DENSITIES, HABITAT-USE, AND MESOPREDATOR RELEASE OF THE OCELOT IN BELIZE

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(ABSTRACT)

The mesopredator release hypothesis suggests that small carnivore populations are negatively affected by competition with larger carnivore species; this could hinder the conservation of mesopredators in areas where large top-carnivores are prioritized. I investigated the ecology of ocelots in Belize and examined the role of mesopredator release in the neotropical carnivore guild to determine if ocelots are limited by competition with jaguars and pumas. I conducted remote camera surveys and sampled habitat within four protected areas: three broadleaf sites and one pine forest site. I measured ocelot activity and habitat-use with respect to the activity of jaguars and pumas at one broadleaf site and one pine forest site; additionally, I calculated estimates of ocelot and jaguar densities within those two sites. Ocelot presence was positively related to jaguar activity in the pine forest and to both jaguar and puma activity in the broadleaf forest. There were few relationships with habitat characteristics; however, in the broadleaf site, ocelot activity was positively related to road width and large avian prey activity. Both jaguar and ocelot densities were low in the pine forest and higher in the broadleaf site. Preliminary findings from the remaining two sites suggest that future results may be similar to those from the first two sites analyzed. I conclude that ocelot populations are not negatively affected by jaguars and that a negative effect of pumas is unlikely. Results imply that mesopredator release does not limit ocelot populations in these areas.

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TABLE OF CONTENTS

Chapter 1 – Ocelot ecology and the potential impact of interspecies competition in the neotropical predator guild ... 1
  Introduction ... 1
  Felid conservation in Central and South America ... 4
  The mesopredator release hypothesis ... 4
  Interactions within guilds of large carnivores and the potential role of mesopredator release (outside of the neotropics). ... 7
  The neotropical felid community and evidence of competition ... 8
    Diet partitioning ... 9
    Habitat-use and activity patterns ... 11
    Aggressive interactions ... 13
  Camera trapping and density estimation ... 13
  Microhabitat sampling of small felids ... 15
Chapter 2 – Habitat-use of the ocelot with respect to jaguar and puma activity in the Mountain Pine Ridge Forest Reserve, Belize. ... 19
  Abstract ... 19
  Introduction ... 19
  Study site ... 21
  Methods ... 22
  Results ... 25
  Discussion ... 28
  Conclusions ... 32
  Acknowledgments ... 33
Chapter 3 – Habitat-use and coexistence of the ocelot with jaguars and pumas in northern Belize. ... 46
  Abstract ... 46
  Introduction ... 46
  Study site ... 48
  Methods ... 49
  Results ... 52
  Discussion ... 54
  Conclusions ... 58
  Acknowledgments ... 59
Chapter 4 – The mesopredator release hypothesis: inferences from felid densities and co-occurrence in Belize ... 72
  Abstract ... 72
  Introduction ... 72
  Methods ... 74
    Fieldwork ... 74
    Individual camera surveys and study site descriptions ... 75
    Density analysis for the MPR and RBCA ... 77
    Estimates of site characteristics for the MPR and RBCA ... 78
    Comparison of presence-absence patterns for the ocelot, jaguar, and puma at all four sites 78
  Results ... 79
    Comparison of site characteristics for the MPR and RBCA ... 80

    Patterns of ocelot, puma, and jaguar co-occurrence 81
    Weather conditions 82
  Discussion 82
    Densities 82
    Comparison of MPR and RBCA site characteristics 83
    Patterns of co-occurrence and implications for upcoming analyses of the CFRNP and CBWS 84
    Mesopredator release and future research 85
  Conclusions 86
  Acknowledgments 87
References 101

LIST OF TABLES

Table 1.1: Felid density estimates (individuals per 100 km^2) previously recorded at study sites in Belize. 17

Table 2.1: Weights used to categorize Mountain Pine Ridge Forest Reserve (MPR) prey and carnivore species into groups for analysis. All species listed were photographically captured during the remote camera survey in the MPR from June to August of 2007......... 34

Table 2.2: Comparison of microhabitat, landscape characteristics and large carnivore activity across locations used or not used by ocelots. Camera stations were established and habitat was sampled at 47 locations in the Mountain Pine Ridge Forest Reserve, Belize, from June to August 2007.......... 35

Table 2.3: Correlation of ocelot trap success with habitat characteristics and large carnivore activity at the 10 camera stations in the Mountain Pine Ridge Forest Reserve, Belize, with ocelots present. Sampling took place from June to August of 2007.......... 36

Table 2.4: Variation among 47 locations with different combinations of jaguar and ocelot presence in the Mountain Pine Ridge Forest Reserve, Belize. Data were collected from June to August of 2007. 37

Table 2.5: Variation among locations with different combinations of puma and ocelot presence in the Mountain Pine Ridge Forest Reserve, Belize. Data were collected from June to August of 2007. 38

Table 2.6: Logistic regression models explaining the presence and absence of ocelots at camera stations in the Mountain Pine Ridge Forest Reserve, Belize. Data used were obtained from 47 locations that were sampled from June to August of 2007. All models are ranked according to Akaike scores (corrected, AIC_c), Δ AIC_c and Akaike weights (ω_i). The 12 proposed models that ranked highest out of the 32 models tested (30 a priori models plus a null and global model) are shown in order of rank. Results of Hosmer and Lemeshow Goodness-of-Fit Tests including Chi-square and *P* values are shown. Null and global models with ranks are displayed for comparison.......... 39

Table 3.1: Weights used to categorize Rio Bravo Conservation and Management Area (RBCA) prey and carnivore species into groups for analysis. All species were photographically captured during the remote camera survey in the RBCA from January to April of 2008. ... 60

Table 3.2: Comparison of microhabitat, landscape characteristics and large carnivore activity across 39 locations used or not used by ocelots in the Rio Bravo Conservation and Management Area, Belize. Camera stations were established and habitat was sampled at 39 locations in the study area from January to April 2008. 61

Table 3.3: Correlation of ocelot trap success with habitat characteristics and large carnivore activity at 29 camera stations in the Rio Bravo Conservation and Management Area, Belize, with ocelots present. Data were collected from January to April of 2008.......... 62

Table 3.4: Variation among locations with different combinations of jaguar and ocelot presence in the Rio Bravo Conservation and Management Area, Belize. Data were collected from January to April of 2008. 63

Table 3.5: Variation among locations with different combinations of puma and ocelot presence in the Rio Bravo Conservation and Management Area, Belize. Data were collected from January to April of 2008. 64

Table 3.6: Zero-inflated negative binomial regression models explaining the counts of ocelot captures at 39 camera stations in the Rio Bravo Conservation and Management Area, Belize. Data used were obtained from 39 locations that were sampled from January to April

of 2008. All models are ranked according to Akaike scores (corrected, AIC_c), Δ AIC_c, and Akaike weights (ω_i) The 12 proposed models ranked highest out of the 32 models tested (including 29 a priori models, one post-hoc model, plus a null and global model) are shown. Results of Pearson correlation between predicted and observed counts are shown. Null and global models with ranks are displayed for comparison. 65

Table 4.1: Characteristics of study sites and camera surveys conducted in each site between June 2007 and August 2008. Sites included the Mountain Pine Ridge Forest Reserve (MPR), the Rio Bravo Conservation and Management Area (RBCA), the Cockscomb Basin and Wildlife Sanctuary (CBWS) and the Chiquibul Forest Reserve and National Park (CFRNP). 88

Table 4.2: Parameters associated with the estimation of abundance, area sampled, tests of population closure and final density estimates for jaguars and ocelots at 3 sites in Belize. Remote camera surveys were completed in the Mountain Pine Ridge Forest Reserve (MPR) from June to August of 2007 and in the Rio Bravo Conservation and Management Area (RBCA) from January to April of 2008. Data from past surveys completed in the Chiquibul Forest Reserve and National Park (CFRNP) in 2003 are presented for comparison. 89

Table 4.3: Summary of habitat and trap success characteristics from 47 camera stations in the Mountain Pine Ridge Forest Reserve (MPR) and and 39 camera stations in the Rio Bravo Conservation and Management Area (RBCA). Data were collected in the MPR from June to August of 2007 and in the RBCA from January to April of 2008. 90

Table 4.4: Similarity of jaguar-ocelot, puma-ocelot, and jaguar-puma co-occurrence patterns within 4 sites in Belize represented using Sørensen's Index. Sites included the Mountain Pine Ridge Forest Reserve (MPR), the Rio Bravo Conservation and Management Area (RBCA), the Cockscomb Basin and Wildlife Sanctuary (CBWS) and the Chiquibul Forest Reserve and National Park (CFRNP). Data were collected at all sites between June 2007 and August 2008. 91

Table 4.5: Mean daily rainfall, minimum and maximum temperatures during survey periods at four study sites in Belize. Sites included the Mountain Pine Ridge Forest Reserve (MPR), the Rio Bravo Conservation and Management Area (RBCA), the Cockscomb Basin and Wildlife Sanctuary (CBWS) and the Chiquibul Forest Reserve and National Park (CFRNP). Data were collected at all sites during indicated survey periods between June 2007 and August 2008. 92

LIST OF FIGURES

Figure 1.1: Location of the four study sites within Belize (Meerman 2006). Remote camera surveys were completed at all sites between June 2007 and August of 2008. See Chapter 4 for details of individual surveys. 18

Figure 2.1: Location of the Mountain Pine Ridge Forest Reserve (MPR) within Belize, Central America. The pine forest of the MPR is separated from the broadleaf forest of the Chiquibul Forest Reserve and National Park by the Macal River. Camera and habitat surveys were completed in this area from June to August of 2007. 40

Figure 2.2: Locations of the 47 camera stations established in the Mountain Pine Ridge Forest Reserve. Each station consisted of two cameras mounted in opposing pairs in a 71 day trapping session from June to August of 2007. 41

Figure 2.3: The total number of capture events (captures) from all cameras throughout the 72-day Mountain Pine Ridge Forest Reserve (MPR) survey and the mean trap success rate averaged across all camera stations for each of the three felid species: the ocelot, the jaguar and the puma. The MPR survey took place from June to August of 2007. 42

Figure 2.4: The areas burned in the Mountain Pine Ridge Forest Reserve in the May 2007 fires are shown along with the distribution of ocelot captures. Data were collected using a remote camera survey from June to August of 2007. Two stations in the southeastern area of the camera grid amidst the burned area and in close proximity to the Macal River, bordering the broadleaf forest, had high trap success (5.36 and 7.69 captures per 100 TN respectively) compared to the other 8 camera stations with ocelots present. 43

Figure 2.5: The distributions of camera stations with either ocelots (black circles), pumas (crosses) or both ocelots and pumas (circles with white crosses) present are shown. Data were collected using a remote camera survey established across the Mountain Pine Ridge Forest Reserve in Belize. Data collection took place from June to August of 2007. Presence was inferred from photos obtained at each location while absence was inferred from lack of photos of that species from that location. Ocelots, but not pumas, were found at 7 camera stations. Pumas, but not ocelots, were found at 8 camera stations. Ocelots and pumas were present at only 3 camera stations in the grid (out of of 47). 44

Figure 2.6: The distribution of camera stations in the Mountain Pine Ridge Forest Reserve with jaguars present (represented by asterisks) is shown. Data were collected using a remote camera survey from June to August of 2007. Presence was inferred from photos obtained at each location while absence was inferred from lack of photos of that species from that location. 45

Figure 3.1: Location of the Rio Bravo Conservation and Management Area in northwestern Belize, Central America (Meerman 2006). It is the largest private reserve in Belize and covers 994.8 km^2. Camera and habitat surveys were completed in this area from January to April 2008 66

Figure 3.2: Thirty-nine camera stations were established in the Rio Bravo Conservation and Management Area; each station consisted of two cameras mounted in opposing pairs for a maximum of 77 days during the survey period from January to April of 2008. The nearby town, Tres Leguas, the general location of La Milpa Field Station, and known locations of the roads and trails (from GPS points taken in 2008) are also shown. 67

Figure 3.3: The total number of capture events (captures) from all cameras throughout the 90-day Rio Bravo Conservation and Management Area survey and the mean trap success rate

averaged across 39 camera stations for each of the three felid species: the ocelot, the jaguar and the puma. Each camera station was operational for a maximum of 77 days during the survey period from January to April of 2008 68

Figure 3.4: The Gallon Jug Road that bisects the Rio Bravo Conservation and Management Area, the nearby town Tres Leguas, and general location of the La Milpa Field Station are shown along with the distribution of ocelot captures. Ocelots were captured at 29 camera stations (out of 39) during the survey period from January to April of 2008. 69

Figure: 3.5: The distributions of camera stations with either ocelots (black circles), jaguars (star) or both ocelots and pumas (circles with inner stars) present are shown. Data were collected using a remote camera survey established across the Rio Bravo Conservation and Management Area in Belize. Data collection took place from January to April of 2008. Presence was inferred from photos obtained at each location while absence was inferred from lack of photos of that species from that location. Ocelots, but not jaguars, were found at 5 camera stations. Jaguars, but not ocelots, were found at only 1 camera station. Ocelots and jaguars were present at 24 camera stations in the grid (out of 39). 70

Figure 3.6: The distributions of camera stations with either ocelots (black circles), pumas (crosses) or both ocelots and pumas (circles with white crosses) present are shown. Data were collected using a remote camera survey established across the Rio Bravo Conservation and Management Area in Belize. Data collection took place from January to April of 2008. Presence was inferred from photos obtained at each location while absence was inferred from lack of photos of that species from that location. Ocelots, but not pumas, were found at 10 camera stations. Pumas, but not ocelots, were found at 3 camera stations. Ocelots and pumas were present at 19 camera stations in the grid (out of 39). 71

Figure 4.1: Density estimates (with standard errors) for the ocelot and jaguar across three study sites are shown. Estimates were calculated using mark-recapture techniques following Nichols and Karanth (2002) using data from remote camera surveys. Remote camera surveys were conducted in the Mountain Pine Ridge Forest Reserve (MPR) from June to August of 2007, and in the Rio Bravo Conservation and Management Area (RBCA) from January to April of 2008. Density estimates for the Chiquibul Forest Reserve and National Park (CFRNP) for ocelots are based on a survey completed from August 2003 to September 2003 (Dillon 2005) and for jaguars are based on a survey completed from June 2003 to July 2003 (Kelly unpublished data). See text for more details on the methods used for density estimation. 93

Figure 4.2: The two camera grids comprising the Mountain Pine Ridge Forest Reserve survey from June to August of 2007 are shown. The “ocelot grid” included 35 cameras spaced approximately 1.5 km apart nested within a larger “jaguar grid” and was used to obtain photographic “captures” of ocelots to produce ocelot density estimates. The effective area sampled of the ocelot grid was estimated to be 189.18 km^2 using ½ the mean maximum distance moved (MMDM) of all ocelots captured. The larger jaguar grid included 12 additional cameras spaced 3 km apart. Captures of jaguars from cameras within both the ocelot and jaguar grids were used to estimate jaguar densities. The effective area sampled of this combined grid was 478.55 km^2 based on ½ MMDM of all jaguars captured. All 47 camera stations were used in estimating site characteristics and evaluating patterns of felid occurrence (based on presence/absence data). 94

Figure 4.3: The two camera grids comprising the Rio Bravo Conservation and Management Area survey from January to April of 2008 are shown. While 52 camera locations are shown they

represent only 40 actual camera stations. Some stations had to be moved early during the survey period due to areas with lower vehicle activity. These stations were moved only short distances and appear in the figure as two or three camera locations spaced less than 500 meters apart. All locations were taken into account in density analyses. The “ocelot grid” included 29 actual camera stations spaced approximately 1.5 km apart nested within a larger “jaguar grid” and was used to obtain photographic “captures” of ocelots to produce ocelot density estimates. The effective area sampled of the ocelot grid was estimated to be 100.49 km^2 using ½ the mean maximum distance moved (MMDM) of all ocelots captured. The larger jaguar grid included 11 additional camera stations spaced 3 km apart. Captures of jaguars from cameras within both the ocelot and jaguar grids were used to estimate jaguar densities. The effective area sampled of this combined grid was 301.71 km^2 based on ½ MMDM of all jaguars captured. All 40 stations were used to evaluate patterns of felid co-occurrence (based on presence/absence data), but only 39 of the 40 camera stations were used in estimating site characteristics as one station was operational for only a short period. 95

Figure 4.4: The two camera grids comprising the Cockscomb Basin Wildlife Sanctuary (CBWS) survey included 40 camera stations operational from April to July of 2008. The “ocelot grid” included 28 cameras spaced approximately 1.5 km apart nested within a larger “jaguar grid”. The larger jaguar grid included 12 additional cameras spaced 3 km apart. Analyses of densities and site characteristics at the CBWS is still underway. All 40 camera stations were used to evaluate patterns of felid occurrence (based on presence/absence data)......... 96

Figure 4.5: The camera stations comprising the Chiquibul Forest Reserve and National Park (CFRNP) survey included 29 camera stations operational from June to August of 2008. Separate ocelot and jaguar grids have yet to be defined. Analyses of site characteristics and possibly densities at the CFRNP are still underway. All 29 stations were used to evaluate patterns of felid occurrence (based on presence/absence data). 97

Figure 4.6: The mean ocelot trap success rate and total number of ocelot capture events from 47 camera stations within the Mountain Pine Ridge Forest Reserve (MPR) survey and 39 camera stations within the Rio Bravo Conservation and Management Area (RBCA) survey are shown. The MPR survey ran for 72 days from June to August of 2007. The RBCA survey ran from January to April of 2008. One additional camera station in the RBCA survey was not included in this summary because it was operational for only a short period. 98

Figure 4.7: The mean puma trap success rate and total number of puma capture events from 47 camera stations within the Mountain Pine Ridge Forest Reserve (MPR) survey and 39 camera stations within the Rio Bravo Conservation and Management Area (RBCA) survey are shown. The MPR survey ran for 72 days from June to August of 2007. The RBCA survey ran from January to April of 2008. One additional camera station in the RBCA survey was not included in this summary because it was operational for only a short period. 99

Figure 4.8: The mean jaguar trap success rate and total number of jaguar capture events from 47 camera stations within the Mountain Pine Ridge Forest Reserve (MPR) survey and 39 camera stations within the Rio Bravo Conservation and Management Area (RBCA) survey are shown. The MPR survey ran for 72 days from June to August of 2007. The RBCA survey ran from January to April of 2008. One additional camera station in the RBCA

survey was not included in this summary because it was operational for only a short period. 100

Chapter 1 – Ocelot ecology and the potential impact of interspecies competition in the neotropical predator guild

Introduction

Due to a high demand for pelts from the 1950's to the 1980's, populations of ocelots (*Leopardus pardalis*) declined throughout their range over the latter 20th century (Murray and Gardner 1997). The populations of all species in the family Felidae are believed to be declining (IUCN 2006), and the rush is on to gain ecological knowledge that will aid in developing effective conservation programs. The conservation of smaller felids, such as the ocelot, may prove even more challenging than that of the larger cats, not only because ocelots are difficult to study due to their elusive nature, but also because they may be overlooked in research projects due to their geographic overlap with other, larger and better known felid species. The ocelot, for example, overlaps with at least seven other felid species over the breadth of its range (Sunquist and Sunquist 2002) including the much-publicized flagship species, the jaguar (*Panthera onca*). While the mechanisms enabling the coexistence of multiple predators in one area are still under investigation, several studies have indicated that the dynamics of sympatric carnivore populations are strongly interrelated (Seidensticker 1976, Crooks and Soule 1999, Caro and Stoner 2003, Donadio and Buskirk 2006, Helldin et al. 2006). A sympatric carnivore community can potentially be upset by any population shifts among its members. For example, cheetahs are influenced by lions where high lion numbers result in reduced cheetah recruitment (Kelly and Durant 2000) – even within protected areas. Wildlife reserves established based upon the ecological needs of one flagship predator, therefore, may not be sufficient to protect all other carnivore species in the community. An understanding of the interplay between the densities of sympatric carnivores is necessary to enact conservation measures that simultaneously preserve all the predators of a community – small and large alike.

Debate in predator ecology revolves around two related questions: 1) What mechanisms allow multiple predators to coexist in the same community? and 2) How is an ecological community affected by changes in the densities of top-carnivore populations? Factors identified as enabling predator coexistence usually involve the reduction of competition through niche differentiation (implied by the competitive exclusion principle; Gause 1934) among the predators of a guild. Unfortunately, the relative importance of this competition is little understood – niche differentiation is variable among sites and within different carnivore communities and is not always related to competitive interactions (Schoener 1982). The second question stems from the idea that top predators often seem to exert a higher degree of influence on their ecological community than would be expected based on local population biomass (keystone species concept; Paine 1966). The potential for top-down effects within a threatened ecological community has increasingly been used to justify and motivate the conservation of large carnivores (Terborgh 1990, Miller et al. 2001, Terborgh et al. 2001). A phenomenon known as “mesopredator release” has been proposed as one mechanism by which top carnivores exert this seemingly disproportionate degree of influence (Brown and Wilson 1956, Crooks and Soule 1999). Mesopredator release theory proposes that with the decline of large predators smaller “mesopredators” experience less competition and are able to expand their functional niche and increase in abundance, resulting in a cascade of population shifts down the food chain (Brown and Wilson 1956, Crooks and Soule 1999). For example, the decline of coyotes has been thought to be responsible for increased levels of songbird nest predation by released mesopredator (raccoon) populations (Rogers and Caro 1998).

In many cases, the mesopredator is considered a “pest species” (e.g. feral cats limited by coyotes, Crooks and Soule 1999). But, what if the mesopredator species involved is also of conservation concern (i.e. endangered or threatened)? Mesopredator release theory should be examined more thoroughly across different communities and ecosystems so that conservation managers can choose an appropriate management plan for their community of interest. While the findings of several studies support mesopredator release theory, research is largely restricted to temperate carnivore communities (Courchamp et al. 1999, Crooks and Soule 1999, Gehrt and Clark 2003, Schmidt 2003) and to the guilds of large predators in the open landscapes of Africa (Kelly et al. 1998, Durant et al. 2004). This raises doubt as to whether mesopredator release is applicable to other carnivore communities around the world. If this phenomenon is ubiquitous, this has implications for many mesopredators such as the ocelot, as they may not do as well in areas of high superpredator numbers.

The presence of accessible field sites in Belize, Central America, already known from previous remote cameras studies to contain differing densities of jaguars (ranging 3.1 - 11.4 per 100km^2; C. Miller, Wildlife Conservation Society, personal communication; M. J. Kelly, Virginia Tech University, personal communication) provides a unique opportunity to examine this theory of competitive release in the understudied guild of neotropical carnivores. I used remote camera surveys to collect data on the density and ecology of the ocelot with respect to the activity of two sympatric large predator species, the puma (*Puma concolor*) and the jaguar, at two sites in Belize. Additionally, I include preliminary data on these species and their patterns of occurrence in two other sites. If mesopredator release occurs in this predator community, ocelot densities should be higher in areas of lower jaguar densities and interspecies competition may result in spatial avoidance and differentiation of habitat-use among the jaguar, puma and ocelot within study sites. Mesopredator release theory has wide-ranging implications for carnivore conservation in a time when we are only beginning to understand the importance of large terrestrial predators to their ecological communities. This project adds to the baseline knowledge of a small felid carnivore, the ocelot, and, by testing mesopredator release theory, examines how small predators may be affected when reserves are designed to maintain high densities of top carnivore species.

This study had four main objectives:

1. Describe patterns of ocelot activity and habitat-use within the Mountain Pine Ridge Forest Reserve and the Rio Bravo Conservation and Management Area by examining correlates of ocelot camera-trap success including microhabitat features, landscape features, and the trap success of jaguars, pumas, other carnivores, prey species, and humans.
2. Estimate the densities of ocelots at two sites in Belize including the Mountain Pine Ridge Forest Reserve and the Rio Bravo Conservation and Management Area.
3. Compare the densities of ocelots to those of the jaguar across three reserves (using previously estimated densities from one additional site in Belize, the Chiquibul Forest Reserve and National Park) to examine the ecology of predator co-existence and potential effects of mesopredator release across those sites.
4. Examine patterns of jaguar, ocelot, and puma co-occurrence among four sites (including the three already listed and one other site the Cockscomb Basin Wildlife Sanctuary) to gain preliminary insight into the role of competition with both pumas and jaguars and to evaluate the potential for mesopredator release effects on a larger scale.

Felid conservation in Central and South America

Ocelots, pumas, and jaguars are the largest felid predators of South and Central America. All three of these species are suffering widespread population declines and are currently threatened by habitat loss and/or persecution (IUCN 2002). As the third largest felid in the world the jaguar is relatively well-known and has been singled out as a flagship, umbrella, and landscape species whose conservation is thought to assist in the preservation of its entire community (Noss 1990, Terborgh 1992, Terborgh et al. 1999, Gittleman et al. 2001, Sanderson et al. 2002b, Coppolillo et al. 2003). These designations cause the jaguar to be the focus of many of the international conservation efforts. In 1986 the Cockscomb Basin Wildlife Sanctuary was established explicitly to protect this charismatic cat. One of the central ideas behind the Mesoamerica Biological Corridor, also known as the Path of the Jaguar or Paseo Pantera (in Spanish; World Bank 1997), is that large stretches of connected forested land through Central America are needed to maintain the integrity of natural ecosystems with a full complement of species which includes top carnivores such as the jaguar (CEPF 2005). This felid has been the focus of other management efforts, including a conservation plan set up for the Brazilian Pantanal (Quigley and Crawshaw 1992) and several international jaguar conservation workshops hosted by the Wildlife Conservation Society. The result of these meetings, which involved jaguar experts from around the world, was the partitioning of South and Central America into priority areas known as "Jaguar Conservation Units" (Sanderson et al. 2002a, Marieb 2005). There are nine other felid species in Central and South America – five of which overlap geographically with the jaguar and are likely to be affected by the institution of management plans and resulting changes in jaguar populations, yet these species have received less attention. Their conservation is thought to be a by-product of the efforts listed above, going hand-in-hand with the preservation of the jaguar and the forests on which it depends. Recently, there has been speculation that a reliance on top predators as conservation tools may be misplaced and may not effectively protect entire communities (reviewed by Sergio et al. 2008). In particular, Sergio et al. (2008) advise that the umbrella species concept has not been well supported by research and may have little relevance in terrestrial systems.

The mesopredator release hypothesis

The mesopredator release hypothesis (MRH) details one route by which the presence and density of large carnivores may have a dramatic effect on the density and even the persistence of smaller carnivore populations. MRH states that populations of these relatively large "superpredators," limit populations of the smaller carnivores or "mesopredators" and, thereby, protect prey populations (upon which the mesopredators feed). Mesopredator release is not a new concept (Latham 1952, Terborgh and Winter 1980, Soule et al. 1988), and, over the years, it has become a popular explanation for the decline of various migratory bird populations in North America (Rogers and Caro 1998, Crooks and Soule 1999, Bolger 2002, Schmidt 2003). Crooks and Soule (1999) showed that coyote (*Canis latrans*) populations had strong negative impacts on mesopredators that preyed on bird species and, therefore, the absence or presence of coyote populations was a significant predictor of bird species diversity in Southern California. However, there is still some debate regarding this theory. Gehrt and Clark (2003) assert that in order for MRH to hold true between a superpredator and a mesopredator pair three predictions must be met: 1) there must be an inverse relationship between abundances of superpredators and mesopredators, 2) populations of the superpredator must be a limiting factor for populations of the mesopredator, and 3) the mesopredator must show behavioral avoidance of areas used by the superpredator. It follows that the same predictions must hold true, at the lower trophic level, for populations of the mesopredator and its prey in order to support the idea that large predator populations do in fact "protect" prey populations. Mesopredator populations should be negatively correlated with their prey populations resulting in an indirect positive correlation between superpredators and mesopredator prey.

To date, most research on this theory has focused on temperate communities of carnivores and has concentrated on the impact experienced by prey populations. Support for mesopredator release has been found in communities involving coyotes, lynx, or raccoons as the large superpredator and involving mongooses, raccoons, domestic cats and opossums as the mesopredators (Palomares et al. 1995, Crooks and Soule 1999, Ginger et al. 2003, Fan et al. 2005, Helldin et al. 2006). There are examples where a species identified as a superpredator in one system has taken the role of mesopredator in another; for example, coyotes seen as superpredators in Texas (Kamler et al. 2003, Gehrt and Prange 2007) were found to be mesopredators suppressed by the recolonization of wolves in Wyoming (Berger and Conner 2008, Berger et al. 2008). Avian populations are almost exclusively the prey populations of interest in these chosen systems (there are exceptions, for example see Berger and Conner 2008). Evidence for this theory is often provided in the form of negative correlations between superpredator and mesopredator populations or activity (Sargeant et al. 1993, Crooks and Soule 1999, Trewby et al. 2008) across different areas (addressing the first prediction listed above). Some studies have been able to go farther and have examined the competitive relationship between sympatric predators (addressing predictions 2 and 3 listed above) by documenting either intraguild predation of the superpredator on the mesopredator (Helldin et al. 2006) or changes in niche after the decline of a predator population (Ginger et al. 2003). For example, Ginger et al. (2003) showed that opossums will expand their niche by selecting different habitat types when raccoons have been experimentally removed. Mathematical support for MRH also has been provided by Courchamp et al. (1999) and Fan et al. (2005) who used models of a hypothetical superpredator-mesopredator-prey system based on cats, rats, and birds to show that the mesopredator release effect exists and could limit shared prey species or even drive them to extinction. This exact scenario (with domestic cats, Pacific rats and Cook's petrels) was later tested and found to hold true by Rayner et al. (2007).

Despite the evidence in support of MRH, the topic remains controversial and has been tested only within a limited range of communities. There is evidence that the strength of mesopredator release effects may be controlled by ecosystem productivity; Elmhagen and Rushton (2007) found that effects were weaker and more difficult to observe in systems where low productivity levels may have limited mesopredator populations before they reached densities where they could be affected by competition with sympatric predators. Additionally, there is concern about the need to collect more detailed evidence of the interactions between superpredator and mesopredator and to ensure that observed correlations are due to interspecies competition effects not just variation in the habitat preferences of the superpredator and mesopredator species (Litvaitis and Villafuerte 1995, Gehrt and Clark 2003, Lariviere 2004). Gehrt and Clark (2003) point out that the interactions between carnivores with large geographic ranges are likely to vary across locations and habitat types resulting in a variation in the importance of mesopredator release effects as well. Thus far MRH has been tested in temperate systems of relatively small carnivores and has almost exclusively been used as motivation to protect declining superpredator populations at the expense of mesopredator "pest" species (ultimately to protect avian prey). One recent exception to this, is a study done by Johnson et al. (2007), who found that the decline of dingoes as a top predator was likely the cause of continent-wide decline in marsupial prey due to introduced mesopredators. Mesopredator release may affect carnivores in a wide range of areas, and needs to be tested in a variety of communities including ones with a mesopredator species that is also of conservation concern.

Interactions within guilds of large carnivores and the potential role of mesopredator release (outside of the neotropics).

When working with communities of large carnivores, it is likely that multiple species are either threatened or endangered, making it important that researchers understand the interactions among these species when developing conservation programs. Is there evidence that mesopredator release functions in these systems? For the phenomenon of mesopredator release to play a role in a community there must be strong enough competition between the superpredators and mesopredators in the system to result in the limiting of mesopredator populations in areas of high superpredator density. While few studies have focused on the role of mesopredator release in carnivore ecology (with one known exception, Moreno et al. 2006, more detail later), there is a large body of evidence outlining the strength of the interactions, and competitive pressure between large carnivores in other areas of the world.

Caro and Stoner (2003) emphasized the high potential for competition among the many sympatric carnivores of Africa and stated that this competition may be apparent in a number of ways. Competitors might avoid each other and leave an area either upon sight or olfactory contact. Competition could also be manifested as the cause of a shift in niche, a change in habitat-use or prey selection usually by the smaller carnivore in order to reduce direct competition with the larger superpredator. There may be aggressive interactions in the form of food stealing or intraguild predation. Intraguild predation occurs widely among carnivores and its occurrence was found to be positively related to the difference between the body size of the killer and the victim by Palomares and Caro (1999). This relationship was further defined by Donadio and Buskirk (2006) who reviewed literature and found that intraguild killings were more frequent when there was an intermediate difference in body size, species were in the same family and showed dietary overlap (with intermediate body size being the most important factor). Cheetah cubs, for example, regularly fall prey to lions (Laurenson 1994;1995). As stated earlier there is evidence that cheetahs, mesopredators in this case, are negatively affected by high lion density (Laurenson 1995, Durant et al. 2004). Furthermore, Kelly and Durant (2000) found if high lion numbers persist, local cheetah populations may be driven to extinction even within a national park. Similarly, both lions and hyenas prey on African wild dogs and significant negative correlations between the densities of these two superpredators and wild dogs have been documented (Creel and Creel 1996). This intraguild predation combined with disease, persecution and a reduced average pack size resulting in an Allee affect is believed to be causing the downhill spiral of this highly endangered species (Woodroffe and Ginsberg 1999, Courchamp et al. 2000).

