

Competition and coexistence in sympatric bobcats and pumas

C. C. Hass

Appleton-Whittell Research Ranch, National Audubon Society, Elgin, AZ, USA

Keywords

bobcat; intraguild predation; interference competition; diet; predation; puma; scat analysis; space use.

Correspondence

Christine Hass, Appleton-Whittell Research Ranch, National Audubon Society, HC 1 Box 44, Elgin, AZ, 85611, USA.
Email: chass@audubon.org

Editor: Andrew Kitchener

Received 8 January 2009; accepted 6 February 2009

doi:10.1111/j.1469-7998.2009.00565.x

Abstract

Space use and diets of sympatric bobcats *Lynx rufus* and pumas *Puma concolor* were compared using sign surveys and scat analysis during 1997–2002 in south-eastern Arizona, USA. Bobcats appeared to use grassland, scrub, riparian and woodland habitats equally, but pumas had higher activity in riparian and woodland habitats. There was little evidence that bobcats avoided pumas in space use. Bobcats ate primarily rodents (33% of items in scats), lagomorphs (32%) and ungulates (16%), whereas pumas ate primarily ungulates (69%) and carnivores (21%). Pumas had a narrower dietary niche breadth than bobcats, and puma diet overlapped bobcat diet by 56%, suggesting that pumas may be more vulnerable to changes in prey density than bobcats. Pumas also killed and consumed bobcats, indicating that interference competition may be manifesting through intraguild predation.

Introduction

Competition for space and food resources is one of the major determinants of community structure (Morin, 1999). Recently, the role of interference competition among predators has been shown to affect space use, diet and behavior among predators (Linnell & Strand, 2000; Tannerfeldt, Elmhagen & Angerbjörn, 2002; Switalski, 2003; Thompson & Gese, 2007). The effects of interference competition, especially when one predator consumes another (intraguild predation, Polis, Myers & Holt, 1989), may extend into other trophic levels, including facilitating prey release (Linnell & Strand, 2000; Finke & Denno, 2005; Vance-Chalcraft *et al.*, 2007). Non-lethal effects, including intimidation, have been shown to be at least as important as lethal effects in ecology of prey and competitors (Lima, 1998; Linnell & Strand, 2000; Preisser, Bolnick & Benard, 2005; Creel & Christianson, 2007).

Studies of felids suggest that interference competition by larger cats may influence the diets and space use of smaller cats (Iriarte *et al.*, 1990; Hart, Ketembo & Punga, 1996; Durant, 2000; Moreno, Kays & Samudio Jr, 2006). For example, the diet of African golden cats *Profelis aurata* in Zaire may be limited by competition with and predation by leopards *Panthera pardus* (Hart *et al.*, 1996). Competition with jaguars *Panthera onca* may influence prey selection by pumas where the two species occur in sympatry (Iriarte *et al.*, 1990). Cheetahs *Acinonyx jubatus* avoid areas where African lions *Panthera leo* are present (Durant, 2000).

Bobcats *Lynx rufus* and pumas *Puma concolor* are sympatric over much of the bobcat's range in western North America, but few studies of space use or diet have been conducted of both species in sympatry. Energetic requirements of mammals scale positively with body mass (McNab, 1980; Nagy, 1987); based on body size alone, with pumas on average three to six times larger than bobcats, competition would be expected to be minimal (Rosenzweig, 1966; Hespeneide, 1975). However, reported diets overlap considerably, with both species consuming prey as diverse as small rodents and deer (*Odocoileus* spp.; Maehr & Brady, 1986; Iriarte *et al.*, 1990).

Predation on bobcats by pumas is well documented (Koehler & Hornocker, 1991; Cashman, Pierce & Krausman, 1992; Harveson *et al.*, 2000; Hansen, 2007). Interference competition by pumas also may influence habitat use of bobcats (Koehler & Hornocker, 1991). Only one study of diet has been conducted on pumas in south-eastern Arizona (Cunningham, Gustavson & Ballard, 1999), and none has been conducted on bobcats in this area. This region includes the northern extent of the Sierra Madre of Mexico and the southern extent of the Rocky Mountains. Floristic and faunal components of both ranges can be found here (Hoffmeister, 1986; Gelbach, 1993). This region hosts an unusual diversity of potential prey and competitors, including 16 species of carnivores, three species of ungulates, four lagomorphs, one marsupial, about 30 species of rodents (Hoffmeister, 1986) and a large diversity of birds (Kaufman, 2000).

The objectives of the study were to determine whether the presence of pumas influenced space use by bobcats; to compare the composition, breadth and overlap of diets of bobcats and pumas in an area of high prey diversity; and to examine the potential role of interference competition in structuring ecological relationships between the two cats.

