

Prey-mediated avoidance of an intraguild predator by its intraguild prey

Oecologia

ISSN 0029-8549

Volume 164

Number 4

Oecologia (2010) 164:921–929

DOI 10.1007/

s00442-010-1797-8

A 21596

Oecologia

In Cooperation with the
International Association for Ecology (Intecol)

Volume 164 · Number 4 · December 2010

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Prey-mediated avoidance of an intraguild predator by its intraguild prey

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Received: 29 June 2010 / Accepted: 16 September 2010 / Published online: 16 October 2010
© Springer-Verlag 2010

Abstract Intraguild (IG) predation is an important factor influencing community structure, yet factors allowing coexistence of IG predator and IG prey are not well understood. The existence of spatial refuges for IG prey has recently been noted for their importance in allowing coexistence. However, reduction in basal prey availability might lead IG prey to leave spatial refuges for greater access to prey, leading to increased IG predation and fewer opportunities for coexistence. We determined how the availability of prey

affected space-use patterns of bobcats (*Lynx rufus*, IG prey) in relation to coyote space-use patterns (*Canis latrans*, IG predators). We located animals from fall 2007 to spring 2009 and estimated bobcat home ranges and core areas seasonally. For each bobcat relocation, we determined intensity of coyote use, distance to water, small mammal biomass, and mean small mammal biomass of the home range during the season the location was collected. We built generalized linear mixed models and used Akaike Information Criteria to determine which factors best predicted bobcat space use. Coyote intensity was a primary determinant of bobcat core area location. In bobcat home ranges with abundant prey, core areas occurred where coyote use was low, but shifted to areas intensively used by coyotes when prey declined. High spatial variability in basal prey abundance allowed some bobcats to avoid coyotes while at the same time others were forced into more risky areas. Our results suggest that multiple behavioral strategies associated with spatial variation in basal prey abundance likely allow IG prey and IG predators to coexist.

Communicated by Janne Sundell.

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Keywords Bobcat · Coexistence · Coyote · Intraguild predation · Spatial refuge

Introduction

Intraguild (IG) predation is increasingly recognized as an important factor influencing community structure (Crooks and Soulé 1999; Berger and Gese 2007). Models suggest that IG predation should be rare (Holt and Polis 1997; Mylius et al. 2001), yet it is frequently documented in natural systems (Palomares and Caro 1999; Donadio and Buskirk 2006). However, these models fail to account for individual antipredator behavior that could lead to

additional scenarios where coexistence can occur (Heithaus 2001; Janssen et al. 2007). Numerous studies have recently shown the importance of avoidance behavior by IG prey towards IG predators for their coexistence (Heithaus 2001; Janssen et al. 2007; Choh et al. 2010). Avoidance can be through the use of spatial refuges by IG prey where IG predators are rare (e.g., Durant 1998), by occupying areas with greater structural complexity, thereby allowing for reduced detectability or enhanced ability to escape detection by IG predators (Janssen et al. 2007), or by temporally avoiding IG predators when they are most active by shifting activity patterns (e.g., Arjo and Pletscher 1999).

While many IG prey species show a preference for areas with reduced probabilities of encountering IG predators (Durant 1998; Sergio et al. 2003; Choh et al. 2010), this often comes at the cost of reduced access to prey (Mills and Gorman 1997; Durant 1998; Heithaus 2001; Thompson and Gese 2007). Thus, IG prey face a tradeoff between access to sufficient prey and avoiding areas with high probabilities of encountering IG predators, just as prey in “traditional” predator–prey relationships (Lima and Dill 1990). In “traditional” predator–prey studies, prey increase their risk of exposure to predators in order to access areas with greater resource abundance when resources are low (e.g., Pettersson and Brömark 1993; Whitham and Mathis 2004).

