s AOK), 2) terrain ruggedness (expected to be inversely related to effort), 3) mean distance to the nearest human settlement (assuming effort decay with distance), 4) mature forest area, 5) wetland area, 6) agriculture area, and 7) second growth forest area, as well as interactions between wetlands or terrain ruggedness and distance to the nearest settlement. Habitat use (Ψ) by jaguar was expected to be positively related to prey diversity (López-González and Miller 2002, Rodríguez-Soto 2011, Zeller *et al.* 2011) and amount of forest cover (Seymour 1989, Chávez *et al.* 2006, Monroy-Vilchis *et al.* 2006), and negatively related to proximity to human activity centers such as roads or settlements (Monroy-Vilchis *et al.* 2006, Zarza *et al.* 2006, Foster *et al.* 2010a). I expected that white-lipped peccary, collared peccary, and red brocket deer would be associated with amount of forest and wetlands in a cell and, further, that white-lipped peccary would be found closer to Protected Areas (Sowls 1997, Fragoso 1999, Reyna-Hurtado 2002, Altrichter and Boaglio 2004, Bello *et al.* 2008, Keuroghlian *et al.* 2009). Because white-tailed deer (Smith 1991), paca (Pérez 1992), agouti, and nine-banded armadillo (Zeller *et al.* 2011) are considered habitat generalists, I modeled their habitat use using models that included all site covariates (Table 1).

All covariates were standardized using the z-transformation method because when the mean values of individual covariates are either very large or small, or the range of the covariates is over several orders of magnitude, the numerical optimization algorithm may fail to find the correct parameter estimates (White 2011), as well as to minimize confounding effects among variables (Quinn and Keough 2009). To guard against collinearity, only covariates having Pearson $r \leq 0.6$ (when $P \leq 0.5$) were included in the same candidate model. To assess model fit I conducted a parametric bootstrapping test (MacKenzie and Bailey 2004) with 1000 simulations. Specifically, the bootstrapping test indicated whether the observed number of sites that displayed each detection history had a reasonable chance of occurring under the assumption that the specified candidate model was correct. Lack-of-fit, either due to an incorrect model structure or non-independent detection histories, would be indicated where $P < 0.05$. Over dispersion was evaluated with models having $\hat{c} \approx 1$ considered to provide an adequate description of the observed data (Mackenzie *et al.* 2006). Model selection was performed using the quasi-likelihood version of AIC (QAIC) in the cases in which the global model was a poor fit to the data (Burnham and Anderson 1998, Mackenzie *et al.* 2006) and parameter standard errors inflated (McCullagh and Nelder 1989). Selection of candidate models was performed by choosing models whose AIC_c were within 2.5 units of the top model (hereafter referred as top models, Burnham and Anderson 2002), being careful to eliminate all uninformative parameters in the modeling process (Arnold 2010). Estimates of habitat use for jaguar and its prey in the study region were estimated using Ψ -cond (conditional occupancy) for all surveyed grids, which is habitat use accounting for detection history (Zeller *et al.* 2011). For the grids that were not surveyed final estimates of habitat use of the target species were estimated using averaged model- Ψ (unconditional occupancy).

Corridor delineation

I delineated the jaguar movement corridor following the approach of Zeller *et al.* (2011), which involves several steps and was applied to the suite of 131 surveyed grid cells given that the prey diversity information was unavailable for unsurveyed cells (see Appendix II). First, final habitat use estimates of target species (jaguar and prey) were achieved using multi-model inference, either averaging the Ψ -cond estimates of the individual surveyed grid cells across the top candidate models, or by estimating the psi-modeled average for the grid cells that were not surveyed. Next, prey was divided between small (agouti, paca, armadillo) and large (peccaries and deer) body sizes. An overall probability of prey habitat use in each grid cell was calculated by estimating the joint probability of habitat use by all small species and at least 2 large prey species in that cell (Appendix II). Finally, I simultaneously varied cutoffs in probability of jaguar and prey habitat use to meet the goal of identifying the most functional corridor, that is, the network of cells that maximized the area of qualifying habitat as well as the width of this network. Using a base criterion of a combined probability of habitat use of 0.70 for jaguar and 0.70 for prey in each grid cell, based on a lower threshold than that established by Zeller *et al.* 2011, I proceeded with 10 combinations of probability cutoffs for both jaguar and prey, using increments of 5% and selecting the combination of habitat use by jaguar and prey that maximized the area of qualifying habitat (Table 4).

Assessing threats to the jaguar corridor

Deforestation trends in the region were analyzed as a potential threat to maintaining integrity of the jaguar corridor. I compared land use and land cover data for Guatemala (1:250,000 topographical maps) for the years 1999 and 2005 (MAGA 2002, 2006). This

comparison was achieved by transforming the original polygon data to raster format (15 m resolution) and reclassifying it into “mature forest” versus “other” while comparing cells of mature forest in 1999 with mature forest cells in 2005 to calculate forest loss in the study region. Additional information of threats to jaguars and the habitat in the corridor was recorded based on information provided by interviewees, community leaders, and Protected Areas’ managers in the study region.

RESULTS

Attitudes regarding jaguar

I performed 427 interviews within 130 grid cells that together comprised a total area of 4,680 km², or 83% of the proposed study region (Appendix III); the remaining 17% was not surveyed due to the inability to access sites due to either security or weather constraints. The majority of surveyed grid cells contained 6 interviews (57%), 27% contained 3-5 interviews, and 16% contained 1-2 interviews. Perceptions of jaguars were predominantly negative including fear (70%) and desire to kill jaguars upon encounter (4%). About half the interviewees (53%) considered jaguars harmful for people, based on the perception that jaguars “attack”¹ cattle, domestic animals, people, and, of frequently expressed concern among these interviewees, children. These feelings were predominant despite none of the interviewees having personal knowledge of an attack on a person in the region. Less than a third of interviewees expressed positive (14%) or neutral (14%) attitudes towards jaguar. Of those, people reported feelings of joy, excitement or surprise upon a jaguar encounter (86%), admiration (7%), and empathy for

¹ This term was frequently used by interviewees whenever they would speak about jaguar effects on their livelihoods.

jaguar (7%). Despite the dominant perception being fear in the region, a substantial portion of interviewees (42%) considered jaguar presence to be neutral to them (no harm or benefit for humans), and 6% reported jaguars as beneficial for people primarily in terms of a potential to attract foreign tourists and thus aiding in higher income for local residents.

The great majority of interviewees (89.1%) perceived declines in jaguar prey over time, although 9.9% perceived an increase in prey species, and 1% perceived no change. From the interviewees that perceived a decrease in prey, 56% attributed this decline to hunting, 30% to forest loss, 11% to a combination of hunting and forest loss, 2% to river flooding, and 1% to the use of pesticides in agriculture.

Occupancy modeling for jaguar and their prey

Jaguar

Jaguars were detected in 38% of the 130 grid cells in which interviews were conducted. Occupancy analysis was restricted to those cells in which ≥ 3 interviews were obtained (58% of surveyed cells) so as to minimize the potential effect of false positives and aid in stability in the modeling process (i.e., including sites with 1-2 surveys generated grossly imprecise or nonsensical parameter estimates; Fig. 2). Only 10% of the cells in which jaguars were detected required more than 3 interviews to document their occurrence. Therefore, a total of 75 grid cells (58%) were retained for analysis (Fig. 2), and jaguars were detected in about half (53%) of the surveyed cells.

