

Foraging in the Landscape of Fear, the Predator's Dilemma: Where Should I Hunt?

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Abstract: Under predation risk, prey species are more abundant in areas of low predation risk even at the expense of forage quality. As a result two predictions are possible, 1) predators should choose to hunt in areas with fewer but easier to catch prey than areas where they are more abundant but harder to catch; and 2) the frequency of prey species in the diet of predators using low risk areas should be greater than, or at least equal to, the diet of predators using high risk areas. To test these two predictions, we used data on coyote *Canis latrans* abundance and diet composition from two habitats in the Chihuahuan Desert of Mexico that have different abundances of jackrabbits (*Lepus californicus*) and rodents. We used the number of coyote scats found in transects in the two areas to assess coyote abundance and analyzed the contents of these scats to determine diet composition. We found significantly more coyote scats/yr (22.6 ± 4.7 (SE) vs. 12.2 ± 2.4 scats/yr, d.f. = 7, paired $t = 3.80$, $P = 0.007$) in the habitat with less jackrabbits and more rodents. However, the percent occurrence of jackrabbits ($54.3 \pm 6.7\%$ vs. $60.1 \pm 7.7\%$) and rodents ($32.6 \pm 6.5\%$ vs. $30.1 \pm 6.0\%$) in coyote scats did not differ between the two habitats. These results supported both the above cited predictions and the hypothesis that prey vulnerability can influence habitat use by coyotes.

Keywords: Optimal foraging, predation risk, predator lethality.

Optimal foraging predicts that an animal should forage where it is most profitable and where it incurs the least costs in obtaining food resources (Sih 1980, Pyke 1984). Based on this theory, animals should forage where food is most abundant or of highest quality (Sih 1980, 1984). However, for prey species, predation risk is an important foraging cost (Brown 1988) and animals will consider it in their foraging decisions (Altendorf *et al.* 2001, Hernández and Laundré 2005, Brown and Kotler 2004). Habitat characteristics, e.g. frequency, availability, and location of cover, can influence the level of predation risk by mediating the lethality of the predator and thus the vulnerability or catchability of the prey (Messier and Barrette 1985, Brown and Kotler 2004, Laundré and Hernández 2003a). Consequently, predation risk will vary over a landscape mosaic of habitat characteristics, i.e. the landscape of fear (Messier and Barrette 1985, Laundré *et al.* 2001, Laundré and Hernández 2003a). Within this landscape, prey must balance forage resources available with their vulnerability to predation within each habitat. The result is a deviance from what is predicted under classic optimal foraging with prey often being more abundant in areas of lower risk even if they provide fewer foraging opportunities (Edwards 1983, Sih 1984, Wolff and Van Horn 2003, Hernández and Laundré 2005, Creel *et al.* 2005).

Relative to foraging strategies of the predator, we can ask: where should they hunt? We traditionally assume they will hunt where prey are more abundant (Andelt and Andelt 1981, Litvatis and Shaw 1982, Gese *et al.* 1996). However, if prey are more abundant in low risk areas, by definition these are areas of lower hunting success for predators. Consequently, it is possible to hypothesize that instead of seeking these more abundant but hard to catch prey, the optimal foraging strategy of a predator should be to hunt more in areas of less abundant but more vulnerable prey individuals (Brown 1988). Some study results support this hypothesis (Sih 1984, Patterson *et al.* 1998, Kunkel and Pletscher 2000, Patterson and Messier 2001, Holmes and Laundré 2006, Hopcraft *et al.* 2005). However, for many of these studies, these results were ancillary to primary study objectives and do not in themselves provide tests of this hypothesis.

To explore this hypothesis, we studied coyotes (*Canis latrans*) in the Chihuahuan Desert of northern Mexico where jackrabbits (*Lepus californicus*) are the principal prey (Hernández and Delibes 1994, Martínez Calderas 2005). We specifically tested two predictions. First, we predicted that coyotes should be more abundant in areas of lower jackrabbit abundance; coyotes will hunt where jackrabbits are less abundant but more vulnerable. Secondly, we tested the prediction that there should be equal or higher occurrence of jackrabbits in coyote diets in the low versus the high jackrabbit areas; there will be higher coyote hunting success per jackrabbit abundance in the low jackrabbit area. We tested the two predictions by comparing, over a study period of eight years and within two distinct areas: (a) the abundance of coyote; and (b) the percent jackrabbit

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occurrence in coyote diets. Here we report the results of our comparisons.