Few studies have investigated similar relationships between IG predator and IG prey, but there is some evidence that IG prey increase exposure to IG predators when prey is low (Polis et al. 1989; Palomares and Caro 1999; Sergio et al. 2003), or when thermal conditions are suboptimal (Webb et al. 2009). Given that the likelihood of encountering IG predators is probably a main factor leading to IG predation (Moehrenschrager et al. 2007), any factor that increases the probability of encounter might reduce the potential for coexistence. Additionally, IG prey are only predicted to use areas of low productivity when overall levels of basal prey are high (Heithaus 2001). Thus, if overall levels of prey decline, IG prey may be forced into riskier areas, possibly leading to increased IG predation. We therefore studied how the availability of basal prey affected space-use patterns of IG prey in relation to the probability of encountering IG predators. We predicted that as basal prey abundance declined, IG prey would increase their exposure to IG predators in order to access areas with more abundant basal prey.

Specifically, we studied the spatial relationships between bobcats (*Lynx rufus*, IG prey) and coyotes (*Canis latrans*, IG predator) in relation to changes in the abundance of small mammals which represent the primary prey of bobcats (Blankenship 2000).

Bobcats and coyotes exhibit a clear IG predator–prey relationship, with numerous accounts of bobcats being killed by coyotes (Knick 1990; Fedriani et al. 2000; Gipson

and Kamler 2002; T.L. Blankenship unpublished data) and bobcats avoiding coyotes at the core area scale (Neale and Sacks 2001; Thornton et al. 2004). Additionally, bobcat populations respond positively to reductions in sympatric coyote population (Henke and Bryant 1999). Bobcat space-use patterns are also strongly influenced by prey abundance, with bobcats ranging much more widely during periods of low prey abundance (Knick 1990; Blankenship 2000).

Materials and methods

Study area

Our study occurred on the Welder Wildlife Foundation Refuge (approx. 3,150 ha), located approximately 10 km north of Sinton, Texas. The study area was located in a transition zone between the gulf prairies and marshes and south Texas plains, and vegetation consisted mainly of mixed grasslands and shrubs (Young et al. 2006).

Coyote territories form a continuous patchwork across the refuge, with approximately seven to eight territories always present and exhibiting high spatial stability through time (Young et al. 2006). Pack sizes range between three and seven adults (Andelt 1985). Bobcats are less abundant on the refuge (approx. 15, Heilbrun et al. 2006), but show extensive home range overlap with coyote territories.

The dietary overlap of coyotes and bobcats is low except for the common use of small mammals. Coyotes tend to have more varied diets, with fruit making up a considerable portion of their diet at many times during the year (Young et al. 2006). Additionally, larger mammals [e.g., whitetail deer (*Odocoileus virginianus*) and feral pigs (*Sus scrofa*)] are a more common constituent of coyote diets (Young et al. 2006) than bobcat diets (Blankenship 2000). The preferred prey of bobcats on the refuge were cotton rats (*Sigmodon hispidus*), wood rats (*Neotoma micropus*), and eastern cottontails (*Sylvilagus floridanus*, Blankenship 2000). However, bobcats switch to a greater proportion of birds (both passerine and waterfowl) during periods of low small mammal abundance (Blankenship 2000).

Bobcat and coyote monitoring

Bobcats were captured using modified Tomahawk live traps (Tomahawk Live Trap Co, Tomahawk, WI; 107 × 38 × 51 cm). An extension (51 × 38 × 51 cm) was added to the trap to house and protect live chickens used as bait (Blankenship 2000). We immobilized captured bobcats with an intramuscular injection of ketamine (i.e., 10–15 mg/kg body mass) and acepromazine (i.e., 0.05 mg/kg body mass). Coyotes were captured using padded leg hold traps

(Victor #3; Softcatch, Lititz, PA), neck snares, or collarums (Wildlife Control Supplies, East Granby, CT). Captured coyotes were not chemically immobilized. Both bobcats and coyotes were fitted with VHF collars (bobcats: Advanced Telemetry Systems, Isanti, MN; coyotes: Lotek, Newmarket, ON, Canada). All captures occurred between April 2007 and November 2008.

We obtained relocations on each bobcat and coyote 4–5 days per week using triangulation and the maximum likelihood estimator in program Locate II (Nams 2006) to estimate animal locations. Locations were estimated using ≥ 3 bearings collected within 20 min, between 20 and 160° of each other. Mean distance between the estimated and true locations was 260 m [standard deviation (SD) 215]. We randomly chose start times and animals for telemetry sessions to ensure the data were not autocorrelated (Fieberg 2007). Both diurnal and nocturnal locations for bobcats and coyotes were collected.