The top models for jaguar showed over dispersion with $\hat{c} = 2.8$ and model selection procedures adjusted to inflate standard errors. There was no statistical support for the effects of sampling or site covariates on jaguar detectability (all models including covariates for \hat{p} yielded

$\Delta\text{QAIC} > 4.46$ compared to the top model shown in Table 2). As a result, jaguar detectability was considered constant throughout the study area at $\hat{p} = 0.45 \pm 0.03$ SE (Table 2). Regarding jaguar habitat use, only the proportion of wetland, proportion forest, and prey diversity in a cell were retained among the top models (those with $\Delta\text{QAIC} < 2.6$). Model selection uncertainty focused on the inclusion or substitution of prey diversity with land cover variables. Overall, the probability of use by jaguar increased given increasing amounts of mature forest, wetlands, or prey diversity (Table 2). After model averaging and zeroing out the effects of other covariates, the probability of habitat use by jaguar appeared most sensitive to the amount of wetland, increasing rapidly from 0.47 in grid cells with no wetlands to essentially 1.0 in grid cells covered 26% (9.3 km²) by wetlands (and remaining stable thereafter; Fig. 3). The probability of jaguar habitat use also reached 0.98 given 97% forest cover (35 km²) in a cell, and reached 0.89 given a prey community that was both rich (all species present) and even (homogeneous relative abundances; $H' = 1.95$). Applying the model-averaged coefficients to the landscape predicted slightly less than half of the study region (42%) to have a high probability of jaguar use ($\Psi = 0.75$ -1.00), with an additional 14% predicted to have intermediate levels of use (Ψ -cond = 0.26-0.75; Fig. 4).

Prey species

Occupancy models were fitted successfully for all prey species except two that were wide-spread (agouti and armadillo, documented in 92% of the surveyed cells) and one that was quite rare (white-tailed deer). Species habitat use and detectability varied differentially with site and survey covariates (Table 3). Detection probability for white-lipped peccary was constant throughout the region ($\hat{p} = 0.16$, SE = 0.05; Table 3), and their probability of habitat use increased

in close proximity to Protected Areas and given higher amounts of forest cover. Detection of collared peccary increased with distance away from human settlements whereas their probability of habitat use, similar to collared peccary, increased with the amount of forest cover in a cell. In contrast, detectability of red brocket deer increased as a function of increasing forest cover in a cell while its probability of habitat use increased with proximity to protected areas. Lastly, for the widespread paca, whose habitat use was high and constant throughout the study area ($\Psi = 0.98 \pm 0.02$ SE), detectability decreased with increasing survey effort and increased in proximity to settlements and in less rugged terrain. Models predicted paca to be the most widespread and white-lipped peccary to be the most habitat restricted prey species, of those modeled, for jaguar in the region (Fig. 4).

Corridor delineation

The combination of probabilities for jaguar and prey habitat use that produced the greatest cell contiguity was $\Psi_{\text{jaguar}} \geq 0.80$ and $\Psi_{\text{prey}} \geq 0.85$. A total of 37% of the 130 grid cells in the region met these criteria, highlighting two potential corridors for jaguar that provide semi-continuous areas of habitat connecting known jaguar populations (Fig. 5). Notably, the previously modeled corridors and my field-validated corridors overlapped only by 353 km² (Fig. 6). In contrast to the previously modeled corridor, I identified core jaguar habitat connectivity across the northern edge of eastern Guatemala coincident with large protected areas (Fig. 5). Although a high probability of jaguar habitat use was predicted in isolated cells overlapping small protected areas along the southern route of the previously hypothesized corridor, my data indicate these areas to be too small and too isolated to meet the criteria for a functional corridor

under current landscape conditions. To achieve a contiguous corridor throughout the southern zone of the study area would require reducing Ψ_{jaguar} to 0.20.

Threats to the jaguar corridor

I documented 3 primary threats to the field-validated jaguar corridor through focal informant interviews, interviews with community leaders, and GIS analysis. These threats included the construction of the Technological Corridor of Guatemala (TCG), which will occur along the border of Guatemala and Honduras; petroleum exploration, already taking place along the coast adjacent to the Belize and Guatemala border; and rapid rates of forest loss in the study region (Fig. 7). From 1998-2005 a total of 595 Km² (6.48%) of mature forest was removed in the region, with the highest deforestation pressure occurring in the middle of the jaguar corridor identified by my study (Fig. 7, see black polygons).

DISCUSSION

Herein I evaluated habitat connectivity for jaguar in Guatemala, comparing empirical habitat use to a previously hypothesized corridor for jaguar and identifying potential threats to continued connectivity for jaguar populations in the region. Foremost, I documented that along the northeastern edge of Guatemala there remains sufficient habitat so as to provide connectivity for jaguar populations from Belize to Honduras. Despite this, minor habitat discontinuity was observed in the east of the corridor, close to the Honduran border (Fig. 5), due potentially to forest loss and cattle ranching. In contrast, habitat discontinuity along the west side of the corridor (close to the Belizean border) stemmed from insufficient data that prevented an assessment of habitat suitability. Moreover, I observed substantial differences in configuration

of the jaguar corridor compared to that previously modeled using least cost paths where costs were identified by expert opinion (Rabinowitz and Zeller 2010) and perhaps underestimated the importance of protected areas for both jaguar and their prey in the region.

Here, as elsewhere, wetlands (Crawshaw and Quigley 1991, Núñez *et al.* 2002, Cullen 2006, Rodriguez-Soto 2011) and mature forest cover were the important habitat elements for jaguar (Núñez *et al.* 2002, Chávez *et al.* 2006, Foster *et al.* 2010a, Monroy-Vilchis *et al.* 2006), likely for reasons related to prey availability (Emmons 1987, Núñez *et al.* 2002, Hatten *et al.* 2005) and protection from human persecution. Whereas some prey species were ubiquitous in the region, such as agouti, armadillo, paca and collared peccary, others, specifically the red brocket deer and white-lipped peccary, were associated with protected areas and showed a predicted distribution most similar to jaguar. Wetlands have persisted in this region most substantially within protected areas, and although jaguar use was not statistically linked to protected areas, 74% of the jaguar sightings fell inside cells containing protected areas. Surprisingly, forest loss has been concentrated within and immediately adjacent to protected areas throughout the region (Fig. 7). Deforestation rates are of concern in Guatemala (IARNA 2012), and I documented forest loss within the study area to be approximately 1.1% per year. The majority of the study region (89.3%) was located in the province of Izabal, which is among the top 3 provinces in terms of deforestation rates, and is part of a group of 5 deforestation fronts (IARNA 2012) in the nation. Large concentrations of forest loss may account in part for the apparent “loss” of the hypothesized jaguar corridor in the southern portion of the study area (Figs 6 and 7), and potentially threatens jaguar population persistence as well as continued population connectivity in the region. Clearly protected areas, while necessary, are not sufficient on their

own for maintaining connected jaguar populations in this region especially in light of ongoing forest loss.

Residents of the study area also indicated far less tolerance of jaguar than expected. . Rabinowitz and Zeller (2010) assigned movement costs to human influenced habitats based on jaguar habitat use patterns observed elsewhere, perhaps from areas where humans exhibited higher levels of tolerance for jaguar and mismatched to the local context in Guatemala. In this region, white-lipped peccary and red brocket deer, both of which are sensitive to disturbances associated with settlement and harvest pressure (Altrichter & Boaglio 2004, Polisar 2002, Keuroghlian *et al.* 2009, Zeller *et al.* 2011, FUNDARY 2004, Jolon 2012), each showed a patchy predicted distribution in the southeastern portion of the study area coincident with the highest human development footprint indicating that either the habitat in that region is too poor, or the cost of living there is too great, for populations to be secure. The same is also likely for jaguar – either the prey is insufficient or the region too risky to persist. Public “education” to shift perceptions more favorably for jaguar may be a viable conservation action, but tying jaguar conservation to something of more fundamental importance to humans, like clean water, may ultimately prove more effective. Conservation of wetlands and forests as a means of securing long-term water supply is of interest to the general public in the region (personal communication with interviewees), and of obvious benefit in terms of jaguar habitat based on my models. Several communities around Sierra de Santa Cruz have partnered with a major environmental NGO (FUNDAECO) to promote protection of the area for its value to their water supply – an action that would benefit jaguar and a concept that could be expanded to promote a broader water-jaguar conservation agenda in the region.