STUDY AREA

The study area is located in the Mapimi Biosphere Reserve of Mexico. Mapimi is a natural protected area in the Chihuahuan Desert of Mexico where hunting of wildlife, including coyotes, is restricted. The area is located between 26° 11' – 27° 00' N and 103° 23' – 104° 07' W and is centered at the junction of the Mexican states of Durango, Chihuahua, and Coahuila. The area is relatively flat with an average elevation of 1100 m and surrounded by mountains that reach to 1400 m. Temperature varies from 4° C in January to 36° C in June. The average annual rainfall is 264 mm and the annual evaporation is 2500 mm. Seventy-eight percent of precipitation is received between June and September. The specific study sites were in two plant communities: a grassland of *Pleurophis mutica* (toboso grass) and a shrubland of *Prosopis glandulosa* (mesquite)-*Larrea tridentata* (creosote bush)-*Opuntia rastrera* (prickly pear cactus).

In Mapimi the main abundant mammalian predator is the coyote. Other mammalian predators include the gray fox (*Urocyon cinereoargenteus*), the kit fox (*Vulpes macrotis*), bobcat (*Lynx rufus*), and puma (*Puma concolor*). However, these species are considered rare to uncommon in the area. Avian predators (hawks and owls) occur in the area but are not common.

The principal prey of coyotes are jackrabbits, with > 70% occurrence in the diet (Martínez Calderas 2005). Various small mammal species, primarily kangaroo rats (*Dipodomys* spp.) and woodrats (*Neotoma albigula*) comprise a lesser portion of the diet (< 30 %; Martínez Calderas 2005). Cottontail rabbits (*Sylvilagus auduboni*) occur in the area but were very rare (abundance index 0.2 sighted/10 km) and had a low occurrence in the diet of coyotes (0.10%, unpublished data). Previous work demonstrated that jackrabbit abundance is higher in open grassland areas compared to closed shrubland habitat (Hernández et al. 2005, Portales 2006). Additionally, the selection of grassland habitat by jackrabbits is based on lower levels of predation risk because of greater visibility (Marín et al. 2003). Conversely, rodent abundance was higher but predation risk lower in shrublands compared to grassland areas (Hernández et al. 2005, Burke 2005).

METHODS

We collected coyote scats by driving along two 15 km routes, one each in the grassland and shrubland areas (Fig. 1). We identified the scats we found as that of coyotes based on their appearance, presence of tracks, and size. We placed the scats in labeled paper bags and left them to dry in the sun. Scat collection occurred over a 6 day period in March and November of each year (2000-2007), however, in 2005 we expanded the collection period to include 10 days each in the months of December, January, and February. In all cases, we collected scats in both areas at the same time, over equal length sample routes, and with equal sample effort (number of days). The two areas receive approximately equal amounts of rainfall (Hernández et al. 2005) so we assumed decomposition rates of scats would be equal in the two areas.

Consequently, we used the total number of scats collected in each area per season as an index of abundance of coyotes in the two areas (Niebauer and Rongstad 1977, MacCracken and Hansen 1987, Stoddart et al. 2001, Bartel et al. 2005). To reduce pseudo-replication, we used the average of the March and November indices for the 8 annual estimates in statistical tests.

We analyzed the scats by breaking them up by hand and then separated the contents into distinct types such as bones, hair, teeth, fruits, etc. (Martínez Calderas 2005). We then identified these contents to the species level when possible or to the genera or order level. Once we identified the contents, we calculated the frequency of occurrence of each type of prey for each habitat and year based on the number of scats that contained a particular prey divided by the number of scats from the given habitat and year, multiplied by 100 (Hernández et al. 2002). The distance between the two collection areas was ≥ 3 km. Telemetry and GPS data on coyote movements indicate that resident animals do not normally move between the two areas (De Ita 2007, unpublished data). Thus, we assumed the results represented diets of distinct individuals in the two areas.