Materials and methods

Study sites

The study was conducted between 1997 and 2002 in and near the Huachuca Mountains, c. 130 km SE of Tucson, AZ, USA. Habitat includes riparian forest (*Populus*, *Fraxinus* and *Juglans*), and grassland, savanna, mesquite bosque and scrub (*Quercus*, *Bouteloua*, *Eragrostis*, *Prosopis*, *Larrea*, *Acacia* and *Opuntia*) habitats at the lowest elevations (c. 1400 a.m.s.l.), and Madread oak and pine woodlands (*Quercus*, *Pinus*, *Juniperus*, *Pseudotsuga* and *Abies*) at middle to high elevations (up to 2800 a.m.s.l.). The study area included Fort Huachuca Military Reservation, the adjacent Coronado National Forest and San Pedro Riparian National Conservation Area, an area encompassing about 300 km² (31°25′–31°45′N, 110°27′–110°05′W).

Space use

Space use of pumas and bobcats was determined from sign surveys along transects established at Fort Huachuca Military Reservation and along the San Pedro River. Transects at Fort Huachuca followed dirt roads and trails which traversed ridges and drainages within oak-pine woodland, grassland and desert scrub habitat. Transects along the San Pedro River consisted of loops that included a trail in the scrub/grassland next to the San Pedro River (0.5–1 km from the river), and a return trip within the riparian forest of the riverbed. For the purposes of analysis, transects were subdivided by habitat type, resulting in 10 transects at Fort Huachuca and 17 transects along the San Pedro. Transects ranged from 0.9 to 9.2 km long (mean = 5.2 km), and were classified by the predominant vegetation type as grassland (45 km of transects), desert scrub (27 km), riparian forest (45 km) or oak-pine woodland (16 km). Each transect was surveyed at least three times between October 1998 and January 2000, and four transects were surveyed four times. At least 2 months separated surveys on any individual transect. Bobcat and puma sign (tracks and scat) were identified from comparison with published sources (Murie, 1975; Aranda Sanchez, 1981; Rezendes, 1999). Location of sign was determined using a GPS receiver in conjunction with a USGS topographic map. Bobcat and puma activity were calculated from track sets per km of transect (tracks km⁻¹), and means and confidence intervals (CI) were calculated for each habitat type for each species by bootstrapping 10 000 times (Mueller & Altenberg, 1985).

Food habits

Felid scats were collected during sign surveys and opportunistically during the course of other field studies (Hass, 2002; Hass & Valenzuela, 2002; Hass & Dragoo, 2006). Scats were identified by odor, size and shape (Murie, 1975; Rezendes, 1999). Scats were frozen immediately after collection, then autoclaved and washed through sieves to separate component parts. All hair, claws, teeth and bone fragments were separated and identified to the lowest taxa possible (Greene & Jaksic, 1983) by comparison to reference collections and published reference materials (Mayer, 1952; Moore, Spence & Dugnolle, 1974; Glass & Thies, 1997). Hairs were mounted following the technique of Carter & Dilworth (1971).

Following Glen & Dickman (2006), the adequacy of the sampling effort was determined by calculating a Brillouin index according to the equation

$$H_b = \frac{\ln N! - \sum \ln n_i!}{N}$$

where H_b is the diversity of prey in the sample, N is the total number of individual prey taxa in all samples and n_i is the number of individual prey taxa in the i th category (Brillouin, 1956; Magurran, 1988). The index ranges from 0 to 4.5. A diversity curve was calculated by sampling with replacement over a range of four to 100 samples, in increments of two. For each sample, a value for H_b was calculated and then resampled 10 000 times to obtain a mean and 95% CI. Adequacy of sampling effort was determined by whether an asymptote was reached in the diversity curve and another curve calculated from the incremental change in each H_b with the addition of two more samples.

Per cent occurrence was calculated as the number of prey items of each taxa divided by the total number of prey items consumed by each predator. Dietary niche breadths for pumas and bobcats were calculated according to Levins (1968), standardized by Hurlbert (1978):

$$B_s = \left(\left(\frac{1}{\sum p_i^2} \right) - 1 \right) / (n - 1)$$

where p_i is the relative proportion of prey taxon i in the diet of predator p and n is the number of prey taxa. B_s ranges from zero to one.

Mean weight of vertebrate prey (MWVP) was calculated as the geometric mean of the weights of individual prey items. Weights were determined from published sources (e.g. Hoffmeister, 1986; *Mammalian Species* accounts) and from animals captured during other field studies. Individual prey animals were assumed to be adult size except where remains indicated those of a juvenile. Because juveniles may be easier for predators to capture than adults, they were considered different taxa for the purpose of analysis. Juveniles weights were assigned as 50% of adult weight.

Dietary overlap was calculated using the MacArthur & Levins (1967) index:

$$\alpha_{bp} = \sum b_i p_i / \sum p_i^2$$

and

$$\alpha_{pb} = \frac{\sum p_i b_i}{\sum b_i^2}$$

where α_{bp} is the overlap of species p on species b , and α_{pb} is the overlap of species b on species p , p_i is the unweighted use of food category i by species p , and b_i is the same for species b . The value of α varies from zero with no overlap to one for complete overlap.