Importantly, properly functioning corridors may facilitate rare and rapid dispersal events, a movement process that is fleeting and difficult to document (Sweaner *et al.* 2000, Stoner *et al.* 2006, Stoner *et al.* 2008). A critical assumption of my approach was that corridors “looked” the same in terms of environmental conditions as landscapes used by jaguar elsewhere in their range. However, large felids have been documented to disperse through “unsuitable” habitats (Sweaner *et al.* 2000, Stoner *et al.* 2006, Stoner *et al.* 2008), and are likely do so as quickly and stealthily as possible. Although I failed to predict a connected corridor of jaguar habitat in the southeastern portion of my study area, I did record jaguar presence there (Fig 4). These sparse detections may represent isolated populations of jaguar, especially given that detections occurred only within protected areas in this part of the study area, or, alternatively, these detections may indicate functional connectivity that was not apparent using my modeling approach. Corroboration of the empirical modeling approach use here is needed before discounting the value of the southeastern portion of my study area for jaguar. Towards this end a landscape genetics approach may be warranted owing to the paucity of jaguar occurrence data in the region, despite the considerable effort invested during this study, combined with the rareness and ephemeral nature of dispersal movements.

To detect jaguar use of the landscape from human interviews, the two-tiered sampling approach recommended by Zeller *et al.* (2011) provided an efficient sampling approach but ultimately provided data that was problematic in an occupancy modeling framework. Estimating detection and habitat use probabilities requires repetitive surveys of the sampling units (Mackenzie *et al.* 2006), and statistical power in an occupancy framework is determined in part by the number of repeat surveys. In this study, grid cells having only one interview created instability in the modeling process, with Program Presence yielding either no confidence

intervals on parameter estimates or intervals that spanned the entire range of the parameter space. Surveying all cells more than once is thus important, and in this study the number of interviews deemed optimal to minimize missing jaguar occurrence was determined to be 3 (accounting for 80% of all jaguar detections). Future applications of the modeling approach used herein may benefit from targeting three or more interviews per cell across the study region. Moreover, my inability to fit occupancy models to generalist species such as white-tailed deer, armadillo, and agouti might be overcome in the future by using covariates measured at finer spatial resolutions, such as food and burrow site availability (Beck-King and Helversen 1999), although requisite landscape data may not exist at finer resolutions.

In addition to deforestation and low human tolerance for jaguar in the region, the construction of the TCG, an alternative route for transferring cargo containers between the Atlantic and Pacific Ocean, is an imminent threat (Cardona 2012). The TCG will affect a zone of approximately 336 km in length and 140 km in width, and will involve construction of a 4-lane road, pipeline, and interoceanic railroad along with industrial parks. Specific information on the location of the TCG is unavailable, making it difficult to assess the likely impact of the project on jaguar habitat in the region. This said, the ICG will involve 4 provinces (Jutiapa, Chiquimula, Zacapa, and Izabal) that parallel the Salvadorian and Honduras border (Cardona 2012, Batres 2013, Corredor Interoceánico S.A 2012), which means the TCG will bisect the jaguar corridor regardless of its specific placement. While it remains unclear whether this TCG will remove forested habitat, the associated development and disturbance may pose physical barriers to jaguar movement (Colchero *et al.* 2002, Miotto 2012) and so should be monitored closely given the critical linkage that Guatemala provides for jaguar populations in Mesoamerica.

CONCLUSION

This study provides further evidence of the importance of wetlands, forest, and prey diversity for jaguar and the critical importance of the regional network of Protected Areas to jaguar population connectivity in Mesoamerica. Conservation of wetlands would not only aid in conserving jaguar populations in eastern Guatemala, but also several other species of high conservation priority in the region (Gibbs 1993, Junk *et al.* 2006), and is important for providing clean water supplies to local communities. Useful habitat management targets specific to conservation of jaguar habitat include maintaining at least 10 km² of mature forest and 3.17 km² of wetlands for every 6 x 6 km landscape unit.

Even in the face of several threats to the jaguar corridor, there are leverage points for strengthening jaguar conservation in the region. The main threats to jaguars and the corridor are the increased urban and industrial developments that threaten to increase habitat fragmentation and decrease habitat quality for jaguars in the region. On the other hand, a significant area of opportunity that would reinforce long-term conservation of the species in the corridor region is a joint water-jaguar conservation agenda. Further efforts are needed to assess the long-term functionality of the corridor delineated herein, as well as verification of the potential loss of connectivity already in the southeastern portion of the study area.

TABLES

Table 1. Occupancy and detection covariates used to assess jaguar and prey species' habitat use in eastern Guatemala.

TYPE	COVARIATE
OCCUPANCY	Shannon-Wiener Diversity index for prey
	Mean distance to the nearest paved roads
	Mean distance to the nearest settlement
	Mean distance to the nearest Protected Areas
	Mature forest area
	Second growth forest area
	Wetland area
	Agriculture area
	Mean terrain ruggedness (coefficient of variation of the slope)
	Wetlands*distance to the nearest settlement
DETECTION	Mean terrain ruggedness (coefficient of variation of the slope)
	Mean distance to the nearest settlement
	Wetlands*distance to the nearest settlement
	Ruggedness*distance to the nearest settlement
	Survey effort
	Mature forest area
	Agriculture area
	Wetland area
	Second growth forest area

Source: Digital Data Base of Guatemala from 1:250,000 scale maps (MAGA 2006), Digital Data Base of Belize from 1:250,000 scale maps (BERDS 2010, CBI 2010), and Digital Data Base of Honduras from 1:250,000 scale maps (ICF 2005). See further details of source, resolution and year for layer type according to country in Appendix I.

Table 2. Top occupancy models for jaguar in eastern Guatemala with respective model ΔAIC_c and AIC weights (w), number of parameters estimated (k), and the untransformed coefficients and standard errors of the covariates influencing occupancy: mature forest (Forest), available wetland (Wetland), and the resulting interaction between amount of wetland and distance to settlements (Wet*sett).

					Untransformed coefficients of covariates (standard errors)			
Model		ΔAIC	w	k	Intercept	Forest	Wetland	Prey
<i>Jaguar</i>								
1	psi(Wetland,forest),p(.)	0	0.48	4	1.57 (0.71)	1.26 (0.39)	4.87 (2.23)	-
2	psi(Wetland,Forest,Prey),p(.)	0.83	0.31	5	1.66 (1.13)	0.95 (0.42)	5.89 (3.77)	0.92 (0.56)
	psi(Prey),p(.)	1.67	0.21	3	-0.09 (0.31)	-	-	1.60 (0.52)
Model averaged site covariates					1.26 (0.85)	0.90 (0.23)	4.19 (1.72)	0.62 (1.11)

Table 3. Top occupancy models for white-lipped peccary, collared peccary, red brocket deer and paca in eastern Guatemala with respective model ΔAIC_c and AIC weights (w), number of parameters estimated (k), and the untransformed coefficients and standard errors of the covariates influencing occupancy: mature forest (Forest), and distance to Protected Areas (PA); as well as detectability: distance to settlements (Sett), Forest (Forest), terrain ruggedness (Rugg), interaction between terrain ruggedness and distance to settlements (Rugg*sett), and effort (Effort).