We conducted abundance counts of jackrabbits in March and November along the same two 15 km roads where we collected coyote scats. The counts were between 20:00 to 22:00 h on nights between the last and first quarters of the moon phase. From the back of a pickup truck driven approximately 10 km/h along the roads (Smith and Nydegger 1985), two persons scanned for jackrabbits with two 1,000,000 candle power Brinkman Q-Beam® spotting lamps. When we observed a jackrabbit, we measured the perpendicular distance from the road to the point where we initially sighted the animal. We standardized the survey counts to number of jackrabbits/10 km and used these as relative abundance indices. As we were only interested in relative abundance between habitats, we did not estimate densities, which require more rigorous assumptions. We reduced pseudo-replication in statistical tests by using the averages of Mar-Nov counts for each year ($n = 8$ years).

Small mammal abundance was estimated in three radial trapping grids or webs (Hernández et al. 2005) per habitat type. We trapped twice per year in March and November over the eight study years. In each web we placed 145 Sherman traps in 12, 100 m lines, each radiating from a central point. We placed 12 traps along each line; the first four were put every five meters and the rest every 10 m. We trapped three days per season, checking and re-baiting the traps in the morning (06:00 - 07:00) and afternoon (17:00 - 18:00). For the first capture of all rodents, we recorded the species and the specific line and trap where they were caught. We marked these individuals with a marking pen and released them. To calculate an abundance index, we converted the total number of new animals caught on all three webs in each habitat for each season into the number captured/1000 trap nights. As with jackrabbit counts, we averaged the March and November indices of each year ($n = 8$).

For all comparisons, we used a paired *t* statistical design and arcsine square root transformed percentage data before the analyses. All means are reported as $\pm$ standard error and the rejection level was $P \leq 0.05$.

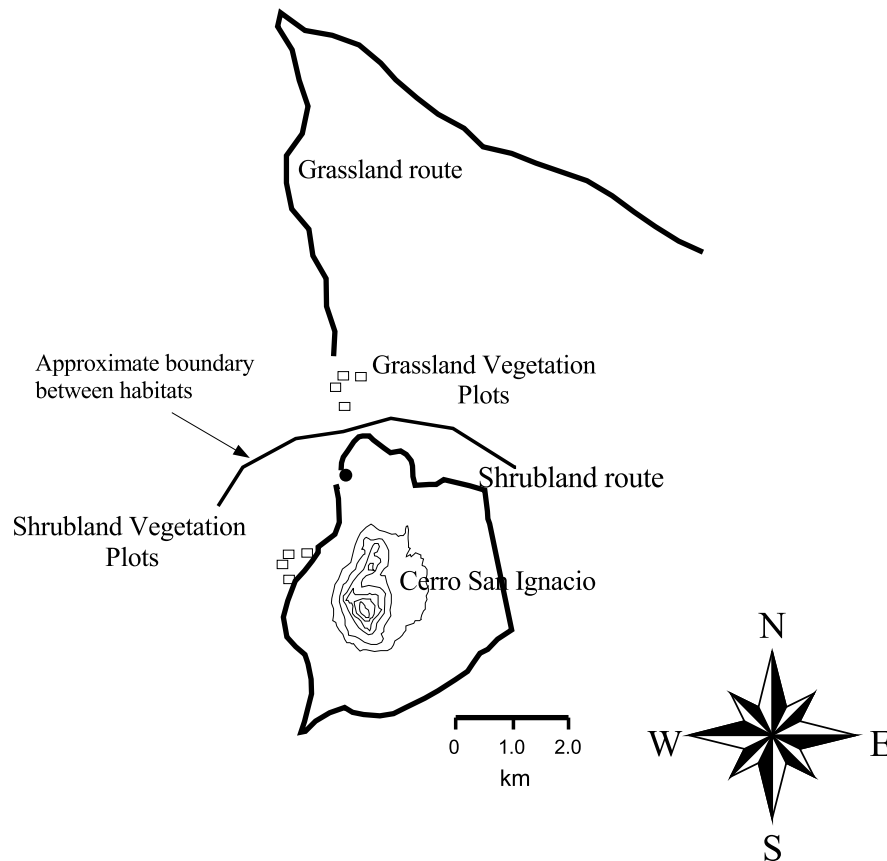


Fig. (1). Locations of the routes used for the jackrabbit surveys and coyote scat collections within the shrubland and grassland habitats. Also indicated are the locations (vegetation plots) of the small mammal trapping webs used to estimate rodent abundance in the two habitat types.