There is evidence of strong competition between sympatric large carnivores outside the open plains of Africa. Seidensticker (1976) found that leopards in Nepal had only transient status (would not maintain a permanent home range) in areas where tigers were present and Arjo and Pletscher (1999) found that the reintroduction of wolves to Yellowstone National Park may have affected the social organization of coyotes in the area, causing an increase in pack size. Wolves have been known to prey on coyotes and Crabtree and Sheldon (1999) documented a 50% drop in the coyote numbers in some areas of Yellowstone following the reintroduction of these superpredators. The existence of these competitive interactions is important because it implies that mesopredator release may indeed play a role in these large predator guilds – producing an inverse relationship between densities of superpredators and their sympatric mesopredators.

The neotropical felid community and evidence of competition

Ten of the 30-40 species of wild cats in the world make their homes in Central or South America (Sunquist and Sunquist 2002). Information on the predator community of the Neotropics has always been especially hard to come by due to the elusive nature of these felids and their dense forest habitat; however, researchers are now realizing that such research may be critical. Around the world the importance of predators as keystone species that maintain the diversity of their communities is being brought to light and it has been suggested that this effect is even more extensive in the Neotropics. Three of these cats, the ocelot, the puma, and the jaguar have been reported to feed opportunistically on all mammalian prey species in almost the exact proportion of their occurrence (Emmons 1987). This could result in prey populations that are kept well below environmental carrying capacity and affect the dynamics of the entire ecosystem. Based on these observations Terborgh (1990) suggested that these Neotropical felids play a unique and even bigger role in the structuring of their communities than do carnivores in other areas of the world. In support of this theory, Terborgh et al. (2001) and Terborgh et al. (2006) found higher densities of herbivore prey species and lower densities of saplings in "predator-free" sites than in sites with a full complement of neotropical predators. Unfortunately, both of these studies focused on a manmade site, Barro Colorado Island, Panama, which may not be adequate for the representation of the typical dynamics within an ecological community. Barro Colorado Island (BCI) is only 6 km^2 in area and was created by the damming of the Chagres River during the construction of the Panama Canal: while convenient for examining the mesopredator release hypothesis, it is difficult to assume that such a site could be an ideal model of natural systems.

At least 6 of the felids resident to Central and South America are known to be simultaneously sympatric in areas of Neotropical forest (Sunquist and Sunquist 2002). This means that opportunities for competition abound, making it highly likely that mesopredator release operates among these felids. Is there evidence that the competition necessary for mesopredator release to occur exists among felids in the understudied Neotropics? As stated by Caro and Stoner (2003), competition can manifest itself through the partitioning of a prey base, habitat-use, or aggressive interactions. The three most common (and largest) of the Neotropical felids, the jaguar, the puma, and the ocelot overlap over the majority of the ocelot's geographic range, feed on a primarily mammalian prey base, and tend to prefer dense forest habitats with minimal disturbance. Ocelots, pumas, and jaguars have been reported to weigh on average between 7.5-13.6 kg, 36.9-53.1 kg, and 42.1-104.5 kg respectively in the Neotropics, although it is interesting to note that jaguars are often smaller in Central America as are the pumas that inhabit tropical areas (Sunquist and Sunquist 2002). It seems likely that these felids, which have already been shown to exert a structuring influence on their community at least at BCI, compete for some of the same resources setting the stage for mesopredator release, which would be observable through negative correlations in densities across sites.

Diet partitioning

There is extensive evidence that ocelots, pumas, and jaguars compete for the same prey resources. These three cats have been shown to collectively consume the full range of mammalian prey species available (Emmons 1987). In fact, Emmons (1987) pointed out that between them, the ocelot and jaguar seem to cover the entire size range of possible mammalian prey, while the size range of prey eaten by the puma falls somewhere in the middle and overlaps that of both the jaguar and the ocelot.

Over the years, many studies have used analysis of scat samples to determine the typical diet of these three species in several areas (Bisbal 1986, Rabinowitz and Nottingham 1986, Konecny 1989, Farrell et al. 2000, Novack et al. 2005, Weckel et al. 2006 to name a few). Ocelots have been found to prey largely on terrestrial mammals less than 1 kg in weight, but have been recorded to eat larger prey than other small felids including deer, agoutis, peccaries, armadillos, capybara, and anteaters (Abreu et al. 2008, De Villa Meza et al. 2002, Konecny 1989, also reviewed by Sunquist and Sunquist 2002). These findings seem to hold true across a variety of habitats; while most take place in broadleaf forests, Abreu et al. (2008) found that ocelots in a pine forest of Brazil rely on small prey, but also consume larger species, such as the grey brocket deer. Abreu et al (2008) speculated that this reliance on small mammals is because ocelots are opportunistic predators and rodents are simply more abundant than many other prey items in neotropical forests. Pumas typically consume prey between 1-15 kg in weight in the tropics - larger prey than ocelots but generally smaller than the prey exploited by sympatric jaguars (Taber et al. 1997, Sunquist and Sunquist 2002, Scognamillo et al. 2003). Jaguars, the largest of these felids, accordingly consume medium to large prey that average around 15 kg in weight. Jaguars have been known to consume the largest mammals in the forest including caimans and tapirs, and have taken domestic cattle when available (reviewed by Sunquist and Sunquist 2002).

Even more interesting is the fact that these three felids show a high degree of adaptability and the composition of their diets varies from one site to the next. Pumas, for example, typically prey on large animals, even moose (*Alces alces*), in temperate zones (where there are no other predators of their size) but focus on animals that weigh less than half their own body weight in tropical areas (Iriarte et al. 1990, reviewed by Sunquist and Sunquist 2002) where it probably suffers from competition due to overlap with the jaguar. This means that while pumas may be concentrating on species of a smaller size, they are actually capable of consuming a broader range of prey sizes – their diet is limited by something other than ability. This limiting factor is likely competition with other carnivores within this predator guild. If this is the case and if mesopredator release functions in this system, then one of these three predators should expand their dietary niche in the absence of one or both of the others. There is already some evidence that this occurs. Taber et al. (1997) suggested that the observation of an unusually small average prey size for both the pumas and jaguars in the Brazilian Chaco may have been due to reduced competition from a low density of ocelots in the area. Meanwhile, the ocelot's preferential use of small mammalian prey likely causes it to suffer from higher levels of competition from other predators including snakes, raptors, and small mammalian carnivores (Emmons 1987) such as tayras (*Eira barbara*), grey foxes (*Urocyon cinereoargenteus*), jaguarundis (*Herpailurus yaguarundi*), and margays (*Leopardus wiedii*). It may, therefore, be ecologically beneficial for the ocelot to expand its prey range if decreased competition from larger predators permitted such a switch. Recently Moreno et al. (2006) found support for this on Barro Colorado Island (BCI) where they found that ocelots consumed larger prey in the absence of jaguars than they generally consume elsewhere in their range where jaguars are present. While the artificiality of BCI brings the widespread application of these results into question, this study is consistent with the mesopredator release hypothesis and confirms that this line of reasoning deserves further attention.

Habitat-use and activity patterns

Evidence of interspecies competition can also be found through the partitioning of habitat-use and activity patterns (spatial and temporal avoidance). In fact, Schoener (1974), concluded in a review of studies on resource partitioning that habitat partitioning was more frequently found to play an important role in the systems studied than dietary or temporal partitioning. Ocelots, pumas, and jaguars are all stalking hunters (Terborgh 1990) and, therefore, depend on adequate cover to approach their prey. All three of these cats show preferences for forested areas with dense understory and canopy cover. The question is how much of their habitat-use and activity patterns is determined by avoidance of each other and how much is determined by the already partitioned prey preferences described above.

The jaguar as the largest, and logically the dominant competitor in this trio has repeatedly been shown to prefer dense, undisturbed, unfragmented forests with close associations to water sources (Mondolfi and Hoogesteijn 1986, Emmons 1987, Crawshaw and Quigley 1991). Jaguars often will patrol riverside areas (also evidenced by their exploitation of caimans as a food source; Emmons 1987). These large cats are active at all times of the day, although occasionally they show nocturnal peaks in activity as well (Rabinowitz and Nottingham 1986, also reviewed by Sunquist and Sunquist 2002). It also has been noted on more than one occasion that the jaguar is particularly negatively impacted by high levels of human activity and habitat fragmentation (Crawshaw and Quigley 1991, Bisbal 1993). If there were to be competition among ocelots, pumas and jaguars, it seems logical that the two relatively smaller felids would show some avoidance of this dominant competitor either spatially or temporally.

Ocelots have specific microhabitat requirements despite their wide geographic range (Ludlow and Sunquist 1987, Emmons 1988). Di Bitetti et al. (2008) found that across Central and South America ocelot density was positively affected by increased rainfall but decreased with latitude. Ocelots select habitats with a dense understory and a high percentage of canopy cover (Ludlow and Sunquist 1987, Sunquist et al. 1989, Shindle and Tewes 1998). In Texas and Northern Mexico ocelots have chosen small fragmented patches of dense forests over large patches featuring open habitat (Jackson et al. 2005, Haines et al. 2006a). Ocelots are markedly nocturnal in many areas and when they are active during the day they keep to areas even more sheltered than those they use at night (Ludlow and Sunquist 1987, Emmons 1988, Sunquist 1989). Lunar phase also can influence habitat-use – ocelots will use open areas during new moons and relatively closed areas as the moon waxes in order to avoid exposure (Emmons et al. 1989, Di Bitetti et al. 2006). This nocturnal behavior may be chosen by ocelots not to avoid jaguars and pumas so much as to maximize their hunting success as they forage for their smaller mammalian prey, which are often nocturnal as well (Ludlow and Sunquist 1987, Emmons 1988, Emmons et al. 1989). Indirectly, however, this behavior could still be due to competition as ocelots seem to be relegated to the smaller sized prey (and possibly to higher levels of competition from other small predators such as snakes and raptors) because of this large competitor, as described above. It is also interesting that ocelots have been reported to be more tolerant of human activity and fragmentation than their sympatric predators the jaguar and puma (Bisbal 1993). There is already evidence of resource partitioning between the ocelot and a sympatric predator in the North (in Texas), the bobcat (*Lynx rufus*), and it is suggested this may be due to competition (Horne 1998). In the neotropics, it is possible that competition with the jaguar and puma may be one factor causing the ocelot to exploit more fragmented areas, which may contain lower densities of competitors, but may also be less desirable due to a lower abundance of prey species.

Pumas, whose prey base overlaps more strongly with that of the jaguar (Emmons 1987, Chinchilla 1997), avoid jaguars spatially and/or temporally in different parts of their range (Schaller and Crawshaw 1980, Rabinowitz and Nottingham 1986, Emmons 1987, Scognamillo et al. 2003). Like jaguars, pumas prefer dense forests and may be active at all times of the day (reviewed by Sunquist and Sunquist 2002). In particular, Schaller and Crawshaw (1980) and Emmons (1987) found that pumas avoided the wetter areas near rivers, which were frequented by jaguars, and also found evidence of temporal avoidance. Competition with the jaguar leading to this spatio-temporal segregation could have an important effect on the puma's diet. For example, avoidance of wetter habitats is likely the reason that pumas in Peru were not recorded to feed on caimans (Emmons 1987) despite the fact that they are physically capable of taking down this large reptile (Sunquist and Sunquist 2002).

Aggressive interactions

Intraguild predation has been found to be more likely when species are in the same family and show high dietary overlap and intermediate differences in body size. In particular, this interaction is more likely when the larger species is 2-5.4 times the mass of the victim (Donadio and Buskirk 2006). The weight ranges already listed for the ocelot, puma, and jaguar imply that intraguild predation is likely to take place between all three of these cats (with the ocelot consistently the victim).

While it is very difficult to observe interactions directly among the elusive large felids within the dense forests of the Neotropics there is evidence that aggressive interactions do occur in the form of intraguild predation. There are at least two instances of ocelot remains being found in jaguar feces (Mondolfi 1986, Chinchilla 1997) and while there are no reports of pumas preying on ocelots, the potential is there – pumas have reportedly been the killer of at least three other sympatric predators including the coyote, the bobcat, and the raccoon (*Procyon lotor*) (reviewed by Palomares and Caro 1999). These may be isolated occurrences rather than evidence of normal interactions among these three felids; however, given the difficulty in witnessing such interactions it is also possible that this intraguild predation takes place on a somewhat regular basis and simply remains unobserved.

Camera trapping and density estimation

To document the effects of mesopredator release it is necessary to demonstrate that competition between sympatric predators causes populations of mesopredators like the ocelot to be negatively affected by the presence or density of superpredators (Gehrt and Clark 2003). As outlined above there is ample opportunity for competition between ocelots, pumas, and jaguars and, in some cases, the evidence of this competition has already been documented. It is still necessary to show that this competition is harmfully affecting the ocelot as a mesopredator. One way to do this is to show a negative correlation between mesopredator and superpredator population densities. The advent of remote triggered infrared cameras has increased the ability of researchers to estimate density relatively quickly and efficiently with minimal impact on the study animal's natural behavior. Camera trapping was first used in conjunction with capture-recapture models to estimate tiger (*Panthera tigris*) population size (Karanth 1995, Karanth and Nichols 1998). Since then the technique has been refined and standardized as it has been repeatedly used to estimate the abundance, densities, and activity patterns of other cryptic and individually recognizable species (Silveira et al. 2003, Trolle and Kery 2003, Karanth et al. 2004, Silver et al. 2004, Wegge et al. 2004, Cuellar et al. 2006, Dillon and Kelly 2007, Dillon and Kelly 2008). When continued for several years, this non-invasive technique has the potential to allow the estimation of other population parameters including survival, and recruitment (Karanth et al. 2006).

As with many techniques used to study large carnivores, small sample sizes are a common challenge faced by projects using remote camera surveys (Wallace et al. 2003, Cuellar et al. 2006). This situation can be improved by increased knowledge of these species' habitat ecology and home range size, and by adjusting the location of camera stations accordingly. For example, Dillon and Kelly (2007) found that by decreasing camera spacing to fit a smaller home range size they were better able to estimate ocelot populations. Carbone et al. (2001) also suggested that capture rates can be directly related to specific population densities. This avoids the need for identification of individuals and for a closed population model, allowing traps to be run for longer periods of time, and can result in increased sample sizes; however, this method may require independent calibrations for each population studied and is still controversial (see Carbone et al. 2002, Jennelle et al. 2002).

In the Neotropics camera trapping has been used to estimate the populations of the spotted cats including: ocelots (Trolle and Kery 2003, Maffei et al. 2005, Di Bitetti et al. 2006, Dillon and Kelly 2007), jaguars (Kelly 2003, Wallace et al. 2003, Maffei et al. 2004, Silver et al. 2004) and Geoffroy's cats (*Oncifelis geoffroyi*) (Cuellar et al. 2006). Traditionally, camera trapping has been used only on these cryptic animals because the technique requires individual identifications to accurately estimate density, but recently Kelly et al. (2008) have pioneered the use of remote camera surveys to estimate the density of pumas by identifying individuals through the use of a variety of characteristics including scars, tail rings, undercoat patterns, subtle markings on the face and underside of the legs, and body carriage. Camera trap surveys had already resulted in density estimates for ocelots, jaguars, and pumas at some of the field sites we used in Belize (Table 1.1; Fig. 1.1). Most importantly, these data aided our choice of sites by showing that estimates of jaguar density vary by almost a factor of 3 between the Chiquibul Forest Reserve and National Park (CFRNP) and the Rio Bravo Conservation and Management Area (RBCA) (C. Miller, Wildlife Conservation Society, personal communication; M. J. Kelly, Virginia Tech, personal communication). Dillon and Kelly (2007, 2008) also found that ocelot densities vary between the CFRNP and the Mountain Pine Ridge Forest Preserve (MPR), which are geographically adjacent, but contain drastically different habitat types. The density of pumas in Belize has, so far, been estimated only in the CFRNP (Kelly et al. 2008). The variations among these study sites could result in an ideal situation for testing the mesopredator release hypothesis by examining sympatric felid densities in relation to each other across sites.

Microhabitat sampling of small felids

To date, very little has been done to assess the microhabitat of small felids in any standardized manner. Many of the studies cited above, which characterized ocelot habitat, either were largely qualitative in nature or used only general classifications of forest type and cover (Emmons 1988, Konecny 1989, Sunquist et al. 1989, Lopez Gonzalez et al. 2003, Jackson et al. 2005, Di Bitetti et al. 2006). Additionally, some of this research took place in the thornscrub habitats of southern Texas and northern Mexico (Shindle and Tewes 1998, Lopez Gonzalez et al. 2003, Jackson et al. 2005, Haines et al. 2006a) where the landscape is very different from that of a tropical forest; therefore, the results of these studies may have limited relevance to ocelot populations in neotropical forests. Past research provides a general idea of factors that may influence ocelot habitat selection, but does not provide strict guidelines for estimating habitat suitability or for sampling felid microhabitat in any detail.

More extensive work has been done to characterize the habitat of the North American small felids, bobcats and lynx, but most of these studies also examine habitat on larger spatial levels often including whole home ranges (Lovallo and Anderson 1996, Chamberlain et al. 2003). This is likely due to the fact that it can be very time-consuming to conduct the manual habitat sampling that would be necessary to characterize finer microhabitat structure. Many researchers limit their habitat assessments to estimates of landcover type and topography taken from aerial photographs, and GIS technology; although some studies have also related carnivore activity and habitat-use to prey abundance and predation behavior (Maletzke et al. 2007, Vashon et al. 2007). Two studies that involved the use of GIS technology, Chamberlain et al. (1996) and Kelly and Holub (2008) suggest that bobcats select habitat over a wide range of spatial scales. It seems likely that ocelots and other small felids may do the same. The study by Kelly and Holub (2008) is also interesting because it is one of the first studies, to my knowledge, that uses GIS in conjunction with remote camera surveys to examine felid habitat at a much smaller scale, through the use of 100 to 750 m buffers surrounding each camera station.

Table 1.1: Felid density estimates (individuals per 100 km^2) previously recorded at study sites in Belize.

Site	Jaguar	Puma	Ocelot
Chiquibul Forest Reserve and National Park (CFRNP)	3.1-7.48 (M. J. Kelly, VirginiaTech, personal communication; Silver et al. 2004)	3.42 (Kelly et al. 2008)	12-25.88 (Dillon 2005, Dillon and Kelly 2007, Dillon and Kelly 2008)
Mountain Pine Ridge Reserve (MPR)	3-7 (M. J. Kelly, Virginia Tech, personal communication)	NE[a]	2.31-3.8 (Dillon 2005, Dillon and Kelly 2007, Dillon and Kelly 2008)
Cockscomb Basin Wildlife Sanctuary (CBWS)	8.8 (Silver et al. 2004)	NE	NE
Gallon Jug/Rio Bravo Conservation and Management Area (RBCA)	11.4 (C. Miller, Wildlife Conservation Society, personal communication)	NE	NE

[a] NE = No density estimates prior to this study

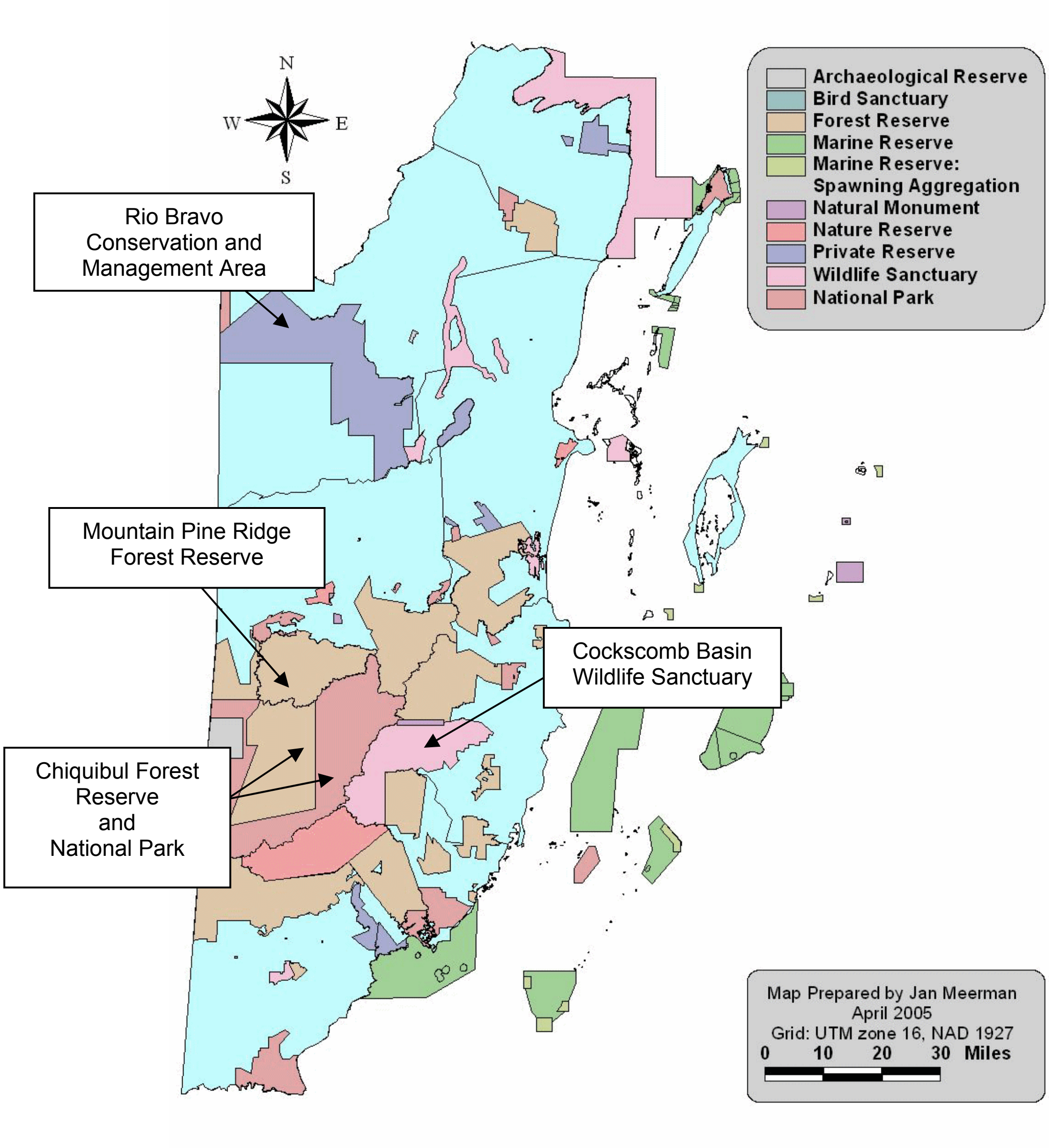

Figure 1.1: Location of the four study sites within Belize (Meerman 2006). Remote camera surveys were completed at all sites between June 2007 and August of 2008. See Chapter 4 for details of individual surveys.

Chapter 2 – Habitat-use of the ocelot with respect to jaguar and puma activity in the Mountain Pine Ridge Forest Reserve, Belize.

Abstract

To manage and protect an intact neotropical carnivore guild it is necessary to understand the relative importance of habitat selection and of intraguild competition to the ecology of individual species. This study examines the habitat-use of ocelots with respect to the activities of jaguars and pumas in the Mountain Pine Ridge Forest Reserve, Belize. For these carnivores, I calculated species-specific trap success from 47 camera stations spaced across the 139 km^2 study site (i.e. MCP surrounding camera stations). I also calculated trap success rates for humans, prey, and other small carnivores. I manually sampled habitat surrounding each camera station to determine canopy cover and height, understory thickness, understory heterogeneity, and tree density. Additionally, I used GIS to retrieve data including the distances to a nearby human settlement and to the neighboring broadleaf forest. I extracted GIS habitat data from 200 and 500 m circular buffers around each trapping site on the length of rivers, roads, and percentage of damaged area due to seasonal fires. Ocelot activity was positively related to roads, but contrary to previous studies was unrelated to other habitat features including canopy and understory characteristics. Ocelot presence was positively associated with jaguar activity but ocelot trap success showed no relation to puma trap success. There were few habitat differences among stations where these felids occurred simultaneously, individually, or were mutually absent. Model selection via AIC revealed that jaguar trap success, plus road and river length, were the strongest predictors of ocelot presence. Results may imply a strong influence of predators on each other and that mesopredator release operates on multiple levels within this carnivore guild.

Introduction

Ocelots (*Leopardus pardalis*), like other neotropical felids, are secretive, difficult to study, and threatened by habitat loss. To ensure the conservation of the ocelot across its range we must understand not only the basic habitat requirements of this species, but also the interplay between ocelot ecology and the activity of coexisting large carnivores. While ocelots have a wide geographic range, they have specific microhabitat requirements (Emmons 1988). Multiple studies have shown that ocelots select areas with dense understories and thick canopies whether in the thornscrub woodlands of Texas or the forests of Argentina (Ludlow and Sunquist 1987, Konecny 1989, Sunquist et al. 1989, Shindle and Tewes 1998).

Throughout much of Central and South America, ocelots co-exist with two larger felid species: the jaguar (*Panthera onca*) and the puma (*Puma concolor*). These felids occupy the same habitats and overlap in the prey species they consume (Rabinowitz and Nottingham 1986, Emmons 1987, Konecny 1989, Sunquist and Sunquist 2002) creating substantial opportunity for competition in this predator guild. Additionally, these three carnivores are likely to exhibit intense competition in the form of intraguild predation due to their close taxonomic relation and intermediate differences in body size (Donadio and Buskirk 2006). The ocelot is the smallest of these species and is likely subordinate to both jaguars and pumas. Moreno et al. (2006) proposed that the absence of jaguars may affect the diet of pumas and ocelots on Barro Colorado Island where these species generally consume larger prey than in other areas with jaguars present. It has also been hypothesized that competition with the jaguar spatially affects puma activity (Rabinowitz and Nottingham 1986, Scognamillo et al. 2003). This implies that mesopredator release, a mechanism through which populations of small carnivores may be limited by the activity of dominant competitors (Brown and Wilson 1956, Crooks and Soule 1999, Gehrt and Clark 2003), could operate in this carnivore guild. It seems likely that competition with jaguars and pumas affects the activity and habitat-use of ocelots; however, this has yet to be documented.

Pine forests are one of many neotropical ecosystems that are inhabited by these three carnivores, but little research has been done on felid populations in this habitat. The Mountain Pine Ridge Forest Reserve (MPR) in Belize, contains one of the few pine habitats for which there exist density estimates of both jaguars and ocelots (no estimate exists for pumas in the MPR). It is estimated that there are roughly 3-7 jaguars per 100 km^2 in both the pine forest and the neighboring broadleaf forests (Kelly, unpublished data; Silver et al. 2004). However, the density estimate for ocelots in the pine forest is only 2.31-3.80 individuals per 100 km^2 and is much lower than the roughly 12-25 per 100 km^2 estimated for the neighboring broadleaf forests (Dillon and Kelly 2007, Dillon and Kelly 2008). The reason for the lower ocelot density in the pine forest is unknown.

My goals are to describe ocelot habitat-use in a little studied neotropical pine forest and to examine co-predator activity and space use in order to elucidate factors contributing to coexistence of ocelots with jaguars, and pumas. I hypothesize that ocelot trap success will increase with canopy cover, canopy height, tree density, understory cover, and understory heterogeneity and that ocelot activity will increase in areas with more streams and roads and decrease in areas affected by dry season fires. I also hypothesize that due to competition, ocelots will avoid areas frequented by jaguars and pumas and that this may result in differences in the habitat characteristics of areas used by ocelots with respect to the activity of these two larger carnivores. These differences could include using sub-optimal areas with lower activity of prey species (especially of larger prey species which jaguars and pumas may focus on) and using areas with higher levels of human activity, which jaguars and pumas may avoid more than ocelots (Crawshaw and Quigley 1991, Bisbal 1993). I also hypothesize that as ocelots compete with jaguars and pumas, they could be forced to rely on smaller prey species and subsequently compete more with other small carnivores (Emmons 1987, Moreno et al. 2006) and hence ocelot activity could be negatively related to small carnivore presence and activity.

Knowledge of the relative impacts of habitat features and predator activity is important for managing populations of co-occurring carnivores in the face of increasing habitat loss. It is especially important to determine whether smaller carnivores such as the ocelot will survive with other top predators especially as reserves shrink in size. It is important to determine whether jaguars do, in fact, function as umbrella species ensuring protection of other species inhabiting their domain (Noss 1990, Gittleman et al. 2001, Sanderson et al. 2002a). In this study, I characterize ocelot habitat-use within the MPR by examining microhabitat characteristics and landscape features in relation to ocelot presence and activity rates across the study site. I also analyze activity levels of mammalian and avian prey species, other small carnivores, and humans as predictors of ocelot presence and activity. Finally, I model ocelot presence across the landscape and compare patterns of ocelot activity to those of jaguars and pumas across the site to assess the influence of co-predator activity on ocelot habitat-use.

Study site

The 433.7 km^2 MPR lies in western Belize near the Guatamalan border (Fig. 2.1, Fig. 2.2). This area contains subtropical lower montane wet and moist climates. The habitat type is a pine forest with pockets of shrubland. The canopy is primarily made up of two pine species: *Pinus caribeae* and *Pinus ocarpa*. The understory is a grassy shrubland dominated by assorted patches of ferns (*Dicranopteris sp.* and *Pteridium caudatum*), grasses (primarily *Scleria bracteata*), and a cane species (*Gynerium saggitatum*). The pine forest is also unique among neotropical habitats because wide swathes of the MPR are periodically burned in naturally occurring fires during the dry season (Kellman and Miyanishi 1982, Kellman and Meave 1997). In May of 2007, approximately 1 month prior to this study, a 167.82 km^2 large area of the MPR succumbed to a particularly large rash of fires. Residual flames and smoke were observed in the study area at the beginning of the camera survey period (personal obs.).

Da Silva Forest Station is a small (roughly 15 people) permanent settlement near the center of the reserve with a network of old logging roads allowing easy access to the study site. Military training activities take place in portions of this reserve on an annual basis. The southern border of the MPR is delineated by the Macal River creating a sharp transition zone between the MPR's pine forest and the broadleaf forest of the Chiquibul Forest Reserve and National Park lying to the south of the Macal River (Fig. 2.2).

Methods

All fieldwork was completed between 6 June and 18 August of 2007. I used standardized techniques for remote camera surveys found to be successful in trapping ocelots, pumas, and jaguars in previous studies (Silver et al. 2004, Maffei et al. 2005, Dillon and Kelly 2007, Kelly et al. 2008). I established 47 camera stations in a systematic grid at intervals of approximately 1.5-3.0 km along roads and trails within the study site. Two of the 47 stations were placed just outside reserve boundaries on forested private land (Fig. 2.2). Each camera station included two cameras mounted on opposing sides of trails/roads. The minimum convex polygon grid covered an area of 139.9 km^2 (i.e. without buffers).

Trap success of ocelots, pumas, and jaguars was calculated as the number of captures of that species at a station divided by the number of trap-nights (TN) multiplied by 100 (Dillon and Kelly 2007). Trap success provides an indication of the local relative activity level of these species. To ensure independence of captures, multiple photographs of an animal taken within an arbitrarily selected 30 minute period were assumed to be the same event (unless individually distinguishable) and counted as only 1 capture. In this manner, I also calculated the trap success of humans (in car or on foot) and several other general "groups" of species.