Home range analysis

The home ranges of individual bobcats were estimated on the basis of ≥ 30 locations to ensure that we obtained a sufficient number of relocations to estimate home ranges (Seaman et al. 1999). We used the fixed kernel method (Worton 1989) with the ad hoc bandwidth selection procedure (see Berger and Gese 2007). In this study, the home range was defined as the area encompassed by the 95% isopleth. To estimate bobcat core areas, we analyzed home ranges for clusters of locations and used Bayesian methods to identify which isopleth partitioned the home range into homogeneous point patterns (Wilson et al. 2010). This method is highly precise for characterizing points as occurring inside or outside the core area. We estimated bobcat home ranges and core areas for all relocation data (day and night combined, hereafter full core area), relocation data obtained during the day (0700–1900 hours, hereafter daytime core area), and relocation data obtained at night (1900–0700 hours, hereafter nighttime core area).

Small mammal trapping

We established 15–45 trapping grids from autumn (September–November) 2007 to spring (February–April) 2009, distributing trapping grids among all of the major vegetative communities on the study area (Blankenship 2000). Each trapping grid consisted of 25 Sherman live traps (H.B. Sherman Traps, Tallahassee, FL) baited with grain (corn-milo mixture), in a 5×5 design, with traps spaced 10 m apart. We opened traps in each grid for three nights and captured small mammals were individually marked by trimming guard hairs in a unique design. Each grid was only sampled once (i.e., open for three nights) each season.

For each grid, we determined the total biomass of all small mammals captured based on average weights found on the study site (Ottens et al. 1972). This is similar to the approach taken by Randa et al. (2009). The number of trapping grids sampled differed each season because of differing levels of field assistance and because weather conditions sometimes hindered our ability to sample a trapping grid each season.

Data analysis

We created kernel intensity maps (Schabenberger and Gotway 2005) of coyote space use based on those territories which had >30 points for a respective season. If multiple coyotes resided in the same territory, we combined their relocations. We created a 100×100 -m grid across the study area, and for each coyote territory, and estimated the kernel density (with ad hoc bandwidth) value at each grid cell using the function 'kde2d' in the MASS library (Venables and Ripley 2002) in the R Statistical Computing Environment (R Development Core Team 2008). We then extracted the grid cells that fell within the 95% isopleth of each coyote territory and scaled each territory's grid cell values to their respective mean value in order to control for interterritorial differences in the number of relocations used for kernel density estimates. If grid cells contained multiple intensity estimates (i.e., the grid cell was contained within multiple territories), we only used the greatest intensity value. We created coyote intensity grids based on day, night, and day and night combined coyote relocations for each season.

A statistical approach was used to spatially predict small mammal biomass across the study area each season and at each observed bobcat location. Our trapping data were zero-inflated (i.e., many grids with no captures); consequently, we were unable to use standard optimal spatial prediction methods (e.g., kriging equations). Instead, we used a hurdle model (e.g., Ver Hoef and Jansen 2007) for the correlated zero process (i.e., locations with no captures) and then a correlated log-Gaussian model at locations with captures. This is essentially a mixture model similar to a zero-inflated model, except that a value of zero can only come from one component of the mixture, rather than two. We used an exponential covariance structure on both the zero and positive processes.

After obtaining spatial prediction maps of small mammal biomass, it was clear that certain regions of the study area had higher overall prey biomass than others (Fig. 1). Given that the availability of prey can influence the level of risk an animal takes while foraging (e.g., Cooper 2000), we determined the mean small mammal biomass in each bobcat's home range for each season as an index of home range quality. Whereas the predicted values of small mammal

