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HABITAT PARTITIONING BY SYMPATRIC OCELOTS AND BOBCATS: IMPLICATIONS FOR RECOVERY OF OCELOTS IN SOUTHERN TEXAS

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Abstract—Populations of ocelots (*Leopardus pardalis*) have declined during the past century due mainly to loss of habitat resulting in the ocelot being listed as endangered by the United States Fish and Wildlife Service. In southern Texas, the northern distribution of the ocelot overlaps the southern distribution of the bobcat (*Lynx rufus*). Because bobcats could adversely affect populations of ocelots through interspecific competition, we examined habitat selection of sympatric ocelots and bobcats to determine if habitat partitioning could be functioning to reduce interspecific interactions. Using radiotelemetry, we analyzed macro-scale (vegetative communities) and micro-scale (structural components) selection of habitats by sympatric ocelots and bobcats on Laguna Atascosa National Wildlife Refuge, Cameron County, Texas. We looked for differences in placement of home ranges within the general study area, selection of cover within home ranges, and use of structural components of vegetation within types of cover. There was substantial evidence for habitat partitioning with ocelots selecting areas with >75% canopy cover, while bobcats selected areas with <75% canopy cover. Thus, coexistence between these two species might be facilitated by resource partitioning of habitat.

Resumen—Las poblaciones de ocelote (*Leopardus pardalis*) han disminuido durante el último siglo debido principalmente a la pérdida de hábitat. Como resultado, esta especie ha sido enlistada en peligro de extinción por el United States Fish and Wildlife Service. En el sur de Texas, la distribución septentrional del ocelote se sobrepone con la distribución meridional del lince rojo (*Lynx rufus*). Debido a que el lince rojo podría afectar negativamente las poblaciones del ocelote con la competencia interespecífica, examinamos la selección de hábitat de las dos especies simpátricas para determinar si la partición de hábitat podía reducir las interacciones interespecíficas. Usando radiotelemetría, analizamos la selección de hábitat a una macro escala (comunidades vegetales) y a una micro escala (componentes estructurales) en Laguna Atascosa National Wildlife Refuge, condado de Cameron, Texas. Buscamos diferencias en la ubicación de rangos de hogar dentro del área general de estudio, la selección del tipo de cobertura dentro del rango de hogar, y el uso de componentes estructurales de vegetación dentro del tipo de cobertura. Encontramos evidencia substancial de la partición de hábitat, con ocelotes seleccionando áreas con >75% de cobertura del dosel mientras que el lince rojo seleccionó áreas con <75% de cobertura del dosel. Por lo tanto, la partición de los recursos del hábitat podría facilitar la co-existencia entre estas dos especies.

The ocelot (*Leopardus pardalis*) is one of the rarest felids in the United States. Historically, populations in the United States ranged from southern through eastern and central Texas to western Louisiana and southern Arkansas (Woodward, 1980). Currently, distribution within the United States is limited primarily to the southern portion of Texas in Cameron and Willacy counties (Haines et al., 2006*b*); size of the population is estimated at 80–100 individuals (Tewes and Everett, 1986; Haines et al., 2006*c*). Loss of habitat is believed to be the main reason for reduction in range and decline in populations of ocelots (Tewes and Everett, 1986), which has led to the ocelot being listed as endangered by the United States Fish and Wildlife Service (1982).

Ocelots and bobcats (*Lynx rufus*) are sympatric from southern Texas to southern Mexico

(Rolley, 1987; Tewes and Schmidly, 1987). Based on competitive-exclusion theory (Gause, 1934), it is believed that ecologically equivalent species cannot coexist (Schoener, 1974; Anderson et al., 2002; Rastetter and Agren, 2002). Therefore, recovery strategies for ocelots should include an understanding of the competitive relationship between ocelots and bobcats. Rosenzweig (1966) stated that differences in size of carnivores provides a means for coexistence, and Schoener (1974) described three forms of ecological partitioning including habitat, temporal, and food that could allow for coexistence. However, ocelots and bobcats are similar in size (Sunquist and Sunquist, 2002), feed mostly on small mammals and birds, and primarily are crepuscular and nocturnal (Rolley, 1987; Tewes and Schmidly, 1987). Thus, differences in selection of habitat may be the primary form of ecological partitioning between ocelots and bobcats.