RESULTS

During the 8 years of this study, jackrabbit abundance was consistently higher in the grassland area for 11 of the 15 seasonal surveys (Portales 2006). The average annual abundance index of jackrabbits was significantly higher ($t = 2.90$, $P = 0.023$, d.f. = 7) in grassland (44.9 ± 7.7 individuals/10 km) than in shrubland (34.6 ± 7.5 individuals/10 km).

Hernández *et al.* (2005) found the occurrence of 13 and 12 species of small mammals in the shrubland and grassland respectively. Of these species, Merriam's kangaroo rat (*D. merriami*) and Nelson's pocket mouse (*Chaetodipus nelsoni*) were consistently the most abundant in shrubland (35.5% and 30.9% of total captures respectively) and Merriam's kangaroo rat was the most abundant in grassland (37.0% of total captures; Hernández *et al.* 2005). During the years of our study, the overall average abundance of rodents was significantly higher ($t = 11.29$, $P < 0.001$, d.f. = 7) in the shrubland (246.5 ± 29.5 individuals/1000 trap nights) than in the grassland (109.2 ± 24.5 individuals/1000 trap nights; unpublished data).

We collected a total of 552 coyote scats (370 in shrubland and 182 in grassland). The average number of coyote scats we found/year in the shrubland was significantly greater than that found in the grassland area (22.6 ± 4.7 vs. 12.2 ± 2.4 scats/year, $t = 3.80$, d.f. = 7, $P = 0.007$).

Although we collected coyote scats each March and November, there were 5 times (November 2000, March and November 2001, March 2004, and November 2006) when we found few scats (2-8) in one or both areas. As the percent occurrence in such small samples can change by > 10% with the presence or absence of jackrabbit or rodent remains in one scat, we decided not to use the data from these months in our seasonal analysis of diet. For the remaining 10 months, percent occurrence of jackrabbits was higher in grassland for 6 sample dates, approximately equal for one sample date, and higher in shrubland for 3 sample dates. Overall, we found no significant difference ($P = 0.30$) in average percent occurrence of jackrabbits between the shrubland (mean = $54.3 \pm 6.7\%$) and grassland (mean = $60.1 \pm 7.7\%$) areas.

Percent occurrence of rodents in coyote diets was higher in shrubland for 4 sample dates and higher in grassland for the other 6 sample dates. Consequently, as with the jackrabbits, we found no significant difference ($P = 0.67$) in percent occurrence of rodents in coyote scats from the shrubland (mean = $32.6 \pm 6.5\%$) and the grassland (mean = $30.1 \pm 6.0\%$).

DISCUSSION

Scat frequency has been successfully used as an index of abundance of coyotes within various habitats (Niebauer and Rongstad 1977, MacCracken and Hansen 1987, Stoddart *et al.* 2001, Bartel *et al.* 2005). However, in comparing between two habitats, scat frequencies could be biased for

various factors. One potential bias is different decomposition rates of scats between the two areas. Because we were comparing two nearby areas, factors affecting decomposition rates between areas, such as rainfall, humidity, or coprophagous insects were assumed to have been minimal. Another bias could result if coyotes preferred to use roads more in one habitat, e.g. the more closed shrubland habitat, than the more open grassland. Telemetry and GPS data on coyotes from both habitat types do not indicate such a bias existed (De Ita 2007, Unpublished data). Thus for the purpose of this study, we were confident that scat frequency was a reliable estimator of relative coyote abundance between the two areas.

Traditionally, it is assumed that prey abundance drives habitat selection by mammalian predators (Sih 1984, Andelt and Andelt 1981, Litvatis and Shaw 1982, Reichel 1991, Lima 2002). This assumption is based on optimal foraging theory. However, it assumes an active predator seeking an inactive or sessile prey (Pulliam 1974, Sih 1984). Based on the landscape of fear model, mobile prey species will alter their foraging patterns because of predation risk, spending more time in safer areas even at the expense of foraging opportunities (Sih 1980, Edwards 1983, Stephens and Peterson 1984, Sweitzer 1996, Gilliam and Fraser 1987, Altendorf et al. 2001, Hernández and Laundré 2005). In our area, previous studies demonstrated this inverse relationship between predation risk and habitat use for jackrabbits and rodents (Marín et al. 2003, Hernández et al. 2005, Burke 2005, Portales 2006).