For comparisons with other studies, a composite index of dietary overlap was calculated according to Pianka (1973):

$$\alpha = \frac{\sum (p_i b_i)}{\sqrt{\sum (p_i^2 b_i^2)}}$$

where p_i and b_i are as above. Both measures of overlap were multiplied by 100 to obtain percentages. To reduce potential bias of small sample sizes, means and 95% CI were calculated by sampling with replacement 10 000 times (Mueller & Altenberg, 1985).

Results

Space use

The 27 transects were surveyed 90 times. Bobcats or pumas were detected on all but one transect. During the course of the study, bobcats only were detected on seven transects, pumas only were detected on only one transect and both species were detected on the remaining 18 transects. Sign of both cats was found on 18 of 27 transects (67%) and 30 of 90 surveys (33%). Transects with sign of both cats included all habitat types (Table 1). CI of bobcat activity overlapped among habitat types, but pumas showed more activity in riparian and woodland habitats than grassland or scrub (Fig. 1). Bobcat activity also did not differ whether or not there was sign of puma on the same survey (bobcat tracks km^{-1} with puma, mean = 0.28, 95% CI: 0.13–0.60; without puma, mean = 0.28, 95% CI: 0.13–0.60).

Table 1 Presence of sign of bobcats *Lynx rufus* and pumas *Puma concolor* by transect and survey in different habitat types

	Neither	Bobcat only	Puma only	Both present	Total
By transect					
Grassland	1	3	0	4	8
Scrub	0	2	0	4	6
Woodland	0	1	0	4	5
Riparian	0	1	1	6	8
Total	1	7	1	18	27
By survey					
Grassland	9	12	0	6	27
Scrub	5	8	0	7	20
Woodland	4	3	4	4	15
Riparian	4	6	5	13	28
Total	22	29	9	30	90

Surveys conducted in south-eastern Arizona, USA, 1998–2000. Each transect was surveyed ≥ 3 times. See text for methods.

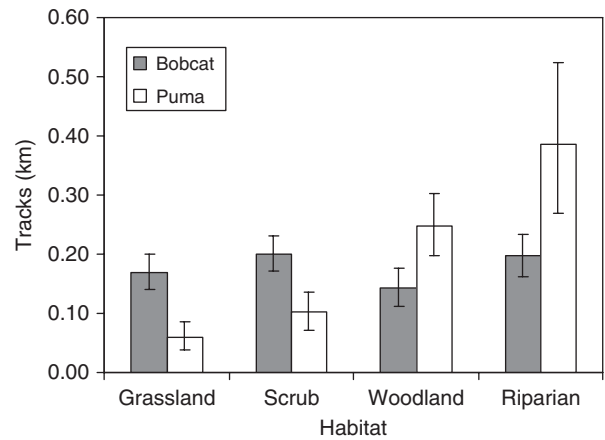


Figure 1 Bobcat *Lynx rufus* and puma *Puma concolor* activity, measured in tracks km^{-1} , along 27 transects surveyed in south-eastern Arizona, 1998–2000. Vertical lines are 95% confidence intervals calculated by bootstrapping 10 000 times.

Food habits

A total of 61 bobcat scats was analyzed, containing 96 items and 17 taxa. A total of 64 puma scats was analyzed, containing 73 items and 14 taxa. For both predators, diversity curves reached an asymptote and the incremental change declined to $< 1\%$ at ≥ 44 samples (Fig. 2), indicating that the sampling effort was adequate.

The most common items in bobcat scats were rodents and cottontails (*Syvilagus* spp.). Cow *Bos taurus* hair was found in one scat; as this was likely scavenged, it was excluded from further analysis. Minor amounts of conspecific hair, in the absence of bones or claws, were considered the results of grooming behavior and were also not included in analyses. Remains of juvenile coatis *Nasua narica*, cottontails and deer (*Odocoileus hemionus* and *Odocoileus virginiana*, identified only to genus) were found in bobcat scats; identifiable juvenile remains made up 7% of the diet. This represents a minimum, as juveniles could not always be identified from remains. Sixty-five per cent of the diet was composed of lagomorphs and rodents (Table 2). Eight taxa each comprised $> 5\%$ of items in bobcat scats: cottontails, *Odocoileus*, small rodents (including *Peromyscus* spp., *Baiomys taylori* and *Reithrodontomys* spp.), small birds, rock squirrels *Spermophilus variegatus*, pocket gophers (*Thomomys* spp.), jackrabbits (*Lepus* spp.) and woodrats (*Neotoma* spp.) (Fig. 3). Standardized diet breadth for bobcats was 0.39 (95% CI: 0.27–0.52), and MWVP was 652 g (95% CI: 397–1014 g). Bobcat diet overlapped that of puma diet by 20% (95% CI = 10–31%).