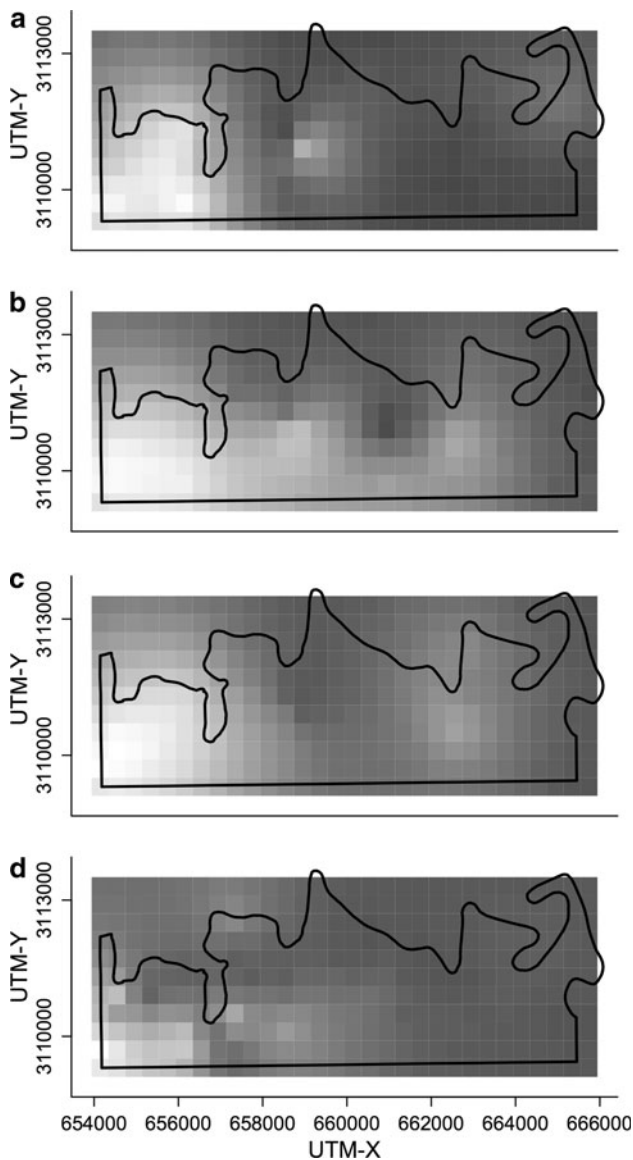


Fig. 1 Predictive map of small mammal biomass obtained with a hurdle model across the study area in autumn 2007 (a), spring 2008 (b), autumn 2008 (a), and spring 2009 (a). Trapping occurred between February and May for spring and between August and November for autumn. Predicted small mammal biomass ranged from 4 (black) to 2,019 g (white). The black outline represents the Welder wildlife refuge, Sinton, Texas boundary

biomass at each bobcat relocation provide information about the spatial distribution of resources at the home range scale, the mean home range biomass (i.e., home range quality) provides a measure of relative prey availability for each bobcat at the study site scale.

For each bobcat relocation, we determined small mammal biomass, intensity of coyote use, and the mean small mammal biomass of the home range where the point occurred. We also determined the distance to water because of the importance of water birds in bobcat diets in the study area during periods of low small mammal abundance

(Blankenship 2000). We used the estimated home range and core areas for each bobcat during each season to determine whether a relocation occurred inside or outside the core area (coded as 1 or 0, respectively). We used the distance to water, coyote space-use intensity, and small mammal biomass as variables and all two-way interactions with mean home range and small mammal biomass for model selection. We also had repeated measures on individuals; thus, we used a logistic generalized linear mixed model [function 'lmer' in R package 'lme4' (Bates 2007)] with bobcat as a random factor to determine which explanatory variables best explained whether a relocation was from inside or outside its core area (Zuur et al. 2009). We standardized all variables prior to analysis (Zuur et al. 2009) and used Akaike Information Criteria (AIC, Burnham and Anderson 1998) to determine the most parsimonious model that best fit the observed data. We used the same procedure to determine the best fitting models for day relocations, night relocations, and day and night relocations combined.