Within the framework of risk and use, a coyote has to make its foraging decisions. Because of the high energy return on their predation investment (Laundré and Hernández 2003b), optimally, coyotes should and do select lagomorphs as their main prey (Niebauer and Rongstad 1977, Patterson et al. 1998, O'Donoghue et al. 1998, Bartel and Knowlton 2005). In the Chihuahuan Desert, the main lagomorph species used by coyotes is the black-tailed jackrabbit (Hernández et al. 2002, Martínez Caldera 2005). Under the traditional optimal foraging view, coyote abundance in Mapimi should be highest in the grassland area because jackrabbit abundance was 1.3 times higher than in the shrubland. Under the landscape of fear model, we predicted the opposite; coyotes should choose an area of less abundant but easier to capture individuals. Our findings of higher coyote scat abundance in the shrubland supported this prediction.

It could be argued that coyotes were more abundant in shrubland because this area had 2.3 times more rodents than the grassland area. This, however, assumes that coyotes are selecting an area solely on prey abundance and are switching to the alternate more abundant rodent prey in the shrubland. There is some evidence that when faced with a lower abundance of their principal prey, coyotes will switch prey (Todd et al. 1981, Patterson et al. 1998, Bartel and Knowlton 2005). However, in these cases, there is a reduction in use of primary prey and a corresponding increase in use of alternate prey. Thus, if coyotes were switching to the more abundant rodent populations in the shrubland, we should have found rodents comprising more and jackrabbits less of their diet in this area compared to each other and to the diet of coyotes in the grassland. We found no difference in use of jackrabbits or rodents between the two habitats. Nor did we find rodents

comprising a majority of the diet in shrubland. Thus, we reject the possibility that higher rodent abundance in the shrubland was supporting a higher coyote population.

Relative to composition of jackrabbits and rodents in the diets of coyotes, as mentioned, we did not find difference in use levels between shrubland and grassland areas for either group. Again, this is in contrast to the finding that during our study period jackrabbit abundance was 1.3 times higher in grassland than shrubland and rodent abundance was 2.3 times higher in shrubland than grassland. From these results we conclude that coyotes were not using either jackrabbits or rodents according to their relative abundance in the two habitats. Based on relative abundance, coyotes actually selected jackrabbits more and rodents less in shrublands vs. grasslands. As a possible alternate explanation of these results, we propose that vulnerability and not abundance was an important factor in determining coyotes' diets in Mapimi. Under this explanation, coyote success in capturing jackrabbits is lower in grassland areas because higher visibility allows jackrabbits to better detect predators (Lechleitner 1958, Daniel et al. 1993, Marín et al. 2003). Because of greater amounts of escape cover for small mammals, the opposite is the case for rodents in the shrubland. One consequence of this explanation would be the pattern of no difference in diet of coyotes between the two habitats. This further supports the hypothesis that the coyotes were selecting habitats based on jackrabbit vulnerability rather than abundance, which directly results from the prey's response to their predation risk due to coyotes.

Our results also corroborate the work of Sih (1984) and Holmes and Laundré (2006) who found predators, notonectid insects (*Notonecta undulata*) and pumas (*Puma concolor*), respectively, used areas of low prey-high risk more than high prey-low risk areas. Hopcraft et al. (2005) also found African lions (*Panthera leo*) were selecting hunting sites based on vulnerability rather than availability of prey. Our results also coincide with ancillary findings of other studies. Kunkel and Pletscher (2000) found higher use by wolves and lower use by moose in open areas, which the authors considered more dangerous for moose because they could be detected easier and could not escape to shelter provided by forests. Higher use areas by moose presumably consisted of greater amounts of this shelter (Kunkel and Pletscher 2000). Patterson and Messier (2000) found areas of high coyote/low deer use related to higher vulnerability of deer to coyotes (Patterson et al. 1998). In this case, vulnerability of deer to coyote predation seemed related to greater snow depth in these regions (Patterson and Messier 2000). These areas were outside of the winter yards used by deer, which seem to provide higher security from coyote predation because of established trails (Messier and Barrette 1985).

In conclusion, the results of our study indicate that prey vulnerability and not just abundance may also influence where a predator selects to hunt. Under this model, the optimal strategy for predators would be to hunt more often in the high risk areas of low prey abundance. If further research supports our findings, these reciprocal interactions between predator and prey in this behavioral response race (Sih 1984) within the landscape of fear could have far reaching consequences in various aspects of predator-prey dynamics.

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