The most common item in puma scats was *Odocoileus*. One scat contained black bear *Ursus americanus* hair; as this was likely scavenged, it was excluded from further analyses. The diet was 55% *Odocoileus*, and only three species each made up $> 5\%$ of the diet: *Odocoileus*, coati and peccary *Pecari tajacu*. Juvenile *Odocoileus*, peccary, puma and hog-nosed skunks *Conepatus leuconotus* were found in puma

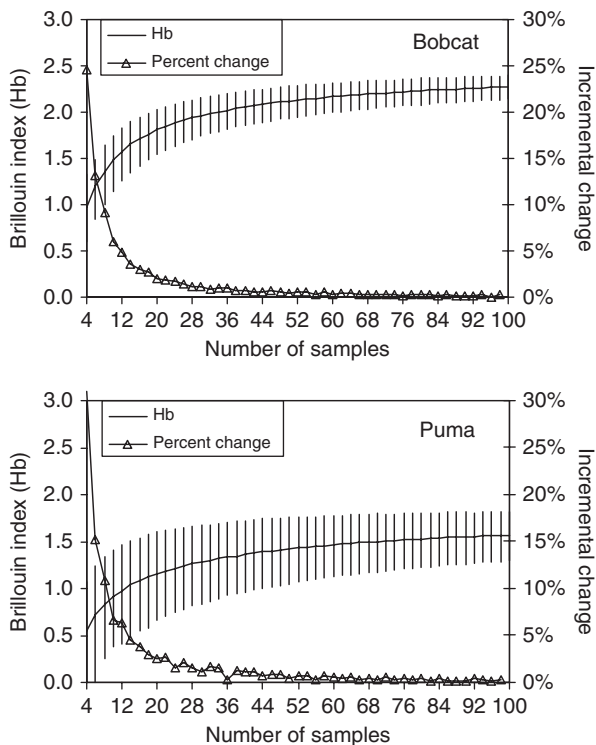


Figure 2 Diversity curves and incremental change curves for bobcat *Lynx rufus* and puma *Puma concolor* scat samples. Mean and 95% confidence intervals obtained by resampling with replacement 10 000 times.

Table 2 Results of analysis of scats of bobcats *Lynx rufus* and pumas *Puma concolor* in south-eastern Arizona, 1997–2002

Taxa	Bobcat (<i>n</i> =61)		Puma (<i>n</i> =64)	
	Mean	95% CI	Mean	95% CI
Lagomorphs	0.32	0.23–0.42	0.03	0–0.07
Rodents	0.33	0.24–0.43	0.06	0.01–0.11
Carnivores	0.08	0.03–0.15	0.21	0.12–0.30
Ungulates	0.16	0.08–0.23	0.69	0.59–0.79
Birds/reptiles	0.10	0.04–0.17	0.01	0–0.04

Means and 95% confidence intervals (CI) of per cent occurrence calculated as number of prey items per sample/total number of prey items.

scats; identifiable juvenile remains made up $\geq 7\%$ of the diet. Eighty-nine per cent of the diet was composed of ungulates and small/medium carnivores (Table 2). Remains of a bobcat were found in one scat. Standardized diet breadth for pumas was 0.13 (95% CI: 0.08–0.21), and MWVP was 13 736 g (95% CI: 8968–18 492 g). Puma diet overlapped that of bobcats by 56% (95% CI: 47–65%). The composite overlap of bobcat and puma diet was 36%, with bobcats consuming, in general, a greater diversity of smaller animals, and puma, fewer species of larger animals (Fig. 3).

Discussion

Bobcats appeared to show similar activity in all habitat types, with little evidence of spatial avoidance of pumas. Bobcats were more active in grassland and scrub habitats than pumas, whereas pumas were more active in woodland and riparian habitats than were bobcats. Previous studies of pumas have found they tend to prefer moderately dense cover for stalking their prey (Hansen, 1992), whereas bobcats are more habitat generalists (Hansen, 2007). No prey availability data were collected during this study, so it could not be determined whether the differences in habitat use were due to seeking of preferred prey items, or avoidance of some habitats by bobcats and pumas. It is possible that bobcats were avoiding pumas on a more temporal scale or finer spatial scale than was measured here (Linnell & Strand, 2000). Koehler & Hornocker (1991) found substantial differences in space use by bobcats and pumas during the summer in Idaho, but not during the winter.

As expected, diets of bobcats and pumas differed by taxa, prey weight and diversity of diet. The results of this study concur with previous studies which found bobcats to prey primarily on lagomorphs and rodents (Maehr & Brady, 1986; Neale & Sacks, 2001) and puma to prey primarily on ungulates (Iriarte *et al.*, 1990; Logan & Sweanor, 2001). Maehr & Brady (1986) reviewed numerous dietary studies of bobcats, and found that rabbits and small mammals constitute 31–85% of bobcat diet (average = 62%, *n* = 25 studies), consistent with this study and a study conducted in central Arizona by Jones & Smith (1979).