Past research suggests that while there is dietary overlap, jaguars consume prey species averaging 15 kg, pumas rely on medium sized prey < 15 kg in weight (reviewed by Sunquist and Sunquist 2002) and ocelots rely on smaller prey, often < 1 kg, but are also reported to regularly take larger prey when available (Konecny 1989, Moreno et al. 2006, Abreu et al. 2008). Mammalian species considered likely prey for ocelots, jaguars, or pumas were assigned to one of 3 groups according to species weights found in literature: small (< 5 kg), medium (5-15 kg), and large (> 15 kg) (Reid 1997; Table2.1). The remote cameras commonly capture ground birds that are likely prey of ocelots, jaguars, and pumas. I designated avian prey species as either small (< 1 kg) or large (> 1 kg) based on weights (Dunning 1993; Table 2.1). Small carnivore species also were placed together in a single category (Table 2.1). I then calculated trap success rates at each station for each group using the sum of the captures for all species in that group.

Sampling of microhabitat concentrated on aspects of habitat structure that ocelots are known to be sensitive to, namely understory thickness and canopy cover (Ludlow and Sunquist 1987, Haines et al. 2006b). To estimate canopy cover I walked a 200 meter long transect at 0, 120, and 240 degrees starting at the camera station and recorded the canopy cover every 20 meters (present or absent) resulting in a total of 10 canopy points per transect. At six points, located at 50 meters and 200 meters along each of these three "canopy transects," I took additional measurements. At these points I estimated canopy height with a clinometer and used the point-centered quarter method to estimate tree density with an unbiased estimator (Pollard 1971). Finally, at these 6 locations, I sampled the understory (defined as 0-2m in height) using point intercepts every 2 m along 40 m long transects perpendicular to the original "canopy transects." This allowed the calculation of percent understory cover. I calculated mean estimates of all of these variables at the 50 and 200 m level and then averaged again to generate overall estimates for the camera station. At 4 of the stations, 1 or 2 transects were abandoned before the 200 m point due to impassable vegetation or cliff edges. In those cases, analyses were completed based on the data from the 50m points and the remaining transect(s) that reached 200m. From the understory cover estimates I also calculated a pooled coefficient of variation (Zar 1999) as a measure of understory heterogeneity at each station.

I used ArcGIS to retrieve landscape variables. I marked camera stations by GPS, entered coordinates into ArcGIS, and created buffers of 200 and 500m around these locations following Kelly and Holub (2008). I intersected the buffers with appropriate GIS layers to retrieve total length of streams, roads, and percent area affected by the May 2007 fires within each circular buffer for each of the 47 stations. Data layers of Belize containing the geographic locations of protected area boundaries, settlements, streams, roads and fires were obtained from their creator, Jan Meerman, in 2007. The layers containing roads and settlements were updated in 2004, while those containing streams and protected area boundaries were updated in 2005. All the layers except those containing the extent of fires are available online (Meerman 2007). I used these layers to create the map figures presented here. The resulting maps of the pine forest were re-examined qualitatively throughout the study period as they were used to navigate the study area and their accuracy was found to be satisfactory for the scale of this analysis. I calculated the distance to the human settlement (Da Silva) and the distance to the nearest point along the Macal River (where the forest transitions from pine to broadleaf) for each camera station using ArcGIS. I completed all operations using the UTM NAD 27 coordinate system in zone 16 North.

In all analyses, individual camera stations with associated habitat estimates and trap success records were treated as the sampling units. I assumed that the habitat characteristics and capture rates of individual stations were independent from each other due to their wide spacing. I assumed that all sampled habitat was accessible (available) to the study species. I also assumed that each capture event of an animal was independent from other capture events of that species as long as they were 30 minutes apart, and that species were truly absent from stations where they were not photographed (no non-detections).

I used SAS for all analyses (SAS Institute 2002) and an $\alpha = 0.05$ to designate significance; *P*-values between 0.05 and 0.1 were considered marginally significant. To test the null hypothesis that the characteristics of areas used versus not used by ocelots were equal, I used a two-sample *t* test. In the case where the assumption of homogeneity of variance between these two groups was rejected, I used the Satterthwaite method. Because ocelot trap success was found to be non-normal, I used a Spearman rank correlation coefficient to test for relationships between ocelot trap success and other variables. For the correlation analyses, only camera stations with ocelots present were used to prevent the stations that did not record ocelots from dominating the results. I used ANOVA, followed by a Tukey-Kramer test (for multiple comparisons with unequal sample sizes), to test for habitat differences among camera stations with different combinations of the presence/absence data for the three cats (ocelot and jaguar, then ocelot and puma). Finally, I developed 30 a priori models including habitat, landscape characteristics (including the 200m level only), and the trap success of jaguars, pumas, humans, mammalian and avian prey groups, and small carnivores. I used logistic regression to model ocelot presence across all the camera stations. I used Akaike's information criterion (Akaike

1973) corrected for low sample sizes (AIC_c; Burnham and Anderson 2002) and Akaike weights to rank and compare all a priori models, a null model (intercept-only) and a global model (containing all variables). I used Hosmer and Lemeshow Goodness-of-Fit Tests (Montgomery et al. 2006) to check for lack of fit of all models (except the null model for which this test is not applicable).

Results

Camera traps were operational for 72 days resulting in 2,894 trap-nights over the study period. Sixteen separate "captures" of ocelots were obtained at 10 different camera stations across the study area. Jaguars were captured on 222 separate occasions at 41 of the stations and pumas were captured on 19 occasions at 11 of the camera stations for a trap success of 7.56 ±1.279 and 0.66 ± 0.200 captures per 100 TN respectively (Fig. 2.3). Ocelot trap success averaged 0.55 ± 0.209 captures per 100 TN over the 47 stations. Two of the 10 stations that captured ocelots had dramatically higher trap success rates (7.69 and 5.36 captures per 100 TN respectively) than the other 8 which averaged 1.60 captures per 100 TN (Fig. 2.4).

Stations with ocelots present yielded twice the jaguar trap success found at stations without ocelot captures ($\bar{x}$'s = 14.1, 5.79 captures per 100TN; df = 45, $t = -2.87$, $P = 0.006$). There was also an average of 122.5m more road within 200m (df = 45, $t = -2.29$, $P = 0.027$) and 334.6m more road within 500 meters of stations (df = 45, $t = -2.16$, $P = 0.037$) with ocelots present than at stations with no ocelot captures. There were no significant differences in any other habitat/landscape variable or in prey, human, small carnivore, or puma trap success between the ocelot present and the ocelot absent sites. However, there were marginally significant differences in human activity rates ($\bar{x}$'s = 78.7, 53.0 captures per 100TN; df = 45, $t = -1.82$, $P = 0.097$) with higher human capture rates at stations with ocelots present than at stations with no ocelots (Table 2.2).

Among the stations with ocelots present, ocelot trap success showed a marginally significant increase with distance to Da Silva ($n = 10$, $r_s = 0.585$, $P = 0.075$) and decrease with distance to the Macal River bordering the Chiquibul broadleaf forest ($n = 10$, $r_s = -0.591$, $P = 0.072$; Table 2.3 and Fig. 2.4). Ocelot activity (i.e. trap success) showed no correlation with any of the other habitat, landscape variables or the prey groups, nor was there a significant correlation between ocelot trap success and the trap success of humans, or the larger carnivores (jaguars and pumas; Table 2.3). Ocelot activity did appear to decrease with small carnivore activity, but this trend was only marginally significant ($n = 10$, $r_s = -0.555$, $P = 0.096$; Table 2.3). Small carnivore captures were dominated by grey fox (*Urocyon cinereoargenteus*) and skunk (*Conepatus semistriatus*) events. Interestingly, all of the stations with ocelots present also yielded photographs of jaguars, while pumas were recorded at only 3 of the 10 stations with ocelots present (Fig. 2.5, Fig. 2.6).

There were 6 stations where neither jaguars nor ocelots were observed, 31 stations with jaguars but no ocelots, 10 stations with both of these species, and 0 stations with ocelots only. Mean canopy height varied significantly among these three categories of camera stations ($F_{2, 44} = 4.43$, $P = 0.018$) as did the length of road within 200m ($F_{2, 44} = 5.29$, $P = 0.009$) and within 500m ($F_{2, 44} = 3.83$, $P = 0.029$). The two groups of stations with jaguars present showed average canopy heights roughly 4 meters higher than the 6 stations with neither ocelots or jaguars (Table 2.4). There was a marginally significant amount of variation in canopy cover among these categories ($F_{2, 44} = 3.00$, $P = 0.060$) with the % canopy cover being higher on average at sites with one or both of these cats than at sites with neither species ($F_{2, 44} = 3.00$, $P = 0.060$). Using both radii of 200m and 500m the 10 stations with both jaguars and ocelots had a significantly higher amount of roads than stations with neither cat species (the group of stations with jaguars but no ocelots was not statistically distinct in this respect; Table 2.4).

Significant variations were found in trap success rates of large mammalian prey ($F_{2, 44} = 3.26$, $P = 0.048$), and small avian prey ($F_{2, 44} = 4.38$, $P = 0.019$) among the ocelot+jaguar camera station categories (Table 2.4). The trap success rates of large mammalian prey were significantly higher at stations with both species than at stations with neither ocelots nor jaguars. While not significantly distinct, large mammal trap success rates at the other stations with jaguars present (but not ocelots) were generally high and reflected those seen at stations with both cats present. Stations with only jaguars present and stations with neither cat species present had lower small avian prey trap success rates than stations with both jaguars and ocelots (Table 2.4). Variation in the trap success rate of humans among these groups of cameras was marginally significant ($F_{2, 44} = 3.00$, $P = 0.060$) with human activity being higher at the ocelot+jaguar stations than at either of the other two groups of stations (Table 2.4).

There were 29 stations with neither ocelots nor pumas observed, 7 stations with ocelots but not pumas, 8 stations with pumas but not ocelots and only 3 stations with both pumas and ocelots. There was marginally significant variation in jaguar trap success rates among these groups ($F_{3, 43} = 2.65$, $P = 0.061$) with jaguar trap success rates being roughly twice as high at the groups of stations with ocelots present (regardless of puma presence or absence) than at either of the groups of stations without ocelots present (Table 2.5). Canopy cover ($F_{3, 43} = 6.82$, $P < 0.001$) and the length of streams within 200m of the station ($F_{3, 43} = 4.06$, $P = 0.013$) varied significantly among these four groups of camera stations. The percent of canopy cover was, on average, 27 % lower at stations with neither cat than at stations with pumas and no ocelots present. There were on average 186 more meters of streams within a 200m radius of stations with neither cat present than at stations with pumas, but no ocelots present (Table 2.5). With both these variables (canopy cover and stream length) larger differences among mean values occurred when examining the stations with both cats present, but this group was represented by a sample size of only 3 locations. There was a marginally significant variation in the % area burned within 500m among these categories ($F_{3, 43} = 2.53$, $P = 0.070$) with the proportion of burned area being higher at stations with neither cat than at stations with one or both species present; stations with pumas only had the lowest proportion of burned area of these categories.

Small avian prey ($F_{3, 43} = 13.8$, $P < 0.0001$), and human trap success rates ($F_{3, 43} = 3.29$, $P = 0.029$) varied significantly among the four ocelot+puma camera station categories. Small avian trap rates were at least 8-13 times higher at stations with both ocelots and pumas than at stations with only one or neither of these carnivores. Finally, human trap success rates were twice as high at stations with only ocelots as at stations with only pumas (the other two camera categories yielded mid-level trap success rates and were not statistically distinct) (Table 2.5).

Among the 30 a priori logistic regression models proposed for ocelot presence, the model based on only jaguar trap success, road length, and river length had the lowest score ($AIC_c = 44.7$) and was ranked first of those examined according to the information theoretic approach with a 26% chance of being the best of the models tested (based on its Akaike weight). One other model based on only jaguar trap success was within 2 AIC_c points and is considered to be competing with a 11% chance of being the best model. While not competing models, other models closely ranked after the first 2 had a greater than 5% chance of being the best model tested and included combinations of jaguar trap success, river length, road length, percent area burned, and prey activity rates (Table 2.6). Null and global models were ranked 15th and 32nd of the 32 models tested. According to the Hosmer and Lemeshow GOF tests none of the models showed evidence of lack of fit (Table 2.6).

Discussion

Of the microhabitat and landscape characteristics measured, only the length of surrounding roads affected ocelot presence or ocelot trap success as I hypothesized. The lack of positive relationships with canopy cover, canopy height, understory cover, and understory heterogeneity is particularly interesting due to the substantial evidence from other studies that canopy and understory characteristics play a key role in determining suitable habitat for ocelots (Tewes 1986, Ludlow and Sunquist 1987, Sunquist et al. 1989, Shindle and Tewes 1998, Haines et al. 2006a, Jackson et al. 2006).

The unique habitat structure of the pine forests in the study site may have caused these unexpected results. In other studies it has been found that habitat may need to provide > 95% canopy cover and a thick understory to be suitable for ocelot use (Shindle 1995, Harveson et al. 2004). Most of these studies were completed in the thornscrub habitats of Texas where ocelot densities are higher than in our study site, possibly implying that the thornscrub provides superior habitat than the pine forests. In the MPR, only one station had an estimated canopy cover of more than 60%. Variation in canopy cover, canopy height, and the other habitat characteristics measured may not be important to ocelots when the canopy cover is below a certain threshold because such habitat is already too poor in quality for intensive use.

Extremely dense understory vegetation, particularly patches of a fern, *Dicranopteris sp.*, and cane, *Gynerium saggitatum*, could cause the lack of a relationship between ocelot trap success and understory cover. Some of these areas are so thickly covered with understory vegetation that it is possible no large mammals could penetrate them. There are no records from the Texas habitats of understory that is too thick for ocelot use (M. E. Tewes, Texas A&M University, personal communication) nor from any other studies (to our knowledge), but this may be the case in the MPR. Extreme understory thickness may make habitat unsuitable for ocelots and make other relationships (e.g. those with prey activity) difficult to observe. A general lack of canopy cover and of thick, yet traversable, understory vegetation may inhibit ocelot hunting success, and could explain the low ocelot density found in the MPR.

The surprising patterns of habitat-use observed may also be related to the locations of the two camera stations that had particularly high ocelot trap success compared to other sampling points. Sample size was small for ocelot captures and these two stations, located near the Macal River and across the study site from Da Silva Forest Station, yielded much higher trap success rates. These stations were along the same road leading down through a lowland area connected to the broadleaf forest of the Chiquibul Forest Reserve and National Park where ocelot densities are much higher (Dillon and Kelly 2007). These locations have also shown high ocelot activity in past surveys (M. J. Kelly, Virginia Tech, personal communication). Ocelot captures at these stations resulted from the activity of the same two widely roaming males (personal obs.); it seems likely that ocelots from the broadleaf cross the Macal River and visit pine forest areas via the roadways containing these stations. This theory is supported by the fact that ocelot activity appears to have increased (albeit non-significantly) with proximity to the Macal River.

Alternatively, the fires that took place in the MPR just prior to our survey could have caused these results. Our 4th best model included percent burned and was nearly a competing model at Δ AIC$_c$ of 2.6. The two stations most frequently visited by ocelots were severely burned in May 2007 (Fig. 2.4). These areas were characterized by large patches of bare open soil, with little understory cover, and a high proportion of trees that had been killed or heavily damaged by fires. Higher levels of ocelot use of these areas could be related to the ocelots' lack of a response to canopy and understory characteristics. New growth in burnt areas may attract prey species, specifically rodents, and burned areas may allow edge-access to locations with prohibitively thick understories that could house prey species.

The lack of a relationship with most prey activity levels could also be a sign that ocelots in the pine forest are making use of marginal habitat. Alternatively, this may be because the use of camera traps at heights suitable for carnivore capture may not be conducive to the capture of the very small (< 1 kg) prey species, that ocelots are typically believed to be dependent on (with occasional use of larger species). Ocelots are opportunistic hunters capable of taking prey as large as peccary and deer (Ludlow and Sunquist 1987, Konecny 1989, Murray and Gardner 1997). In particular, ocelots released from competitive pressure may make use of larger prey (> 1 kg) such as agouti (*Dasyprocta punctata*) (Moreno et al. 2006), which were photographed frequently in the pine forest. Ocelots in the Cockscomb Basin Wildlife Sanctuary, in central Belize, were recorded to rely heavily on opossum (Konecny 1989), which were captured often in the MPR. Therefore, the lack of a relationship with the small mammalian prey activity may also indicate that ocelots in the MPR have not been released from top-down competitive pressure; but more information (particularly on the relationship to the activity of < 1 kg prey species) is needed to address this theory.

While competition may lead ocelots to avoid other small carnivores, I found only a marginally significant negative relationship between ocelots and other small carnivores. Perhaps there is little competition with the smaller carnivore species. These smaller non-felid species, especially the gray fox (*Urocyon cinereoargenteus*), whose captures dominated this group may have substantially different feeding habits that could result in few competitive interactions.

While only marginally significant, human trap success appeared to be higher at stations with ocelots than at stations without ocelots and this may prove important with a larger sample size. The lack of influence of human activity on ocelot trap success is contrary to our predictions, but supports the idea that ocelots may be more tolerant of human disturbance as has been hypothesized previously (Bisbal 1993).

Contrary to our hypothesis, ocelots appear to use sites with higher jaguar activity rather than avoiding them. There was, however, no such relationship between ocelot trap success and puma trap success. Ocelots may be less prone to favor areas with high puma activity because of higher degrees of competition between the two smaller felids. Ocelots and pumas both feed on smaller species (on average) than jaguars and likely have more dietary overlap than ocelots and jaguars (Emmons 1987). Additionally, pumas have been shown to avoid areas of high jaguar activity (Schaller and Crawshaw 1980, Emmons 1987, Scognamillo et al. 2003). It is possible, therefore, that in the MPR ocelots may prefer sites with jaguar activity because jaguars deter pumas as they have been recorded to do in these other studies.

It is difficult to determine if large predator activity levels affected ocelot habitat-use. Our findings suggest that jaguar activity at least could play a large role in determining ocelot habitat-use, but the results show little variation in habitat characteristics between the areas used and not used by ocelots. Jaguar trap success and length of surrounding roads were the only habitat variables to differ between stations with ocelot present and ocelots absent, and jaguar trap success appears to have been stronger than the influence of other habitat characteristics measured. The differences between sites used by neither ocelots nor jaguars and the other two groups (sites used by both cats, and sites used by only jaguars) may indicate jaguar habitat selection for taller canopies, more roads, large mammalian prey activity and may be locations ocelots must choose if they prefer high jaguar activity. Selection for higher canopy height would be consistent with previous studies on jaguar habitat-use suggesting that jaguars prefer dense undisturbed forests (Sunquist and Sunquist 2002) and the use of areas with more roads is consistent with the idea that these felids use human tracks to forage for prey. Within the two groups of stations used by jaguars, it seems that ocelots have chosen sites with higher small avian prey activity and possibly higher levels of human activity; however, it does not appear that ocelots are selecting for any other specific habitat features. This lack of selection may be because the pine forest habitat in the MPR is poor quality for ocelot use or because ocelots are selecting for another unknown habitat characteristic not measured in this study.

The analysis considering puma presence and habitat characteristics is inconclusive. These results tentatively suggest, once again, that ocelots are choosing areas with high jaguar activity, while pumas show no evidence of doing the same. The higher canopy cover and length of surrounding streams (within 200m) observed at sites with only pumas present, not ocelots, could mean that ocelots are relegated from using those sites with higher canopy cover and more streams if they are avoiding centers of puma activity. The high small avian trap success rate observed at the only 3 stations with both cats present imply that perhaps this high prey activity induced their coexistence at this site, but a larger sample size would make this conclusion more reliable. Most interesting among this set of results may be the evidence that ocelots used areas with higher human activity than locations chosen by pumas alone. This is consistent with Bisbal (1993) who reported that ocelots seemed more tolerant of human activity than pumas and could be a sign of ocelots avoiding sites used by pumas, which may have been chosen due to lower human activity. Previous studies also found jaguars to be particularly negatively affected by human activity (Crawshaw and Quigley 1991, Bisbal 1993), but this was not reflected in our results. That being said, there was no negative response of ocelots to puma activity observed in this study and, with the exclusion of human activity and small avian prey activity, there were no differences found between the stations used by ocelots and those not, so there is little evidence for habitat selection by ocelots at this level.

When modeling ocelot presence, the best model was simple and included only jaguar trap success, length of roads, and length of streams. It is likely that the effectiveness of this model is primarily due to the first two variables listed and not the effect of streams, which would be consistent with the other results of this study. It appears that simple models containing jaguar trap success, prey trap successes, and few other habitat variables are most effective. Other than the model containing only the effect of roads and streams, models lacking the trap success of jaguars, or prey as a variable did not rank as well. These a priori models ranked high in comparison to the null and global models indicating the importance of these variable combinations when modeling ocelot presence in the MPR. Past efforts at modeling ocelot activity have concentrated on habitat (Lopez Gonzalez et al. 2003, Haines et al. 2006b) and, to my knowledge, have not included the activity of prey or other carnivores. These results suggest such an omission may be misleading. For future studies in other areas, I suggest developing models that include other carnivores and prey trap success values in addition to habitat/landscape features, and testing them with a larger sample size.

Conclusions

Findings imply that jaguars may have large positive effects on the spatial activity of ocelots and these influences may outweigh the effects of other species' activity and of many of the other habitat characteristics within the MPR. While ocelots used sites with a higher degree of jaguar activity, their trap success did not appear to be related to puma activity. This could mean that mesopredator release operates on multiple levels within this carnivore guild; high jaguar activity may indirectly protect ocelots by limiting competitive puma activity. Further studies on competition and interacting activity levels in this community are necessary if we are to understand the intricacies of this carnivore guild.

Results from the MPR suggest that the jaguar may function as an umbrella species for the conservation of the ocelot populations. Ocelots used areas with high jaguar activity and did not appear to avoid preferable habitat areas with high prey activity due to any form of competition with this top predator. However, this is a unique study area and research in areas with higher ocelot density is needed. It is possible that in other areas (specifically broadleaf forests) jaguars could have a negative effect on ocelot populations; if this is the case then it may be necessary to select some protected areas not inhabited by jaguars but more hospitable to ocelots. Additionally, negative effects of pumas on ocelot populations have not been ruled out, and areas with few jaguars and many pumas could potentially pose a problem for ocelot conservation if mesopredator release is found to operate on multiple levels within this system. It may be necessary to design reserve systems and prioritize conservation areas not by ensuring that a full complement of predators are present in all locations, but rather that a variety of guild compositions, with different proportions of predatory species, are involved.

Acknowledgments

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Table 2.1: Weights used to categorize Mountain Pine Ridge Forest Reserve (MPR) prey and carnivore species into groups for analysis. All species listed were photographically captured during the remote camera survey in the MPR from June to August 2007.

Scientific name	Common name	Weight from literature (kg) [a]	Group assignment for trap success calculation
Dasyprocta punctata	Agouti	3 – 4	Small mammalian prey
Dasypus novemcinctus	Nine-banded armadillo	3 – 7	Small mammalian prey
Coendou mexicanus	Porcupine	1.4 – 2.6	Small mammalian prey
Didelphis marsupialis	Common opossum	0.6 – 2.4	Small mammalian prey
Agouti paca	Paca	5 – 12	Medium mammalian prey
Tamandua mexicana	Tamandua	3.8 – 8.5	Medium mammalian prey
Nasua narica	Coatimundi	2.7 – 6.5	Medium mammalian prey
Tayassu tajacu	Collared peccary	12 – 26	Large mammalian prey
Dicotyle pecari	White-lipped peccary	27 – 40	Large mammalian prey
Mazama americana	Red brocket deer	12 – 32	Large mammalian prey
Odocoileus virginianus	White-tailed deer	25 – 43	Large mammalian prey
Tapirus bairdii	Tapir	180 – 300	Large mammalian prey
Columbina passerina	Common ground dove	0.022 – 0.041	Small avian prey
Nyctidromus albicollis	Common pauraque	0.0532	Small avian prey
Ortalis vetula	Plain chachalaca	0.439 – 0.794	Small avian prey
Penelope pupurascens	Crested guan	2.000 – 2.150	Large avian prey
Crax rubra	Great currasow	4.050 – 4.225	Large avian prey
Meleagris ocellata	Ocellated turkey	5.525	Large avian prey
Mustela frenata	Long-tailed weasel	0.108 – 0.450	Small carnivore
Conepatus semistriatus	Striped hog-nosed skunk	< 5	Small carnivore
Urocyon cinereoargenteus	Grey fox	1.8 – 3.5	Small carnivore
Leopardus wiedii	Margay	2.6 – 5	Small carnivore
Eira barbara	Tayra	3 – 6	Small carnivore
Lutra longicaudis	Neotropical river otter	5 – 9.5	Small carnivore
Herpailurus yaguarundi	Jaguarundi	4 – 9	Small carnivore

[a] Weights used were obtained from Reid (1997) in the case of mammalian species and Dunning (1993) in the case of avian species.

Table 2.2: Comparison of microhabitat, landscape characteristics and large carnivore activity across locations used or not used by ocelots. Camera stations were established and habitat was sampled at 47 locations in the Mountain Pine Ridge Forest Reserve, Belize, from June to August of 2007.

Variable	Mean at sites with ocelots present $n = 10$ [a]	SE	Mean at sites with ocelots absent $n = 37$	SE	*t*-stat [f]	*P* value
Jaguar trap success (captures per 100 trap nights) [b]	14.1	2.61	5.79	1.34	-2.87	0.006
Puma trap success (captures per 100 trap nights)	0.95	0.54	0.59	0.21	-0.73	0.467
% canopy cover [c]	31.33	5.86	24.14	3.21	-1.04	0.303
Canopy height (m)	12.7	1.11	11.6	0.57	-0.95	0.348
% understory cover	82.75	4.8	77.67	2.8	-0.86	0.397
Understory heterogeneity (%) [d]	16.61	5.11	17.515	2.13	0.19	0.853
Tree density (No. per ha.)	1029	234.8	879	98.41	-0.66	0.510
Road width	423	23.19	419	19.80	-0.09	0.930
Length of streams within 200m (m) [e]	178	54.9	165	28.4	-0.21	0.835
Length of streams within 500m (m)	1922	141.1	1611	106.8	-1.42	0.162
Length of road within 200m (m)	447	32.8	324	26.3	-2.29	0.027
Length of road within 500m (m)	1424	93.3	1089	76.3	-2.16	0.037
% area burned within 200m	30.31	14.50	46.30	7.74	0.96	0.343
% area burned within 500m	29.99	13.21	48.36	7.13	1.20	0.238
Distance to Da Silva (km)	7.8	0.95	8.9	0.43	1.11	0.272
Distance to nearest point along Macal River (km)	7.5	0.81	7.1	0.53	-0.32	0.751
Small mammalian prey trap success	2.04	0.885	0.95	0.356	-1.32	0.193
Medium mammalian prey trap success	1.72	0.707	1.31	0.287	-0.62	0.540
Large mammalian prey trap success	3.16	1.036	2.26	0.534	-1.64	0.108
Small avian prey trap success	14.32	6.734	2.81	1.039	-1.69	0.124
Large avian prey trap success	1.15	0.725	2.50	0.814	1.23	0.227
Small carnivore trap success	32.5	12.34	33.7	7.412	-1.84	0.093
Human trap success	78.7	13.32	53.0	4.097	-1.82	0.097

[a] Presence was inferred from photos obtained at each location while absence was inferred from lack of photos of that species from that location.

[b] Trap success values were calculated from the photographs obtained from two opposing remotely triggered cameras at each location. Multiple photos of the same animal within 30 minutes were counted as only 1 capture.

[c] Habitat data were obtained from sampling along 3 transects within a 200 m radius of the camera location. See methods for more details on sampling plot design.

[d] Understory heterogeneity was calculated as the coefficient of variation from 6 separate estimates (2 along each of 3 transects) at each habitat plot.

[e] Landscape data were obtained using GIS. See methods for more details on data extraction.

[f] A *t* test was used to test for significant differences.

Table 2.3: Correlation of ocelot trap success with habitat characteristics and large carnivore activity at the 10 camera stations in the Mountain Pine Ridge Forest Reserve, Belize, with ocelots present. Sampling took place from June to August of 2007.

Habitat characteristic[a]	Spearman correlation coefficient (r_s)	*P* value
Jaguar trap success (captures per 100 trap-nights)	-0.171	0.637
Puma trap success (captures per 100 trap nights)	-0.270	0.450
% canopy cover	0.144	0.691
Canopy height (m)	-0.459	0.182
% understory cover	-0.262	0.464
Understory heterogeneity (%)	0.195	0.589
Tree density (No. per ha.)	-0.280	0.433
Road width (cm)	-0.461	0.180
Length of streams within 200m (m)	0.396	0.257
Length of streams within 500m (m)	0.317	0.372
Length of roads within 200m (m)	0.159	0.662
Length of roads within 500m (m)	0.079	0.828
% area burned within 200m	0.407	0.243
% area burned within 500m	0.463	0.177
Distance to Da Silva (km)	0.585	0.075
Distance to nearest point along Macal River (km)	-0.591	0.072
Small mammalian prey trap success	-0.358	0.310
Medium mammalian prey trap success	-0.306	0.390
Large mammalian prey trap success	0.116	0.749
Small avian prey trap success	-0.475	0.166
Large avian prey trap success	-0.293	0.412
Small carnivore trap success	-0.555	0.096
Human trap success	-0.067	0.854

[a] See Table 2.2 for details of the sampling protocol for these variables.

Table 2.4: Variation among 47 locations with different combinations of jaguar and ocelot presence in the Mountain Pine Ridge Forest Reserve, Belize. Data were collected from June to August of 2007.

Variable [a]	*F* value[b]	*P* value	Mean at stations with neither ocelots nor jaguars *n* = 6	Mean at stations with jaguars, but no ocelots *n* = 31	Mean at stations with both jaguars and ocelots *n* = 10
Puma trap success (captures per 100 trap nights)	0.92	0.406	0^c	0.70^c	0.95^c
% canopy cover	3.00	0.060	8.89^c	27.10^c	31.33^c
Canopy height (m)	4.43	0.018	8.2^c	12.2^d	12.7^d
% understory cover	0.59	0.556	81.94^c	76.84^c	82.75^c
Understory heterogeneity (%)	0.38	0.683	13.13^c	18.36^c	16.60^c
Tree density (No. per ha.)	0.28	0.756	965^c	863^c	1029^c
Road width (cm)	0.17	0.844	395^c	424^c	423^c
Length of streams within 200m (m)	0.51	0.602	101^c	177^c	178^c
Length of streams within 500m (m)	1.34	0.273	1422^c	1647^c	1922^c
Length of roads within 200m (m)	5.29	0.009	205^c	347^{cd}	447^d
Length of roads within 500m (m)	3.83	0.029	821^c	1141^{cd}	1424^d
% area burned within 200m	0.47	0.628	50.0^c	45.6^c	30.3^c
% area burned within 500m	0.77	0.468	54.4^c	47.1^c	30.0^c
Distance to Da Silva (km)	2.26	0.116	10.6^c	8.5^c	7.8^c
Distance to nearest point along the Macal River (km)	1.16	0.324	5.4^c	7.5^c	7.5^c
Small mammalian prey trap success	1.49	0.236	0^c	1.14^c	2.04^c
Medium mammalian prey trap success	0.72	0.495	2.02^c	1.18^c	1.72^c
Large mammalian prey trap success	3.26	0.048	0^c	2.69^{cd}	4.16^d
Small avian prey trap success	4.38	0.019	0.27^c	3.30^c	14.3^d
Large avian prey trap success	1.01	0.372	0.55^c	2.87^c	1.15^c
Small carnivores trap success	0.26	0.775	21.9^c	36.0^c	32.5^c
Human trap success	3.00	0.060	50.6^c	53.5^c	78.7^c

[a] See Table 2.2 for details of the sampling protocol for these variables

[b] A one-way ANOVA was used to test for statistically significant variation among groups. In the case of significance, a Tukey-Kramer test was conducted for differences between specific pairs. Means not followed by the same letter (either c or d) are statistically different at the α = 0.05 level.

Table 2.5: Variation among locations with different combinations of puma and ocelot presence in the Mountain Pine Ridge Forest Reserve, Belize. Data were collected from June to August of 2007.