Data indicating differences in habitat between ocelots and bobcats are inconclusive. Whereas ocelots are habitat specialists with spatial patterns strongly linked to dense thornshrub communities (i.e., ≥95% canopy cover; Harveson et al., 2004; Haines et al., 2006*a*, 2006*c*), selection of habitat by bobcats in Texas is equivocal. Lariviere and Walton (1997) suggested that bobcats are ecologically flexible and occur in a variety of habitats in Texas. However, other studies of radio-monitored bobcats in southern Texas have concluded that bobcats selected dense thornshrub communities (Bradley and Fagre, 1988; Cain et al., 2003). None of these studies on selection of habitat by bobcats were conducted in areas where bobcats occur sympatrically with ocelots. Our objective was to simultaneously radio-monitor ocelots and bobcats on Laguna Atascosa National Wildlife Refuge to determine if differences in habitat could be detected where these species co-occur. Because selection of habitat, and thus partitioning of habitat, occurs along a hierarchy of scales (Johnson, 1980), we looked for differences in placement of home range within the general study area, selection of type of cover within home ranges, and use of micro-scale structural components of vegetation within types of cover.

Materials and Methods—*Study Site, Captures, and Radiotelemetry*—We used data collected on Laguna Atascosa National Wildlife Refuge and parts of adjoining private land in the Lower Rio Grande Valley of southern Texas during March 1996–June 1997. The Laguna Atascosa National Wildlife Refuge (26°13′N, 97°22′W) encompasses 19,680 ha; is located 32 km E Harlingen, Cameron County, Texas, and contains ca. 40–50% of the total population of ocelots in southern Texas (Haines et al., 2006*c*). Topography is flat with elevations of 0–10 m and <1% slope (Williams et al., 1977). Common vegetative associations include salt flats, marshes, chaparral, and brush-grasslands (Lonard et al., 1991).

We trapped ocelots and bobcats using single-door, wire box traps (Tomahawk Trap Co., Tomahawk, Wisconsin) with live bait (i.e., chickens or pigeons) placed in an adjoining compartment. We immobilized ocelots and bobcats with a 9:1 ratio of ketamine hydrochloride and acepromazine maleate (Beltran and Tewes, 1995) and injected this mixture with a pole syringe at a dosage of 20 mg/kg body weight. We fitted immobilized ocelots and bobcats with a collar-mounted radiotransmitter (Advanced Telemetry Systems, Isanti, Minnesota; Telonics, Mesa, Arizona) and returned them to the trap until the dissociative effects of anesthesia were no longer apparent.

We located individuals by triangulation using a handheld receiver and two-element H-antenna during June 1996–June 1997. Locations for each species were distributed equally among six 4-h time periods during the day with >24 h between successive relocations (Poole, 1994). To minimize error in radiotelemetry that could bias analyses of selection of habitat (White and Garrott, 1986; Samuel and Kenow, 1992), a maximum distance of 100 m was allowed between the cat and researcher during each attempt at relocation. After triangulation, we left the area and returned for measurements of microhabitat after the cat had moved to a new location.

Separation of Macrohabitats—We investigated macrohabitat partitioning by evaluating differences in selection of major vegetative associations (i.e., types of cover) by ocelots and bobcats. We divided the study area into four types of cover based on floristics and amount of structural cover. Types of cover included three classes of canopy (closed, mixed, and open) that were partitioned according to amount of vegetative cover >1 m above the ground, as well as a fourth category, bare ground, that had little or no vegetative cover and generally consisted of cultivated fields and tidal-salt flats. We created a Geographic Information System (GIS) for the study area by digitizing types of cover from 61 by 61 cm black and white aerial photos (United States Department of Agriculture-Farm Service Agency, Salt Lake City, Utah) taken in 1995. Two other types of cover (i.e., developed land and water) were digitized but not considered available habitat because no cat was located in these areas.