Previous studies have found that the majority of a puma's diet in temperate habitats consisted of ungulates, whereas in tropical habitats the diet was more varied and composed of smaller prey (Iriarte *et al.*, 1990; Nuñez, Miller & Lindzey, 2000). This study found that 89% of the diet of pumas was ungulates. Nearby studies of pumas also found a high percentage of ungulates (65–95%) in the diet (Cashman *et al.*, 1992; Cunningham *et al.*, 1999; Logan & Sweanor, 2001; Rosas-Rosas *et al.*, 2003).

Bobcats can extract more nutrients from larger prey, like *Odocoileus*, than from small mammals or rabbits (Powers, Mautz, & Pekins, 1989). Although Sunquist & Sunquist (1989) suggested that felids may forage most effectively by choosing the largest available prey, a larger felid competitor may exercise both exploitative and interference competition by usurping carcasses that cannot be consumed at one time, possibly killing the smaller competitor in the process.

Bobcats are quite capable of killing *Odocoileus*. *Odocoileus* make up the highest proportion of bobcat diets in the north-eastern US (Hansen, 2007) – an area in which pumas were extirpated many years ago (Hansen, 1992). *Odocoileus* are also important in the diet of bobcats in Florida (Labisky & Boulay, 1998) and Pennsylvania (McLean, McCay & Lovallo, 2005), areas where pumas are rare enough to have been classified as federally endangered (Hansen, 1992). *Odocoileus* comprised 23–47% of the diet of bobcats reintroduced onto an island in Georgia where no pumas were present (Baker *et al.*, 2001). It is possible that bobcats are

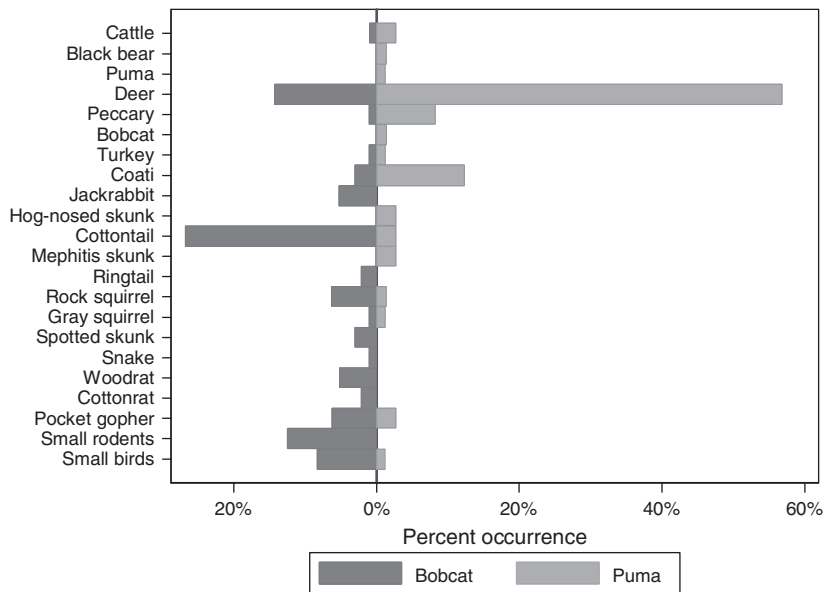


Figure 3 Per cent occurrence of different prey found in scats of bobcats *Lynx rufus* and pumas *Puma concolor* in the Huachuca Mountains of Arizona. Listed in descending order of prey weight. For graphical simplicity, all prey were calculated at adult weights. Deer = *Odocoileus hemionus* and *Odocoileus virginiana*; Turkey = *Meleagris gallopavo*; gray squirrel = *Sciurus arizonensis*; cottontail = *Sigmodon* spp.; ringtail = *Bassariscus astutus*; spotted skunk = *Spilogale gracilis*; Mephitis skunk = *Mephitis mephitis* and *Mephitis macroura*. Small rodents include *Peromyscus*, *Reithrodontomys* and *Baiomys*.

killing fewer *Odocoileus* in areas where they are sympatric with pumas to reduce predation risk. Pumas have been documented scavenging *Odocoileus* killed by bobcats, and killing bobcats that scavenge from their kills (Koehler & Hornocker, 1991). More information is needed on the role of competitors in shaping dietary niche breadths.