Variable	*F* value[b]	*P* value	Stations with neither ocelots nor pumas observed *n* = 29	Stations with pumas, but no ocelots observed *n* = 8	Stations with ocelots, but no pumas observed *n* = 7	Stations with both pumas and ocelots observed *n* = 3
Jaguar trap success (captures per 100 trap nights)	2.65	0.061	5.57^{c}	6.60^{c}	14.0^{c}	14.4^{c}
% canopy cover	6.82	<0.001	18.21^{c}	45.62^{d}	35.71^{cd}	11.11^{cd}
Canopy height (m)	0.93	0.433	11.2^{c}	13.0^{c}	12.5^{c}	13.3^{c}
% understory cover	0.49	0.688	76.41^{c}	82.24^{c}	82.20^{c}	84.02^{c}
Understory heterogeneity (%)	0.13	0.939	18.23^{c}	14.91^{c}	16.93^{c}	15.85^{c}
Tree density (No. per ha.)	0.15	0.931	886^{c}	856^{c}	1019^{c}	1052^{c}
Road width (cm)	1.95	0.136	400^{c}	490^{c}	396^{c}	487^{c}
Length of streams within 200m (m)	4.06	0.013	125^{c}	311^{d}	235^{cd}	43^{cd}
Length of streams within 500m (m)	1.28	0.293	1558^{c}	1802^{c}	1806^{c}	2195^{c}
Length of roads within 200m (m)	2.25	0.097	317^{c}	349^{c}	482^{c}	364^{c}
Length of roads within 500m (m)	1.71	0.179	1060^{c}	1194^{c}	1403^{c}	1472^{c}
% area burned within 200m	1.92	0.141	54.9^{c}	15.3^{c}	28.6^{c}	34.4^{c}
% area burned within 500m	2.53	0.070	57.1^{c}	16.7^{c}	29.6^{c}	31.0^{c}
Distance to Da Silva (km)	0.66	0.579	8.9^{c}	8.7^{c}	8.3^{c}	6.7^{c}
Distance to nearest point along the Macal River (km)	0.65	0.585	6.8^{c}	8.2^{c}	7.0^{c}	8.6^{c}
Small mammalian prey trap success	0.65	0.589	0.95^{c}	0.96^{c}	1.79^{c}	2.62^{c}
Medium mammalian prey trap success	0.96	0.420	1.30^{c}	1.37^{c}	1.12^{c}	3.13^{c}
Large mammalian prey trap success	1.55	0.215	2.15^{c}	2.66^{c}	5.07^{c}	2.05^{c}
Small avian prey trap success	13.8	<0.0001	2.69^{c}	3.24^{c}	4.67^{c}	36.8^{d}
Large avian prey trap success	0.27	0.848	2.60^{c}	2.14^{c}	1.44^{c}	0.50^{c}
Small carnivore trap success	1.94	0.138	36.3^{c}	24.0^{c}	12.5^{c}	79.3^{c}
Human trap success	3.29	0.029	56.0^{cd}	42.1^{c}	87.3^{d}	58.5^{cd}

[a] See Table 2.2 for details of the sampling protocol for these variables

[b] A one-way ANOVA was used to look for statistically significant variation among all groups. In the case of significance this was followed by a Tukey-Kramer test for differences between specific pairs. Means not followed by the same letter (either c or d) are statistically different at the α = 0.05 level.

Table 2.6: Logistic regression models explaining the presence and absence of ocelots at camera stations in the Mountain Pine Ridge Forest Reserve, Belize. Data used were obtained from 47 locations that were sampled from June to August of 2007. All models are ranked according to Akaike scores (corrected, AIC$_c$), Δ AIC$_c$ and Akaike weights (ω_i). The 12 proposed models that ranked highest out of the 32 models tested (30 a priori models plus a null and global model) are shown in order of rank. Results of Hosmer and Lemeshow Goodness-of-Fit Tests including Chi-square and *P* values are shown. Null and global models with ranks are displayed for comparison.

Model[a]	Rank	K	AIC$_c$	Δ AIC$_c$	ω_i	Chi-square[c]	*P* value
Y = jaguar trap success, road length, river length	1	3	44.71	0	0.2564	8.3143	0.3057
Y = jaguar trap success	2	1	46.41	1.694	0.1099	6.1576	0.5215
Y = road length, river length	3	2	46.89	2.176	0.0864	6.4112	0.4926
Y = jaguar trap success, percent area burned	4	2	47.36	2.647	0.0683	4.5506	0.7146
Y = all prey trap success variables	5	5	47.58	2.869	0.0611	8.6058	0.2822
Y = small mammalian prey trap success, small avian prey trap success	6	2	47.66	2.944	0.0588	3.1148	0.5388
Y = small avian prey trap success, large avian prey trap success	7	2	47.69	2.972	0.0580	3.1084	0.6833
Y = jaguar trap success, understory cover, understory heterogeneity	8	3	48.05	3.332	0.0485	8.8304	0.2651
Y = jaguar trap success, puma trap success	9	2	48.17	3.455	0.0456	4.1055	0.7676
Y = puma trap success, road length, river length	10	3	48.22	3.503	0.0445	5.4103	0.6111
Y= jaguar trap success, puma trap success, small mammalian prey trap success, small avian prey trap success	11	4	48.44	3.727	0.0397	4.9233	0.6693
Y = distance to Da Silva, human trap success	12	2	49.73	5.019	0.0208	5.5115	0.5978
Null Model (contains intercept only – no predictor variables)	15	0	50.65	5.939	0.0132	NA	NA
Global Model (contains all variables considered as predictors)	32	20	74.37	29.66	0	0.0325	0.9999

[a] See Table 2.2 for details of the sampling protocol for data used in models.

[b] The term “all prey trap success variables” indicates the inclusion of the activity measures for all 5 prey groups including: small mammalian prey, medium mammalian prey, large mammalian prey, small avian prey, and large avian prey.

[c] The Hosmer and Lemeshow Goodness-of-fit Test is not applicable (NA) to the null (intercept-only) mode

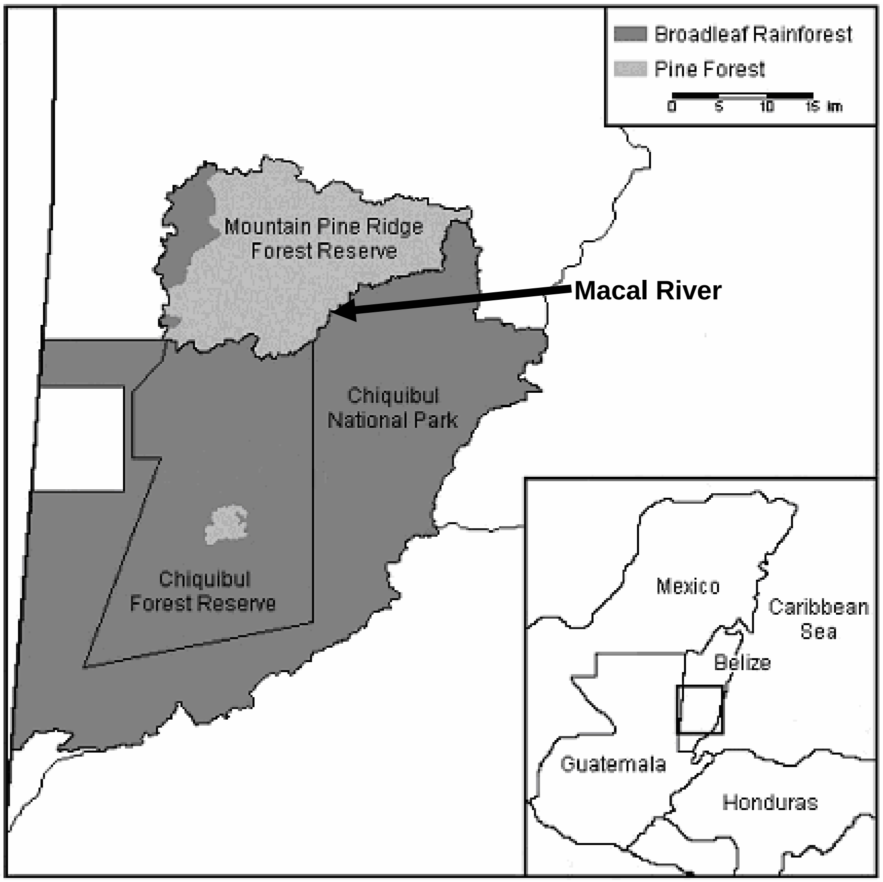

Figure 2.1: Location of the Mountain Pine Ridge Forest Reserve (MPR) within Belize, Central America. The pine forest of the MPR is separated from the broadleaf forest of the Chiquibul Forest Reserve and National Park by the Macal River. Camera and habitat surveys were completed in this area from June to August of 2007.

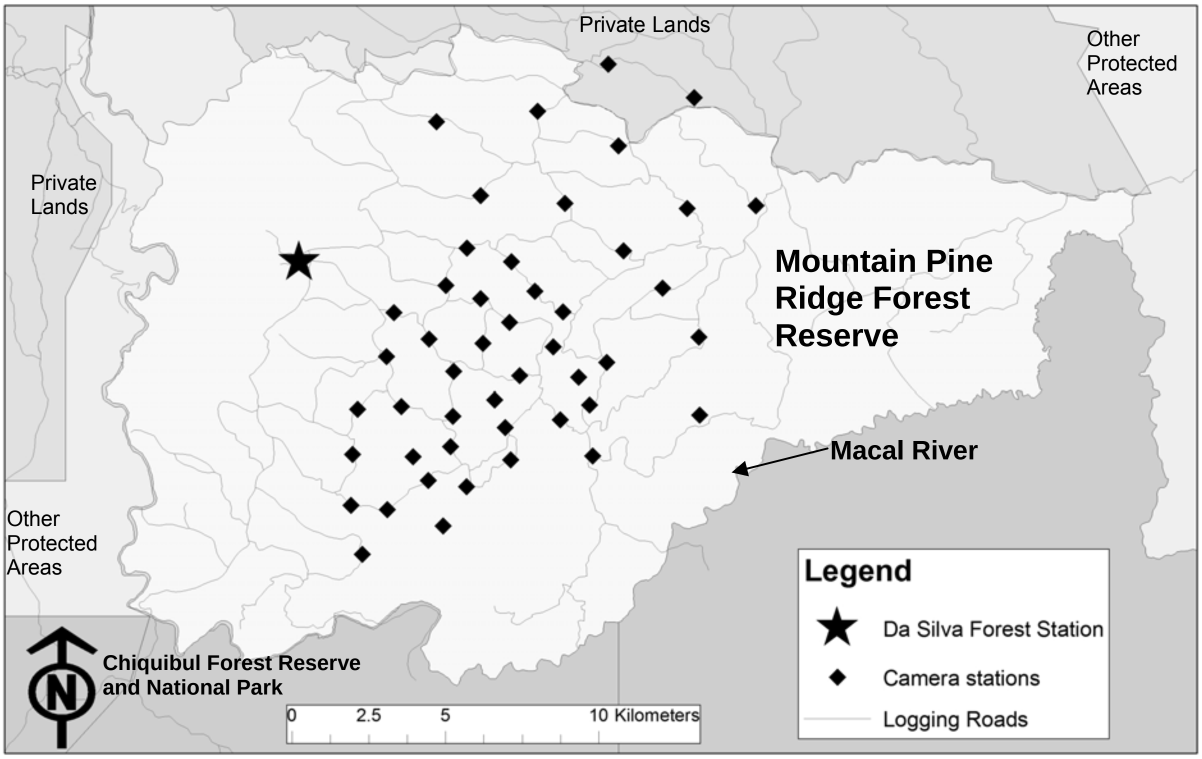

Figure 2.2: Locations of the 47 camera stations established in the Mountain Pine Ridge Forest Reserve. Each station consisted of two cameras mounted in opposing pairs in a 71 day trapping session from June to August of 2007.

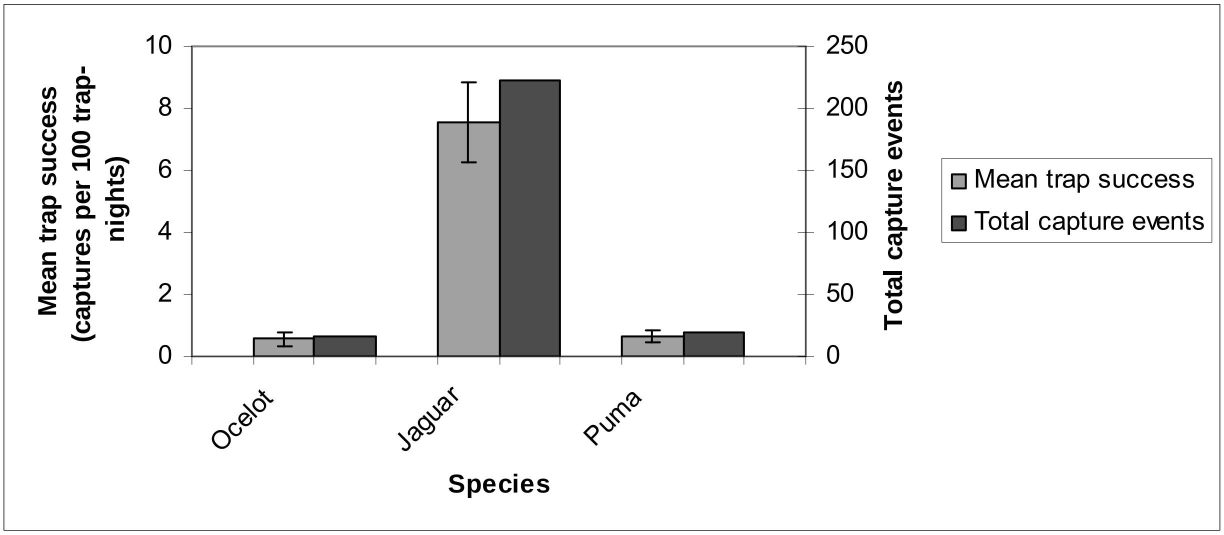

Figure 2.3: The total number of capture events (captures) from all cameras throughout the 72-day Mountain Pine Ridge Forest Reserve (MPR) survey and the mean trap success rate averaged across all camera stations for each of the three felid species: the ocelot, the jaguar and the puma. The MPR survey took place from June to August of 2007.

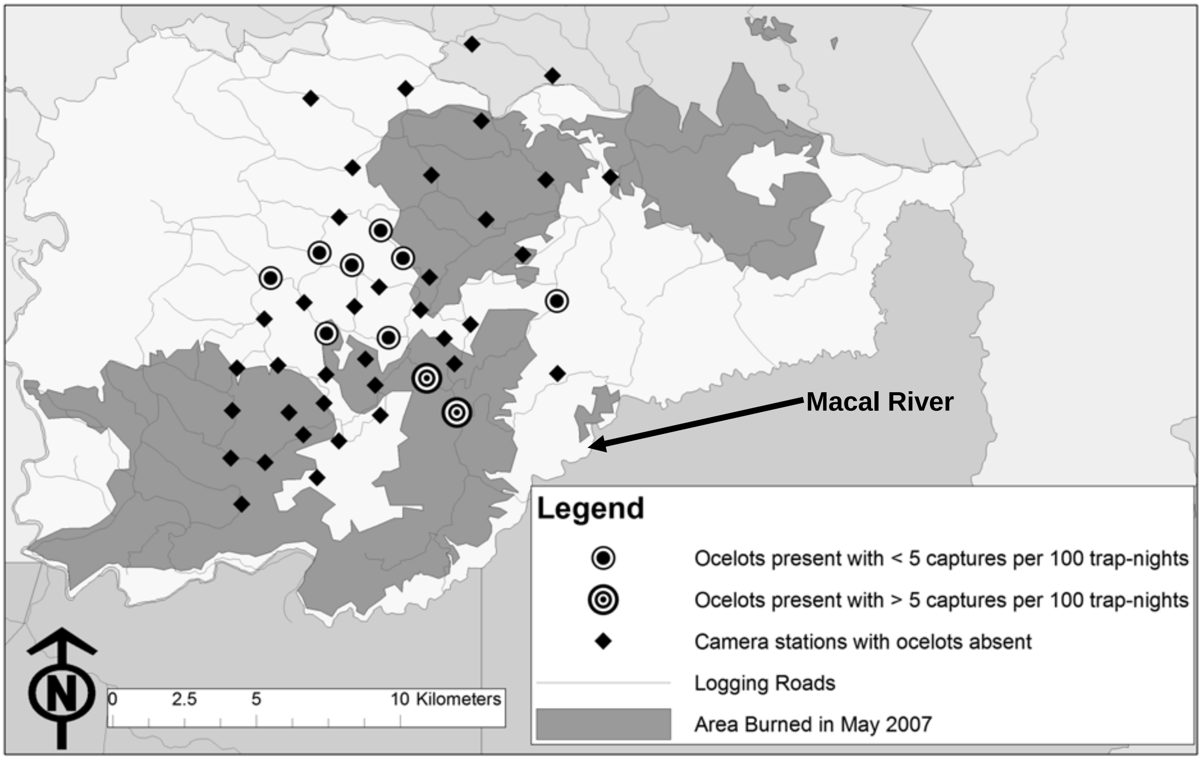

Figure 2.4: The areas burned in the Mountain Pine Ridge Forest Reserve in the May 2007 fires are shown along with the distribution of ocelot captures. Data were collected using a remote camera survey from June to August of 2007. Two stations in the southeastern area of the camera grid amidst the burned area and in close proximity to the Macal River, bordering the broadleaf forest, had high trap success (5.36 and 7.69 captures per 100 TN respectively) compared to the other 8 camera stations with ocelots present.

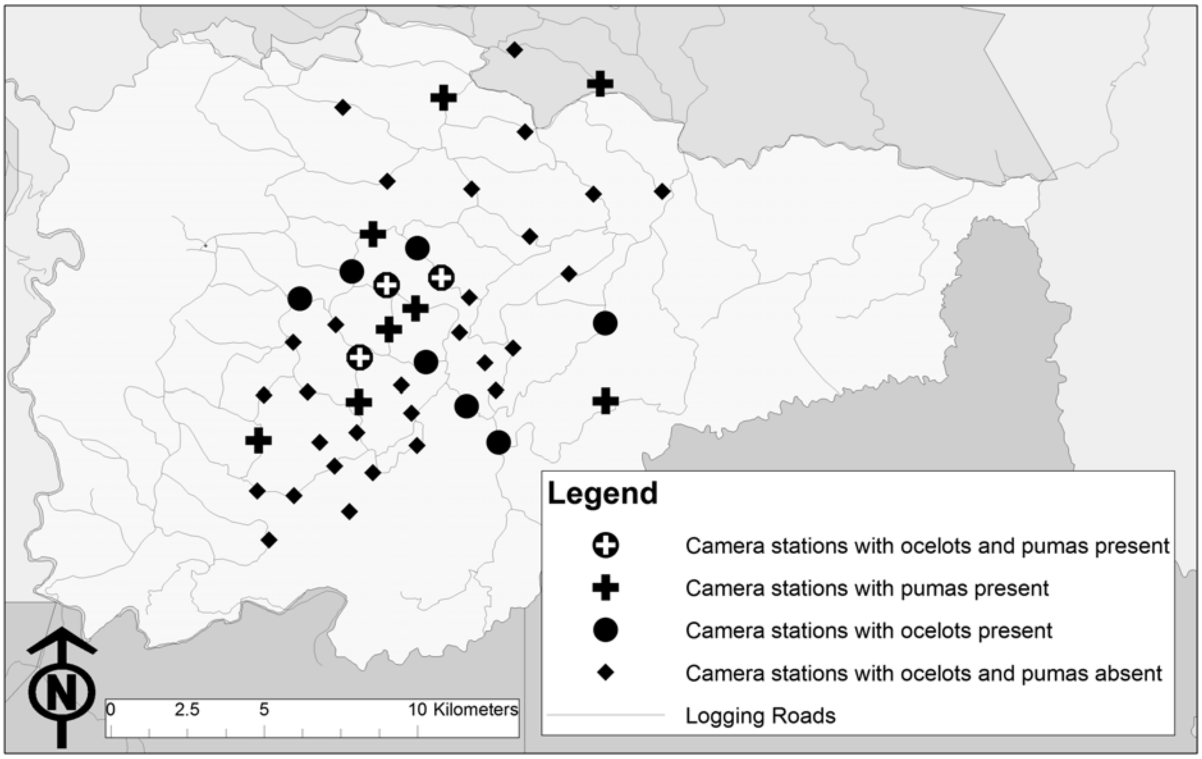

Figure 2.5: The distributions of camera stations with either ocelots (black circles), pumas (crosses) or both ocelots and pumas (circles with white crosses) present are shown. Data were collected using a remote camera survey across the Mountain Pine Ridge Forest Reserve from June to August of 2007. Presence was inferred from photos obtained at each location while absence was inferred from lack of photos of that species from that location. Ocelots, but not pumas, were found at 7 camera stations. Pumas, but not ocelots, were found at 8 camera stations. Ocelots and pumas were present at only 3 camera stations in the grid (out of of 47).

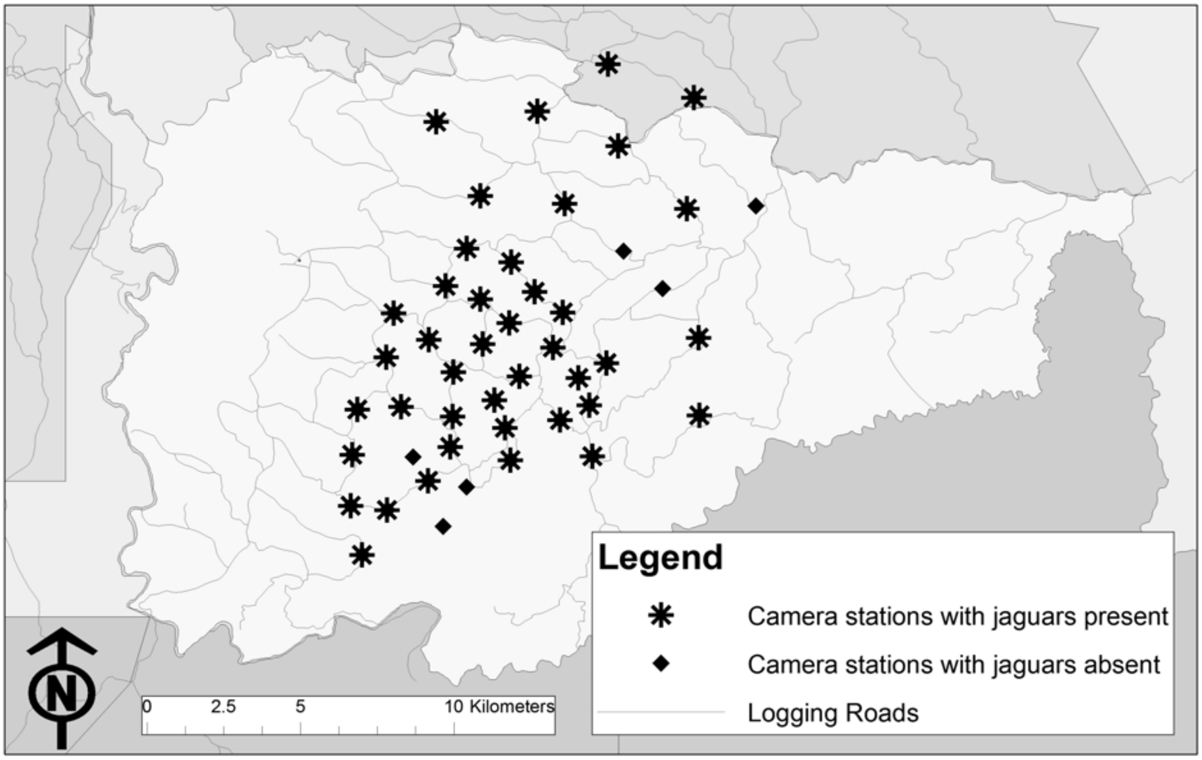

Figure 2.6: The distribution of camera stations in the Mountain Pine Ridge Forest Reserve with jaguars present (represented by asterisks) is shown. Data were collected using a remote camera survey from June to August of 2007. Presence was inferred from photos obtained at each location while absence was inferred from lack of photos of that species from that location.

Chapter 3 – Habitat-use and coexistence of the ocelot with jaguars and pumas in northern Belize.

Abstract

Understanding carnivore coexistence and interspecies effects on habitat-use is critical to the design of conservation programs that protect and maintain an intact, neotropical community. I examined the activity and habitat-use of ocelots compared with the activity of large carnivores in the Rio Bravo Conservation and Management Area, Belize. I calculated species-specific trap success rates for the ocelot, jaguar and puma at 39 camera stations across the 121 km^2 study site (i.e. MCP surrounding camera stations). I also calculated trap success rates for humans, small carnivores and prey groups. I manually sampled a number of variables relating to vegetation structure and human disturbance. Ocelot presence was positively related to the activity of jaguars, pumas, and large avian prey; however, ocelots chose not to use areas with higher levels of the medium sized mammalian prey used by pumas. Ocelot trap success was positively related to path width, but showed no relationship to other structural habitat parameters or human activities. While ocelots, jaguars, and pumas appeared to have used the same areas characterized by high activity levels of large avian prey there was little evidence of resource partitioning due to structural habitat characteristics. Comparison of a priori models using AIC similarly implied that the activity of other carnivores and prey are the best predictors of ocelot trap success. Results suggest that levels of competition among carnivores in the site do not negatively affect ocelot resource use and that high prey activity may facilitate coexistence in the neotropical carnivore guild.

Introduction

The carnivore guild containing the jaguar (*Panthera onca*), puma (*Puma concolor*), and the ocelot (*Leopardus pardalis*), is believed to exert a strong structuring influence within neotropical forest communities (Terborgh 1990). These cats may be responsible for limiting prey abundance to levels below carrying capacity (Emmons 1987) and have other top down cascading effects that extend throughout the neotropical system, including affecting plant community dynamics (Asquith et al. 1997, Terborgh et al. 2001, Terborgh et al. 2006). Protecting these carnivores and thereby maintaining intact ecosystems requires a better understanding of neotropical carnivore ecology. This may not be a straight-forward endeavor because jaguars, pumas, and ocelots are likely to compete with each other; these felids overlap not only in a number of the mammalian and avian species they prey upon, but also in their preference for areas of dense forest (Rabinowitz and Nottingham 1986, Emmons 1987, Sunquist and Sunquist 2002). Potential for high levels of competition mean that mesopredator release, a process through which small carnivores may be restricted by the activity of dominant predator species, may operate in the neotropics (Brown and Wilson 1956, Crooks and Soule 1999, Gehrt and Clark 2003). Managing for the benefit of one top carnivore species, such as the jaguar, could theoretically harm others in the guild, such as the ocelot. Unfortunately, because jaguars, pumas and ocelots are solitary animals, elusive and challenging to study, we know little about the mechanisms currently enabling the coexistence of these competitors.

Niche differentiation through the partitioning of habitat and prey resources may facilitate coexistence of carnivore species. It may also mean that the dominant competitor exploits the resources it prefers to the detriment of subordinate species, which are forced to avoid desirable locations used by the top carnivore (Caro and Stoner 2003). In the neotropics, preferable areas with high prey activity, good hunting cover, and low human activity may be occupied by jaguars and pumas, and subsequently may be used relatively infrequently by the much smaller ocelot. Given evidence that ocelots have specific microhabitat requirements, (for example, ocelots have been reported to almost exclusively use areas with > 95 % canopy cover in Texas; Shindle 1995, Harveson et al. 2004), this could prove detrimental to their populations in areas of high jaguar and puma densities.

Supporting mesopredator release theory, Moreno et al. (2006) argued that ocelots and pumas on Barro Colorado Island, Panama, may have a wider dietary niche in the absence of jaguars than in other areas of their range where pumas and ocelots overlap (and possibly compete) with jaguars. In the Mountain Pine Ridge Forest Reserve (MPR), Belize, contrary to predictions, I found that ocelots used areas with high jaguar activity more frequently, implying that this dominant competitor did not negatively affect ocelots (Chapter 2). These apparently incongruent findings may be because the pine forest is characterized by extremely low canopy cover and thick understory vegetation that are inhospitable to ocelots. These habitat features could cause the low ocelot population density in the Belizean pine forest and prevent competition with jaguars and pumas from playing as large a role in the ecology of that particular ocelot population (Chapter 2). To determine how representative the results are from the MPR, I need to conduct research in high productivity areas with habitat suitable to ocelot use and with healthy populations of the ocelot's potential competitors, the jaguar and the puma.

I chose a high productivity broadleaf forest site to maximize the chances of observing an ocelot population strongly influenced by competitive pressures with these larger carnivores. The Rio Bravo Conservation and Management Area (RBCA) in northwestern Belize is reputed to house a high diversity of vegetational communities and a particularly robust faunal community including a complete complement of predators (Casado Internet Group 2002). The Gallon Jug Reserve just south and contiguous with the RBCA has an estimated jaguar density of 11.4 individuals per 100 km^2 (C. Miller, Wildlife Conservation Society, personal communication; M. J. Kelly, Virginia Tech, personal communication) and while there is no existing puma density estimate, these cats are frequently seen within the study site and on surrounding lands (C. Miller, Wildlife Conservation Society, personal communication; personal obs.).

I expect that ocelot activity will increase with canopy cover, canopy height, understory cover, understory heterogeneity, and tree density. I predict that ocelots will avoid areas with high levels of human disturbance and more frequently use areas with high prey activity. However, I also hypothesize that ocelots will avoid other carnivores (particularly jaguars and pumas). The avoidance of competitors may conflict with the desire for optimal habitat. Ocelots may be driven to use less suitable habitat because in doing so, they avoid their major competitors. For example, ocelots may use lower quality areas with low canopy cover, high human activity, and low medium and large prey activity in an effort to avoid areas with high levels of puma activity.

In this chapter, I examine the relationship between ocelot activity rates, and the microhabitat characteristics across the RBCA. I also analyze ocelot activity as a response to activity levels of humans, other small carnivores and prey. Last but not least, I assess the influence of jaguars and pumas on ocelot ecology by considering all these variables as I compare patterns of ocelot activity to those of jaguars and pumas across the site. Understanding the role of interspecies competition and resource partitioning in this carnivore guild is critical to the development of future neotropical conservation efforts.

Study site

The RBCA in Northwestern Belize is approximately 994.8 km^2 in size and is the largest private reserve in Belize (Fig 3.1). The RBCA contains a range of habitat types including savannah, marsh, tropical pine forest, and tropical broadleaf forest. La Milpa Field Station is the only settlement within this area and houses conservation employees, and roughly 30 visitors (tourists and researchers) on a routine basis. Gallon Jug Road is the main track running north-south through the study site and connects the Mennonite communities in the north to the field station, tourist destinations and eventually the Western highway in south-central Belize. Many old logging roads and trails (used by researchers to reach Mayan archaeological sites) branch off from Gallon Jug road allowing further access to the study site. There is a Mennonite farming community, Tres Leguas, located to the north of the site (Casado Internet Group 2002). While not officially documented, there have been many reports of illegal hunting of jaguars by locals (usually when the animals are seen outside the reserve, near agricultural fields). Despite this and other possible negative interactions with humans near the borders of the study site, wildlife within the reserve is relatively bold and common. Species such as white-tailed deer, ocellated turkey, and great curassow are frequently observed in forest clearings and along road-sides.

Methods

All fieldwork was completed between 6 January 2008 and 9 April 2008. I established a grid of 40 camera stations spaced approximately 1.5-3.0 km^2 apart across the study area. Thirty-nine of these stations were sampled for habitat (Fig 3.2) and the minimum convex polygon of this grid covered an area of 121.5 km^2 (i.e. without buffers). When possible I used established roads and trails; however, many of these paths had fallen into disrepair and required extensive clearing. Some areas were not accessible by established paths, therefore over 20 km of new trails were cut to provide access to camera sampling locations. When establishing a station I recorded the width of the path (road or trail) where the cameras were placed and included this among other habitat variables (see below) for analysis. Thirty-seven stations were set up within the first month of fieldwork as trail clearing progressed and camera-traps at these stations were operational for a maximum of 77 days during the survey period. The final two stations (of the 39 used in the analysis) were established on 20 February and 25 February 2008 and ran until 31 March 2008.

I used camera-trap success rates as a measure of local relative activity for individual species and for groups of species. I calculated species-specific trap success rates for all species including humans (in car or on foot) as the number of captures at a camera station divided by the number of trap-nights (TN) multiplied by 100. When an animal was photographed multiple times at the same station within an arbitrarily selected 30 minute period I designated these photos collectively as only one capture event (unless the animal was individually distinguishable). I similarly calculated trap success rates for groups of species at individual stations by summing the captures of all species I assigned to that group. Small carnivore species were combined into one group for analysis. I divided probable prey species into size categories based on previous research on ocelot, puma and jaguar diets. Despite overlap among all three felids, it appears that ocelots rely primarily on small prey < 1 kg in size (reviewed by Sunquist and Sunquist 2002), pumas often consume prey < 15 kg in weight, and jaguars prey upon species averaging 15 kg (Emmons 1987, Scognamillo et al. 2003). Using weights from Reid (1997) I assigned mammal prey species to one of three groups: small (< 1 kg), medium (> 1 kg and < 15 kg), or large (> 15 kg; Table 3.1). Avian prey species, including many ground birds regularly captured by the remote cameras, were divided into two groups: small (< 1 kg) and large (> 1 kg) using weights from Dunning (1993, 2007; Table 3.1).