Closed cover included communities with >75% canopy cover. Dominant vegetative species included a variety of mixed thornshrub. Shindle and Tewes (1998) provided a detailed description of thornshrub communities on Laguna Atascosa National Wildlife Refuge including percentage composition of vegetative species. Mixed cover (>25–75% canopy cover) consisted mainly of thornshrub but had a greater proportion of honey mesquite (*Prosopis glandulosa*), blue sage (*Salvia ballotaiflora*), yucca (*Yucca treculeana*), Texas prickly pear (*Opuntia engelmannii*), and various grasses. Open cover had 0–25% canopy cover and was dominated by grasses and cordgrass (*Spartina spartinae*) with honey mesquite contributing most of the canopy cover. Open cover also included old channels of the Rio Grande (i.e., resacas) that were dominated by sea ox eye (*Borrichia frutescens*) and cattail (*Typha domingensis*).

We determined selection of each type of cover for each species by comparing use of each type with their corresponding availability (Thomas and Taylor, 2006). We assessed selection of type of cover at two scales; the first (second-order selection; Johnson, 1980) compared the proportion of each type within individual home ranges (use) to the proportion of that type of cover within the study area (availability) and the second (third-order selection; Johnson, 1980) compared the proportion of telemetry locations of an individual in each type of cover (use) to proportion of each type within the home range (availability). At each scale, we calculated selection ratios (i.e., proportion used per proportion availabile) for each individual and type of cover (Manley et al., 2002; Alldredge and Griswold, 2006). If there was no partitioning, we expected mean ratios of selection across individuals to be similar for ocelots and bobcats. We defined availability on the study area by using the boundaries of Laguna Atascosa National Wildlife Refuge and parts of adjacent private lands that were accessible to researchers. Because we used boundaries of home ranges simply to describe availability of type of cover (second order) and use (third order), we chose to describe these boundaries for individual cats using a 100% minimum convex polygon.

Separation of Microhabitats—We used seven measurements describing vegetational structure at locations to determine if ocelots and bobcats were using micro-scale characteristics of habitat similarly when located within the same general type of cover. Measurements included percentage canopy cover, percentage horizontal cover at three height-profiles, and height of canopy. The sampling unit consisted of 5-m transects radiating from four cardinal directions from the point of relocation. We used the point-intercept method with 21 points spaced at 1-m intervals along each transect to estimate percentage canopy cover (James and Shugart, 1970; Higgins et al., 1994). Profiles of canopy cover were 0–1 m, >1 m, and total canopy cover that included all vegetative cover above ground. We calculated percentage of horizontal cover at three profiles (0–0.5, >0.5–1, and >1–2 m) using a cover pole (2-m high by 3-cm wide) marked at 1-dm intervals (Higgins et al., 1994). We placed the pole at the estimated location of the cat and visually estimated the percentage of the pole obscured by vegetation from 5 m in each of the cardinal directions (Shindle and Tewes, 1998). The mean of the four observations (i.e., each cardinal direction) for each profile was used to estimate percentage horizontal cover. Height of canopy was determined by the mean of five measurements taken at the point of relocation and at each end of the 5-m transects.

Differences in characteristics of micohabitat between locations of ocelots and bobcats within the same type of cover were analyzed using univariate tests for differences in means. To more closely approximate normality for statistical tests, we took the square root of height of canopy and transformed percentage data using an angular transformation (Snedecor and Cochran, 1989).

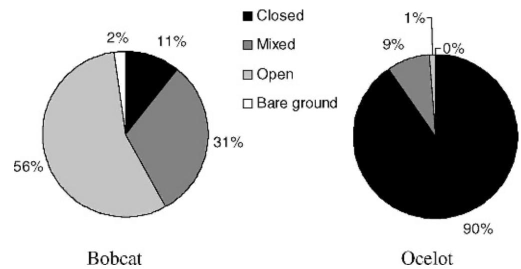

Fig. 1—Percentage of telemetry locations in four types of cover for ocelots (*Leopardus pardalis*; $n = 93$) and bobcats (*Lynx rufus*; $n = 93$) on Laguna Atascosa National Wildlife Refuge, Cameron County, Texas, June 1996–June 1997.

Results—We captured 10 adult ocelots (six males, four females) and 8 adult bobcats (five males, three females). Three ocelots (two males, one female) and two bobcats (both males) had <10 locations and were not used in the analysis resulting in comparisons between seven ocelots (four males, three females) and six bobcats (three males, three females). We collected 186 locations, with 93 observations each on ocelots and bobcats. Median number of locations per individual was 15 and range was 10–20. The majority of locations of ocelots (90%) occurred in closed cover, whereas most locations of bobcats (87%) were in the open and mixed cover (Fig. 1).