Results

We captured seven bobcats (5 males, 2 females) and 13 coyotes (8 males, 5 females), with each having a portion of its home range overlapping with the opposite species' home range. The 13 captured coyotes resided in seven distinct territories on the refuge. We obtained 1,201 bobcat locations that overlapped with ≥ 1 coyote territory for bobcat home ranges estimated with day and night locations over all seasons and individuals. Of those locations, 680 were classified as occurring inside core areas, and 521 outside. For daytime bobcat home ranges, we obtained 348 (227 inside, and 121 outside core areas) bobcat locations that overlapped with coyote daytime territory estimates. For nighttime bobcat home ranges, 334 (197 inside, and 137 outside core areas) bobcat locations overlapped with coyote nighttime territory estimates. For day and night combined, individual bobcats had 66.7 ± 5.9 [mean \pm standard error (SE)] locations that overlapped with estimated coyote territories each season (37.8 ± 3.7 and 28.9 ± 4.0 from inside and outside of core areas, respectively). For daytime bobcat home ranges, there were 31.6 ± 4.4 locations for individual bobcats used for analysis each season (20.6 ± 3.8 , and 11.0 ± 2.2 , from inside and outside of core areas, respectively). Finally, for nighttime bobcat home ranges, there were 27.8 ± 4.1 locations for individual bobcats used for analysis each season (16.4 ± 3.0 , and 11.4 ± 2.1 , from inside and outside of core areas, respectively). Mean small mammal biomass in bobcat home ranges varied from 6.5 to 1,199 g.

The top-ranked model for the full bobcat core area included intensity of coyote use and distance to water, each

Table 1 Results of Akaike Information Criteria analysis for the top ten of 27 candidate logistic generalized linear mixed models with the individual as a random effect explaining the location of core areas within bobcat home ranges based on day and night relocations combined ($n = 1,201$)

Model	AIC	Δ AIC	k	w_i
Coy, D2W, HRQ, Coy \times HRQ, D2W \times HRQ	1,617	0	7	0.535
SmMam, Coy, D2W, HRQ, Coy \times HRQ, D2W \times HRQ	1,619	2	8	0.197
SmMam, Coy, D2W, HRQ, SmMam \times HRQ, Coy \times HRQ, D2W \times HRQ	1,621	4	9	0.072
D2W, HRQ, D2W \times HRQ	1,621	4	5	0.072
Coy, D2W, HRQ, D2W \times HRQ	1,622	5	6	0.044
SmMam, D2W, HRQ, D2W \times HRQ	1,623	6	6	0.027
Coy, SmMam, D2W, HRQ, D2W \times HRQ	1,623	6	7	0.027
SmMam, D2W, HRQ, SmMam \times HRQ, D2W \times HRQ	1,624	7	7	0.016
SmMam, Coy, D2W, HRQ, SmMam \times HRQ, D2W \times HRQ	1,625	8	8	0.010
SmMam, Coy, HRQ, SmMam \times HRQ, Coy \times HRQ	1,637	20	7	0.000

Variables for models included small mammal biomass (SmMam), coyote space use intensity (Coy), distance to water (D2W), home range quality (HRQ) and all two-way interactions with HRQ (denoted by \times)

AIC Akaike Information Criteria values, Δ AIC differences from the model with the lowest AIC value, k , number of parameters, w_i , Akaike weights

Table 2 Regression coefficients of best fitting logistic generalized linear mixed models with individual as a random effect and assessed by AIC

Data	Variables	Coefficient	SE	P value
Day + night	Intercept	0.205	0.105	0.051
	HRQ	-0.119	0.103	0.249
	Coy	0.060	0.062	0.336
	Coy \times HRQ	-0.165	0.063	0.009
	D2W	0.070	0.065	0.278
	D2W \times HRQ	0.347	0.072	<0.001
Day	Intercept	0.655	0.371	0.078
	HRQ	0.004	0.379	0.992
	SmMam	-0.589	0.290	0.042
	D2W	-0.420	0.164	0.010
	D2W \times HRQ	0.360	0.155	0.020
	Coy	-0.007	0.164	0.968
Night	Intercept	0.344	0.242	0.155
	HRQ	-0.231	0.222	0.298
	Coy	0.380	0.130	0.003
	Coy \times HRQ	-0.288	0.106	0.006

Models are for bobcat home range and core area estimates based on day (day), night (night), and day and night relocations combined (day + night)

interacting with home range quality (Table 1). This model accounted for 53.5% of the Akaike weights (Table 1). The only other competing model (i.e., Δ AIC < 2) included the small mammal biomass term, but the slope was not different from 0 ($P = 0.60$), and it only accounted for 19.7% of the Akaike weights (Table 1). Coefficient estimates for the top-ranked model (Table 2) indicated that as prey abun-

