

Niche overlap between sympatric coyotes and bobcats in highland zones of Olympic Mountains, Washington

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Abstract

The 20th century extensive range expansion of coyote *Canis latrans* throughout North America may impose negative effects on native carnivores. We investigated the interspecific niche relationships to assess potential for competition between sympatric coyote and a similar-sized felid – bobcat *Lynx rufus* – throughout the highland zones (elevation >1000 m) of Olympic National Park, Olympic Peninsula, Washington. Through systematic collection and analyses of scats for both carnivores (May–September 2005–2006), we determined food habits (composition, diversity, overlap of diets) and habitat use patterns. To ensure correct determination of carnivore species, we used mtDNA analysis of scats. Scat analysis indicated extensive dietary overlap between coyote and bobcat (Pianka's overlap index = 0.97). For both carnivores medium-sized mammals comprised the predominant prey: mountain beaver *Aplodontia rufa* and snowshoe hare *Lepus americanus*; each occurring in about 50% of the scats. High dietary similarity indicated the potential for interspecific exploitative competition for mammalian prey, especially in harsh climatic conditions of high mountains. However, observed patterns of habitat selection inferred from scat distribution showed differences between coyotes and bobcats, implying some degree of habitat partitioning. Bobcats preferred relatively dense montane forests (canopy cover >40%) at lower elevations, and avoided the alpine zone, while coyotes inhabited mainly alpine and subalpine zones and mostly avoided forest. We conclude that observed habitat separation may alleviate foraging competition between coyote and bobcat. Whether this habitat separation will decrease potential negative effects of coyote colonization on bobcat abundance, or whether it indicates ongoing displacement of bobcats by coyotes, remains an open question.

Introduction

Invading species can create new competitive interactions with resident species, by occupying similar ecological niches (Grinnell, 1917; Elton, 1927; Hutchinson, 1957). If the species requirements are much alike and the resources they use are limiting, competitive interactions can lead to the exclusion of the weaker competitor by the superior one (Gause, 1932; Hardin, 1960) or to niche partitioning (resource differentiation by coexisting species) that affects the breadth of their realized niches (Hutchinson, 1959; MacArthur & Levins, 1967). In practice, the most commonly assessed niche dimensions for animal species are the food niche and the habitat niche. The overlap in these two niche dimensions between potential competitors may indicate the potential for mutual persistence in a given community. Competition between sympatric carnivores can be expressed as interference (direct aggression) or exploitative through consuming the same limited resources. Competitive interactions can significantly

alter demographic vital rates of carnivore populations, affecting their distribution and numbers (Linnell & Strand, 2000).

The coyote *Canis latrans* has recently spread throughout most of the North America (Moore & Parker, 1992; Gompper, 2002; Levy, 2012) and in many locations have been shown to compete with other carnivores (Cypher & Spencer, 1998; Kitchen, Gese & Schauster, 1999; Fedriani *et al.*, 2000; Kamler *et al.*, 2003). As a result of coyote expansion, its present range overlaps that of bobcat *Lynx rufus* throughout the contiguous United States and most of Mexico. Coyotes are considered a superior competitor with bobcats due to higher reproductive rates, more opportunistic diet and habitat use, and higher tolerance of humans (Bunnell *et al.*, 2007). For example, negative relationships in abundance between coyotes and bobcats have been documented (Robinson, 1961; Nunley, 1978; Henke & Bryant, 1999), with mechanisms including both exploitative (Litvaitis & Harrison, 1989) and interference competition whereby larger coyotes kill bobcats (Toweill, 1986; Fedriani *et al.*, 2000; Gipson & Kamler, 2002). These

patterns are not universal, however, as other studies suggested no negative interactions between these carnivores (Major & Sherburne, 1987; Neale & Sacks, 2001; Thornton, Sunquist & Main, 2004).

The range of coyotes has expanded considerably to the eastern part of North America, but also throughout the west coast (Levy, 2012). One of the last areas colonized by coyotes in the Pacific Northwest was the Olympic Peninsula of Washington. Available data suggest that coyotes first arrived on the peninsula early in the 20th century, but until at least 1940 they were rare and inhabited only low-elevation logged areas (Schwartz & Mitchell, 1945). The subsequent increase in coyote abundance closely paralleled a dramatic decrease and eventual extinction of the wolf *Canis lupus* population (Scheffer, 1995). Coyote colonization of the Olympic Mountains, the relatively pristine interior of the peninsula, appears to have imposed negative effects on prey populations (e.g. endemic Olympic marmots *Marmota olympus*; Griffin, 2007; Witczuk, Pagacz & Mills, 2013). Moreover, coyotes have been identified as predators of Pacific fishers *Pekania pennanti*, designated as an endangered species in Washington State and recently reintroduced to the Olympic Mountains (Lewis, 2014; Wengert *et al.*, 2014). Competition between coyotes in the Olympic mountains and large carnivores such as cougars *Felis concolor* and black bears *Ursus americanus* is unlikely due to dissimilar body size, home range and metabolic requirements (Gittleman & Harvey, 1982). Therefore, we focused on potential competitive interactions between invasive coyotes and similar-sized bobcats.