				Untransformed coefficients of covariates (standard errors)			
Model	ΔAIC	w	k	Intercept	Forest	PA	Additional: detection covariates
<i>White-lipped peccary</i>							
1 psi(PA), p(.)	0	0.58	3	-0.68 (0.68)	-	-1.81 (0.77)	-
2 psi(Forest, PA), p(.)	0.63	0.42	4	-0.77 (0.59)	0.63 (0.56)	-1.52 (0.65)	-
Model averaged covariates				-0.71 (0.47)	0.26	-1.69 (0.53)	-
<i>Collared peccary</i>							
1 psi(Forest), p(Sett)	0	0.56	4	2.14 (0.50)	1.27 (0.66)	-	Sett, 1.32 (0.31)
2 psi(.), p(Sett)	0.49	0.44	3	1.74 (0.33)	-	-	Sett, 1.32 (0.31)
Model averaged covariates				1.96 (2.64)	0.71	-	Sett, 1.31 (0.05)
<i>Red brocket deer</i>							
1 psi(PA),p(Forest)	0	0.47	4	-	-	-0.59 (0.30)	Forest, 0.23 (0.11)
2 psi(.),p(Forest)	0.95	0.29	3	-	-	-	Forest, 0.24 (0.11)
3 psi(PA),p(.)	1.41	0.23	3	-	-	-0.6 (0.30)	
Model averaged covariates				-	-	-0.42 (0.18)	Forest, 0.18 (0.12)
<i>Paca</i>							
1 psi(.),p(Sett, Rugg, Rugg*sett, Effort)	0	0.50	6	4.03 (1.10)	-	-	Sett, -0.46 (0.43); Rugg, -0.45 (0.44); Rugg*sett, 1.31 (0.67); Effort, -0.29 (0.12)
2 psi(.),p(Sett, Rugg, Rugg*sett)	1.32	0.26	5	4.07 (1.04)	-	-	Sett -0.44 (0.43); Rugg, -0.49 (0.43); Rug*sett, 1.36 (0.66)
3 psi(.),p(Rugg)	1.39	0.25	3	3.83 (0.89)	-	-	Rugg, 0.37 (0.12)
Model averaged covariates				3.99 (1.22)	-	-	Sett, -0.25 (0.33) ; Rugg, -0.25 (0.31); Rugg*sett, 1.00 (0.41); Effort, -0.14

Table 4. Probability cutoffs of jaguar and prey habitat use applied for the delineation of the corridor for jaguar movement in eastern Guatemala. Table shows, in decreasing order of total corridor area, the results of applying each specific criterion for corridor delineation: number of qualifying grid cells in the study region (Qualifying grids₁), the number of qualifying grid cells included in a final delineation of a corridor (Qualifying grids₂), the total area of corridor in km² (including non-qualifying grid cells embedded in the final corridor to increase continuity and width). The cutoff information used in the delineation of the corridor in the present study is in bold.

Cutoff		Qualifying grids ₁	Qualifying grids ₂	Corridor area (Km ²)
Jaguar	Prey			
0.90	0.90	51	46	1656
0.90	0.75	54	47	1692
0.80	0.80	58	51	1836
0.80	0.85	58	51	1836
0.80	0.90	56	49	1764
0.85	0.85	56	49	1764
0.75	0.75	59	51	1836
0.75	0.80	59	51	1836
0.75	0.85	59	51	1836
0.75	0.90	57	49	1764
0.70	0.70	59	51	1836

FIGURES

Figure 1. Study region in eastern Guatemala. Interviews of local people were conducted May-October 2012 to document occurrence of jaguar and 7 key prey species within each of the 6x6 km cells indicated. Dark yellow grid cells required a sample effort of 6+ interviews while light yellow grid cells required 1-2 interviews. (Source: Panthera 2011).

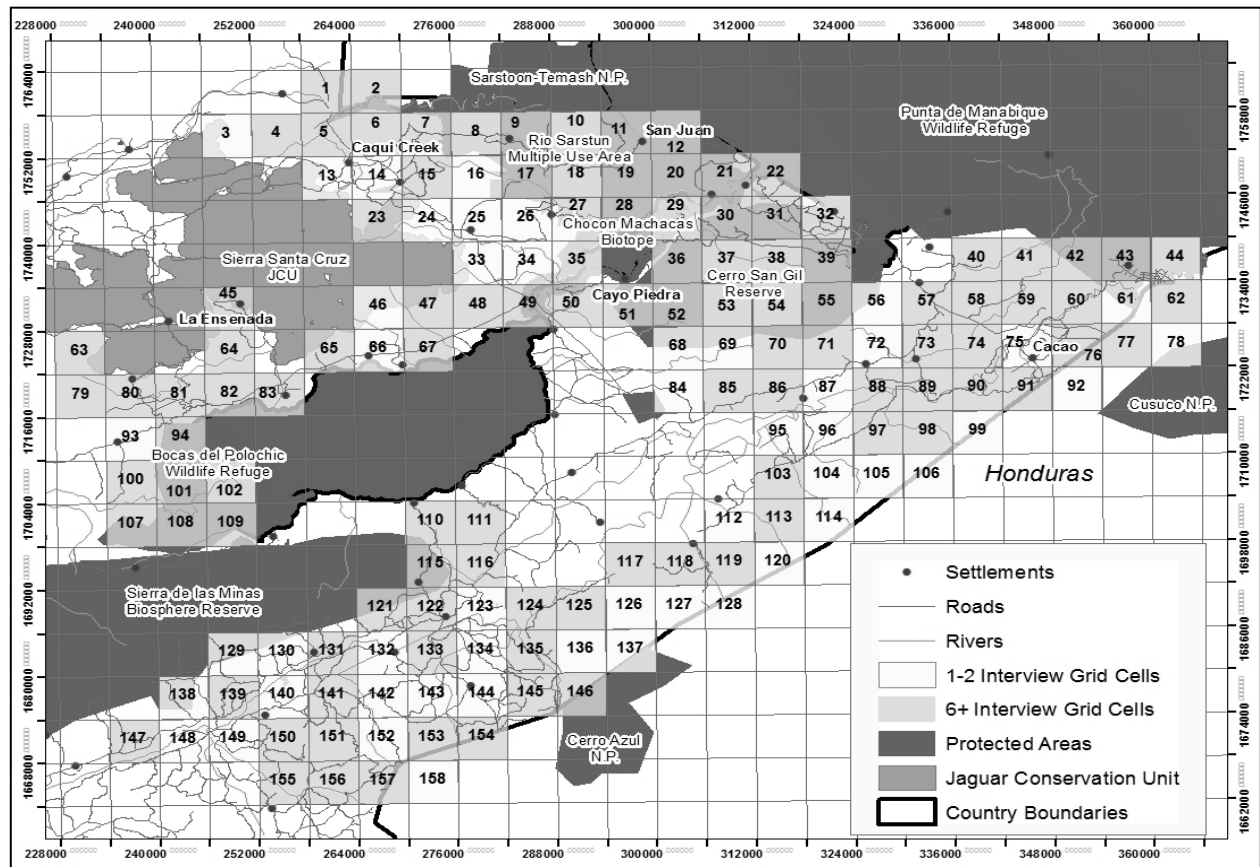


Figure 2. Contemporary Sightings of jaguar or their sign as reported within the subset of study grids having data from ≥ 3 interviewees.