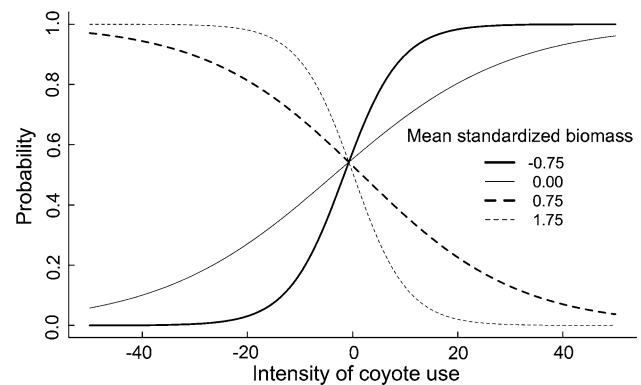


Fig. 2 Estimated logistic functions for the best fitting model for the full bobcat core area (i.e., day and night combined) with changes in standardized values of coyote space-use intensity and mean home range prey biomass. Other variables were held constant (e.g., distance to water, and its interaction with mean home range biomass)

dance increased in home ranges, core areas increasingly occurred further from water and had lower coyote use (Table 2; Fig. 2).

The top-ranked model for daytime core areas included the small mammal, coyote, and distance to water covariates, with home range quality interacting with coyote use and distance to water (Table 3). Coefficient estimates for this model indicated that bobcat core areas were negatively associated with small mammal biomass and occurred further from water and areas intensely used by coyotes with increasing home range quality (Table 2). There were two competing models, one which included the interaction between small mammal biomass and home range quality, and the other which excluded any small mammal biomass variables (Table 3). Coefficients for the model with the interaction between small mammal biomass and home

Table 3 Results of Akaike Information Criteria analysis for the top ten of 27 candidate logistic generalized linear mixed models with individual as a random effect explaining the location of bobcat core areas within home ranges based on daytime relocations (i.e., 700–1900 hours, $n = 348$)

Model	AIC	Δ AIC	k	w_i
SmMam, Coy, D2W, HRQ, Coy \times HRQ, D2W \times HRQ	408.4	0	8	0.359
SmMam, Coy, D2W, HRQ, SmMam \times HRQ, Coy \times HRQ, D2W \times HRQ	409.7	1.3	9	0.188
Coy, D2W, HRQ, Coy \times HRQ, D2W \times HRQ	410.4	2	7	0.132
Coy, D2W, HRQ, Coy \times HRQ	410.8	2.4	6	0.108
SmMam, D2W, Coy, HRQ, Coy \times HRQ	411.6	3.2	7	0.073
SmMam, Coy, D2W, HRQ, SmMam \times HRQ, Coy \times HRQ	413.6	5.2	8	0.027
SmMam, D2W, HRQ, D2W \times HRQ	413.7	5.3	6	0.025
SmMam, Coy, HRQ, Coy \times HRQ	414.4	6	6	0.018
SmMam, D2W, HRQ, SmMam \times HRQ, D2W \times HRQ	414.7	6.3	7	0.015
Coy, HRQ, Coy \times HRQ	415.3	6.9	5	0.011

range quality indicated that as home range quality increased, the probability of the daytime core area occurring in high prey areas decreased.

The top-ranked model for nighttime core areas only included the interaction between coyote intensity and home range quality (Table 4). Coefficient estimates indicated that as home range quality increased, core areas had an increased probability of occurring in areas with low coyote use (Table 2). There were two additional competing models, each of which contained the interaction between coyote and home range quality (Table 4). The second-ranked model contained the small mammal biomass covariate, indicating core areas occurred in areas of the home range with greater small mammal biomass. The third-ranked model contained the distance to water variable (Table 4), indicating core areas occurred further from water than areas outside the core area.

Discussion

Our results support the concept that the stability of IG predation in our system is most likely influenced by bobcats “safety matching” (Heithaus 2001) rather than outcompeting coyotes for shared resources—although bobcat safety

matching is context-dependent. Bobcats tended to safety match when basal prey populations were high inside an individual’s home range, but forewent safety matching when prey levels were low. If prey abundance were to be constant across the entire population, this could lead to an unstable system wherein during periods of low prey abundance, all bobcats would be forced to leave spatial refugia, increasing the probability of negative interactions with coyotes. An interesting result of our analysis, however, is that even within a population, prey abundance was found to vary spatially, allowing some individuals to continue safety matching while others were required to use riskier areas to access sufficient prey.