When sampling microhabitat I focused on features such as canopy cover and understory thickness that are believed to influence ocelot activity in other areas (Ludlow and Sunquist 1987, Haines et al. 2006b). I estimated canopy cover by completing 100 meter long transects at 0, 120, and 240 degrees starting at each camera station. I recorded the canopy cover (present or absent) every 10 meters; this resulted in a total of 10 canopy points per transect. At 50 and 100 meters along each transect I also estimated canopy cover using a clinometer and tree density using the point-centered quarter method and an unbiased estimator (Pollard 1971). I estimated understory cover (defined as < 2 m in height) using 40 meter long point intercept transects running perpendicular to the original "canopy transects" at these 6 locations. I calculated mean estimates of all of these measures at the 50 and 100 m level and then averaged these means to generate overall estimates of microhabitat features for each camera station.

At two stations one transect had to be abandoned before reaching the 100 m point because of exceptionally steep terrain and impassable vegetation; at those stations I relied on the data from the 50 m level and from the remaining 2 completed transects to generate the 100 meter estimates. Using understory cover estimates I also was able to estimate understory heterogeneity using a pooled coefficient of variation for the 50 and 100 meter transects at each station (Zar 1999).

I used ArcGIS to create maps of the camera grid and to calculate the distance to human centers. I acquired data layers of Belize containing the geographic locations of protected area boundaries, and settlements from Jan Meerman, their originator, in 2007. Claudia Wultsch provided GPS coordinates of the roads and trails used to establish the camera grid. These points, along with coordinates of the camera stations, were taken using a Garmin 60 CSx throughout the study period. All maps presented here were created using layers created from this GPS data or layers provided by Jan Meerman. I calculated the distance to the human settlement (Tres Leguas) and the distance to the nearest point along the Gallon Jug Road for each camera station using ArcGIS. The UTM NAD 27 coordinate system in zone 16 North was used for all of these operations. I found that the available GIS layers were not accurate for extracting data on roads and streams within the study area.

When analyzing these data, each camera station (of the 39 at which habitat was sampled) was considered one experimental unit. I assumed sites were accessible to the target species and that if a species was not photographed at a camera station then it was absent from that location (no false absences). I also assumed that captures of a species that were 30 minutes apart were independent of each other and the habitat characteristics and capture rates of each camera station were independent of surrounding stations due to their wide spacing.

I conducted analyses in the statistical program SAS (SAS Institute 2002) and used $\alpha = 0.05$ to determine significance; I considered *P*-values between 0.05 and 0.1 marginally significant. I used two-sample *t* tests to look for differences between the characteristics of stations used and not used by ocelots; if the variance of a variable was not found to be homogenous for the two groups, I used the Satterthwaite method. I used Spearman correlation coefficients to test for relationships between ocelot trap success and other variables as many of the variables (including ocelot trap success) were non-normal. In this correlation analysis I used only stations with ocelots present; this was done to prevent the absent sites from dominating the results. To compare the groups of stations with different combinations of ocelot, jaguar, and puma presence or absence I used an ANOVA followed by a Tukey-Kramer test for multiple comparisons. To model ocelot activity across the site I used zero-inflated negative binomial models with absolute counts of ocelot captures at each station as the response variable. Zero-inflated negative binomial models model "zeros" separately from positive values of the response variable and have been shown to perform well when data contains a disproportionately large number of zeros (as is often the case with animal count data; Sileshi 2008). Because stations were operational for varying lengths of time, I included the number of trap-nights at each station as a covariate (as an offset variable). I developed 29 a priori models using different combinations of the habitat and trap success variables as predictors. Because preliminary results from these models suggested that jaguar trap success and path width performed well as predictors, I also developed one post-hoc model including both of these variables simultaneously. I ranked and compared these 30 models, plus a null and a global model using Akaike's information criterion (Akaike 1973) corrected for low sample sizes (AIC_c) and Akaike weights (Burnham and Anderson 2002). To evaluate the predictive value of each model, I used Pearson's correlation coefficient to measure the correlation between observed counts at each station and counts predicted by the model.

Results

After accounting for occasional camera malfunctions, the 39 camera stations resulted in 2,510 trap-nights over the study period. Ocelots were captured 122 times at 29 camera stations yielding an average of 4.90 ± 0.743 captures per 100 TN (Fig. 3.3 and Fig 3.4). Jaguars were captured 64 times at 25 stations with an average trap success of 2.46 ± 0.423 captures per 100 TN. Pumas had an average trap success of 2.49 ± 0.485 captures per 100 TN and were captured 65 times at 22 stations (Fig. 3.3).

Stations with ocelots present had higher levels of jaguar activity ($\bar{x}$'s = 3.20, 0.30 captures per 100TN; df = 37, $t = -5.06$, $P < 0.0001$) and puma activity ($\bar{x}$'s = 3.19, 0.46 captures per 100TN; df = 37, $t = -4.29$, $P = 0.0001$) than stations without ocelots (Table 3.2). No significant differences were found in any of the structural habitat characteristics (including canopy cover, canopy height, understory cover, understory heterogeneity, tree density, and road width), or in the distance to Tres Leguas or the Gallon Jug Road. When considering prey groups, stations where ocelots were present yielded higher large avian prey trap success rates ($\bar{x}$'s = 22.6, 2.69 captures per 100TN; df = 37, $t = -3.16$, $P = 0.0035$). There was also a marginally significant difference in the activity of medium-sized mammalian prey; species in this group were captured only half as often at stations with ocelots as at stations without any ocelot activity ($\bar{x}$'s = 1.05, 2.56 captures per 100TN; df = 37, $t = 1.99$, $P = 0.0540$). Human activity, small carnivore activity and the activity levels of small, large mammalian prey and small avian prey did not differ between ocelot presence and absence sites (Table 3.2).

Among the 29 camera stations where ocelots were photographed ocelot trap success increased with both puma ($n = 29$, $r_s = 0.396$, $P = 0.034$) and large avian prey activity ($n = 29$, r_s

= 0.440, $P = 0.017$). Ocelot activity also showed marginally significant positive correlations with small carnivore trap success ($n = 29$, $r_s = 0.340$, $P = 0.071$) and human trap success ($n = 29$, $r_s = 0.329$, $P = 0.081$). Ocelot trap success also increased with increasing path width ($n = 29$, $r_s = 0.559$, $P = 0.002$), but was uncorrelated with all other habitat and trap success variables (Table 3.3).

Twenty-four out of 39 stations captured both jaguars and ocelots while both species were absent from 9 camera locations (Fig 3.5). Ocelots, but not jaguars, were captured at 5 stations, while jaguars were captured only at one station where ocelots were absent. While the one station with jaguars present and ocelots absent is listed for comparison, it could not be included in the ANOVA used to compare the other ocelot+jaguar camera groups (Table 3.4). There was significant variation in puma trap success among the three groups analyzed ($F_{2, 36} = 3.37$, $P = 0.0459$); puma trap success was lowest at stations where both ocelots and jaguars were absent and highest at stations where both jaguars and ocelots were present ($\bar{x}$'s = 0.34, 3.23 captures per 100 TN). Stations with only ocelots present (not jaguars) had a mid-range puma activity level ($\bar{x} = 3.03$ captures per 100 TN) as did the one station with only jaguars and not ocelots ($x = 1.49$ captures per 100 TN). Stations with both ocelots and jaguars had high levels of large avian prey activity ($\bar{x} = 25.0$ captures per 100 TN) while stations with neither species had low large avian activity levels ($\bar{x} = 1.50$ captures per 100 TN) and the mean for stations with only ocelots was mid-range ($\bar{x} = 11.0$ captures per 100 TN); however, these values were not statistically distinct (Table 3.5). There were no significant variations in the other habitat and trap success variables among these groups. The one station with jaguars present, but no ocelot captures, had the lowest tree density of all the sites sampled with only 487 trees per ha. (Table 3.4; mean tree density among all sites was 1,354 trees per ha. with a standard error of 64.7).

Both ocelots and pumas were present at 19 sites; both species were mutually absent from 7 sites. Pumas but not ocelots were captured at 3 sites and ocelots were captured at 10 sites from which pumas were absent (Fig. 3.6). There was significant variation in jaguar activity among these four categories ($F_{3, 35} = 5.99$, $P = 0.0021$). Jaguar trap success was lower at sites with neither pumas nor ocelots than at sites with both pumas and ocelots ($\bar{x}$'s = 0.00, 3.88 captures per 100 TN). The two camera groups with only ocelots or pumas present had mid-range jaguar activity levels and were not statistically distinct in this respect (Table 3.5). The trap success rates of medium mammalian prey varied significantly among the ocelot+puma station groups ($F_{3, 35} =$

5.78, $P = 0.0026$). The activity of medium mammalian prey was at least 4 times higher at the stations where only pumas were captured than at all other groups of stations. There was marginally significant variation in the trap success rates of large avian prey among these groups ($F_{3, 35} = 2.50$, $P = 0.0754$). There was marginally significant variation in the activity of large avian prey among these categories; stations with both ocelots and pumas had high levels of large avian prey activity ($\bar{x} = 29.9$ captures per 100 TN) while stations with neither species had low large avian activity levels ($\bar{x} = 0.86$ captures per 100 TN) and stations with only pumas or ocelots fell in between these two extremes ($\bar{x}$'s = 6.97, 8.69 captures per 100 TN; Table 3.5). No other comparisons among the ocelot+puma station groups were statistically significant.

Among the zero-inflated negative binomial models proposed for ocelot captures in the RBCA, the post-hoc model based on jaguar activity and path width had a 44 % chance of being the best (based on Akaike weight) with the lowest AIC_c value ($AIC_c = 165.6$; Table 3.6). There were two competing models (i.e. within 2 ΔAIC of the top model). The first had a 25 % chance of being the best model tested and included jaguar activity only. The third ranked model included both jaguar and puma activity and had a 16 % chance of being the best model of those considered. The only model between 2 - 4 ΔAIC_c, ranked fourth, was based on jaguar, puma, and small carnivore activity. Many other high-ranking models included a combination of prey activity rates. The null and global models were ranked 13th and 32nd, respectively, out of the 32 models tested. All models except the null model showed highly significant correlations between observed and predicted counts across stations (Table 3.6).

Discussion

Ocelot activity in the RBCA does not appear to be influenced by any of the structural habitat characteristics examined in this study with the exception of path width. While there is little distinguishing the vegetative features at the sites used by ocelots, these cats more frequently visited stations set up along wider roads and trails. This is consistent with previous camera trapping studies in Belize (Dillon and Kelly 2007) and is likely caused by preference for established logging roads (as opposed to newly cut trails) within the study site that may be clear, easy to travel, known to individuals, and used by prey.

Lack of a response to other habitat characteristics, particularly the lack of a positive relationship with canopy and understory cover, is more surprising and implies that ocelots in the neotropical broadleaf forests may not be as sensitive to these features as ocelots in the thornscrub habitats of Texas and northern Mexico. Ocelots in these northern areas were repeatedly found to use only densely vegetated areas often characterized quantitatively by at least 95 % canopy cover (Navarro-Lopez 1985, Tewes 1986, Shindle 1995, Horne 1998, Harveson et al. 2004). Nevertheless, canopy and understory cover ranged 50 – 95 % and 58 – 98 % respectively across the RBCA stations and is what may be described as dense forest. Use of these areas seems consistent with qualitative observations from other neotropical broadleaf sites where ocelots avoided exposed areas with the exception of a few nocturnal forays (Emmons 1987, Ludlow and Sunquist 1987, Emmons et al. 1989, Sunquist et al. 1989).

It is likely that prey activities play a much more important role in determining ocelot habitat-use in the RBCA than structural habitat characteristics, consistent with results from the pine forest (Chapter 2). Ocelots showed a strong positive relationship with the activity of large avian prey species (including ocellated turkey, great curassow, plain chachalaca, crested guan and great tinamou; Table 3.1) and used the areas more frequently visited by these birds. These species are exceptionally common in the RBCA, and may be a very reliable food source. No relationship was found with the smaller prey that ocelots depend upon in other areas. However, this is likely because camera traps are unable to capture the small rodent prey (< 1 kg in size) important to ocelots (Emmons 1987, Ludlow and Sunquist 1987) or because other prey in the RBCA are plentiful and ocelots meet their dietary requirements more efficiently by pursuing those groups (such as large avian prey). Ocelots also appear unaffected by large mammalian prey; this is unsurprising as these species are likely taken during opportunistic encounters and are typically consumed less frequently due to increased size (Emmons 1987, Ludlow and Sunquist 1987). Finally, ocelots in the RBCA used areas with lower levels of medium mammalian prey activity; this may be because these prey species are actively preferred by another large carnivore, causing ocelots to avoid those areas, as discussed below.

Human activities within the RBCA do not appear to have negatively influenced ocelot activity. Indeed, these felids may have visited locations with high levels of human activity (both by foot and vehicle) more frequently. Nor was there an implied effect of proximity to the nearby town, Tres Leguas, or to the high-traffic Gallon Jug Road. Visually, ocelot activity appears to have been distributed evenly throughout the study site and many of the sites yielding high capture rates were set up along Gallon Jug Road or adjacent to La Milpa Field Station (Fig. 3.4). Ocelots in the RBCA may be habituated to the relatively benign activities of tourists and researchers within the site. The favorable effects of wider paths and higher prey activity may also offset costs of proximity to humans.

Despite the fact that ocelots, jaguars, and pumas appear to be abundant in the RBCA and were captured at most stations, there is little support for the mesopredator release hypothesis in this study site. Contrary to expectations, ocelots did not show signs of avoiding locations used by jaguars, pumas, or other small carnivores. In fact, the areas ocelots used were more frequently visited by jaguars and pumas. Presence of ocelots and either jaguars or pumas at a station was associated with an increased probability of observing the third felid species. Nor did small carnivores appear to avoid these areas; locations more frequently used by ocelots may have had higher levels of small carnivore activity. These results imply that levels of competition between these carnivores are low and top carnivore activity is unlikely to have negative effects on ocelots.

It seems likely that multiple carnivores find the same features desirable causing the co-occurrence observed in this study, but it does not appear that the areas used were chosen due to any structural habitat characteristics measured. Nor do the carnivores appear to have partitioned habitat due to variation in these features. These results are similar to those found by Taber et al. (1997) and Scognamillo et al. (2003) who reported little evidence of habitat selection or partitioning by jaguars and pumas. This may be because prey activity rates have a more direct effect on the ecology of these felids. Ocelots, jaguars, and pumas all use areas with high levels of large avian prey activity. Areas with abundant large bird prey may be a factor enabling the coexistence of these felids in the RBCA. This may be similar to the situation in Venezuela where Scognamillo et al. (2003) suggested that an abundance of medium-sized prey facilitated jaguar-puma coexistence. Abundant large bird activity may “saturate” this carnivore community and minimize competition for prey. Additionally, this could reduce the need for carnivores to separate their niches by exploiting other prey groups. Jaguars did not seem drawn to areas of large mammalian prey activity, nor did ocelots make more use of areas with small mammalian prey activity. For the ocelot, high activity levels of prey in one location (surrounding one of the camera stations for example), may also mean that the benefits of exploiting that area’s resources outweigh the cost of proximity to the dominant puma and jaguar.

There is some evidence that pumas exploit different prey resources and that this, in turn, may affect ocelot activity. Stations with high levels of medium mammalian prey activity were used by pumas, but not ocelots; in fact, these results suggest that ocelots generally chose not to use locations with high activity levels of this prey group throughout the study site. This is consistent with other research suggesting that neotropical pumas rely on medium-sized prey up to around 15 kg in size (Emmons 1987, Scognamillo et al. 2003). Pumas may actively defend sites with medium sized mammalian prey against other carnivores such as the ocelot; perhaps, pumas prefer mammalian prey to avian prey species or are unable to meet their energetic requirements by relying only upon the large avian species. Avoiding areas with these particular mammalian prey may be of little concern to the ocelot considering the availability of other prey in the study site and the ocelot's tendency to consume smaller species.

Consistent with the other results of this study, ocelot activity in the RBCA was best modeled using carnivore activity, path width, and prey activity rates, as predictors. The fact that the three best (and only competing) models included jaguar and puma trap success rates highlights the point that while these carnivores may not be negatively influencing ocelots as I predicted, their activity may play an important role in ocelot ecology. The inclusion of path width in the top ranked model implies that this could also be an important factor in determining ocelot activity patterns and should be taken into account in future models (perhaps as a covariate). Other high-ranking models included the activity levels of the small carnivore and prey groups. Models containing structural habitat characteristics (other than road width) performed poorly relative to the other models. The high correlations found between observed and predicted counts of the proposed models in addition to the relatively poor performance of the null and global models confirms the importance of these variable combinations. The activity rates of other species within the neotropical community, especially of sympatric carnivores, appear to be the best predictors of ocelot activity.

Scognamillo et al. (2003) and Taber et al. (1997) suggested that documenting the use of roads and trails by cats does not necessarily imply active use of surrounding habitat patches, merely travel through those areas, and this may bias results. Lack of evidence for habitat partitioning in the RBCA could be a sign that path activity does not correctly identify the habitat actively used by felids, or that I am not measuring the habitat characteristics of importance to their activity. My analysis of prey activity may also be too indirect and general to illustrate partitioning of prey resources among these felids. I have not directly measured dietary consumption, only relationships between predator activity and that of possible prey. Jaguars and pumas in Peru, Venezuela, and Guatemala appear to concentrate on different individual prey species and age-classes within species at different sites (Emmons 1987, Taber et al. 1997, Novack et al. 2005). Similarly, ocelots in Peru were found to take juvenile agouti more often than adult agouti, and not to prey upon adult paca (Emmons 1988). My examination of prey size groups would not be sensitive to such patterns of consumption. Neotropical felids are believed to be opportunistic hunters with highly adaptable diets (Emmons 1987); the results of this and the other studies mentioned imply that prey partitioning among the ocelot, jaguar and puma may vary widely among sites.

Alternatively, it is possible that competition within this guild is taking place, but is manifested in other ways such as temporal avoidance, more active sensory avoidance, or intraguild predation (Schoener 1974, Palomares and Caro 1999, Caro and Stoner 2003). Ocelots could be avoiding other carnivores temporally; these mesopredators may visit areas at different times of the day or only after signs of recent visit by these larger carnivores have faded. Competition could be displayed more actively through aggressive interactions including intraguild predation (Palomares and Caro 1999, Donadio and Buskirk 2006), but not affecting overall patterns of space-use. The benefits of exploiting the resources in a certain location may be too great to consistently avoid an area used by large carnivores. Detecting such interactions directly is beyond the scope of this study; however, if intraguild predation is a regular occurrence within this guild and an important ecological force, it seems likely it would have resulted in noticeable spatial avoidance.

Finally, while not causing detectable differences in resource use by ocelots, competition with jaguars and pumas could have negative effects that may be discernable only at the population level. Aggressive interactions and decreased access to resources can reduce the health and reproductive success of carnivore populations (Laurenson 1995, Kelly et al. 1998, Caro and Stoner 2003). If this is the case, ocelot population density should be lower in areas of high jaguar and puma population densities. Conversely, if these carnivore populations do not negatively affect one other, but are capable of thriving in the same resource-rich areas, then their densities should be positively related and positively related to prey resources. Data on estimated population densities from multiple sites are needed to evaluate this possibility.

Conclusions

I provide evidence that ocelots in the neotropical broadleaf forest of the Rio Bravo Conservation and Management Area, Belize, are not forced to use areas with sub-optimal habitat to avoid competition with pumas and jaguars as would be expected according to the mesopredator release hypothesis. Despite some evidence that pumas may limit ocelots in the use of some prey, likely non-essential to their diet, there is no evidence that competition within the neotropical guild is causing spatial avoidance. These results also imply that the activities of prey are more important in determining carnivore spatial activity patterns than the habitat characteristics measured and I propose that coexistence may be due to high levels of prey activity.

Similar to results from the Belizean pine forest (Chapter 2), this study tentatively suggests that the jaguar could fill the role of an umbrella species with respect to its sympatric carnivores in broadleaf areas as well; neither ocelots nor pumas appear to have avoided areas used by jaguars. Further research examining the relationship between prey abundance and the activity of sympatric carnivores could elucidate mechanisms driving carnivore coexistence and aid in the prioritization of conservation areas. Preserving areas with healthy jaguar populations and with abundant prey resources is likely to simultaneously protect healthy populations of other carnivores in the community.

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Table 3.1: Weights used to categorize Rio Bravo Conservation and Management Area (RBCA) prey and carnivore species into groups for analysis. All species were photographically captured during the remote camera survey in the RBCA from January to April of 2008.

Scientific name	Common name	Weight from literature (kg)[a]	Group assignment for trap success calculation
Dasyprocta punctata	Agouti	3 – 4	Small mammalian prey
Dasypus novemcinctus	Nine-banded armadillo	3 – 7	Small mammalian prey
Sciurus deppei	Deppe's squirrel	0.191 – 0.219	Small mammalian prey
Didelphis marsupialis	Common opossum	0.6 – 2.4	Small mammalian prey
Agouti paca	Paca	5 – 12	Medium mammalian prey
Tamandua mexicana	Tamandua	3.8 – 8.5	Medium mammalian prey
Nasua narica	Coatimundi	2.7 – 6.5	Medium mammalian prey
Tayassu tajacu	Collared peccary	12 – 26	Large mammalian prey
Dicotyle pecari	White-lipped peccary	27 – 40	Large mammalian prey
Mazama americana	Red brocket deer	12 – 32	Large mammalian prey
Odocoileus virginianus	White-tailed deer	25 – 43	Large mammalian prey
Tapirus bairdii	Tapir	180 – 300	Large mammalian prey
Columbina passerina	Common ground dove	0.022 – 0.041	Small avian prey
Ortalis vetula	Plain chachalaca	0.439 – 0.794	Small avian prey
Tinamus major	Great tinamou	0.885 – 1.249	Large avian prey
Penelope pupurascens	Crested guan	2.000 – 2.150	Large avian prey
Crax rubra	Great currasow	4.050 – 4.225	Large avian prey
Meleagris ocellata	Ocellated turkey	5.525	Large avian prey
Conepatus semistriatus	Striped hog-nosed skunk	< 5	Small carnivore
Urocyon cinereoargenteus	Grey fox	1.8 – 3.5	Small carnivore
Leopardus wiedii	Margay	2.6 – 5	Small carnivore
Eira barbara	Tayra	3 – 6	Small carnivore
Herpailurus yaguarundi	Jaguarundi	4 – 9	Small carnivore

[a] Weights used were obtained from Reid (1997) in the case of mammalian species and Dunning (1993, 2007) in the case of avian species.

Table 3.2: Comparison of microhabitat, landscape characteristics and large carnivore activity across 39 locations used or not used by ocelots in the Rio Bravo Conservation and Management Area, Belize. Camera stations were established and habitat was sampled at 39 locations in the study area from January to April 2008.

Variable	Mean at sites with ocelots present *n* = 29[a]	SE	Mean at sites with ocelots absent *n* = 10	SE	*t*-stat[f]	*P* value
Jaguar trap success (captures per 100 trap nights)[b]	3.20	0.489	0.30	0.299	-5.06	<0.0001
Puma trap success (captures per 100 trap nights)	3.19	0.596	0.46	0.23	-4.29	0.0001
% canopy cover[c]	76.22	2.645	81.50	2.761	1.10	0.2798
Canopy height (m)	11.5	0.50	10.6	0.82	-0.89	0.3772
% understory cover	79.61	1.410	82.88	2.57	1.15	0.2557
Understory heterogeneity (%)[d]	15.28	1.420	12.60	1.280	-1.05	0.2989
Tree density (No. per ha.)	1346	78.05	1374	117.5	-0.18	0.8553
Path width	256	16.03	223	25.42	-1.08	0.2870
Distance to Tres Leguas (km)	11.3	0.98	11.3	1.26	0	0.9982
Distance to nearest point along Gallon Jug Road (km)	1.55	0.283	1.25	0.266	-0.59	0.5592
Small mammalian prey trap success	5.11	1.362	4.38	1.975	-0.28	0.7820
Medium mammalian prey trap success	1.05	0.343	2.56	0.836	1.99	0.0540
Large mammalian prey trap success	3.72	0.586	8.87	4.422	1.15	0.2769
Small avian prey trap success	2.92	1.567	2.22	1.918	-0.24	0.8125
Large avian prey trap success	22.6	6.159	2.69	1.326	-3.16	0.0035
Small carnivore trap success	6.42	2.027	2.90	1.291	-1.47	0.1512
Human trap success	233	125.9	25.8	2.144	-1.64	0.1114

[a] Presence was inferred from photos obtained at each location while absence was inferred from lack of photos of that species from that location.

[b] Trap success values were calculated from the photographs obtained from two opposing remotely triggered cameras at each location. Multiple photos of the same animal within 30 minutes were counted as only 1 capture.

[c] Habitat data were obtained from sampling along 3 transects within a 100 m radius of the camera location. See methods for more details on sampling plot design.

[d] Understory heterogeneity was calculated as the coefficient of variation from 6 separate estimates (2 along each of 3 transects) at each habitat plot.

[e] Landscape data were obtained using GIS. See methods for more details on data extraction.

[f] A *t* test was used to test for significant differences.

Table 3.3: Correlation of ocelot trap success with habitat characteristics and large carnivore activity at 29 camera stations in the Rio Bravo Conservation and Management Area, Belize, with ocelots present. Data were collected from January to April of 2008.

Habitat characteristic[a]	Spearman Correlation Coefficient (r_s)	*P* value
Jaguar trap success (captures per 100 trap-nights)	0.294	0.122
Puma trap success (captures per 100 trap nights)	0.396	0.034
% canopy cover	-0.306	0.106
Canopy height (m)	-0.070	0.718
% understory cover	-0.101	0.603
Understory heterogeneity (%)	0.173	0.369
Tree density (No. per ha.)	-0.039	0.840
Path width (cm)	0.559	0.002
Distance to Tres Leguas (km)	-0.176	0.361
Distance to nearest point along Gallon Jug Road (km)	0.055	0.776
Small mammalian prey trap success	0.199	0.301
Medium mammalian prey trap success	-0.126	0.514
Large mammalian prey trap success	-0.122	0.529
Small avian prey trap success	0.061	0.752
Large avian prey trap success	0.440	0.017
Small carnivore trap success	0.340	0.071
Human trap success	0.329	0.081

[a] See Table 3.2 for details of the sampling protocol for these variables.

Table 3.4: Variation among locations with different combinations of jaguar and ocelot presence in the Rio Bravo Conservation and Management Area, Belize. Data were collected from January to April of 2008.

Variable [a]	*F* value[b]	*P* value	Mean at stations with neither ocelots nor jaguars *n* = 9	Mean at stations with ocelots, but no jaguars *n* = 5	Mean at stations with both jaguars and ocelots *n* = 24	Estimate at station with jaguars, but no ocelots *n* = 1 (Not included in ANOVA) [c]
Puma trap success (captures per 100 trap nights)	3.37	0.0459	0.34^{d}	3.03^{de}	3.23^{e}	1.49
% canopy cover	0.39	0.6780	80.74^{d}	76.74^{d}	76.11^{d}	88.33
Canopy height (m)	1.09	0.3471	10.8^{d}	10.1^{d}	11.8^{d}	9.14
% understory cover	0.93	0.4057	82.64^{d}	82.50^{d}	79.01^{d}	85.00
Understory heterogeneity (%)	0.35	0.7104	13.08^{d}	14.81^{d}	15.38^{d}	8.320
Tree density (No. per ha.)	1.72	0.1938	1473^{d}	1596^{d}	1295^{d}	487
Path width (cm)	0.80	0.4554	222^{d}	235^{d}	263^{d}	160
Distance to Tres Leguas (km)	0.05	0.9518	10.7^{d}	11.4^{d}	11.3^{d}	16.8
Distance to nearest point along the Gallon Jug Road (km)	1.45	0.2473	1.39^{d}	2.48^{d}	1.36^{d}	0.03
Small mammalian prey trap success	0.36	0.7012	4.87^{d}	2.65^{d}	5.62^{d}	0
Medium mammalian prey trap success	1.99	0.1521	2.52^{d}	0.36^{d}	1.20^{d}	2.99
Large mammalian prey trap success	1.82	0.1770	9.20^{d}	4.61^{d}	3.54^{d}	5.97
Small avian prey trap success	0.70	0.5047	0.31^{d}	0.63^{d}	3.39^{d}	19.4
Large avian prey trap success	2.26	0.1190	1.50^{d}	11.0^{d}	25.0^{d}	13.4
Small carnivores trap success	0.88	0.4244	2.39^{d}	3.28^{d}	7.07^{d}	7.46
Human trap success	0.79	0.4620	25.5^{d}	20.2^{d}	277^{d}	28.4

[a] See Table 3.2 for details of the sampling protocol for these variables

[b] A one-way ANOVA was used to test for statistically significant variation among groups. In the case of significance, a Tukey-Kramer test was conducted for differences between specific pairs. Means not followed by the same letter (either d or e) are statistically different at the $\alpha = 0.05$ level.

[c] There was only one station which had jaguars present but no ocelots. The habitat estimates for this station are presented here but were not included in the analysis of variance as there were no mean estimates available for this category.

Table 3.5: Variation among locations with different combinations of puma and ocelot presence in the Rio Bravo Conservation and Management Area, Belize. Data were collected from January to April of 2008.

Variable	*F* value[b]	*P* value	Mean at stations with neither ocelots nor pumas *n* = 7	Mean at stations with pumas, but no ocelots *n* = 3	Mean at stations with ocelots, but no pumas *n* = 10	Mean at stations with both pumas and ocelots *n* = 19
Jaguar trap success (captures per 100 trap nights)	5.99	0.0021	0^{c}	1.00^{cd}	1.91^{cd}	3.88^{d}
% canopy cover	0.62	0.6078	79.76^{c}	85.56^{c}	78.09^{c}	75.24^{c}
Canopy height (m)	0.55	0.6516	10.3^{c}	11.5^{c}	12.0^{c}	11.3^{c}
% understory cover	0.59	0.6235	81.73^{c}	85.56^{c}	89.75^{c}	79.53^{c}
Understory heterogeneity (%)	0.42	0.7393	12.98^{c}	11.72^{c}	14.60^{c}	15.63^{c}
Tree density (No. per ha.)	1.14	0.3463	1505^{c}	1070^{c}	1446^{c}	1295^{c}
Path width (cm)	1.08	0.3719	214^{c}	218^{c}	233^{c}	272^{c}
Distance to Tres Leguas (km)	1.65	0.1958	11.1^{c}	11.9^{c}	14.1^{c}	9.90^{c}
Distance to nearest point along the Gallon Jug Road (km)	0.68	0.5693	1.41^{c}	0.90^{c}	1.98^{c}	1.33^{c}
Small mammalian prey trap success	0.69	0.5643	4.48^{c}	4.16^{c}	2.55^{c}	6.45^{c}
Medium mammalian prey trap success	5.78	0.0026	1.26^{c}	5.60^{d}	1.38^{c}	0.88^{c}
Large mammalian prey trap success	1.46	0.2421	10.4^{c}	5.42^{c}	3.55^{c}	3.81^{c}
Small avian prey trap success	0.67	0.5748	0.40^{c}	6.47^{c}	1.18^{c}	3.83^{c}
Large avian prey trap success	2.50	0.0754	0.86^{c}	6.97^{c}	8.69^{c}	29.9^{c}
Small carnivore trap success	1.15	0.3427	2.65^{c}	3.47^{c}	2.56^{c}	8.45
Human trap success	0.82	0.4897	25.6^{c}	26.4^{c}	42.8^{c}	333^{c}

[a] See Table 3.2 for details of the sampling protocol for these variables

[b] A one-way ANOVA was used to look for statistically significant variation among all groups. In the case of significance this was followed by a Tukey-Kramer test for differences between specific pairs. Means not followed by the same letter (either c or d) are statistically different at the α = 0.05 level.