When we compared proportions of each type of cover present within home ranges to proportions in the study area, there was little evidence that bobcats established home ranges in parts of the study area differently than would be expected at random (i.e., selection ratios ca. 1; Fig. 2a). In contrast, ocelots tended to establish home ranges that included a greater proportion of closed and mixed cover and a smaller proportion of bare ground (Fig. 2a). Although ocelots generally selected areas with more closed cover than bobcats, 90% confidence intervals on selection ratios overlapped between ocelots and bobcats for all but bare ground, suggesting little tendency for ocelots and bobcats to establish home ranges in different parts of the study area.

When we compared the proportion of telemetry locations in each type of cover to the availability in individual home ranges, there was

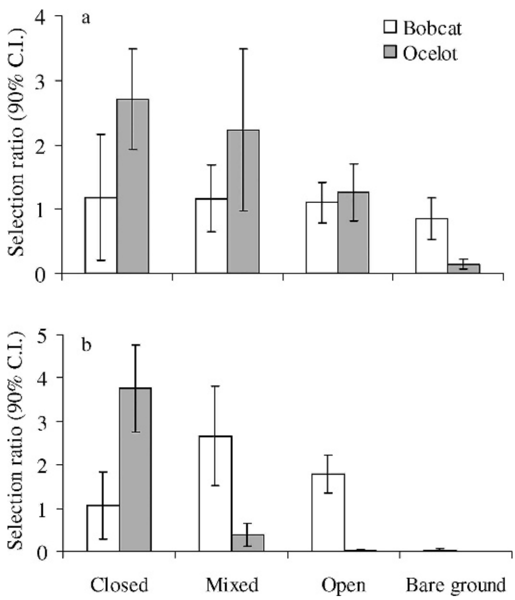

FIG. 2—Mean selection ratio (90% confidence interval) for home ranges of six bobcats (*Lynx rufus*) and seven ocelots (*Leopardus pardalis*). Availability was determined by proportion of each type of cover within the study area and use was determined by the proportion of each type of cover within the 100% minimum convex polygon for the home range of an individual on Laguna Atascosa National Wildlife Refuge, Cameron County, Texas, June 1996–June 1997: a, second-order selection (Johnson, 1980); b, third-order selection (Johnson, 1980).

substantial evidence for habitat partitioning between ocelots and bobcats. Ocelots selected almost exclusively for the closed cover while avoiding all other types of cover (Fig. 2b). Bobcats demonstrated an opposite selection pattern by favoring mixed and open cover within their home range (Fig. 2b). None of the 90% confidence intervals on selection ratios, except bare ground, which both species strongly avoided, overlapped between ocelots and bobcats.

Comparisons of the seven structural variables indicated several differences between mean measurements of microhabitat taken at locations of ocelots versus bobcats within the same type of cover (Table 1). Sites for ocelots were characterized by higher canopies, greater canopy cover >1 m, and greater horizontal cover 1–2 m than sites for bobcats.

DISCUSSION—Our results suggest a distinct boundary of separation in selection of type of cover with ocelots relying almost exclusively on closed-canopy cover while bobcats selected mixed and open types of cover. While we acknowledge that sizes of samples (i.e., number of individuals and number of locations per individual) used in this study were below those reported as being sufficient to describe habitat selection (e.g., Alldredge and Ratti, 1986; Leban et al., 2001), we suggest the following reasons why we believe these results are not spurious. Because Laguna Atascosa National Wildlife Refuge includes ca. 40–50% of the total population of ocelots in the United States and is more amenable to management than surrounding private lands, our goal was to make inferences about habitat partitioning within Laguna Atascosa National Wildlife Refuge. Because we are making inferences on a finite population (i.e., ocelots and bobcats within Laguna Atascosa National Wildlife Refuge) of ca. 20 adult ocelots (Haines et al., 2006*c*) and a similar number of bobcats, our number of individuals (seven ocelots and six bobcats) constitute about one-third of the population for which inferences are being made. The power to detect differences is not only a function of sample size (number of individuals) but also the effect size. If there are large differences in habitat selection as our results suggest, we can be confident these differences can be detected with smaller samples than would otherwise be necessary to detect smaller differences. Finally, because we used individuals as the sample unit, too few locations per individual would only increase variability of the estimated selection ratio for each individual. This increased variability would manifest in decreased power to detect differences among ocelots and bobcats. Despite this decrease in power, we were able to detect significant differences in selection of type of cover and demonstrate a consistent pattern of ocelots selecting areas with greater canopy cover than bobcats.