A key missing link in our understanding of IG predation is the identification of which factors affect the dynamics of IG predator–prey interactions (Polis et al. 1989; Palomares and Caro 1999; Donadio and Buskirk 2006; Gehrt and Prange 2007; Thompson and Gese 2007). Our results, however, suggest that the dynamics of IG predator–prey interactions generally follow the same rules as those for “traditional” predator–prey systems. Within predator–prey systems, there are areas where prey remain relatively invulnerable to predation (Matter and Mannan 2005) as a result of inaccessibility by predators or a high probability of escape (Creswell et al. 2010). The increased risk of preda-

Table 4 Results of Akaike Information Criteria analysis for the top ten of 27 candidate logistic generalized linear mixed models with individual as a random effect explaining the location of bobcat core areas within home ranges based on nighttime relocations (i.e., 1900–700 hours; $n = 334$)

Model	AIC	Δ AIC	k	w_i
Coy, HRQ, Coy \times HRQ	437.1	0	5	0.381
SmMam, Coy, HRQ, Coy \times HRQ	439.1	2	6	0.140
D2W, Coy, HRQ, Coy \times HRQ	439.1	2	6	0.140
Coy, D2W, HRQ, Coy \times HRQ, D2W \times HRQ	440.8	3.7	7	0.060
SmMam, Coy, HRQ, SmMam \times HRQ, Coy \times HRQ	441	3.9	7	0.054
SmMam, D2W, Coy, HRQ, Coy \times HRQ	441.1	4	7	0.052
Coy	441.7	4.6	3	0.038
SmMam, Coy	442.1	5	4	0.031
SmMam, Coy, D2W, HRQ, Coy \times HRQ, D2W \times HRQ	442.8	5.7	8	0.022
SmMam, Coy, D2W, HRQ, SmMam \times HRQ, Coy \times HRQ	443	5.9	8	0.020

tion outside of these refuges can significantly restrict prey space use. For example, Heithaus and Dill (2002) showed that bottlenose dolphins (*Tursiops aduncus*) avoided high-quality foraging areas when their predators, tiger sharks (*Galeocerdo cuvier*), were present, even at a relatively low density. Only when sharks were absent in the system would dolphins forage in those areas. Even though prey are capable of restricting use to areas with low predation risk, numerous studies have shown prey to take greater risks to acquire resources when other needs become more pressing, such as avoiding starvation (Sih 1992; Pettersson and Brömark 1993; Whitham and Mathis 2004; Creswell et al. 2010). Creswell et al. (2010) found that redshanks (*Tringa tetanus*) avoided areas with greater risk of predation from Eurasian sparrowhawks (*Accipiter nisus*) and subsequently avoided >25% of their available habitat when temperatures were >5°C. However, when temperatures were <5°C and the risk of starvation more imminent, redshanks increased their use of those risky areas. Thus, prey must constantly balance multiple risks and the need to find strategies to minimize those risks (Sih 1980).

Our results clearly show a similar pattern between IG predator–prey relationships. When basal prey was low within a home range, bobcats were forced to use riskier areas to meet their energetic needs. The importance of the interaction between home range quality and intensity of coyote use is further supported by the fact that models with the interaction accounted for 80–92% of the total AIC weights. Bobcats in high-quality home ranges are likely not food stressed and have access to sufficient prey; both factors allow them to restrict space use to areas with a lower risk of encountering coyotes. Webb et al. (2009) found a similar relationship with IG predator interactions in snakes: in their study, juvenile snakes of the IG prey species took greater risks of IG predation to use areas with favorable microclimates, whereas adults did not take those risks because of their greater thermal tolerance.