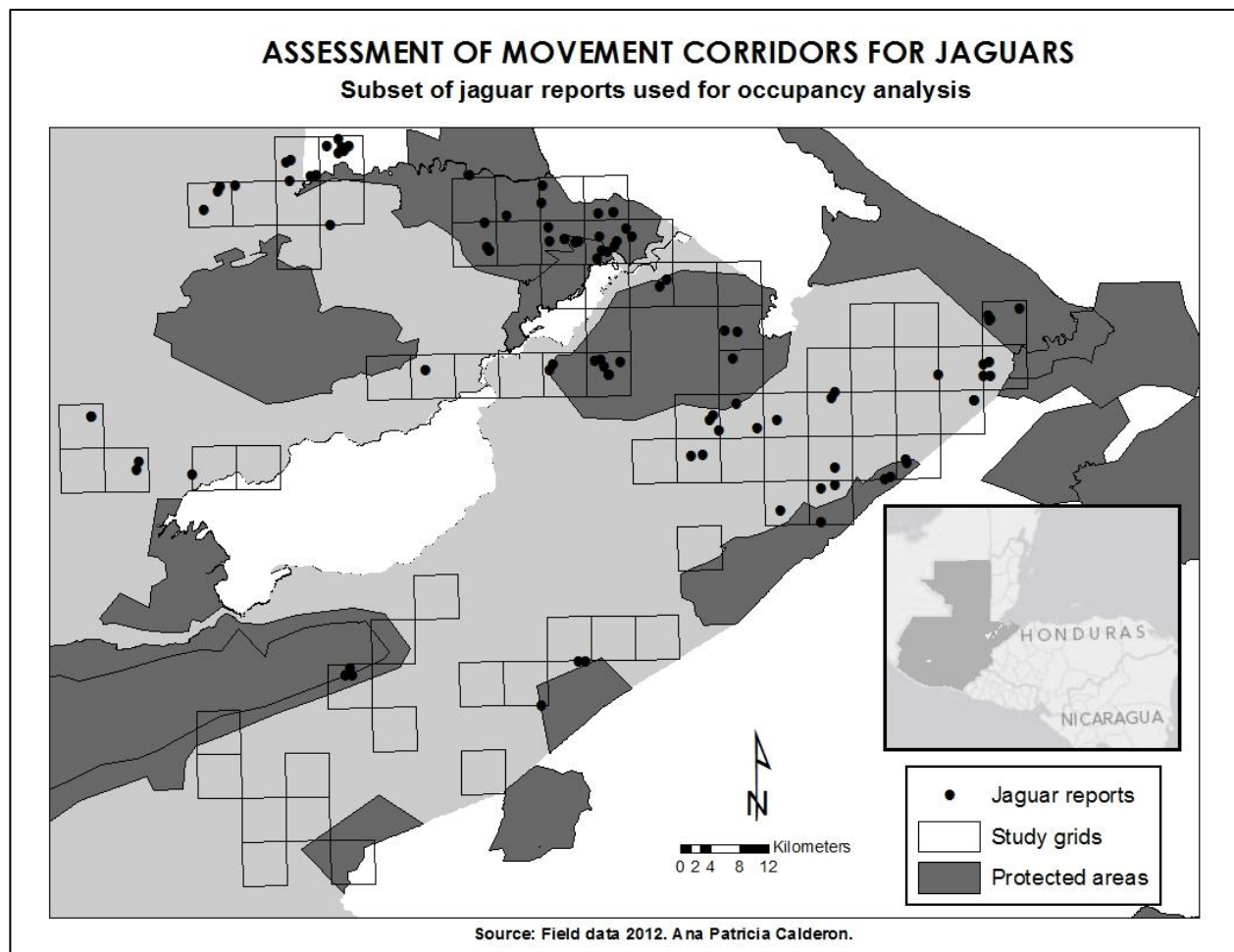


Figure 3. Partial probability of jaguar habitat use (Ψ) as a function of either prey diversity, area of wetlands, or mature forest area of a cell after setting the effects of other covariates to zero. Variable values are rescaled to -1 to +1 for minima and maxima, respectively.

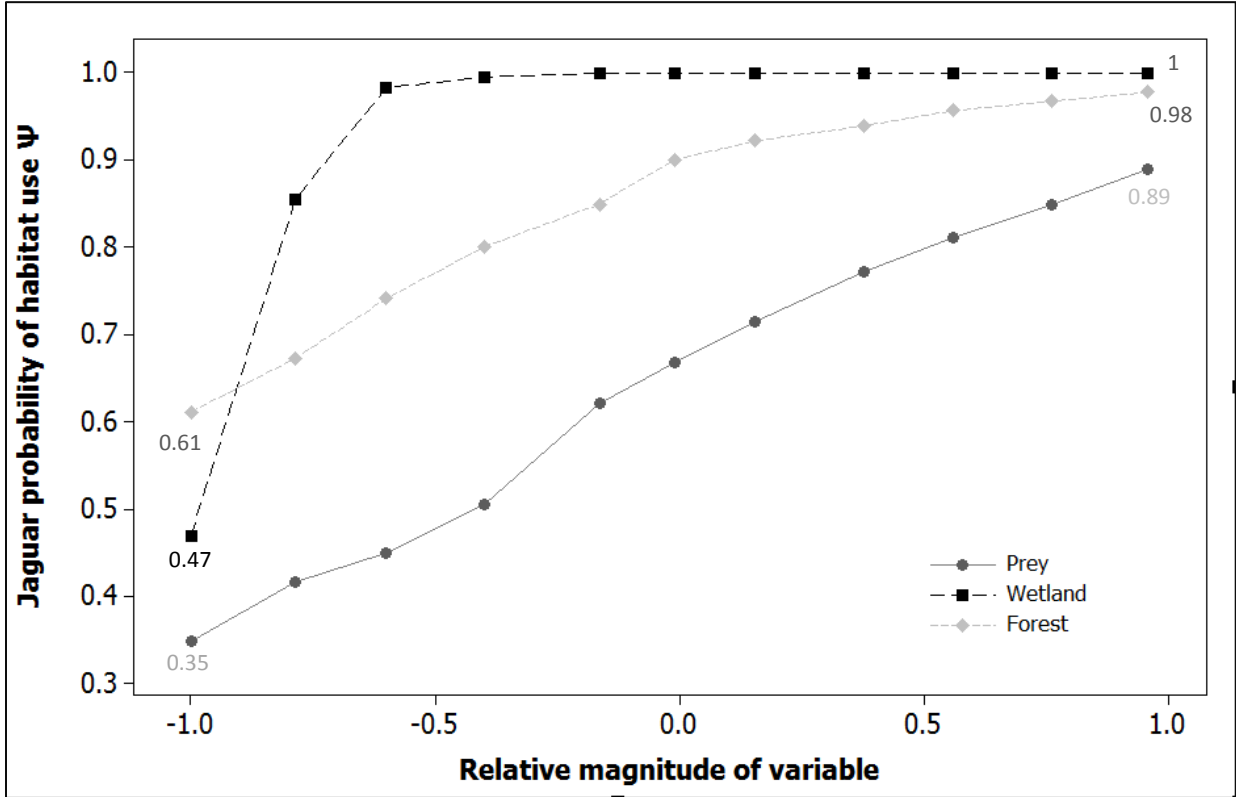


Figure 4. Predicted probabilities of habitat use by jaguar (with points = reported jaguar records within the last year of study), white-lipped peccary, collared peccary, red brocket deer, and paca in eastern Guatemala.



Figure 5. Corridor design for jaguar movement in eastern Guatemala based on field-validated assessment of jaguar occurrence. Cells were included in the corridor based on high probability of use by both jaguar and their prey (see text for details).