Our results agree with others that have suggested that ocelots are habitat specialists with spatial patterns strongly linked to closed woody cover in southern Texas (Shindle and Tewes, 1998; Haines et al., 2006*a*, 2006*c*; Harveson et al., 2004). Our results also supported the conclusion of Lariviere and Walton (1997) who suggested that bobcats occur in a variety of habitats in Texas. Indeed, we determined that composition of type of cover within home ranges of bobcats

Table 1—Characteristics[a] of microhabitat for 93 locations of ocelots (*Leopardus pardalis*) and 93 locations of bobcats (*Lynx rufus*) by type of cover on Laguna Atascosa National Wildlife Refuge, Cameron County, Texas, June 1996–June 1997.

Microhabitat variable	Type of cover	Ocelot	Bobcat	*P*-value[b]
Canopy cover				
total	Across all (88, 89)[c]	94.7 (9.1)	73.0 (19.0)	<0.001
	Closed (79, 10)	96.3 (5.4)	81.2 (13.8)	<0.001
	Mixed (8, 26)	79.2 (20.2)	75.5 (14.6)	0.392
	Open (1, 51)	NA	71.1 (20.3)	NA
<1 m	Across all	72.8 (17.3)	63.4 (20.3)	<0.001
	Closed	74.8 (15.0)	59.1 (22.9)	0.008
	Mixed	53.6 (26.4)	62.1 (15.5)	0.250
	Open	NA[d]	65.6 (21.4)	NA
>1 m	Across all	80.4 (16.7)	26.4 (26.9)	<0.001
	Closed	81.9 (15.7)	61.0 (23.6)	0.001
	Mixed	67.3 (21.5)	36.0 (24.1)	0.004
	Open	NA	15.6 (21.3)	NA
Horizontal cover				
<0.5 m	Across all	93.5 (14.4)	96.3 (11.5)	0.030
	Closed	95.1 (9.7)	99.4 (1.6)	0.095
	Mixed	76.9 (34.2)	99.0 (2.4)	<0.001
	Open	NA	94.3 (14.8)	NA
0.5–1 m	Across all	94.2 (15.0)	62.9 (30.5)	<0.001
	Closed	95.7 (11.8)	86.8 (16.5)	0.009
	Mixed	79.1 (30.7)	79.8 (19.3)	0.448
	Open	NA	50.6 (30.5)	NA
1–2 m	Across all	90.4 (14.6)	30.1 (32.9)	<0.001
	Closed	91.3 (13.6)	82.1 (21.0)	0.089
	Mixed	81.3 (21.9)	38.1 (28.5)	<0.001
	Open	NA	16.5 (25.3)	NA
Height of canopy				
	Across all	2.4 (0.5)	1.1 (0.5)	<0.001
	Closed	2.5 (0.4)	1.8 (0.7)	<0.001
	Mixed	2.3 (0.6)	1.3 (0.5)	<0.001
	Open	NA	0.9 (0.3)	NA

[a] Values reported are untransformed means with standard deviations in parentheses.

[b] To more closely approximate normality, tests on means (*t*-test) were performed on the square root of height of canopy and we transformed percentage data using an angular transformation.

[c] Size of sample by type of cover are provided in parentheses for ocelots and bobcats, respectively. Size of samples were the same for each variable. Two locations of bobcats recorded in bare-ground cover are not included in this table.