Table 3.6: Zero-inflated negative binomial regression models explaining the counts of ocelot captures at remote cameras in the Rio Bravo Conservation and Management Area, Belize. Data were obtained from 39 camera station locations sampled from January to April of 2008. All models are ranked according to Akaike scores (corrected, AIC_c), Δ AIC_c, and Akaike weights (ω_i) The 12 proposed models ranked highest out of the 32 models tested (including 29 a priori models, one post-hoc model, plus a null and global model) are shown. Results of Pearson correlation between predicted and observed counts are shown. Null and global models with ranks are displayed for comparison.

Model [a]	Rank	K	AIC_c	Δ AIC_c	ω_i	r [c]	*P* value
Y = jaguar trap success, path width [b]	1	2	165.6	0	0.4334	0.667	< 0.0001
Y = jaguar trap success	2	1	166.7	1.109	0.2490	0.522	0.0007
Y = jaguar trap success, puma trap success	3	2	167.5	1.934	0.1648	0.570	0.0002
Y = jaguar trap success, puma trap success, small carnivore trap success	4	3	169.2	3.639	0.0703	0.687	< 0.0001
Y = jaguar trap success, puma trap success, medium mammalian prey trap success, large mammalian prey trap success, large avian prey trap success	5	5	170.3	4.746	0.0404	0.731	< 0.0001
Y = small avian prey trap success, large avian prey trap success	6	2	171.0	5.435	0.0286	0.631	< 0.0001
Y = jaguar trap success, distance to Gallon Jug Rd	7	2	173.3	7.673	0.0093	0.550	0.0003
Y = path width	8	1	177.0	11.37	0.0015	0.494	0.0014
Y = jaguar trap success, understory cover, understory heterogeneity	9	3	178.3	12.71	0.0008	0.534	0.0005
Y = medium mammalian prey trap success, large mammalian prey trap success, large avian prey trap success	10	3	178.6	13.06	0.0006	0.649	< 0.0001
Y = puma trap success	11	1	178.9	13.29	0.0006	0.489	0.0016
Y = puma trap success, distance to Gallon Jug Rd	12	2	179.8	14.22	0.0004	0.483	0.0018
Null Model (contains intercept only – no predictor variables)	13	0	181.0	15.38	0.0002	0.058	0.7262
Global Model (contains all variables considered as predictors)	32	17	3018	2853	0	0.838	< 0.0001

[a] See Table 3.2 for details of the sampling protocol for data used in models.

[b] The model including jaguar trap success and path width was developed as a post-hoc model based on preliminary results from the a priori models indicating the high predictive value of these two variables.

[c] Pearson's correlation coefficient (r) was used to measure the correlation between observed and predicted counts at each station.

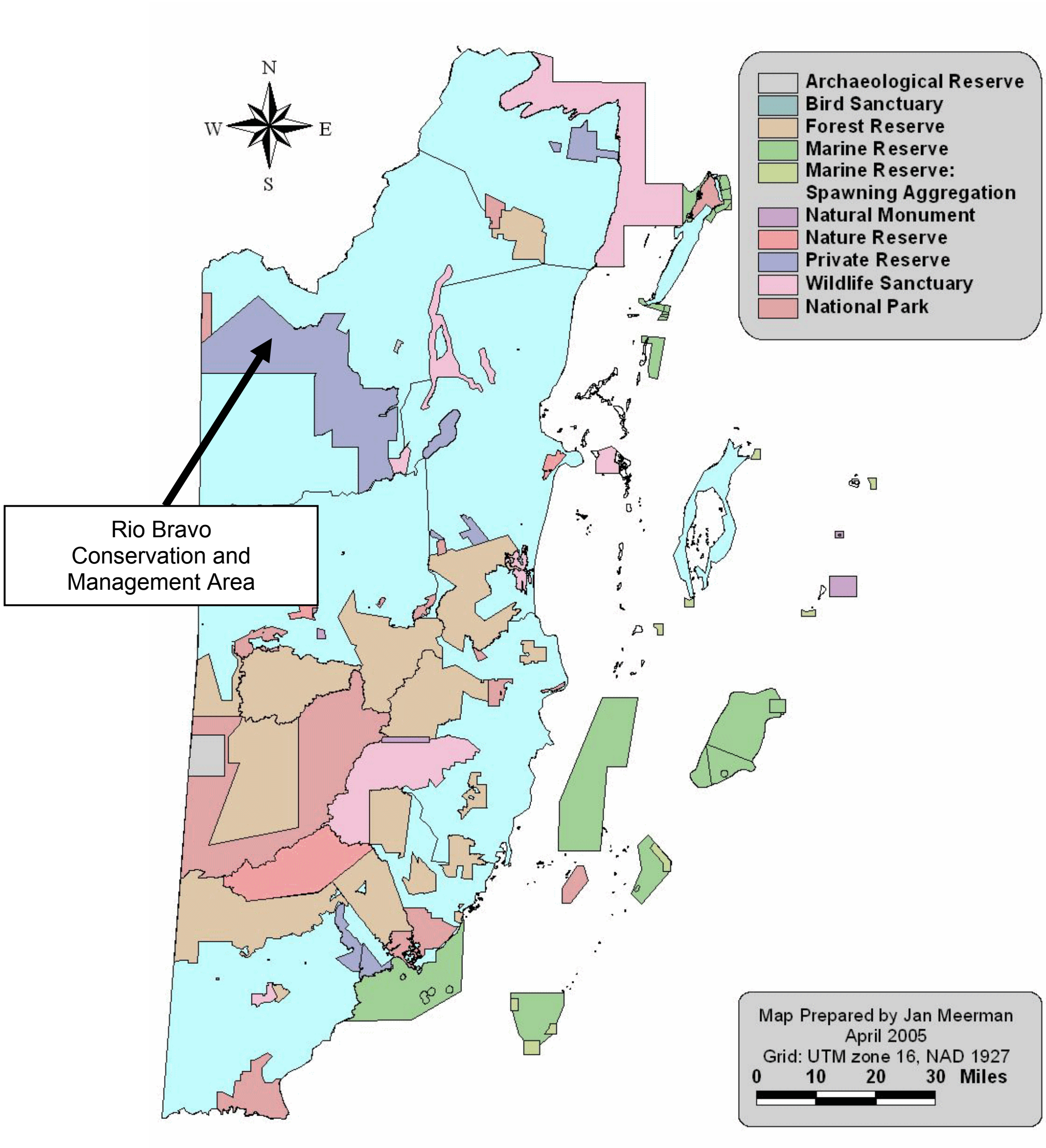

Figure 3.1: Location of the Rio Bravo Conservation and Management Area in northwestern Belize, Central America (Meerman 2006). It is the largest private reserve in Belize and covers 994.8 km^2. Camera and habitat surveys were completed in this area from January to April of 2008.

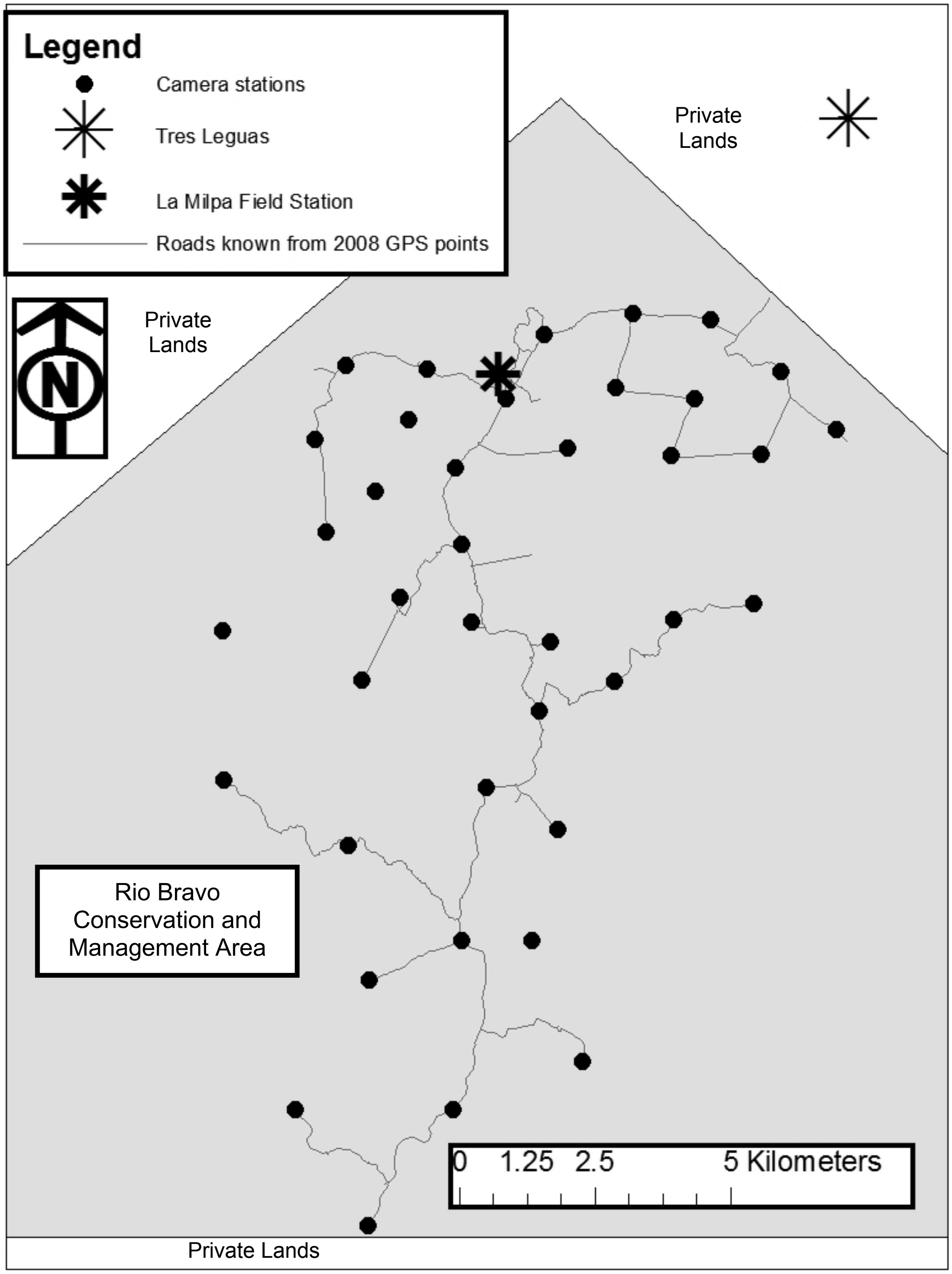

Figure 3.2: Thirty-nine camera stations were established in the Rio Bravo Conservation and Management Area; each station consisted of two cameras mounted in opposing pairs for a maximum of 77 days during the survey period from January to April of 2008. The nearby town, Tres Leguas, the general location of La Milpa Field Station, and known locations of the roads and trails (from GPS points taken in 2008) are also shown.

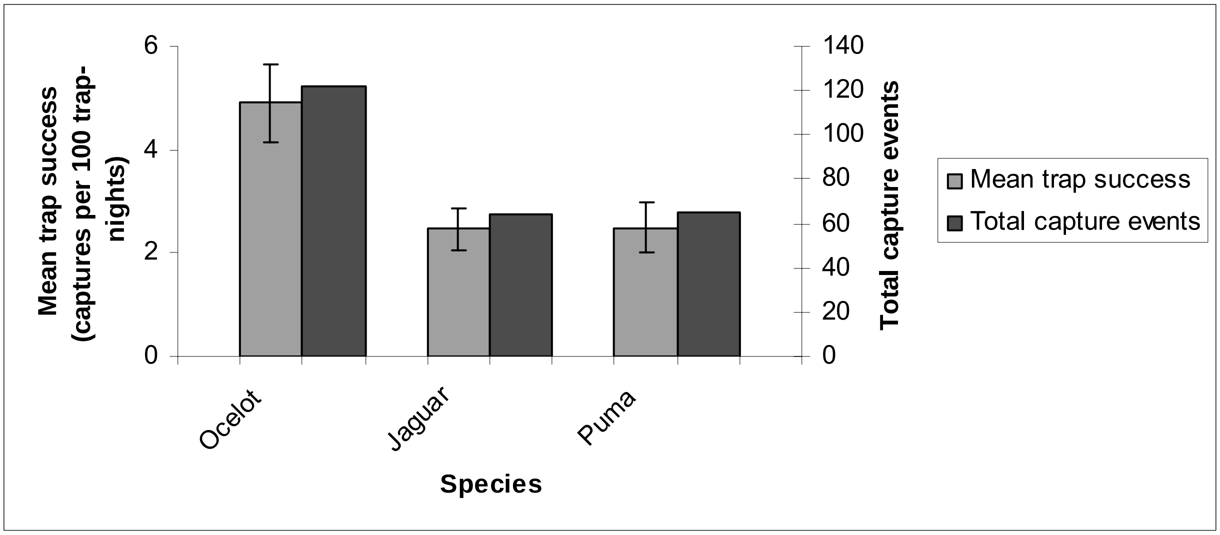

Figure 3.3: The total number of capture events (captures) from all cameras throughout the 90- day Rio Bravo Conservation and Management Area survey and the mean trap success rate averaged across 39 camera stations for each of the three felid species: the ocelot, the jaguar and the puma. Each camera station was operational for a maximum of 77 days during the survey period from January to April of 2008.

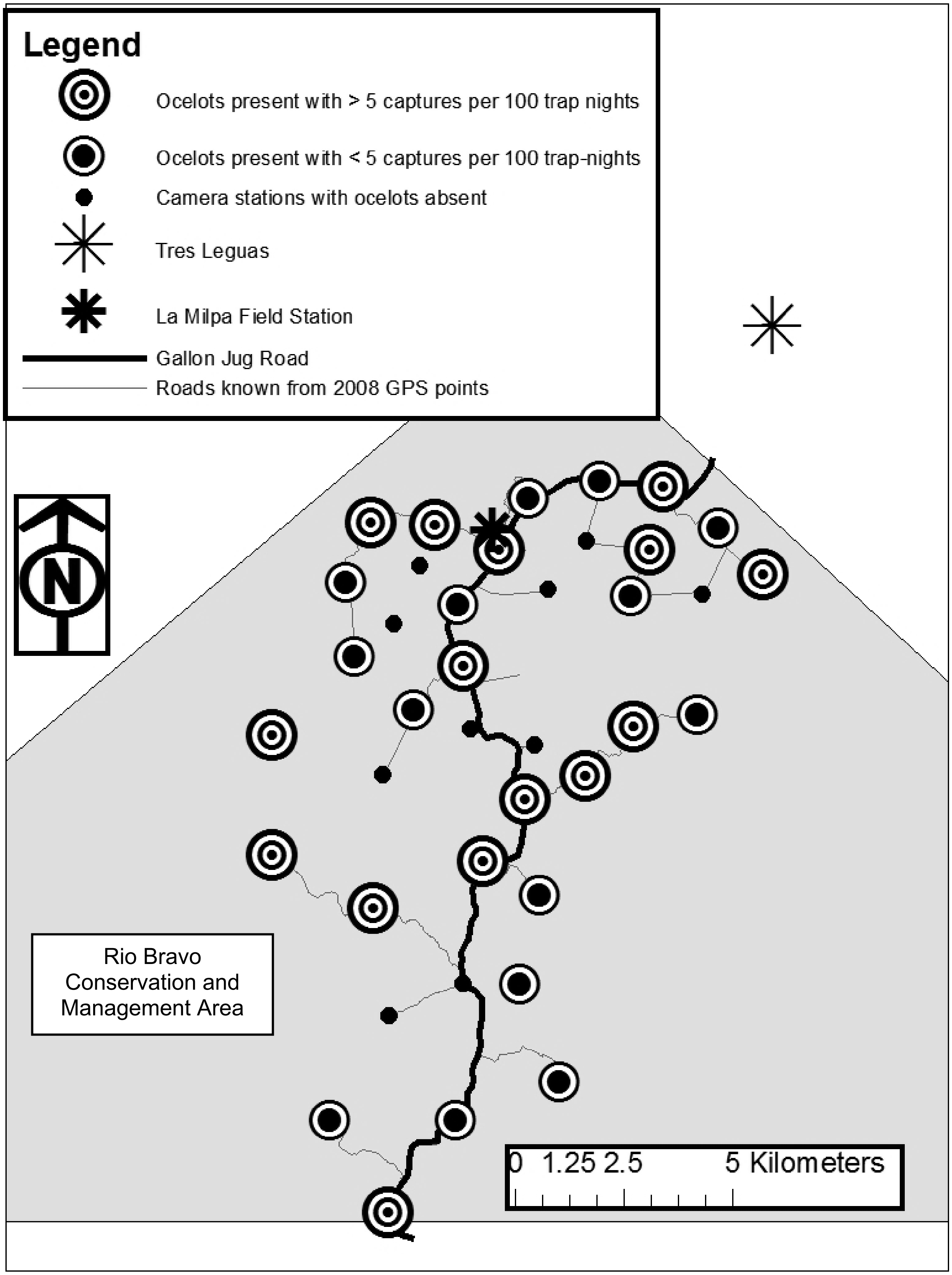

Figure 3.4: The Gallon Jug Road that bisects the Rio Bravo Conservation and Management Area, the nearby town Tres Leguas, and general location of the La Milpa Field Station are shown along with the distribution of ocelot captures. Ocelots were captured at 29 camera stations (out of 39) during the survey period from January to April of 2008.

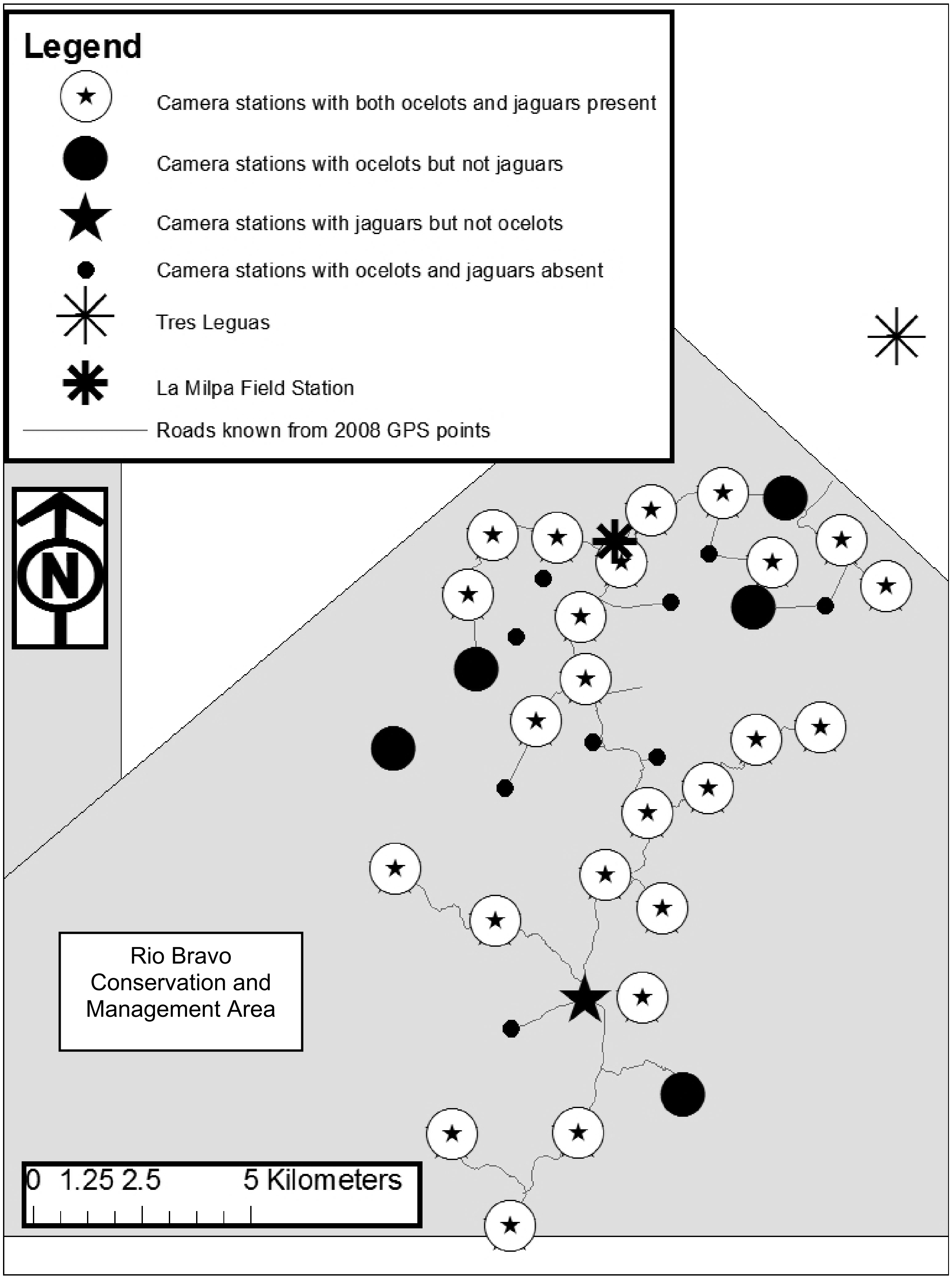

Figure: 3.5: The distributions of camera stations with either ocelots (black circles), jaguars (star) or both ocelots and pumas (circles with inner stars) present are shown. Data were collected using a remote camera survey across the Rio Bravo Conservation and Management Area in Belize. Data collection took place from January to April of 2008. Presence was inferred from photos obtained at each location while absence was inferred from lack of photos of that species from that location. Ocelots, but not jaguars, were found at 5 camera stations. Jaguars, but not ocelots, were found at only 1 camera station. Ocelots and jaguars were present at 24 camera stations in the grid (out of 39).

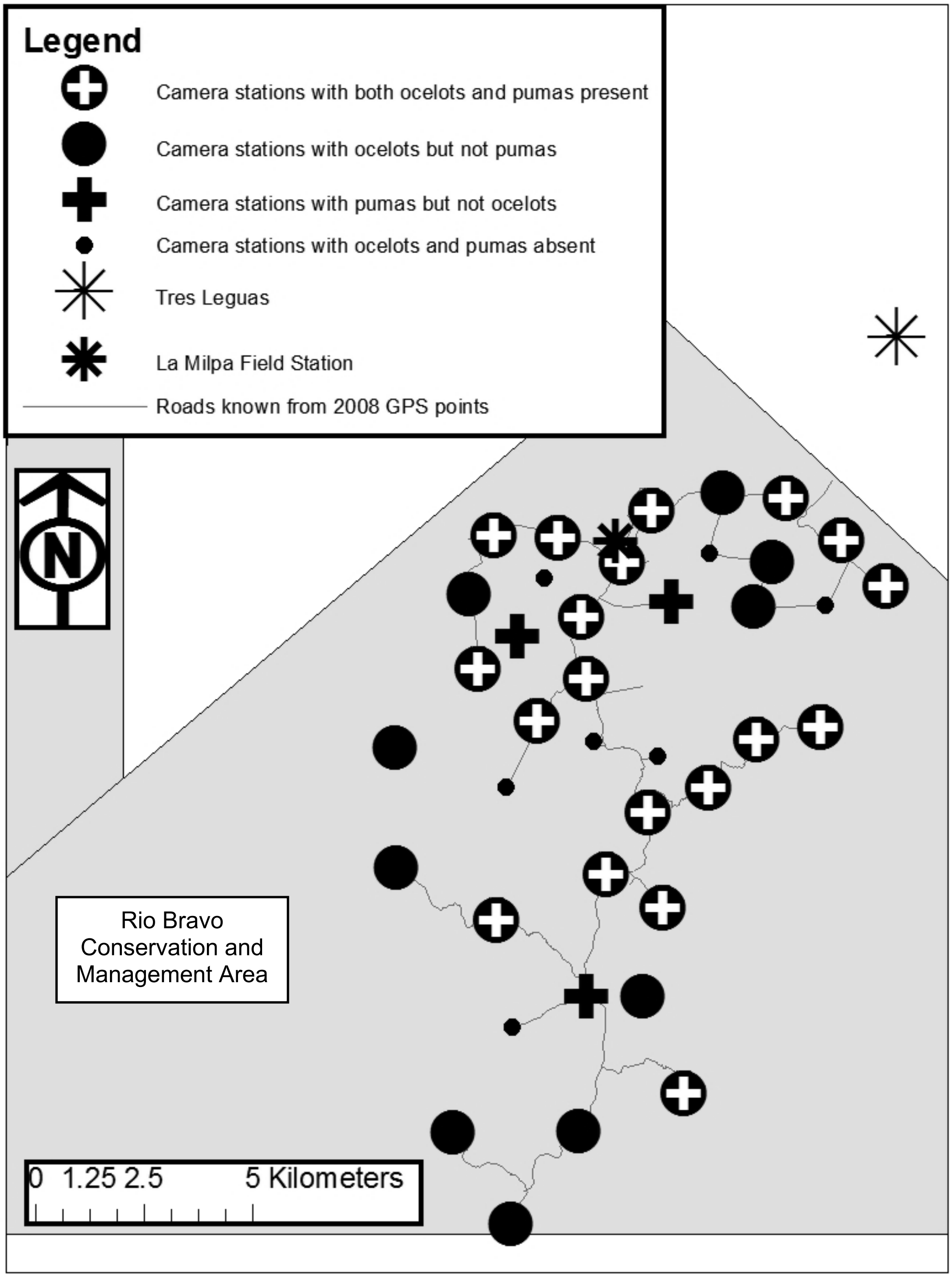

Figure 3.6: The distributions of camera stations with either ocelots (black circles), pumas (crosses) or both ocelots and pumas (circles with white crosses) present are shown. Data were collected using a remote camera survey established across the Rio Bravo Conservation and Management Area, Belize. Data collection took place from January to April of 2008. Presence was inferred from photos obtained at each location while absence was inferred from lack of photos of that species from that location. Ocelots, but not pumas, were found at 10 camera stations. Pumas, but not ocelots, were found at 3 camera stations. Ocelots and pumas were present at 19 camera stations in the grid (out of 39).

Chapter 4 – The mesopredator release hypothesis: inferences from felid densities and co-occurrence in Belize

Abstract

Top-carnivores are often described as umbrella species and are targeted by conservation initiatives meant to preserve entire communities. To evaluate the effectiveness of this strategy it is necessary to determine if top predators negatively impact smaller predators as described by the mesopredator release hypothesis. This study examines jaguar (top-carnivore) and ocelot (mesopredator) densities and patterns of ocelot, puma, and jaguar co-occurrence at four sites in Belize to evaluate mesopredator release within the neotropical carnivore guild. I determined densities and activity rates through remote-camera surveys and analyzed these with respect to habitat characteristics and trapping rates of humans, prey, and other carnivores. I used Sørensen's index to compare patterns of ocelot, jaguar, and puma co-occurrence within all four study sites. Densities ranged from 2.11 to 38.81 ocelots per 100km^2 and from 2.09 jaguars to 5.63 jaguars per 100 km^2 across sites. While there were few differences in structural habitat features between the two sites with intensive habitat data, canopy cover was higher in the Rio Bravo Conservation and Management Area (RBCA). Additionally, three of the five prey groups examined had higher trap success rates in the RBCA. Sørensen's index indicated that patterns of co-occurrence for jaguar-ocelot and puma-ocelot species pairs were alike but also suggested more spatial separation between pumas and ocelots than between jaguars and ocelots. This trend was consistent across 4 study sites. Results suggest that ocelot populations are not negatively affected by high jaguar density, and that high densities in the RBCA may be driven by high canopy cover and prey activity. Preliminary results from the 2 other sites suggest that ocelots are not negatively affected by jaguar or puma activity. These results show that mesopredator release is unlikely to operate in this predator guild and that with careful prioritization of protected areas, jaguars may perform well as an umbrella species for ocelot populations.

Introduction

The ocelot, (*Leopardus pardalis*), and other small predators receive relatively little attention in neotropical conservation. The system's top predator, the jaguar (*Panthera onca*) is considered a potential umbrella, flagship, and landscape species and, therefore, is generally the focus of conservation efforts (Rabinowitz and Nottingham 1986, Noss 1990, Quigley and Crawshaw 1992, Terborgh 1992, Sanderson et al. 2002a, Sanderson et al. 2002b). According to the umbrella species concept preserving the large areas of land required by jaguars should inherently protect all other species in the community whose resource requirements are less extensive than those of the jaguar (Noss 1990, Quigley and Crawshaw 1992, Lambeck 1997). However, there are few studies that directly support this assumption (Sergio et al. 2008) and other ecological considerations involving interspecies competition and intraguild predation could complicate the situation. The mesopredator release hypothesis (MRH) suggests that competition with sympatric carnivores may limit mesopredator populations in areas of high superpredator densities (Brown and Wilson 1956, Crooks and Soule 1999). This implies that selecting areas for the preservation of the jaguar, could be detrimental to smaller carnivores such as the ocelot and calls the umbrella species concept into question. The design of successful conservation programs that protect multiple carnivore species in one area depends on illuminating the relationships between sympatric carnivore populations and on elucidating the strength of mesopredator release effects within ecological systems.

Gehrt and Clark (2003) propose that support for the operation of mesopredator release in a system rests on three predictions: 1) the local abundances of superpredator and mesopredator species should be negatively related, 2) superpredator populations must be a factor limiting mesopredators, and 3) the mesopredator should avoid areas frequented by the superpredator. These predictions depend on high levels of competition between sympatric predator species and the third, in particular, suggests that the mesopredator may be restricted from using certain habitat and prey resources, consistent with competitive niche partitioning (Gause 1934, Schoener 1974). My investigation into the role of mesopredator release in the neotropical carnivore guild, including the ocelot, jaguar, and puma (*Puma concolor*), has concentrated on the third of these predictions; I have provided evidence that ocelots in two sites do not avoid areas used by larger sympatric carnivores and are not restricted to areas of low resource quality as a result (Chapters 2 and 3). To continue this investigation, it is necessary to evaluate the effects of mesopredator release at the population level and to compare multiple sites simultaneously, addressing the first prediction made by Gehrt and Clark (2003).

The population densities of ocelots and jaguars can be readily estimated using modern camera-trapping field techniques and capture-recapture methods due to their individual spot patterns (Silver et al. 2004, Dillon and Kelly 2007). If ocelots are negatively affected by competition with jaguars their densities should be lower in areas of high jaguar density;

conversely, if the umbrella species concept holds true the densities of ocelots and jaguars may be positively related. While such analysis for pumas is more difficult, preliminary data from multiple study areas can be used to provide insight into their role in this guild. The combined results of the previous two chapters suggest that neither pumas nor jaguars negatively affect ocelots. A comparison of within site patterns of puma and jaguar co-occurrence with ocelots may suggest if these findings are supported in other areas.

My objectives for this chapter are as follows:

1) To estimate ocelot and jaguar densities within two sites, the Rio Bravo Conservation Area (RBCA) and Mountain Pine Ridge Forest Reserve (MPR) and compare these to previous estimates from the Chiquibul Forest Reserve and National Park (CFRNP).
2) To discuss the possible implications of those densities in light of the overall site characteristics and previous findings in those areas and to evaluate evidence for the MRH based on those results.
3) To examine patterns of jaguar, ocelot, and puma occurrence among four sites to gain preliminary insight into the role of competition with both pumas and jaguars and to evaluate the potential for MRH effects on a larger scale.

Methods

Fieldwork

We conducted surveys at four study sites following standardized remote camera-trapping techniques designed to target ocelots, pumas, and jaguars as in previous studies (Silver et al. 2004, Maffei et al. 2005, Dillon and Kelly 2007, Kelly et al. 2008). Camera stations included a pair of remote-sensing cameras mounted on opposing sides of a path, trail, or road. Each field site included two camera grids – one nested within the other. The cameras in the larger grid were placed at intervals of approximately 3 km apart, designed for estimating the density of jaguars. The 3 km spacing was chosen based on the smallest home range size estimated for a jaguar of 10km^2 (Rabinowitz and Nottingham 1986) so that every 9 km^2 area will have a camera – minimizing holes in the grid. I then used a smaller camera grid nested inside the jaguar camera grid for the estimation of ocelot density following Dillon and Kelly (2007) who found that using 3 km spacing underestimated ocelot densities. Camera stations in these ocelot grids were placed in between jaguar cameras at approximately 1.5 km apart to accommodate the smallest estimated home range of 2 km^2 maintained by ocelots (Emmons 1988). The aim was to establish at least 40 camera stations per grid (25 forming the jaguar grid, and at least 15 additional nested cameras forming the ocelot grid).