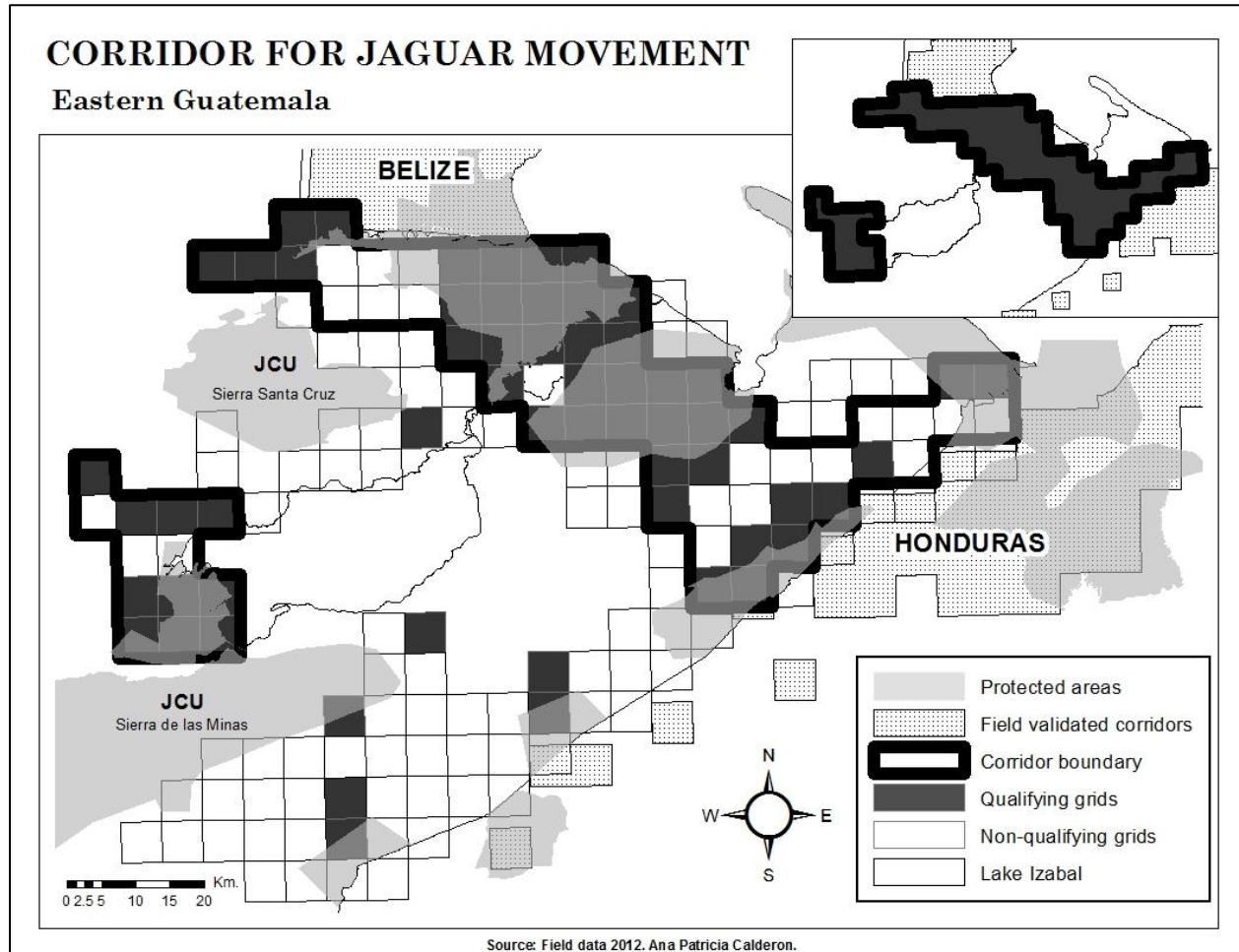


Figure 6. Area of overlap between the originally proposed corridor by Rabinowitz and Zeller (2010) and the field-validated corridor in eastern Guatemala.

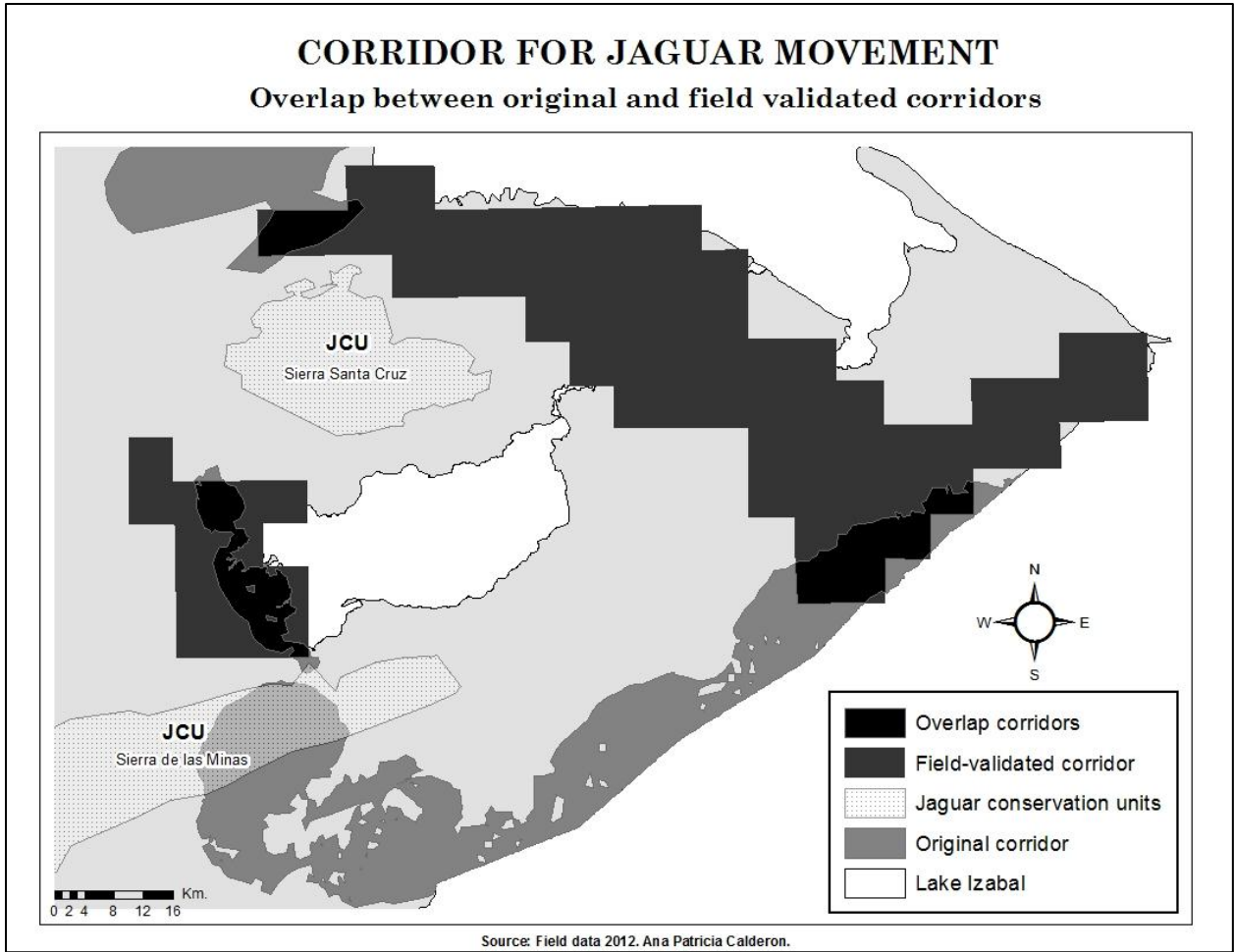
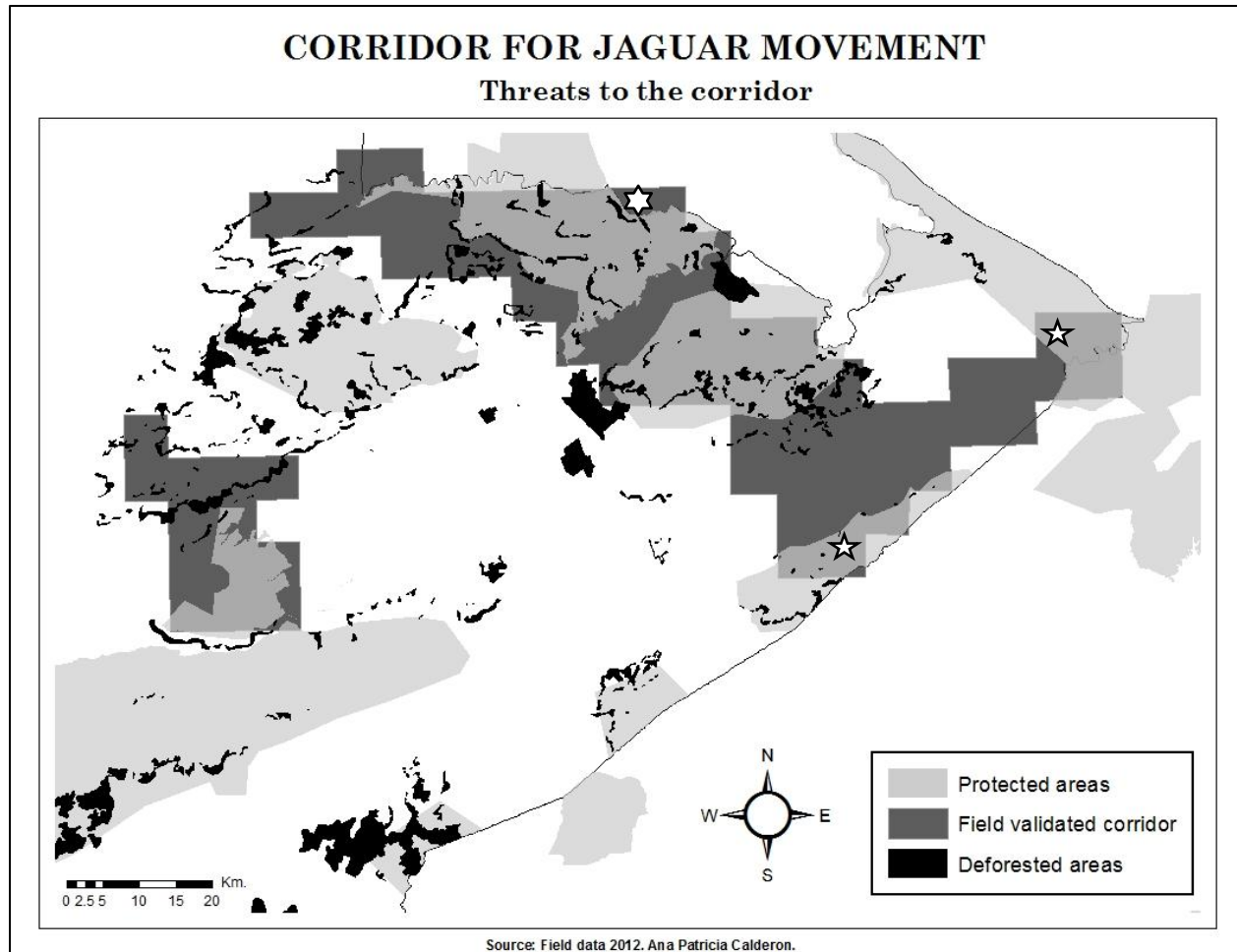