Although the composite index of overlap was only 36%, puma diets overlapped bobcat diets by 56%, and pumas exhibited a narrower dietary niche breadth. These two factors may reflect a diet more vulnerable to environmental perturbations that affect prey populations, such as drought, than the diet of bobcats (*sensu* Fedriani *et al.*, 2000). Bobcats consume many species which have high rates of reproduction, which may lessen the effects of food shortages for bobcats. Competition might not fully manifest itself until resources drop below some critical threshold (Wiens, 1993). When food resources become limiting, competitors have three primary options for reducing competition: changing foraging behaviour (e.g. spatially or temporally), changing diets (Hespenheide, 1975) or reducing the competition by killing or intimidating competitors (Linnell & Strand, 2000).

Both bobcats and pumas are strongly territorial (Fendley & Buie, 1982; Sunquist & Sunquist, 1989; Lovallo & Anderson, 1996; Logan & Swenor, 2001; Chamberlain, Leopold, & Conner, 2003). However in some studies, bobcats changed movement rates and intensity of home-range use (Chamberlain *et al.*, 2003) and exhibited seasonal changes in home-range use or home-range size (Koehler & Hornocker, 1989; Lovallo & Anderson, 1996). Both bobcats and pumas appear to modify their diet based on prey availability (Leopold & Krausman, 1986; Maehr & Brady, 1986; Iriarte *et al.*, 1990). Therefore, it appears that bobcats and pumas can minimize competition by modifying both diet and foraging behavior within their home ranges. Scognamiglio *et al.* (2003) suggested that although jaguars and

pumas exhibited a high degree of spatial overlap, temporal differences in activity patterns and in food habits promoted coexistence.

In addition, pumas may reduce competition with bobcats through intraguild predation or interference competition. In most cases, pumas do not appear to consume the bobcats they have killed (Koehler & Hornocker, 1991; Hansen, 2007; pers. obs.), so it appears that interference competition may reduce the number and behavior of potential competitors. Moreno *et al.* (2006) suggested that interference competition might be more effective among competitors that differ substantially in body size. Minimizing predation risk has pronounced effects on prey behavior, including space use, time spent foraging, sociality and diet (Lima, 1998; Preisser *et al.*, 2005; Creel & Christianson, 2007). It seems reasonable to hypothesize that, in areas of sympatry, bobcats may adjust their foraging behaviour or diet to reduce predation risk from pumas. However, it was not possible in this study to rule out the alternative hypothesis that bobcat diet and habitat use reflected prey availability and not interference competition (Baker *et al.*, 2001). Additional studies in other habitats and environmental conditions, and including more putative competitors and prey availability may further illuminate coexistence patterns among these species.

Acknowledgments

Field work was supported by Arizona Game and Fish Heritage Funds (grants I95028, I20001, U20003), The Nature Conservancy through a Rodney Johnson/Katherine Ordway Stewardship Endowment and USAIC & Fort Huachuca Wildlife Office. Microscopes were provided by Arizona Game & Fish and the Fort Huachuca Wildlife Office. Thanks to M. Tuegel for field assistance, H. Richter

for support of the tracking study, H. Shaw for collecting some puma scats and S. Stone and anonymous reviewers for comments on the paper.