Habitat sampling took place around camera stations within the grids according to the methods outlined in Chapters 2 and 3. I also measured the width of the road or path where each camera was placed. For each study site, I recorded daily rainfall, minimum temperature and maximum temperature for the duration of the field survey at each site. These data were averaged across the study period at each site to document differences in the weather conditions among the four sites as they were surveyed at different times of the year and during different seasons.

Individual camera surveys and study site descriptions

Survey layouts varied by field site due the landscape and specific challenges presented by each area. The four study sites are distributed throughout Belize with varying climates and habitat types (Figure 1.2). The 513.2 km^2 Mountain Pine Ridge Forest Reserve (MPR) and the Chiquibul Forest Reserve and National Park (CFRNP) are adjacent to each other (North to South) in midwestern Belize (Figure 1.2) where rainfall averages 1,500 mm per year with a rainy season from June to January (Johnson and Chaffey 1973). The MPR was established in 1944 and consists primarily of tropical pine forest habitat with some small pockets of broadleaf forest. It has been carefully, but consistently logged since that time. The MPR survey included 47 camera stations and covered a minimum convex polygon (MCP) area of 139.9 km^2 without buffers; 35 of these formed the ocelot grid. Cameras were in operation from 6 June to 18 August 2007 (Table 4.1).

The Rio Bravo Conservation and Management Area (RBCA) study site is in northwestern Belize on the other side of the Western Highway from the CFRNP and MPR. It is approximately 994.8 km^2 in size. The RBCA contains a wide variety of habitat types including savannah, marsh, and pine forest, but is primarily composed of tropical broadleaf forest. This area receives 1,575 mm of rainfall per year and, similar to the other sites, has an annual wet season from June until January (Casado Internet Group 2002). La Milpa Field Station is the only settlement within the RBCA, housing roughly 30 people. A large, high traffic road, Gallon Jug Road, bisects the study site. The camera survey in the RBCA included 40 camera stations, 11 of these stations were originally established on Gallon Jug Road and had to be relocated to a nearby path because of high car traffic and film constraints; this was done within the first month of the study. Data from the original locations of these stations and one other station established late in the survey were included in the density analysis, but were not sampled for habitat characteristics or included in the trap success calculations for this site (Chapter 3) as they were only operation for brief periods of time. Of the 40 stations, 29 were included in the ocelot grid. The entire survey (all cameras included) covered an area of 121.7 km^2 (MCP without buffers) and lasted from 6 January to 9 April 2008 (Table 4.1).

The Cockscomb Basin Wildlife Sanctuary (CBWS) is located on the eastern side of the Maya Mountain divide (opposite from the CFRNP) and generally receives more rainfall than the other study sites. The CBWS is composed of broadleaf forest, which receives an average of 2,500 mm of rain per year and has a wet season lasting from June to February (Ostro 1998). Containing 351.8 km^2 of land, the CBWS is the world's only Jaguar Preserve and was established in 1986. The area is a popular tourist location and has an extensive trail network. The CBWS survey included 40 cameras and covered an area of 100.1 km^2 (MCP without buffers). Fieldwork at this site was conducted from 5 April 2008 until 30 July 2008 and resulting in an 116 day survey with 2,467 trap-nights (Table 4.1). While an ocelot grid including 28 of the stations was established and habitat was sampled at all 40 stations, the data analysis for this site (including the calculation of density estimates) is still underway; only preliminary results based on presence-absence data of the ocelot, puma, and jaguar are presented here.

The final site, the Chiquibul Forest Reserve and National Park (CFRNP) is located to the southeast of the MPR. This protected area was established in 1956 and now covers 1,671.9 km^2. The CFRNP has a subtropical moist climate and consists mostly of tropical broadleaf forest. There is one field research station, Las Cuevas Research Station, inside the reserve and some parts of the area have been and still are selectively logged (Casado Internet Group 2002). The CFRNP survey included 29 camera stations and covered an area of 146.5 km^2 (MCP without buffers). Establishing camera stations in the CFRNP was hindered by poor road conditions and by the activity of poachers within the protected area. Increased illegal activity, theft of equipment, and safety risks caused me to end the survey prematurely. Cameras were operational for 59 days between 21 June and 19 August 2008, but this resulted in only 644 trap-nights (Table 4.1). These problems may reduce the reliability of the estimates of density and activity (based on trap success). Therefore, I will use previous density estimates for comparison with the MPR and

RBCA estimates. In addition, I will present preliminary results based on more robust presence-absence data of ocelots, pumas and jaguars at the 29 stations.

Density analysis for the MPR and RBCA

To estimate ocelot and jaguar densities within the MPR and RBCA, I identified individuals by their distinct spot patterns and recorded the date and location of each photographic capture. For ocelots, I used only photographic captures from cameras forming the ocelot grids to create individual capture histories. For jaguars, captures from all cameras in the site surveys were included. I collapsed survey periods (72 days for the MPR and 90 days for the RBCA) into multiple 4, 5, or 6 day long capture occasions to increase the estimated daily probability of capture for ocelots and jaguars at that study site allowing for more precise density estimation. I created a capture history for each individual; if an individual was photographed at least once during each capture occasion it was recorded as a 1, while the lack of a capture within one of these periods was recorded as a zero. A list of capture histories for each species (jaguar or ocelot) and site were analyzed using the program CAPTURE (Otis et al. 1978, Rexstad and Burnham 1991), which tests for population closure and uses a variety of models to generate abundance estimates based on the number of individuals photographed and their capture probabilities. Models tested vary some combination of individual capture probabilities (M(h): heterogeneity model), rates of initial capture versus recapture (M(b): behavior model), and the influence of time on capture probabilities (M(t): time model), or none of these (M(o): the null model, assuming a constant capture probability for all individuals); CAPTURE uses discriminant function analysis procedures to allow selection of the model best suited to each dataset.

The effective trap area of each grid was determined by calculating a buffer value equal to one-half the mean maximum distance moved (½ MMDM) among all individuals (of the target species) recaptured at least once and using this buffer as a radius around each camera station (Wilson and Anderson 1985, Karanth and Nichols 1998). Buffers were then dissolved and the total area estimated using ArcGIS. To determine the maximum distance moved by each individual, captures from all camera stations were used for both ocelots and jaguars (whether or not they were a part of the ocelot grid); I did not include distances for individuals who were captured only once and therefore had a MMDM of 0 km. Due to the high number of one-sided ocelot and jaguar photos at RBCA, I used only photos from left sides for ocelots and right sides for jaguars to create the capture histories and estimate abundances. These particular sides were used because camera malfunctions and field errors meant that the dates and locations associated with some photos were lost and by chance, these malfunctions affected captures of opposite sides for each species. After calculating abundance estimates, I then divided by the effective area sampled to estimate densities of jaguars and ocelots in the MPR and RBCA and calculated 95% confidence intervals on these densities using methods outlined by Nichols and Karanth (2002).

Estimates of site characteristics for the MPR and RBCA

To characterize the habitat features and relative activity levels of other animals (including humans) in MPR and RBCA I averaged the values estimated from each camera station as outlined in Chapters 2 and 3. Trap success rates calculated as the number of captures per 100 trap-nights (TN) at a station were used as a measure of relative activity for species and groups of species. Habitat sampling and calculation of trap success values for ocelots, jaguars, pumas, humans (both in car and on foot), other small carnivores and prey groups was completed for 47 stations in the MPR and 39 stations in the RBCA. Prey groups included small mammalian prey (< 5 kg), medium mammalian prey (5 – 15 kg), large mammalian prey (> 15 kg), small avian prey (< 1 kg), and large avian prey (> 1 kg). All small carnivore species (not ocelots, jaguars, or pumas) were also combined into one group for analysis.

Comparison of presence-absence patterns for the ocelot, jaguar, and puma at all four sites

We recorded the presence and absence of ocelots, jaguars, and pumas at all camera stations; if a species was captured at a station at least once it was recorded as present, and if it was not captured during the survey period I assumed that species was absent from that location. For the RBCA I did not include the original location of stations that had been moved early in the study; I included all other camera locations (40 stations total). I used Sørensen's index of similarity to compare patterns of jaguar-ocelot, puma-ocelot, and jaguar-puma co-occurrence within the MPR, RBCA, CBWS, and CFRNP; this was calculated using species presence-absence data from camera stations within each site. Sørenson's index was calculated for these species pairs as $\frac{2a}{2a+b+c}$ where a is the number of stations with both species present, b is the number with one present (ocelots in this study), and c is the number of stations with only the second species present (either pumas or jaguars) (Pielou 1984). This is a relative index of similarity used only to compare similarity of species pairs within sites (not among sites). I used a nonparametric bootstrapping procedure to calculate confidence intervals. This procedure included 100 iterations in which n traps (n = number of stations included at that study site) were sampled with replacement and Sørensen's index was recalculated. I then took the inner 95 % quantile of these results.

Results

Density estimates were completed for both ocelot and jaguar populations in the MPR and RBCA and estimates from a previous survey in the CFRNP were used for comparison (Table 4.2, Fig. 4.1). The MPR camera survey lasted 72 days and resulted in a total of 2,894 trap-nights. Based on the captures of 3 individuals, CAPTURE yielded an abundance estimate of 4 ocelots in the area surveyed. The best model was the heterogeneity model, M(h), which assumes that each individual has a unique capture probability. Based on ½ of the MMDM the estimated effective area sampled was 189.2 km^2 and ocelot density for the MPR was estimated to be 2.11 ± 0.83 individuals per 100 km^2 (Table 4.2, Fig. 4.1, Fig. 4.2).

Jaguar density in the MPR was very similar to that estimated for ocelots. Ten individual jaguars were captured in the MPR resulting in an abundance estimate of 10 jaguars for the area sampled. Results from CAPTURE suggested that the behavior model, which allows for a different rate of initial capture and recapture, was most appropriate; initial probability of capture was 0.22 while probability of recapture was 0.48. Based on ½ MMDM, an effective area surveyed of 478.6 km^2 was calculated and jaguar density was estimated to be 2.09 ± 0.36 per 100 km^2 (Table 4.2, Fig. 4.1, Fig. 4.2).

The RBCA survey lasted 90 days and resulted in 2,510 trap-nights. Density estimates for both jaguars and ocelots were higher in the RBCA than in the MPR. Twenty-eight individual ocelots were captured in the RBCA resulting in an abundance estimate of 39 ocelots using the heterogeneity model, M(h). The estimated effective area sampled, based on ½ MMDM, was 100.5 km^2 producing a density estimate of 38.8 ± 6.69 ocelots per 100 km^2. However, it should be noted that 12 of the 28 individuals captured were photographed only once and the population violated the assumption of closure (Table 4.2; Fig. 4.1, Fig 4.3). While this means that the accuracy of this density estimate may be uncertain, the use of the heterogeneity model, M(h), yields density estimates with larger standard errors and is likely more robust to violations of model assumptions than other models used (such as M(o), M(b), or M(t); Nichols and Karanth 2002).

The capture of 15 individuals led to an abundance estimate of 17 jaguars in the RBCA using the heterogeneity model, M(h). Buffering the grid with ½ the MMDM of the jaguars captured resulted in an effective area sampled of 301.7 km^2, and finally a density estimate of 5.63 ± 1.20 jaguars per 100 km^2 (Table 4.2, Fig 4.1, Fig. 4.3). This is more than twice the jaguar density estimated in the MPR; however, it should be noted that the 95 % confidence intervals for the jaguar density estimates in these two areas show slight overlap (Table 4.2).

Previous estimates of jaguar and ocelot densities from surveys completed in 2003 (Dillon 2005; Kelly unpublished data) were used for the CFRNP. Dillon (2005) conducted a camera survey in this study area from 20 August to 24 September 2003. The capture of 9 ocelots led to an abundance estimate of 11 individuals using M(h). The estimated effective area sampled based on a small ocelot grid was 38.64 km^2, leading to a density estimate of 28.5 ± 12.54 ocelots per 100 km^2 (Dillon 2005; Table 4.1, Fig. 4.1). The jaguar survey from that year lasted from 16 June until 22 July 2003 and photographically captured 11 jaguars and resulted in an estimate of 13 individuals using M(h). The effective area sampled was estimated to be 343.18 km^2 and a density estimate of 3.79 ± 1.19 jaguars per 100 km^2 was calculated (Kelly unpublished data; Table 4.1, Fig 4.1).

Comparison of site characteristics for the MPR and RBCA

The mean habitat and trap success characteristics of the MPR and RBCA are listed for comparison in Table 4.3. Mean ocelot trap success in the RBCA (4.90 ± 0.74 captures per 100 TN) was nearly 9 times the mean trap success rate observed in the pine forest (0.55 ± 0.21 captures per 100 TN; Fig. 4.6). Similarly, puma trap success was over 3 times higher in the RBCA ($\bar{x}$ = 2.49 ± 0.48 captures per 100 TN) than in the MPR ($\bar{x}$ = 0.66 ± 0.20 captures per 100 TN; Fig. 4.7); however, jaguar trap success in the RBCA ($\bar{x}$ = 2.46 ± 0.42 captures per 100 TN) was only one third of that observed in the pine forest ($\bar{x}$ = 7.56 ± 1.28 captures per 100 TN; Fig. 4.8).

Many of the structural habitat characteristics including canopy height, understory cover and understory heterogeneity varied little between the MPR and RBCA (Table 4.2). Only canopy cover, and path width were notably different between the two areas; canopy cover in the RBCA averaged 77.6 ± 2.11 % compared to a mean canopy cover of only 25.7 ± 2.83 % in the MPR. Mean road or path width was generally higher in the MPR ($\bar{x}$ = 420 ± 16.25 cm) than in the RBCA ($\bar{x}$ = 248 ± 13.62 cm). Tree density in the RBCA ($\bar{x}$ = 1354 ± 64.7 trees per ha) was also higher than in the MPR ($\bar{x}$ = 911 ± 91.3 trees per ha) but showed much within site variation (indicated by large standard errors; Table 4.3).

Small mammalian prey trap success rates were on average four times higher in the RBCA (4.92 ± 1.12 captures per 100 TN) compared to the MPR (1.19 ± 0.34 captures per 100 TN). Large avian trap success rates were almost 8 times higher in the RBCA ($\bar{x}$ = 17.50 ± 4.78 captures per 100 TN) as those observed in the MPR ($\bar{x}$ = 2.21 ± 0.66); however, the standard error for the RBCA is high indicating a lot of within site variation. Large mammalian prey trap success rates were also higher in the RBCA, while small avian trap success rates were lower in that area (higher in the MPR), but both of these groups showed much within site variation and had large standard errors; medium mammalian trap success rates showed almost no difference between the two study sites (Table 4.3).

Small carnivore trap success was much higher in the MPR ($\bar{x}$ = 33.42 ± 6.34) than in the RBCA ($\bar{x}$ = 5.51 ± 1.55). However, the recorded captures from this group were dominated by the activity of grey fox (*Urocyon cinereoargenteus*) in the MPR; this species was captured more often than any other non-human species – 912 times throughout the survey period. Finally human trap success was lower in the MPR ($\bar{x}$ = 58.45 ± 4.49) than in the RBCA ($\bar{x}$ = 179.77 ± 94.35) where two camera stations were set up along the high-traffic Gallon Jug road; however, the RBCA showed much within site variation in human trap success (large standard error; Table 4.3).

Patterns of ocelot, puma, and jaguar co-occurrence

In the MPR, ocelots were present at 10 stations, pumas at 11, and jaguars at 41 stations (out of 47 camera stations total). In the RBCA, 40 stations were examined for felid presence; ocelots were present at 30 stations, jaguars at 25 stations and pumas at 22 stations. In the CBWS, there were 40 stations; ocelots were captured at 28 of those locations, jaguars at 28 stations and pumas at 24 stations. There were 29 stations established in the CFRNP; ocelots were photographed at 10 locations, jaguars at 9 locations and pumas at 7 camera locations in that area.

At all sites (MPR, RBCA, CBWS, and CFRNP) Sørensen’s index for jaguar-ocelot co-occurrence was higher than the index for puma-ocelot co-occurrence, implying a consistent pattern with a higher degree of similarity between ocelots and jaguars than between ocelots and pumas. Sørensen’s index for jaguar-puma co-occurrence was the highest of all 3 pairs examined in the CBWS and MPR, relatively low in the RBCA and was mid-range in the CFRNP.

However, confidence intervals were wide and overlapped among all pairs within each study site suggesting that the observed differences were not statistically significant (Table 4.4).

Weather conditions

Mean temperatures were generally higher in the MPR and CBWS than in the RBCA and CFRNP; but there was generally little variation in minimum and maximum daily temperatures among or within study sites (Table 4.4). Daily rainfall was much lower in the RBCA ($\bar{x}$ = 2.24 ± 0.652 mm per day) compared to the MPR, CBWS, and CFRNP where mean rainfall ranged from 6.76 to 10.4 mm per day among sites (Table 4.5).

Discussion

Densities

Density estimates for the ocelot and jaguar in the MPR, RBCA and previous estimates for the CFRNP (Dillon 2005 (ocelots); Kelly, unpublished data (jaguars)) suggest that the populations of these two felids are not negatively related (Fig. 4.1) and this conflicts with the predictions of the mesopredator release hypothesis (Gehrt and Clark 2003). Mesopredator release mediated by jaguar populations does not appear to play a strong role in ocelot ecology in these protected areas in Belize. This finding is consistent with previous results from these sites suggesting that competition levels are low and that jaguars do not negatively affect ocelot activity (Chapters 1 and 2). The two broadleaf sites, RBCA and CFRNP have similar and relatively high densities compared to the pine forest of the MPR. The coexistence of high population densities in the RBCA and CFRNP could be particularly important for conservation efforts as it implies that by prioritizing areas with high jaguar densities it may be possible to protect ocelot populations as well (umbrella species concept), especially if high resource areas with abundant prey are selected (see below).

Because the ocelot density estimate for the RBCA resulted from a population that violated the assumption of population closure this estimate may be inflated and should be treated cautiously. This violation most likely occurred because many of the 28 individuals identified were captured only once, suggesting they may be transient in the study area. However, given the magnitude of the RBCA density estimate (38.81 ocelots per 100 km^2) compared to that found in the MPR (2.11 ocelots per 100 km^2) it is very likely that the actual density of the ocelot population is higher than that found in the MPR. Additionally, the identification of 28 individuals, transient or not, suggests that the RBCA despite its high jaguar density is more suited to ocelot use than the MPR where only 3 individuals were identified.

These results are further supported by the higher ocelot activity level (based on trap success) seen in the RBCA. However, the use of trap success as a relative index of abundance without identification of individuals has been criticized (Carbone et al. 2002, Jennelle et al. 2002) and a comparison of jaguar trap success levels between the two sites highlights the pitfalls of this index. The higher jaguar trap success found in the low density MPR is reflected in the relatively low number of individuals identified (10 compared to 15 in RBCA) and high probability of recapture (compared to that of initial capture); this indicates that jaguars in the MPR are "trap-happy" as suggested by the selection of M(b) as the best model. This may be because the jaguars captured in the MPR are highly dependent on the road system and if captured once are likely to be captured again while foraging for prey. Alternatively, it could indicate that pine forest habitat may be less than ideal for jaguars; low resource levels may necessitate wide-ranging behavior resulting in high capture rates from relatively few individuals.

Comparison of MPR and RBCA site characteristics

While MPR is composed of pine forest and RBCA of broadleaf, the two sites differed noticeably in only two structural habitat variables measured by this study: canopy cover and mean road width. Low canopy cover observed in the pine forests could be one cause of the low cat densities seen there. Both jaguars and ocelots are known to prefer dense forest areas (Rabinowitz and Nottingham 1986, Ludlow and Sunquist 1987, Emmons 1988, Sunquist and Sunquist 2002) and ocelots in particular have been known to be sensitive to low levels of canopy cover (Shindle 1995, Horne 1998, Harveson et al. 2004). While I did not observe a relationship between ocelot activity and canopy cover on a local scale within sites, it may be that ocelots are responding to this feature on a larger landscape scale. Ocelots may be responding to the consistently high canopy cover seen with the RBCA. Higher canopy cover is a typical characteristic of broadleaf forests, may provide better cover for hunting and may also be associated with higher prey abundances in broadleaf areas. Road width, the other variable to differ between the two sites, is unlikely to cause the observed difference in densities. Cats seem likely to respond positively to wider roads that may offer better foraging routes; this is supported by the positive relationship between ocelot activity and road width in the RBCA (Chapter 3).

Prey activity levels were higher in the RBCA than in the MPR for three of the five prey groups examined. In fact, only small avian prey showed an indication of higher activity levels in the pine forest site. Despite caveats regarding the use of trap success rates as indicators of local abundance this seems to imply that abundant prey resources may also be partially responsible for the high densities of jaguars and ocelots in the RBCA study site. This seems especially likely given that ocelots and jaguars in the RBCA showed a particularly strong association with large avian prey, the prey group that showed the highest activity rates in the broadleaf RBCA and low activity in the pine forest (Table 4.3). Low prey activity may consequently be one reason for the low densities observed in the MPR. Additionally, based on trap success comparisons it appears that pumas are also more active in the RBCA and may similarly benefit from higher quality resources of the broadleaf forest, but as explained above such conclusions based on trap success rates must be treated cautiously.

Finally, it is also possible that differences between these sites could be attributed to seasonal differences in species activity patterns. Lower daily rainfall and temperatures in the RBCA may cause cats (and other species) to be more active, travel more widely, and elevate trap success rates. While I cannot completely rule out the influence of these patterns on my results the difference in mean temperatures between the two sites is low and previous studies conducted at different times of the year within the same study site showed no differences between wet and dry season density estimates (Dillon 2005; Kelly unpublished data), therefore these differences in temperature and rainfall from site to site are unlikely to cause the patterns in these results. The results presented here support the conclusions of Chapter 2 and 3 that unsuitable habitat may cause the low ocelot (and jaguar) abundance seen in the MPR and that predator coexistence in the RBCA may be facilitated by abundant prey resources.

Patterns of co-occurrence and implications for upcoming analyses of the CFRNP and CBWS

While there were no definitive differences between jaguar-ocelot and puma-ocelot patterns of occurrence within sites, there is an interesting trend suggesting that ocelots may overlap less with pumas than jaguars at all four sites visited. This would make sense given evidence from the RBCA implying that there may be some partitioning of prey resources between ocelots and pumas. Ocelots are closer in body size to pumas, and likely overlap more with pumas in their use of prey resources than they do with jaguars; studies show that jaguars rely more on larger prey than either pumas or ocelots. This fact and the positive relationships seen between ocelot and jaguar activity in the MPR and RBCA (Chapters 2 and 3) could mean that mesopredator release operates on multiple levels with in this guild; pumas have been known to show spatial avoidance of jaguars in other parts of the neotropics (Schaller and Crawshaw 1980, Emmons 1987, Scognamillo et al. 2003) and this could indirectly result in ocelots using areas with jaguar activity more frequently to avoid pumas. However, levels of spatial overlap (as measured by Sørensen's index) between jaguars and pumas are relatively high and similar to those recorded for the other felid pairs considered. Additionally, since there is little evidence from the RBCA and MPR that ocelots are negatively affected by puma activity (Chapters 2 and 3), the possible resource partitioning between pumas and ocelots appears unlikely to be causing mesopredator release effects.

The lack of support for the MRH is consistent across all sites considered, including both pine and broadleaf sites. This could imply that the underlying interspecies interactions are independent of the variations in felid abundance, community composition, and habitat structure among sites. Conducting similar habitat and density analyses to those done in the MPR and RBCA at the remaining two field sites (the CBWS and CFRNP) will allow me to determine how representative the results are from the first two surveys and to characterize patterns of felid coexistence within this guild over a wider geographic area. Additionally, identifying individual pumas using scars, tail kinks, undercoat patterns and other features will allow the estimation of puma density at all four sites following the methods of Kelly et al. (2008) and provide insight into the intensity of puma-ocelot interactions in this system.

Mesopredator release and future research

The apparent similarity of felid co-occurrence patterns at the MPR and RBCA to those at CBWS and CFRNP, suggests that forthcoming analyses at the latter sites will confirm findings from the first two study sites. The observation of mesopredator release effects in this carnivore guild is unlikely because competition levels do not appear to be limiting ocelot populations as required for mesopredator release to take place.

Consistent results from the CBWS and CFRNP would indicate a lack of mesopredator release effects across four different study sites and two different forest types (pine and broadleaf), and may mean that levels of interspecies competition within this guild are generally very low. Ocelot, jaguar, and puma populations may be limited by other ecological mechanisms allowing all three predators to simultaneously exploit areas with abundant prey populations that reduce competition. Given the territorial nature of felids and the relatively low rates of reproduction within this family (for a review of all felid species see Sunquist and Sunquist 2002), these populations may be self-limiting through intraspecies competition and inherent reproductive ceilings. Additionally, competitive effects among species may be further reduced by the dense forest environment these cats inhabit; actual encounters between these wide-ranging felids may be too uncommon for interspecies territoriality to be an ecologically important force. Previous studies of mesopredator release have often focused temperate forests or on mesopredator pest species that are locally abundant such as raccoons, opossums or rats (Crooks and Soule 1999, Ginger et al. 2003, Helldin et al. 2006, Rayner et al. 2007) unlike the rare felids examined here.

Future studies should concentrate on validating these results at other study sites over a wider geographic area and over a longer period. All of the study sites are in Belize, a country that covers only a small part of the ocelots and jaguars' geographic range; therefore, extrapolations to other neotropical areas should be undertaken with caution. Furthermore, due to time constraints, I am unable to overcome the effects of seasonal variation among study periods at the different sites within Belize; differences in temperature and rainfall could affect species activity patterns. Monitoring activity and population levels in the same areas over multiple years would allow the comparison of trends over time and would provide stronger evidence for relationships between the densities of these carnivores. Finally, the sensitivity of techniques used here should be validated in other sites, and possibly with other species. This study may rely too heavily on monitoring activity along roads and may not fully illustrate the patterns of avoidance and resource partitioning I am investigating (for more discussion of this issue see Chapter 3); it would be good to verify the usefulness of these methods in a community where mesopredator release has already been observed using other techniques.

Conclusions

The neotropical carnivore guild includes at least three large felid species of conservation concern: the ocelot, the puma, and the jaguar. While the umbrella species concept suggests that protecting the largest of the three should be enough to simultaneously protect the other two, the mesopredator release hypothesis raised doubts about the validity of the assumptions made when designing conservation plans based on one top predator species. I present evidence that this is not the case, and mesopredator release may not operate in this predator community as I had hypothesized. I found evidence that jaguar and ocelot densities for the RBCA, MPR, and CFRNP are not negatively related across sites. The RBCA and the MPR had the highest and lowest densities, respectively, of both jaguars and ocelots. Differences between these two sites suggest that higher canopy cover and prey abundance could be at least partially responsible for the ability of high density populations of ocelots and jaguars thrive in the same area. Results suggest that the other large felid, the puma, may compete more with ocelots resulting in some spatial separation. While in theory this could result in mesopredator release operating on multiple levels with this guild (with ocelots using areas of high jaguar activity that may be avoided by pumas), levels of overlap between pumas and jaguars were relatively high and it does not appear that such an effect is likely to play a strong role in ocelot ecology. Additionally, preliminary information on the co-occurrence patterns of ocelots, pumas, and jaguars within the CFRNP and CBWS suggests that the results from the RBCA and MPR may be representative of other protected areas in Belize. When designing conservation plans based on the distribution of top carnivore populations, priority should also be given to sites with high productivity and high prey abundance. Evidence from this and previous chapters suggests that ocelot populations are not restricted by mesopredator release and that the jaguar could, when managed with caution, act as an umbrella species for the ocelot.

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Table 4.1: Characteristics of study sites and camera surveys conducted in each site between June 2007 and August 2008. Sites included the Mountain Pine Ridge Forest Reserve (MPR), the Rio Bravo Conservation and Management Area (RBCA), the Cockscomb Basin and Wildlife Sanctuary (CBWS) and the Chiquibul Forest Reserve and National Park (CFRNP).

Site	Dominant forest type	Reserve Size (km^2) [a]	Yearly rainfall (mm)	Number of stations [b]	Camera grid size (MCP without buffers)	Survey length	Trap-nights
MPR	Pine	513.2	1500	47	139.9	72	2894
RBCA	Broadleaf	994.8	1575	40	121.7	90	2510
CBWS	Broadleaf	351.8	2500	40	100.1	116	2467
CFRNP	Broadleaf	1671.9	1500	29	146.5	59	644

[a] Data on size and rainfall obtained from Johnson and Chaffey (1973), Casado Internet Group (2002), and Ostro (1998).

[b] Cameras stations were set up in a grid spaced 1.5 – 3.0 km apart. See text for detailed survey methods.

Table 4.2: Parameters associated with the estimation of abundance, area sampled, tests of population closure and final density estimates for jaguars and ocelots at 3 sites in Belize. Remote camera surveys were completed in the Mountain Pine Ridge Forest Reserve (MPR) from June to August of 2007 and in the Rio Bravo Conservation and Management Area (RBCA) from January to April of 2008. Data from past surveys completed in the Chiquibul Forest Reserve and National Park (CFRNP) in 2003 are presented for comparison.

Model parameter [a]	Ocelot			Jaguar		
	MPR	RBCA	CFRNP	MPR	RBCA	CFRNP
No. of individuals captured	3	28	9	10	15	11
Capture occasions [c]	14	15	16	18	18	17
Model used [d]	M(h)	M(h)	M(h)	M(b)	M(h)	M(h)
Mean capture probability; recapture probability [e]	0.1607	0.1060	0.0660	0.2222;0.4815	0.1340	0.0314
½ MMDM (km)	3.31	1.48	1.23	4.59	3.57	5.59
Abundance Estimate	4	39	11	10	17	13
Effective area sampled (km^2)	189.2	100.5	38.64	478.6	301.7	343.2
Test for violation of closure						
Z-score	0.079	-3.394	-0.739	-1.355	-1.146	-0.416
P-value	0.5315	0.0002	0.2300	0.0878	0.1259	0.3388
Density estimate (individuals per 100 km^2)	2.11	38.8	28.5	2.09	5.63	3.79
95 % confidence intervals						
Lower limit	0.49	25.70	3.89	1.39	3.29	1.46
Upper limit	3.74	51.9	53.1	2.79	7.98	6.12

[a] Density estimates were completed for the Mountain Pine Ridge Reserve (MPR) in 2007 and Rio Bravo Conservation and Management Area (RBCA) in 2008 at the same time other data on site characteristics was collected.

[b] Density estimates for the Chiquibul Forest Reserve and National Park (CFRNP) for ocelots are based on a survey completed from 20 August 2003 to 24 September 2003 (Dillon 2005) and for jaguars are based on a survey completed from 16 June 2003 to 22 July 2003 (Kelly unpublished data).

[c] Surveys were collapsed into multi-day capture occasions. The 72 day MPR survey was collapsed into 5-day periods for ocelots and 4-day periods for jaguars. The 90 day RBCA survey was collapsed by 6-day periods for ocelots and 5-day periods for jaguars. See methods in text for more details.

[d] The most appropriate model type for the data was selected using program capture. The heterogeneity model, M(h), assumes that different individuals may have different capture probabilities. The behavior model, M(b), assumes that the probability of recapture may be different from the probability of first capture.

[e] Recapture probabilities are only calculated in the case that M(b) is used.

Table 4.3: Summary of habitat and trap success characteristics from 47 camera stations in the Mountain Pine Ridge Forest Reserve (MPR) and and 39 camera stations in the Rio Bravo Conservation and Management Area (RBCA). Data were collected in the MPR from June to August of 2007 and in the RBCA from January to April of 2008.