Figure 7. Threats to the movement corridor for jaguar in eastern Guatemala. Shown are locations likely to be impacted by the TCG (five-pointed stars) and locations impacted by oil and gas exploration (six-pointed star). Also shown are recently deforested areas (black polygons) indicating forest loss through the corridor from the period of 1999 to 2005.



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APPENDICES

APPENDIX I: Geographic data sets used for measuring the spatial covariates in the single-state, single-season occupancy models analysis. The table shows the country, data type, resolution, year, and author for each of the data sets used.

Country	Data set	Scale/ resolution	Year	Author
Guatemala	Roads	1:250,000	2005	Guatemalan Ministry of Agriculture and Cattle
	Rivers	1:250,000	2005	Guatemalan Ministry of Agriculture and Cattle
	Protected Areas	1:250,000	2005	Guatemalan Ministry of Agriculture and Cattle
	Land Use and land cover	1:250,000	2005	Guatemalan Ministry of Agriculture and Cattle
	Settlements	1:50,000	2002	National Institute of Statistics
	Settlements	1:50,000	2005	Guatemalan Ministry of Agriculture and Cattle
Belize	Land use and land cover	1:250,000	2011	Jan Meerman, Belize Tropical Forest Studies
	Roads	1:250,000	2005	U.K. Directorate of Overseas Surveys/Belize Land Information Center
	Settlements	1:250,000	2010	Conservation Biology Institute
	Protected Areas	1:250,000	2011	Jan Meerman, Belize Tropical Forest Studies
Honduras	Roads	1:250,000	2010	Honduran Institute for Conservation, Forest development, Protected Areas, and Wildlife
	Rivers	1:250,000	2005	Honduran Institute for Conservation, Forest development, Protected Areas, and Wildlife
	Protected Areas	1:250,000	2012	Honduran Institute for Conservation, Forest development, Protected Areas, and Wildlife
	Land use and land cover	1:250,000	2005	Honduran Institute for Conservation, Forest development, Protected Areas, and Wildlife
	Settlements	1:250,000	2005	Honduran Institute for Conservation, Forest development, Protected Areas, and Wildlife

APPENDIX II: Procedure for calculating prey species probability of habitat use for the delineation of the functional corridor for jaguar movement.

Probabilities of prey habitat use were calculated in several steps. First, the conditional probabilities for the prey species were calculated. Conditional probability takes into account probability of detection in a sampling unit, and it is equal to one in the sampling sites where there was at least one detection, as presence of the species is unambiguously established in these sites.

$$\psi_{cond} = \frac{\psi \times Q}{1 - \psi + \psi \times Q}$$

where $Q = (1-p)^k$, being k the number of interviews performed in the sampling site. The probabilities of detection for each of these species were calculated averaging all detection probabilities in the competing models (models that summed 90% of the AIC weights).

Second, probabilities of habitat use for agouti, paca, armadillo, and white-tailed deer; for which none of the single-state, single-season occupancy models fitted the observed data, equaled 0 for sites where species were not reported and one for sites where it was (species presence was unambiguously established). This approach, although very coarse, was considered to add less uncertainty to the prediction of prey habitat use and because most prey species were widespread and easily detected by the interviewees in the study area, as well as the highly selective procedure used for targeting interviewees, it is unlikely that the species were present but went undetected in the study region. It is important to note though, that regardless of whether these probabilities were derived directly from the capture data ($P=1$ for reported presence and $P=0$ for unreported presence) or model based (Ψ -averaged-cond), they all represent the same response variable, which is probability of habitat use.

Third, probability of habitat use by all small (Step 1) and at least 2 big prey species (Step 2-4) were calculated for each grid cell using the following equations. For practical purposes, probability of prey habitat use in the following equations, model-based or not, was denoted as P . The outputs from the steps above were multiplied to get the overall prey probability estimate as shown in step 5.

Step 1: Probability of all small prey

$$P_1 = P_{ag} \times P_{pac} \times P_{arm}$$

Step 2: Probability of no prey species

$$P_2 = (1 - (1 - P_{wlp}) \times (1 - P_{cp}) \times (1 - P_{wtd}) \times (1 - P_{bd}))$$