Because coyote colonization of the Olympic highlands occurred relatively recently, we could assess interspecific relations of sympatric bobcats and coyotes during the early stage of coexistence. To date, most studies of early effects of coyote invasion on bobcat populations have been conducted mainly in eastern North America [e.g. Maine (Major & Sherburne, 1987; Litvaitis & Harrison, 1989); Florida (Thornton *et al.*, 2004)], with very different environmental conditions, prey base and human population density.

To assess interspecific niche overlap and potential for competition between bobcats and coyotes throughout the highland zones of Olympic Mountains, we investigated food habits (composition, diversity, overlap of diets) and habitat use based on systematic scat collection and analyses. To ensure correct determination of carnivore species from scats, we used diagnostic DNA tests. Given limiting food resources in harsh, mountainous conditions and similar size of carnivores we predicted high overlap of their diet and spatial/habitat segregation.

Materials and methods

Study area

The study was conducted in the high country of the Olympic Mountains within Olympic National Park, Washington, at the core of the Olympic Peninsula. Climate is characterized by wet winters and dry summers and a steep west–east precipitation gradient, with mean annual rainfall exceeding 400 cm on the

western slopes and averaging about 100 cm at high elevations of the eastern rain shadow part of the range (Houston & Schreiner, 1994). The Olympic Mountains are characterized by a short growing season and long winter with the snowpack lingering until June/July. The terrain is rugged with the highest peaks reaching over 2000 m and some covered with glaciers. This study was concentrated within three upper (>1000 m) vegetation zones of the Olympic Mountains: (1) montane forests predominated by silver fir *Abies amabilis*, western hemlock *Tsuga heterophylla* and Douglas fir *Pseudotsuga menziesii*; (2) subalpine zone with patches of subalpine fir *Abies lasiocarpa* and mountain hemlock *Tsuga mertensiana*; and (3) alpine meadows occurring above 1500 m (Fonda & Bliss, 1969; Houston & Schreiner, 1994).

Scat collection and genetic species verification

Field work consisted of systematic monthly scat collection during the snowfall-free period (May–September) of 2005 and 2006 (Witczuk *et al.*, 2013). We collected scats from a total of 125 km of transects placed along stretches of hiking trails and roads (see Supporting Information Fig. S1). Transects within the elevation range of about 1000–2000 m constituted 30% of all designated trails and roads in the highland zones of Olympic National Park. Approximately 41% of the total length of transects traversed montane forests, 20% traversed mixed meadow/forest subalpine habitats, whereas the remaining 39% were in alpine meadows. Microsatellite analysis of coyote scats during parallel studies (Witczuk *et al.*, 2013) revealed that at the time of the research, sample transects were used by at least 12 coyote individuals. We also collected some scats (11% of total) opportunistically (away from trails) during transit and while conducting other research activities. All carnivore scats were collected except those of bear, whose scats were easily distinguishable from other carnivores. For each scat, GPS coordinates were recorded and a 1-cm segment was stored with silica gel for genetic verification of the species, and the remainder in a plastic bag for diet analysis.

A random sample of approximately 50% of collected scats (453 of 958) was subjected to molecular identification of the carnivore species (Witczuk *et al.*, 2013). Genetic species verification is essential because physical characteristics of scats are not diagnostic for carnivore species and so can lead to misleading diet analyses (Farrell, Romant & Sunquist, 2000; Davison *et al.*, 2002; Reed *et al.*, 2004; Monterroso *et al.*, 2013). For diagnostic species identification, we used polymerase chain reaction (PCR) and primers CanidL1 and HCarn200 (Paxinos *et al.*, 1997; Bidlack *et al.*, 2007) to amplify a short (196 bp) fragment of the cytochrome *b* region of mtDNA that we assigned to species by comparison with sequences in GenBank (Benson *et al.*, 2012).

Diet analysis

Analysis of carnivore diet was based solely on scats with species identity determined through molecular testing. We

determined prey species composition of scats based on macroscopic examination of teeth and bone fragments and microscopic examination of hair (Witzczuk *et al.*, 2013). Carnivore diet was expressed as the frequency of occurrence for each food item (the percentage of scats containing each food item). Sporadic prey items occurring in <1% of scats were excluded from analysis. We quantified food niche overlap between coyotes and bobcats using Pianka's equation (1973):

$$O = \sum (p_i q_i) / \sqrt{\sum p_i^2 \sum q_i^2} \quad (1)$$

where p_i is the proportion of food item i in coyote scats (i.e. number of occurrences of food item i / total number of occurrences of all food items in all coyote scats examined) and q_i is the proportion of food item i in bobcat scats. An index value of 1 indicates complete similarity, whereas 0 indicates complete dissimilarity of the diet (no food items in common).