	MPR (n = 47)			RBCA (n = 39)		
Site characteristic [a]	Mean (SE)	Min	Max	Mean (SE)	Min	Max
Ocelot trap success (captures per 100 trap nights) [b]	0.55 (0.21)	0	7.69	4.90 (0.74)	0	17.88
Jaguar trap success (captures per 100 trap nights)	7.56 (1.28)	0	42.19	2.46 (0.42)	0	8.96
Puma trap success (captures per 100 trap nights)	0.66 (0.20)	0	4.84	2.49 (0.48)	0	10.45
% canopy cover [c]	25.7 (2.83)	0	96.7	77.6 (2.11)	50.0	95.0
Canopy height (m)	11.80 (0.50)	6.56	20.94	11.3 (0.42)	6.47	21.4
% understory cover	78.8 (2.42)	26.7	100	80.4 (1.13)	57.5	97.5
Understory heterogeneity (%)	17.3 (1.97)	0	53.5	14.6 (1.01)	3.58	42.9
Tree density (No. per ha.)	911 (91.3)	120	3327	1354 (64.7)	487	2360
Path or road width	420 (16.25)	230	700	248 (13.62)	115	570
Small mammalian prey trap success	1.19 (0.34)	0	9.84	4.92 (1.12)	0	29.41
Medium mammalian prey trap success	1.40 (0.27)	0	7.14	1.44 (0.34)	0	7.94
Large mammalian prey trap success	2.66 (0.48)	0	12.12	5.04 (1.23)	0	45.76
Small avian prey trap success	5.26 (1.74)	0	65.67	2.74 (1.25)	0	41.54
Large avian prey trap success	2.21 (0.66)	0	25.00	17.50 (4.78)	0	148.61
Small carnivore trap success	33.42 (6.34)	0	216.07	5.51 (1.55)	0	48.44
Human Trap Success	58.45 (4.49)	17.74	184.38	179.77 (94.35)	10.71	2865.63

[a] Site characteristics are based on fieldwork completed in MPR from June – August 2007 and in RBCA from January – April 2008.

[b] Trap success, a measure of relative activity levels, was calculated for each species/group as the number of photographic captures per 100 trap-nights.

[c] Habitat was characteristics were sampled at each camera station for the MPR (n = 47) within a 200 m radius and for the RBCA (n = 39) within a 100 m radius according to the methods outline in Chapters 2 and 3. Values from all stations sampled within each site were averaged to produce site estimates.

Table 4.4: Similarity of jaguar-ocelot, puma-ocelot, and jaguar-puma co-occurrence patterns within 4 sites in Belize represented using Sørensen's Index. Sites included the Mountain Pine Ridge Forest Reserve (MPR), the Rio Bravo Conservation and Management Area (RBCA), the Cockscomb Basin and Wildlife Sanctuary (CBWS) and the Chiquibul Forest Reserve and National Park (CFRNP). Data were collected all sites between June 2007 and August 2008.

Study site [a]	Species pair	Number of stations sampled within site	Number of stations with at least one species of pair present	Sørensen's Index	Bootstrap 95% confidence intervals Lower limit	Bootstrap 95% confidence intervals Upper limit
MPR [b]	Jaguar-ocelot	47	41	0.39	0.25	0.55
	Puma-ocelot	47	18	0.29	0.26	0.54
	Jaguar-puma	47	41	0.42	0.23	0.58
RBCA	Jaguar-ocelot	40	31	0.87	0.77	0.95
	Puma-ocelot	40	33	0.73	0.57	0.85
	Jaguar-puma	40	30	0.72	0.54	0.84
CBWS	Jaguar-ocelot	40	35	0.75	0.60	0.88
	Puma-ocelot	40	34	0.69	0.54	0.82
	Jaguar-puma	40	32	0.77	0.64	0.86
CFRNP	Jaguar-ocelot	29	15	0.42	0.12	0.70
	Puma-ocelot	29	15	0.24	0	0.53
	Jaguar-puma	29	14	0.25	0	0.56

[a] Sørenson's index was calculated using data on the presence of each felid species in two pairs (jaguar-ocelot, puma-ocelot, and jaguar-puma) following Pielou (1984). Presence (or absence) of each species at each camera station with each site was recorded. If a species was photographed at a station during the survey period it was considered present; if no photographs were obtained it was assumed to be absent from that location.

[b] This index is comparable only between species pairs within study sites; comparisons of absolute values across study sites are not supported.

Table 4.5: Mean daily rainfall, minimum and maximum temperatures during survey periods at four study sites in Belize. Sites included the Mountain Pine Ridge Forest Reserve (MPR), the Rio Bravo Conservation and Management Area (RBCA), the Cockscomb Basin and Wildlife Sanctuary (CBWS) and the Chiquibul Forest Reserve and National Park (CFRNP). Data were collected at all sites during indicated survey periods between June 2007 and August 2008.

Site	Survey Period	Mean (SE) daily rainfall (mm)	Mean (SE) daily temperature minimum (°C)	Mean (SE) daily temperature maximum (°C)
MPR	June – August 2007	10.4 (4.716)	22.8 (0.189)	30.8 (0.290)
RBCA	January – April 2008	2.24 (0.652)	18.7 (0.296)	30.2 (0.277)
CBWS	April – July 2008	6.76 (2.296)	23.2 (0.355)	31.7 (0.380)
CFRNP	June – August 2008	7.58 (2.210)	20.5 (0.200)	30.0 (0.250)

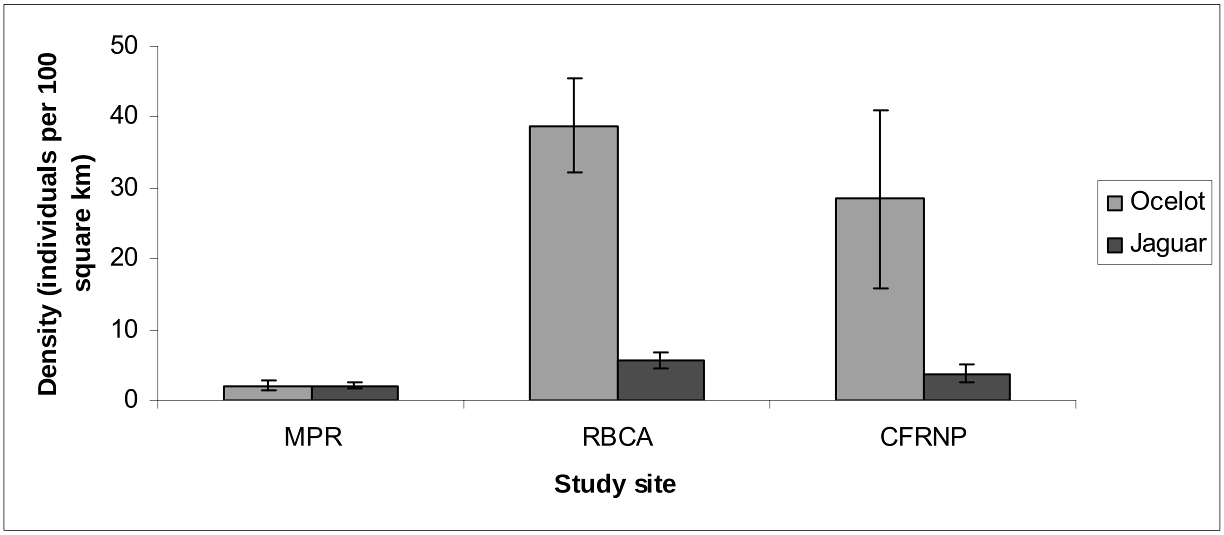

Figure 4.1: Density estimates (with standard errors) for the ocelot and jaguar across three study sites are shown. Estimates were calculated using mark-recapture techniques following Nichols and Karanth (2002) using data from remote camera surveys. Remote camera surveys were conducted in the Mountain Pine Ridge Forest Reserve (MPR) from June to August of 2007, and in the Rio Bravo Conservation and Management Area from January to April of 2008. Density estimates for the Chiquibul Forest Reserve and National Park (CFRNP) for ocelots are based on a survey completed from August 2003 to September 2003 (Dillon 2005) and for jaguars are based on a survey completed from June 2003 to July 2003 (Kelly unpublished data). See text for more details on the methods used for density estimation.

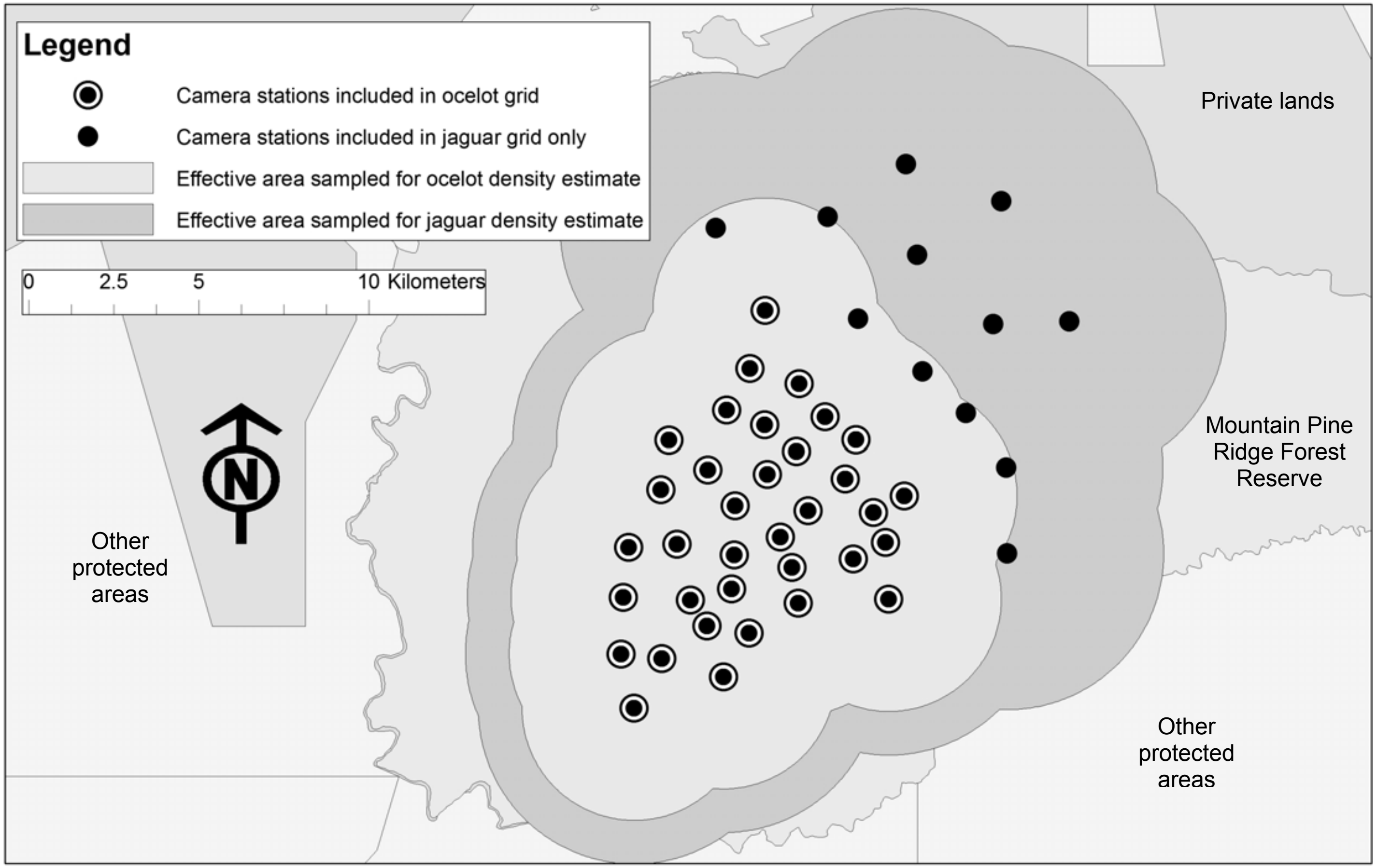

Figure 4.2: The two camera grids comprising the Mountain Pine Ridge Forest Reserve survey from June to August of 2007 are shown. The "ocelot grid" included 35 cameras spaced approximately 1.5 km apart nested within a larger "jaguar grid" and was used to obtain photographic "captures" of ocelots to produce ocelot density estimates. The effective area sampled of the ocelot grid was estimated to be 189.18 km^2 using ½ the mean maximum distance moved (MMDM) of all ocelots captured. The larger jaguar grid included 12 additional cameras spaced 3 km apart. Captures of jaguars from cameras within both the ocelot and jaguar grids were used to estimate jaguar densities. The effective area sampled of this combined grid was 478.55 km^2 based on ½ MMDM of all jaguars captured. All 47 camera stations were used in estimating site characteristics and evaluating patterns of felid occurrence (based on presence/absence data).

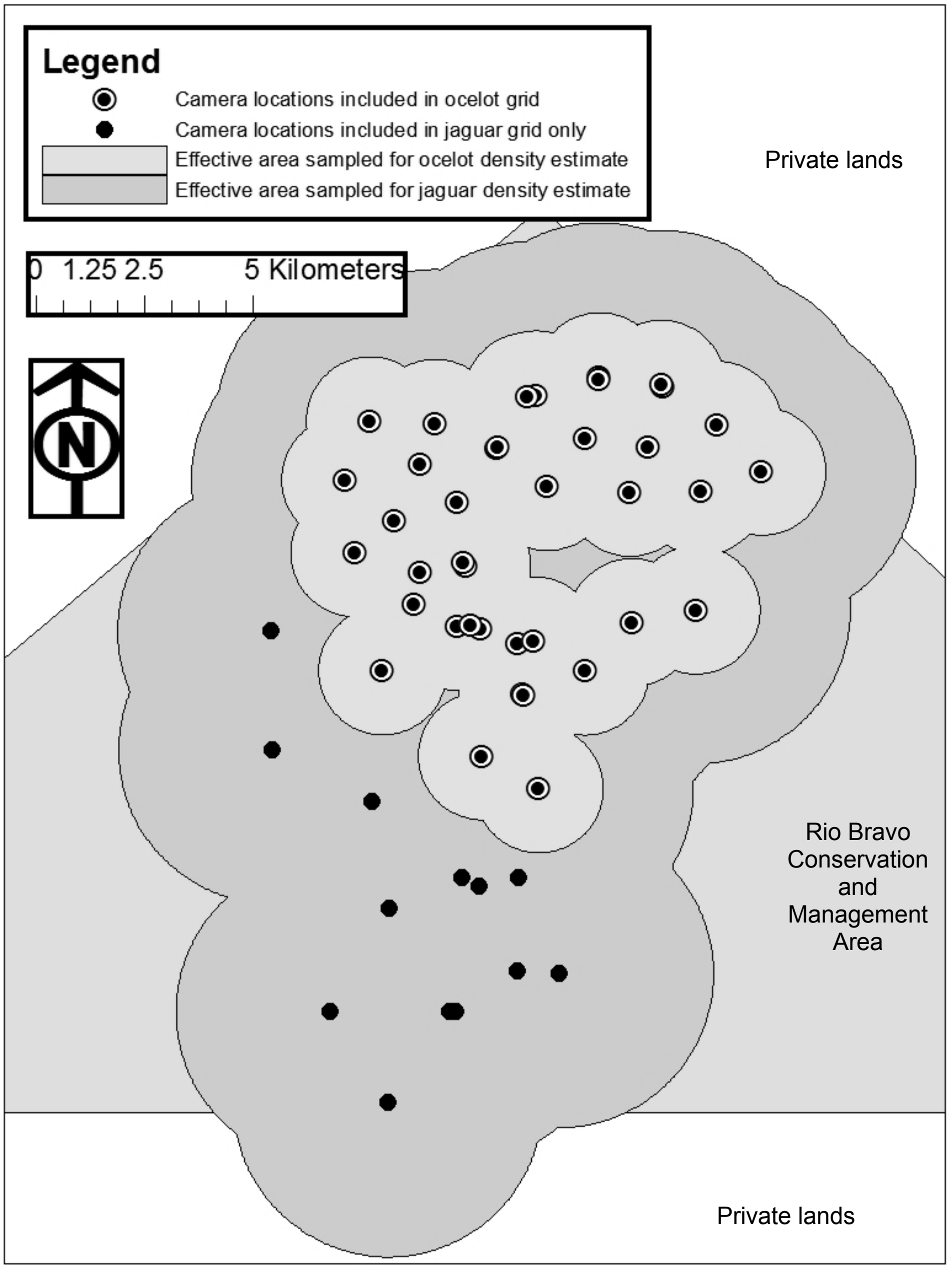

Figure 4.3: The two camera grids comprising the Rio Bravo Conservation and Management Area survey from January to April of 2008 are shown. While 52 camera locations are shown they represent only 40 actual camera stations. Some stations had to be moved early during the survey period due to areas with lower vehicle activity. These stations were moved only short distances and appear in the figure as two or three camera locations spaced less than 500 meters apart. All locations were taken into account in density analyses. The "ocelot grid" included 29 actual camera stations spaced approximately 1.5 km apart nested within a larger "jaguar grid" and was used to obtain photographic "captures" of ocelots to produce ocelot density estimates. The effective area sampled of the ocelot grid was estimated to be 100.49 km^2 using ½ the mean maximum distance moved (MMDM) of all ocelots captured. The larger jaguar grid included 11 additional camera stations spaced 3 km apart. Captures of jaguars from cameras within both the ocelot and jaguar grids were used to estimate jaguar densities. The effective area sampled of this combined grid was 301.71 km^2 based on ½ MMDM of all jaguars captured. All 40 stations were used to evaluate patterns of felid co-occurrence (based on presence/absence data), but only 39 of the 40 camera stations were used in estimating site characteristics as one station was operational for only a short period.

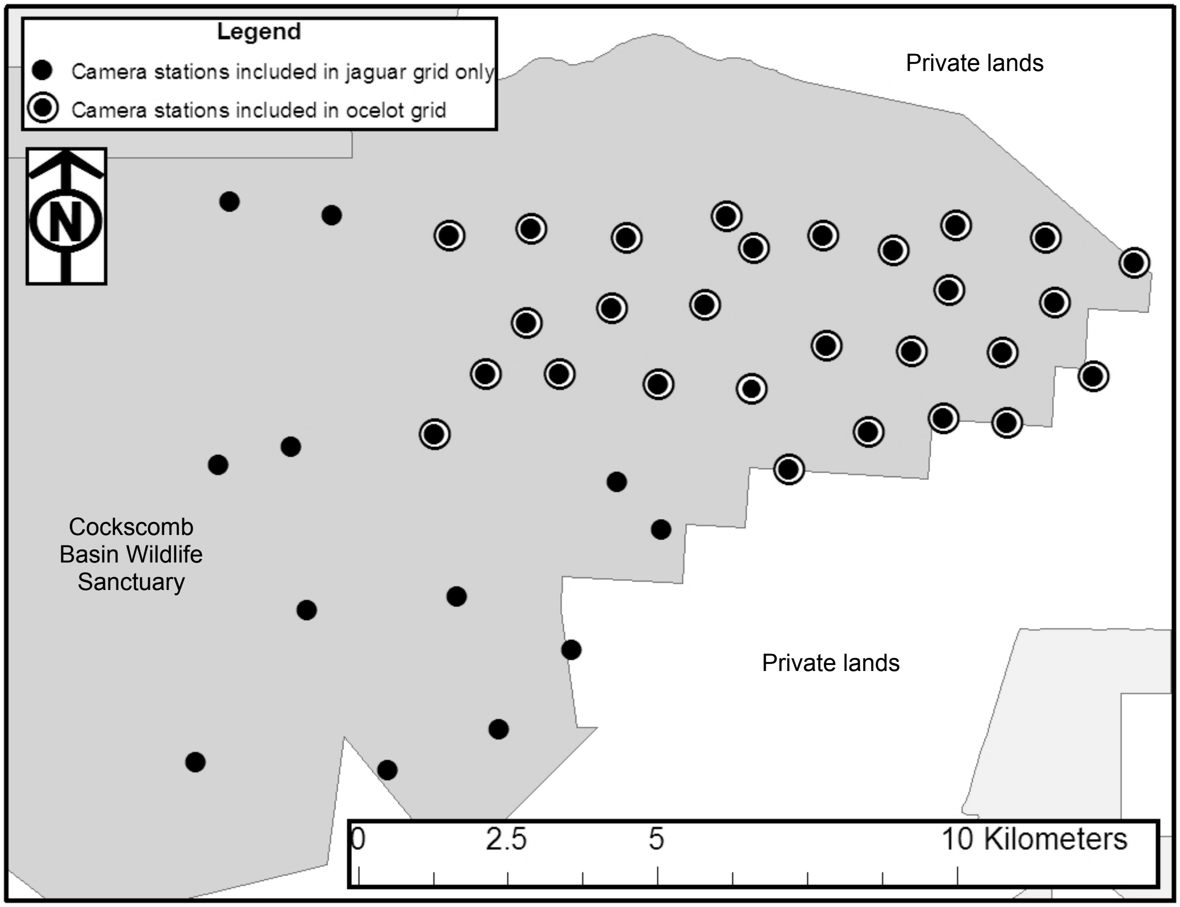

Figure 4.4: The two camera grids comprising the Cockscomb Basin Wildlife Sanctuary (CBWS) survey included 40 camera stations operational from April to July of 2008. The “ocelot grid” included 28 cameras spaced approximately 1.5 km apart nested within a larger “jaguar grid”. The larger jaguar grid included 12 additional cameras spaced 3 km apart. Analyses of densities and site characteristics at the CBWS is still underway. All 40 camera stations were used to evaluate patterns of felid occurrence (based on presence/absence data).

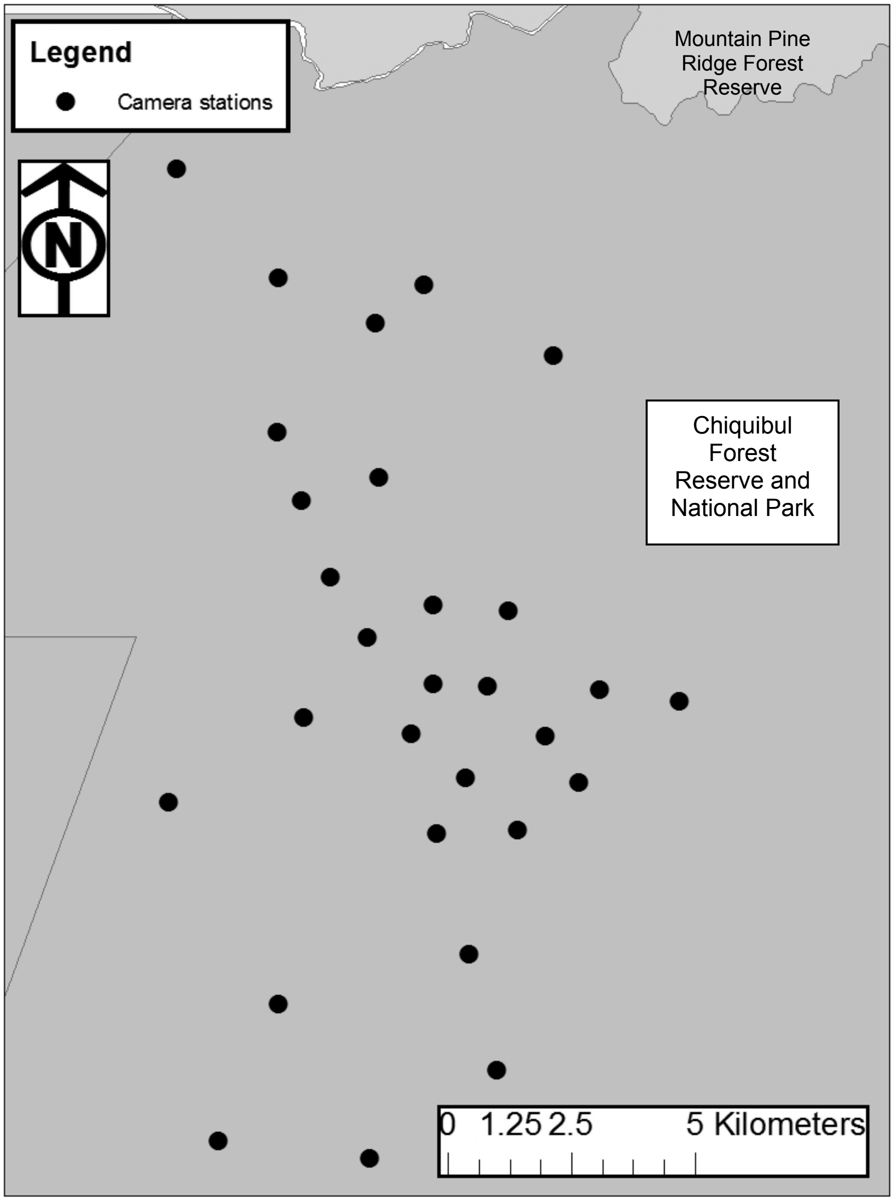

Figure 4.5: The camera stations comprising the Chiquibul Forest Reserve and National Park (CFRNP) survey included 29 camera stations operational from June to August of 2008. Separate ocelot and jaguar grids have yet to be defined. Analyses of site characteristics and possibly densities at the CFRNP are still underway. All 29 stations were used to evaluate patterns of felid occurrence (based on presence/absence data).

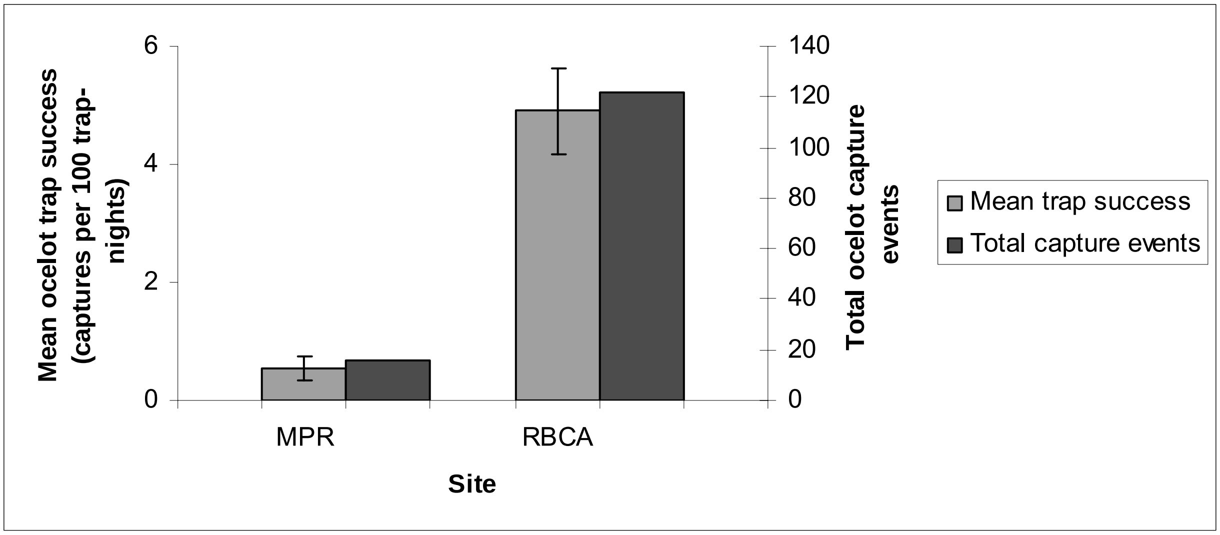

Figure 4.6: The mean ocelot trap success rate and total number of ocelot capture events from 47 camera stations within the Mountain Pine Ridge Forest Reserve (MPR) survey and 39 camera stations within the RBCA survey are shown. The MPR survey ran for 72 days from June to August of 2007. The Rio Bravo Conservation and Management Area (RBCA) survey ran from January to April of 2008. One additional camera station in the RBCA survey was not included in this summary because it was operational for only a short period.

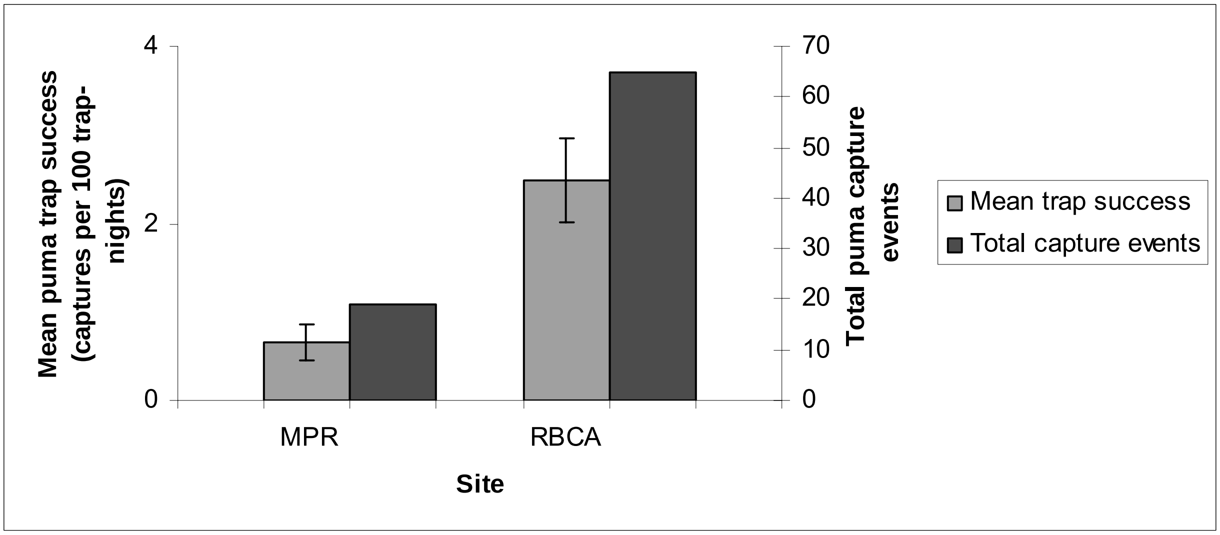

Figure 4.7: The mean puma trap success rate and total number of puma capture events from 47 camera stations within the Mountain Pine Ridge Forest Reserve (MPR) survey and 39 camera stations within the Rio Bravo Conservation and Management Area (RBCA) survey are shown. The MPR survey ran for 72 days from June to August of 2007. The RBCA survey ran from January to April of 2008. One additional camera station in the RBCA survey was not included in this summary because it was operational for only a short period.

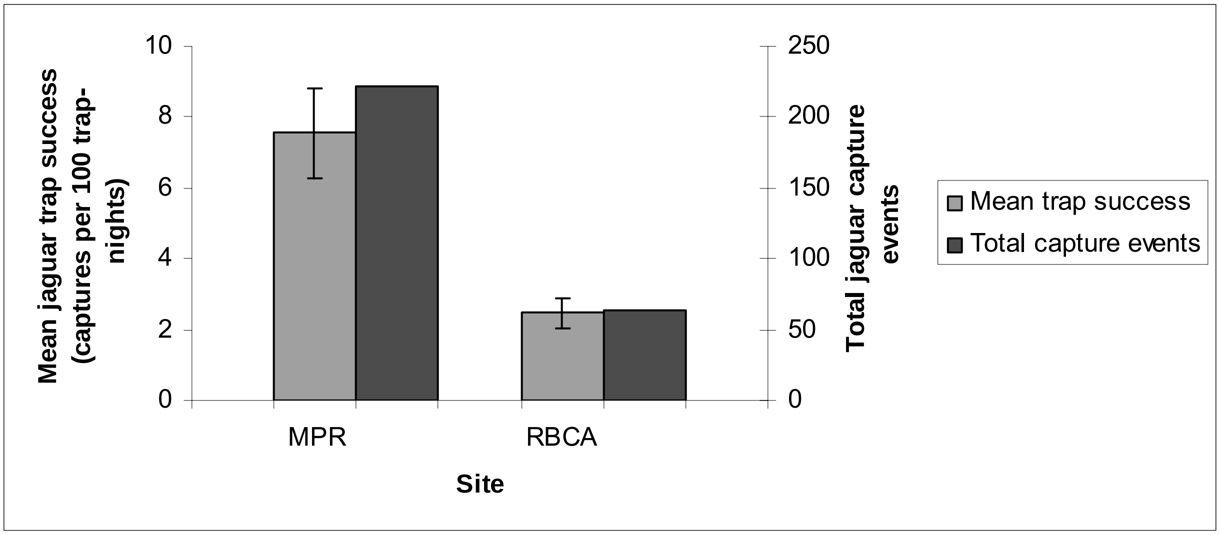

Figure 4.8: The mean jaguar trap success rate and total number of jaguar capture events from 47 camera stations within the Mountain Pine Ridge Forest Reserve (MPR) survey and 39 camera stations within the Rio Bravo Conservation and Management Area (RBCA) survey are shown. The MPR survey ran for 72 days from June to August of 2007. The RBCA survey ran from January to April of 2008. One additional camera station in the RBCA survey was not included in this summary because it was operational for only a short period.

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