Bobcats are generally considered to be nocturnal (Neale and Sacks 2001), but our results suggest that when small mammal abundance decreases, bobcats increase their daytime activity to gain access to water birds when they are most active (Brisbin and Mowbray 2002). This shift in bobcat activity is further supported by the fact that the top-ranked nighttime core area models did not include distance to water as a covariate, or if it did, the model showed that core areas were located further from water. Our top daytime core area models also suggest that bobcats increased daytime foraging for small mammals when the latter were low in abundance, as indicated by a higher probability of core areas occurring where small mammal abundance was higher in the home range during periods of low prey abundance than during periods of high prey abundance. By having to forage during the day, bobcats likely increase their

exposure to IG predation, especially because daytime core areas shift to areas with greater coyote use when prey abundance is low. Other normally nocturnal IG prey species have been shown to increase their daytime activity for increased access to food, even though exposure to IG predation increases (Sunde et al. 2003). While coyotes at the study site have been shown to be most active at night, they still are active at all other times of the day (Young et al. 2006), so temporal avoidance of bobcats towards coyotes seems unlikely.

The relationship we found between bobcats and coyotes is intriguing given the relative rarity of coyote predation on bobcats. Others have also shown that IG prey can exhibit a behavioral response towards IG predators, even though predation is rarely observed (Sergio et al. 2007; Zuberogoitia et al. 2008) and indirect predator effects can have an equal or greater effect on prey population (Creel and Christianson 2008) and community dynamics (Creswell et al. 2010). Bobcats on the study site have been found to react negatively to the perceived presence of coyotes: when presented with a coyote call playback at a relatively short distance (approx. 20 m), a bobcat immediately ran for the closest dense vegetative cover (R. Wilson, personal observation). While no bobcats were killed by coyotes during our study, during a previous study on the refuge, a bobcat was killed by a coyote, coinciding with a period of low prey abundance (T.L. Blankenship, unpublished data). The relatively rarity of IG predation suggests that the space-use strategy employed by bobcats is relatively effective at avoiding coyotes.

One assumption of our analysis is that uncollared bobcats and coyotes did not influence our results. This could be problematic, for instance, if uncollared coyotes intensively used space estimated as used infrequently by collared coyotes. We do not believe this is a problem, however, because we had 23–62% of the coyote population collared given the number of territories present on the refuge and average pack sizes (Andelt 1985). Because coyote space use on the refuge is relatively stable over time (Young et al. 2006) and because coyote movements within territories are typically highly correlated, space-use data obtained from collared coyotes should be representative of uncollared coyotes in the territory. An increase in the number of coyotes collared in a territory would only result in more precise estimates of use, but it would not influence the general pattern of intensity of use. Additionally, because coyote intensity maps were bounded by the estimated territory boundaries and we restricted our use of bobcat relocations to those that overlapped with those intensity maps, we reduce the likelihood of associating a location with an artificially low coyote use value. Given that we had approximately 50% of the bobcat population collared (approx. 15; Heilbrun et al. 2006) and that bobcats are solitary felids, the presence of uncollared bobcats likely had limited influence on our results.

Finally, our results provide some insight into the underlying behaviors that lead to the development of bobcat core areas. Few studies have tested hypotheses on how animals use core areas (e.g., Barg et al. 2006), and most have assumed they represent foraging areas (Powell et al. 1997; Plowman et al. 2006). Our results indicate, however, that bobcat core area behavior is not just a function of prey abundance, but a balance between prey abundance and coyote avoidance. Spatial variation in basal prey abundance allowed individuals in the population to employ multiple behavioral strategies to deal with the coyote risk. Thus, at any given time, some bobcats remained relatively invulnerable to IG predation, while others increased the likelihood of encountering coyotes. These multiple behavioral strategies employed over such a small area likely enhance the potential for IG competitors to coexist. Future research should continue to focus on how local-scale heterogeneity might influence IG predation dynamics within a given community and use existing information on predator–prey dynamics to inform research on IG predator–prey dynamics.

Acknowledgments This research was funded by the Welder Wildlife Foundation, American Society of Mammalogists, and USDA Wildlife Services National Wildlife Research Center. We thank S.N. Glasscock for valuable discussion and the staff of the Welder Wildlife Foundation for support throughout. J. du Toit, E.M. Gese, J.A. Powell, and J.A. Bissonette, and two anonymous reviewers provided valuable comments on earlier versions of this manuscript. We thank P. Darrow, S. Meggers, C. Burnett, J. Williams, M. Bales, and O. Chan for assistance in data collection. This is Welder Wildlife Foundation Publication Number 962.

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