References

- Aranda Sanchez, J.M. (1981). *Rastros de los mamíferos silvestres de México*. Xalapa, Veracruz: Instituto Nacional de Investigaciones sobre Recursos Bioticos.
- Baker, L.A., Warren, R.J., Diefenbach, D.R. & James, W.E. (2001). Prey selection by reintroduced bobcats (*Lynx rufus*) on Cumberland Island, Georgia. *Am. Midl. Nat.* **145**, 80–93.
- Brillouin, L. (1956). *Science and information theory*. New York: Academic Press.
- Carter, B.C. & Dilworth, T.G. (1971). A simple technique for revealing the surface pattern of hair. *Am. Midl. Nat.* **85**, 260–262.
- Cashman, J.L., Pierce, M. & Krausman, P.R. (1992). Diets of mountain lions in southwestern Arizona. *Southwest Nat.* **37**, 324–326.
- Chamberlain, M.J., Leopold, B.D. & Conner, L.M. (2003). Space use, movements, and habitat selection of adult bobcats (*Lynx rufus*) in central Mississippi. *Am. Midl. Nat.* **149**, 395–405.
- Creel, S. & Christianson, D. (2007). Relationships between direct predation and risk effects. *Trends Ecol. Evol.* **23**, 194–201.
- Cunningham, S.C., Gustavson, C.R. & Ballard, W.B. (1999). Diet selection of mountain lions in southeastern Arizona. *J. Range Mgmt.* **52**, 202–207.
- Durant, S.M. (2000). Living with the enemy: avoidance of hyenas and lions by cheetahs in the Serengeti. *Behav. Ecol.* **11**, 624–632.
- Fedriani, J.M., Fuller, T.K., Sauvajot, R.M. & York, E.C. (2000). Competition and intraguild predation among three sympatric carnivores. *Oecologia* **125**, 258–270.
- Fendley, T.F. & Buie, D.E. (1982). Seasonal home range and movement patterns of the bobcat on the Savannah River Plant. In *Cats of the world: biology, conservation, and management*: 237–259. Miller, S.D. & Everett, D.D. (Eds). Washington, DC: National Wildlife Federation.
- Finke, D.L. & Denno, R.F. (2005). Predator diversity and the functioning of ecosystems: the role of intraguild predation in dampening trophic cascades. *Ecol. Lett.* **8**, 1299–1306.
- Gelbach, F.R. (1993). *Mountain islands and desert seas. A natural history of the US–Mexican borderlands*. College Station, TX: Texas A & M University Press.
- Glass, B.P. & Thies, M.L. (1997). *A key to the skulls of North American mammals*, 3rd edn. Stillwater, OK: Oklahoma State University.
- Glen, A.S. & Dickman, C.R. (2006). Diet of the spotted-tailed quoll (*Dasyurus maculatus*) in eastern Australia: effects of season, sex and size. *J. Zool. (Lond.)* **269**, 241–248.
- Greene, H.W. & Jaksic, F.M. (1983). Food–niche relationships among sympatric predators: effects of level of prey identification. *Oikos* **40**, 151–154.
- Hansen, K. (1992). *Cougar: the American lion*. Flagstaff, AZ: Northland Publishing.
- Hansen, K. (2007). *Bobcat: master of survival*. New York: Oxford University Press.
- Hart, J.A., Ketembo, M. & Punga, K. (1996). Diet, prey selection and ecological relations of leopard and golden cat in the Ituri forest, Zaire. *Afr. J. Ecol.* **34**, 364–379.
- Harveson, L.A., Tewes, M.E., Silvy, N.J. & Rutledge, J. (2000). Prey use by mountain lions in southern Texas. *Southwest Nat.* **45**, 472–476.
- Hass, C.C. (2002). Home-range dynamics of white-nosed coatis in southeastern Arizona. *J. Mammal.* **83**, 934–946.
- Hass, C.C. & Dragoo, J.W. (2006). Rabies in hooded and striped skunks in Arizona. *J. Wildl. Dis.* **42**, 825–829.
- Hass, C.C. & Valenzuela, D. (2002). Anti-predator benefits of group-living in white-nosed coatis (*Nasua narica*). *Behav. Ecol. Sociobiol.* **51**, 570–578.
- Hespenheide, H.A. (1975). Prey characteristics and predator niche width. In *Ecology and evolution of communities*: 158–180. Cody, M.L. & Diamond, J.M. (Eds). Cambridge, MA: Harvard University Press.
- Hoffmeister, D.F. 1986. *Mammals of Arizona*. Tucson, AZ: The University of Arizona Press.
- Hurlbert, S.H. (1978). The measurement of niche overlap and some relatives. *Ecology* **59**, 67–77.
- Iriarte, J.A., Franklin, W.L., Johnson, W.E. & Redford, K.H. (1990). Biogeographic variation in food habits and body size of the American puma. *Oecologia* **85**, 185–190.
- Jones, J.H. & Smith, N.S. (1979). Bobcat density and prey selection in central Arizona. *J. Wildl. Mgmt.* **43**, 666–672.
- Kaufman, K. (2000). *Birds of North America*. New York: Houghton Mifflin Co.
- Koehler, G.M. & Hornocker, M.G. (1989). Influence of seasons on bobcats in Idaho. *J. Wildl. Mgmt.* **53**, 197–202.
- Koehler, G.M. & Hornocker, M.G. (1991). Seasonal resource use among mountain lions, bobcats, and coyotes. *J. Mammal.* **72**, 391–396.
- Labisky, R.F. & Boulay, M.C. (1998). Behavior of bobcats preying on white-tailed deer in the Everglades. *Am. Midl. Nat.* **139**, 275–281.
- Leopold, B.D. & Krausman, P.R. (1986). Diets of 3 predators in Big Bend National Park, Texas. *J. Wildl. Mgmt.* **50**, 290–295.
- Levins, R. (1968). *Evolution in changing environments*. Princeton, NJ: Princeton University Press.
- Lima, S.L. (1998). Nonlethal effects in the ecology of predator–prey interactions. *BioScience* **48**, 25–34.
- Linnell, J.D.C. & Strand, O. (2000). Interference interactions, co-existence and conservation of mammalian carnivores. *Divers. Distrib.* **6**, 169–176.
- Logan, K.A. & Sweanor, L.L. (2001). *Desert puma. Evolutionary ecology and conservation of an enduring carnivore*. Washington, DC: Island Press.