Step 3: Probability of only one prey species

$$P3 = P(wlp) \times (1 - Pcp) \times (1 - Pbd) \times (1 - Pwtd)$$

$$P4 = (Pcp) \times (1 - Pwlp) \times (1 - Pbd) \times (1 - Pwtd)$$

$$P5 = (Pbd) \times (1 - Pwlp) \times (1 - Pcp) \times (1 - Pwtd)$$

$$P6 = (Pwtd) \times (1 - Pwlp) \times (1 - Pcp) \times (1 - Pbd)$$

Step 4: Probability of only two prey species

$$P7 = (Pwlp \times Pcp) \times (1 - Pbd) \times (1 - Pwtd)$$

$$P8 = Pwlp \times Pbd \times (1 - Pcp) \times (1 - Pwtd)$$

$$P9 = (Pwlp \times Pwtd) \times (1 - Pcp) \times (1 - Pbd)$$

$$P10 = (Pcp \times Pbd) \times (1 - Pwlp) \times (1 - Pwtd)$$

$$P11 = (Pcp \times Pwtd) \times (1 - Pwlp) \times (1 - Pbd)$$

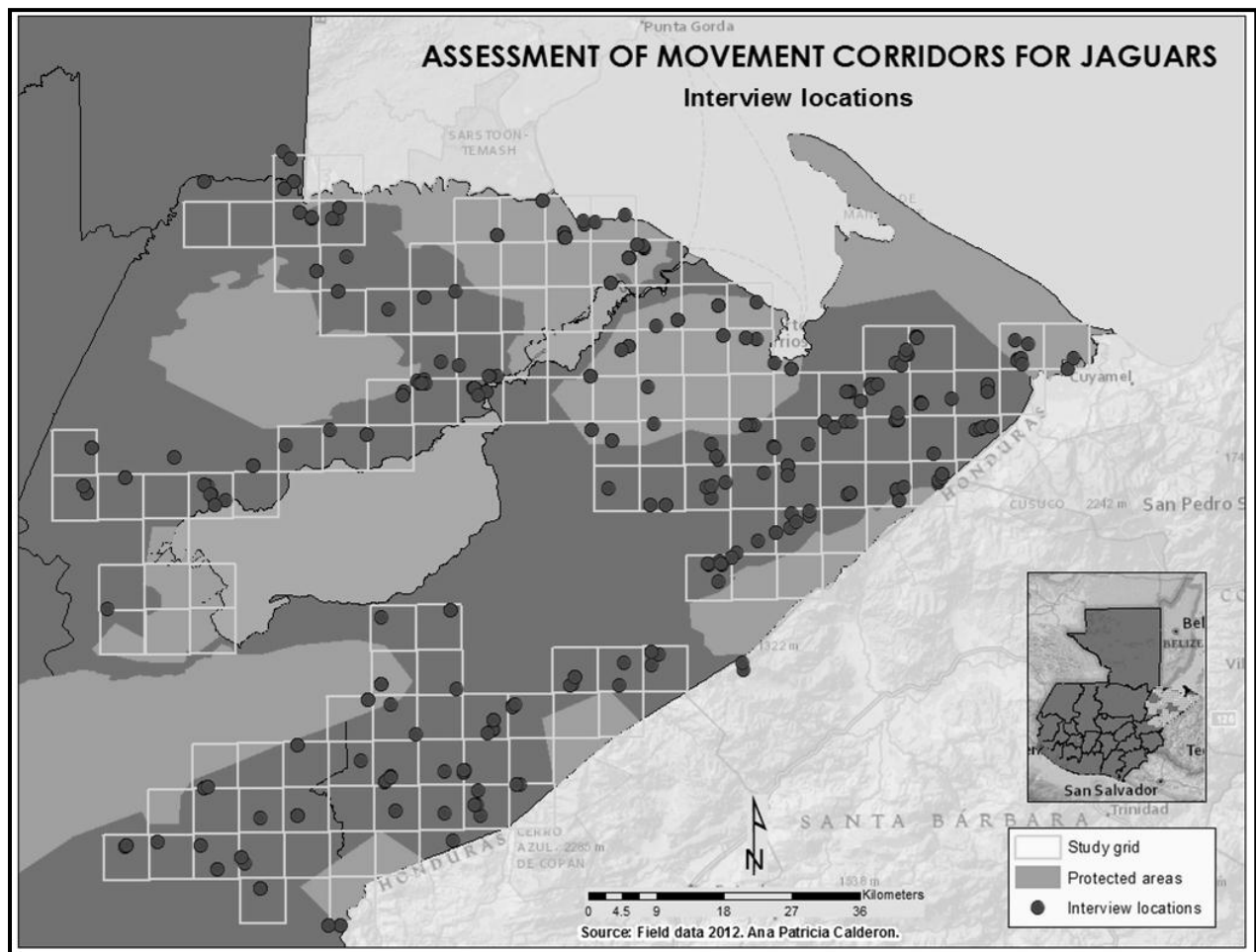
$$P12 = (Pbd \times Pwtd) \times (1 - Pwlp) \times (1 - Pcp)$$

Step 5: Probability of all small and at least two big prey species

$$P_{prey} = (1 - P2 - (P3 + P4 + P5 + P6) - (P7 + P8 + P9 + P10 + P11 + P12))$$

where P_{ag} , P_{arm} , P_{pac} , P_{cp} , P_{bd} , P_{wtd} , P_{wlp} , equal the probability of habitat use of agouti, armadillo, paca, collared peccary, red brocket deer, white-tailed deer, and white-lipped peccary respectively.

APPENDIX III: Locations of the interviews performed to resident people in eastern Guatemala during May to October 2012 for assessing patterns of occurrence of jaguars and 7 prey species.



APPENDIX IV: All single-state, single-season occupancy models for jaguar. Covariates influencing occupancy: mature forest (Forest), available wetland (Wetland), prey diversity (Prey), interaction between wetland and settlements (wet*sett), and mean distance to settlements (Sett).

Model	QAIC	ΔQAIC	AIC weight	Model Likelihood	Number parameters	-2*LogLike
psi(wetland,forest),p(.)	150.37	0.00	0.34	1.00	4	389.38
psi(forest,wetland,prey) p(.)	151.20	0.83	0.22	0.66	5	386.16
psi(preyn diversity),p(.)	152.04	1.67	0.15	0.43	3	399.41
psi(forest),p(.)	153.34	2.97	0.08	0.23	3	402.97
psi(wetland, sett, wet*sett),p(.)	153.52	3.15	0.07	0.21	5	392.51
psi(wetland),p(.)	153.90	3.53	0.06	0.17	3	404.5
psi(sett),p(.)	153.91	3.54	0.06	0.17	3	404.51
psi(.),p(.)	154.82	4.45	0.04	0.11	2	412.48

APPENDIX V: All single-state, single-season occupancy models for white-lipped peccary.
Covariates influencing occupancy: mature forest (Forest), mean distance to Protected Areas (PA).

Model	QAIC	ΔQAIC	AIC weight	Model Likelihood	Number parameters	-2*LogLike
psi(PA.),p(.)	169.45	0	0.572	1	3	163.45
psi(forest, PA),p(.)	170.08	0.63	0.4175	0.7298	4	162.08
psi(forest),p(.)	177.68	8.23	0.0093	0.0163	3	171.68
psi(.),p(.)	181.88	12.43	0.0011	0.002	2	177.88

APPENDIX VI: All single-state, single-season occupancy models for collared peccary. Covariates influencing occupancy: mature forest (Forest). Covariates influencing detection: mean distance to settlements (Sett), terrain ruggedness (Rugg), interaction between terrain ruggedness and settlements (Rugg*sett).

Model	QAIC	ΔQAIC	AIC weight	Model Likelihood	Number parameters	-2*LogLike
psi(forest),p(Sett)	174.00	0.00	0.43	1.00	4.00	413.55
psi(.),p(Sett)	174.49	0.49	0.34	0.78	3.00	419.75
psi(forest),p(Sett,Rug, Rugg*sett)	176.69	2.69	0.11	0.26	6.00	410.28
psi(.),p(Sett, Rugg, Rugg*sett)	177.18	3.18	0.09	0.20	5.00	416.47
psi(Forest),p(.)	180.72	6.72	0.02	0.03	3.00	435.27
psi(.),p(.)	181.20	7.20	0.01	0.03	2.00	441.44

APPENDIX VII: All single-state, single-season occupancy models for red brocket deer.
Covariates influencing occupancy: mean distance to Protected Areas (PA). Covariates influencing detection: Forest (Forest).

Model	QAIC	ΔQAIC	AIC weight	Model Likelihood	Number parameters	-2*LogLike
psi(PA),p(Forest)	405.11	0.00	0.42	1.00	4.00	506.83
psi(.),p(Forest)	406.06	0.95	0.26	0.62	3.00	510.60
psi(PA),p(.)	406.52	1.41	0.21	0.49	3.00	511.18
psi(.),p(.)	407.76	2.65	0.11	0.27	2.00	515.32

APPENDIX VIII: All single-state, single-season occupancy models for the paca. Covariates influencing detection: mean distance to settlements (Sett), Terrain ruggedness (Rugg), interaction between terrain ruggedness and mean distance to settlements (Rugg*sett), effort (Effort).

Model	QAIC	ΔQAIC	AIC weight	Model Likelihood	Number parameters	-2*LogLike
psi(.),p(Sett, Rugg, Rugg*sett, Effort)	266.19	0	0.4517	1	6	420.79
psi(.),p(Sett, Rugg, Rugg*sett)	267.51	1.32	0.2335	0.5169	5	426.28
psi(.),p(Rugg)	267.58	1.39	0.2254	0.4991	3	433.02
psi(.),p(Effort)	270.05	3.86	0.0656	0.1451	3	437.11
psi(.),p(.)	272.07	5.88	0.0239	0.0529	2	443.76

RESUME
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