[d] Samples were too small (i.e., ≤2) to calculate means and standard deviations.

did not differ from composition in the study area and selection of type of cover within the home range included a variety of vegetative communities with canopy cover <75%. Our results contrast somewhat from a previous study in southern Texas that suggested bobcats prefer dense thornshrub cover (i.e., Cain et al., 2003). However, we believe this discrepancy could be the result of the study by Cain et al. (2003) being conducted where the two species did not co-occur or inconsistent definitions of types of cover. For example, ''dense'' thornshrub on Laguna Atascosa National Wildlife Refuge can be substantially thicker than thornshrub communities in more northern areas of Texas.

The tendency for spatial segregation that we detected in analyses of macrohabitats also was observed in our micro-scale analysis of vegetational measurements taken within the same type of cover. For example, mixed cover had >25–75%

woody canopy cover >1 m. Within this type of cover, ocelots were in areas with greater canopy cover (67% mean canopy cover >1 m), while bobcats were in areas with less canopy cover (36% mean canopy cover >1 m). This pattern was consistent in closed cover (>75% canopy cover) as well. Ocelots were in areas with 82% mean canopy cover >1 m, whereas bobcats were in areas with less than typical canopy cover (61% mean canopy cover >1 m). Despite these differences, the micro-scale measurements revealed that both felids were rarely in habitats with little or no screening cover (i.e., horizontal cover 0–0.5 m) despite the abundance of these areas as indicated by the amount of the bare ground in the study area (48%). Therefore, both felids might require a certain amount of cover near the ground for concealment from predators and prey (Kleiman and Eisenberg, 1973).

Implications of habitat partitioning for populations of ocelots and bobcats will be dependent on the type and consequences of the interaction resulting in segregation. Arthur and Mitchel (1989) described three types of populational interactions including neutralism in which neither species is affected by presence of the other, amensalism in which individuals of one species adversely affect those of the other but are unaffected themselves, and competition in which both species are affected negatively. It is possible that habitat partitioning between ocelots and bobcats originated independent of any competitive interactions (Schoener, 1982). Thus, the observed differences simply reflect different evolutionary paths merging in southern Texas with no adverse affect on fitness of either species (neutralism). Although this is possible, we believe the sharp distinction between habitats selected by ocelots and bobcats suggests some type of competitive interaction. If the type of interaction is one in which ocelots are affected negatively by bobcats (amensalism or competition), then reducing populations of bobcats in areas of sympatry could allow ocelots to increase in population density or occupy habitats previously unused.

It is important to note that our study does not identify the type of interaction between ocelots and bobcats, but future research could address this question. Observational studies can be conducted to evaluate differences in densities of bobcats and ocelots in areas where the species do and do not co-occur (Stevens and Willig, 2000). However, to conduct this type of analysis, density of prey and structure of habitat have to be similar in all areas, a situation that is unlikely for ocelots and bobcats. Another option is to conduct a manipulative study in southern Texas by determining response of ocelots to removal of bobcats within a study area. Hairston (1980) conducted a similar type of manipulative study of salamanders in the mountains of North Carolina and reported that removal of one species of terrestrial salamander resulted in a significant increase in distribution and abundance of the other. In addition, other studies have noted that changes in density of one species of carnivore can profoundly impact the density of another species of carnivore (Linnell and Strand, 2000). Therefore, an hypothesis that could be tested through a manipulative study is that abundance of ocelots within a study site will increase in response to removal of bobcats.

Our study is one of the few that have addressed resource partitioning between wild felids, especially two species with such similar morphology. Seidensticker (1976) analyzed use of space through radiotelemetry between tigers (*Panthera tigris*) and leopards (*Panthera pardus*) in Nepal and concluded that coexistence between the two species was facilitated by large biomass of prey, a larger proportion of biomass of ungulates in small size classes, and by dense structure of vegetation. Schaller and Crawshaw (1980) and Scognamillo et al. (2003) radio-monitored jaguars (*Panthera onca*) and cougars (*Puma concolor*) in South America and both concluded that the two species exhibited mutual avoidance through fine-scale separation of habitat and food habits. In addition, Haines (2006) further analyzed coexistence between sympatric jaguars and cougars and reported that studies on partitioning of prey between these two felids were conflicting and that coexistence between the species may be mediated by specialization of jaguars on Neotropical species of prey. Based on distinct differences in habitat selection between sympatric ocelots and bobcats radio-monitored in this study, coexistence between these two felids appears to be the result of resource partitioning of habitat.

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