- Lovallo, M.J. & Anderson, E.M. (1996). Bobcat (*Lynx rufus*) home range size and habitat use in northwest Wisconsin. *Am. Midl. Nat.* **135**, 241–252.
- MacArthur, R.H. & Levins, R. (1967). The limiting similarity, convergence, and divergence of coexisting species. *Am. Nat.* **101**, 377–358.
- Maehr, D.S. & Brady, J.R. (1986). Food habits of bobcats in Florida. *J. Mammal.* **67**, 133–138.
- Magurran, A.E. (1988). *Ecological diversity and its measurement*. London: Chapman & Hall.
- Mayer, W.V. (1952). The hair of California mammals with keys to the dorsal guard hairs of California mammals. *Am. Midl. Nat.* **48**, 480–512.
- McLean, M.L., McCay, T.S. & Lovallo, M.J. (2005). Influence of age, sex and time of year of the diet of the bobcat (*Lynx rufus*) in Pennsylvania. *Am. Midl. Nat.* **153**, 450–453.
- McNab, B.K. (1980). Food habits, energetics, and the population biology of mammals. *Am. Nat.* **116**, 106–124.
- Moore, T.D., Spence, L.E. & Dugnolle, C.E. (1974). Identification of the dorsal guard hairs of some mammals of Wyoming. *Wyoming Game Fish Dept. Bull.* **14**, 1–174.
- Moreno, R.S., Kays, R.W. & Samudio, R. Jr (2006). Competitive release in the diets of ocelot (*Leopardus pardalis*) and puma (*Puma concolor*) after jaguar (*Panthera onca*) decline. *J. Mammal.* **87**, 808–816.
- Morin, P.J. (1999). *Community ecology*. Oxford, UK: Blackwell Science Inc.
- Mueller, L.D. & Altenberg, L. (1985). Statistical inference on measures of niche overlap. *Ecology* **66**, 1204–1210.
- Murie, O.J. (1975). *A field guide to animal tracks*, 2nd edn. Boston, MA: Houghton Mifflin Co.
- Nagy, K.A. (1987). Field metabolic rate and food requirement scaling in mammals and birds. *Ecol. Monogr.* **57**, 111–128.
- Neale, J.C.C. & Sacks, B.N. (2001). Resource utilization and interspecific relations of sympatric bobcats and coyotes. *Oikos* **94**, 236–249.
- Núñez, R., Miller, B. & Lindzey, F. (2000). Food habits of jaguars and pumas in Jalisco, Mexico. *J. Zool. (Lond.)* **252**, 373–379.
- Pianka, E.R. (1973). The structure of lizard communities. *Ann. Rev. Ecol. Syst.* **4**, 53–74.
- Polis, G.A., Myers, A.H. & Holt, R.D. (1989). The ecology and evolution of intraguild predation: potential competitors that eat each other. *Ann. Rev. Ecol. Syst.* **20**, 297–330.
- Powers, J.G., Mautz, W.W. & Pekins, P.J. (1989). Nutrient and energy assimilation of prey by bobcats. *J. Wildl. Mgmt.* **53**, 1004–1008.
- Preisser, E.L., Bolnick, D.I. & Benard, M.F. (2005). Scared to death? The effects of intimidation and consumption in predator–prey interactions. *Ecology* **86**, 501–509.
- Rezendes, P. (1999). *Tracking and the art of seeing: how to read animal tracks and sign*, 2nd edn. New York, NY: HarperCollins Publishers Inc.
- Rosas-Rosas, O.C., Valdez, R., Bender, L.C. & Daniel, D. (2003). Food habits of pumas in northwestern Sonora. *Wildl. Soc. Bull.* **31**, 528–535.
- Rosenzweig, M.L. (1966). Community structure in sympatric carnivores. *J. Mammal.* **47**, 602–612.
- Scognamillo, D., Esperanza Maxit, I., Sunquist, M. & Polisar, J. (2003). Coexistence of jaguar (*Panthera onca*) and puma (*Puma concolor*) in a mosaic landscape in the Venezuelan llanos. *J. Zool. (Lond.)* **259**, 269–279.
- Sunquist, M.E. & Sunquist, F.C. (1989). Ecological constraints on predation by large felids. In *Carnivore behavior, ecology, and evolution*: 283–301. Gittleman, J.L. (Ed.). Ithaca, NY: Cornell University Press.
- Switalski, T.A. (2003). Coyote feeding ecology and vigilance in response to gray wolf reintroduction in Yellowstone National Park. *Can. J. Zool.* **81**, 985–993.
- Tannerfeldt, M., Elmhagen, G. & Angerbjörn, A. (2002). Exclusion by interference competition? The relationship between red and arctic foxes. *Oecologia* **132**, 213–220.
- Thompson, C.M. & Gese, E.M. (2007). Food webs and intraguild predation: community interactions of a native mesocarnivore. *Ecology* **88**, 334–346.
- Vance-Chalcraft, H.D., Rosenheim, J.A., Vonesh, J.R., Osenberg, C.W. & Sih, A. (2007). The influence of intraguild predation on prey suppression and prey release: a meta-analysis. *Ecology* **88**, 2689–2696.
- Wiens, J.A. (1993). Fat times, lean times and competition among predators. *TREE* **8**, 348–349.