For each species, we calculated dietary niche breadth (B) using the inverse of Simpson's diversity index (Simpson, 1949; Magurran, 2004, p. 115):

$$B = \frac{1}{\sum_{i=1}^s \left(\frac{n_i(n_i-1)}{N(N-1)} \right)} \quad (2)$$

where n_i is the number of occurrences of food item i , N is the total number of occurrences of all food items and s is the number of all identified food items. Greater values of the index correspond with greater diet diversity.

To evaluate whether the sample size of scats analyzed was sufficient, we plotted the values of the inverse Simpson's diversity index (B) against the number of analyzed scats for each species (Magurran, 2004). Mean and bootstrap standard deviation were obtained in program EstimateS 8.2.0 (Colwell, 2013) by sampling with replacement 1000 times.

Habitat analysis

We assessed carnivore habitat selection based on relative abundances of scats confirmed to species in the three habitat zones: montane forests, subalpine and alpine. Delineation of the zones was based on a GIS raster layer with tree crown cover (Dalby, 1996). Categories of cover in the original raster were grouped into three zones as: (1) forest zone – tree cover 71–100%, tree cover 41–70%, shrub; (2) subalpine zone – tree cover 11–40%; (3) alpine zone – rock, snow, meadows, heather. For raster reclassification, we used program GME v.0.4.0 (<http://www.spatial ecology.com>) and ArcGIS 9.3 (ESRI). In a new raster for each pixel, corresponding to a 25 × 25 m square on the ground, one of three zones was assigned, leading to relative proportions throughout the whole Park highlands of forest 67%, subalpine 10% and alpine 23%. We computed total length of all transect sections crossing each zone and assigned each scat to a given zone. The total length of all transect sections in each zone gave an estimate of habitat sampled: forest 41%, subalpine 20%, alpine 39%.

Proportion of scats of each carnivore species found in a given zone was treated as an estimate of its use (Hass, 2009; Lovari *et al.*, 2013). For such an estimate to be valid, two

assumptions must be met. First, trails must be representative survey units for bobcats and coyotes. Second, scat detection must be constant across habitats and carnivore species. Wild canids and felids are known to prefer trails and roads for travel, and sampling along trails is more effective than using off-trail methods (Gompper *et al.*, 2006; Harmsen *et al.*, 2010). Although the level of human activity may differentially affect use of trails by coyotes and bobcats (George & Crooks, 2006), this should not be an issue in Olympic National Park because of limited hiker activity on most of our surveyed transects. Detectability of scats did not differ across habitats, as the sampled transects were bare ground of similar width, where scats were distinct and visible. Although sometimes bobcats attempted to cover their scats (scratch marks on the ground accompanied 17% of their scats) lack of litter made this ineffective.

Data on scat distribution and availability of different habitats were used in computations of Manly's habitat selectivity index for each carnivore species (Manly *et al.*, 2002, p. 51):

$$\hat{w}_i = \frac{o_i}{\pi_i} \quad (3)$$

where o_i is the proportion of scats found in zone i and π_i is the proportion of transect length crossing zone i .

Values of index >1 indicate preference of a given zone; <1 indicate avoidance. Standard error and confidence intervals were computed with the formulas (Manly *et al.*, 2002, p. 55):

$$se(\hat{w}_i) = se\left(\frac{o_i}{\pi_i}\right) = \sqrt{\frac{o_i(1-o_i)}{u_i \pi_i^2}} \quad (4)$$

$$\hat{w}_i \pm z_{\alpha/2} se(\hat{w}_i) \quad (5)$$

where π_i and o_i are as above, u_i is the total number of scats of a given carnivore species and $z_{\alpha/2}$ is the percentage point of the standard normal distribution exceeded with probability $\alpha/2$. We used Bonferroni-corrected alpha level ($\alpha = 0.05/3$) to reduce type I errors due to multiple tests.

All computations were conducted in R (R Core Team, 2012) with package 'adehabitat' (Calenge, 2006).

Results

Diets

Among the 381 (of 453) scats that successfully amplified for diagnostic mtDNA species identification, 260 were confirmed as from coyote and 104 from bobcat. The remaining 17 samples were identified as cougar and not considered further. Among identified coyote and bobcat scats, 8% (30 scats) were found opportunistically off-transect (off trail), with only two of these collected >1 km from the sample transects. Proportions of carnivore species in this subset (24 and 6 scats for coyote and bobcat, respectively) were similar to those found on transects.

Diets of coyote and bobcat inferred from scat analysis show a high degree of similarity (Pianka's overlap index = 0.97)

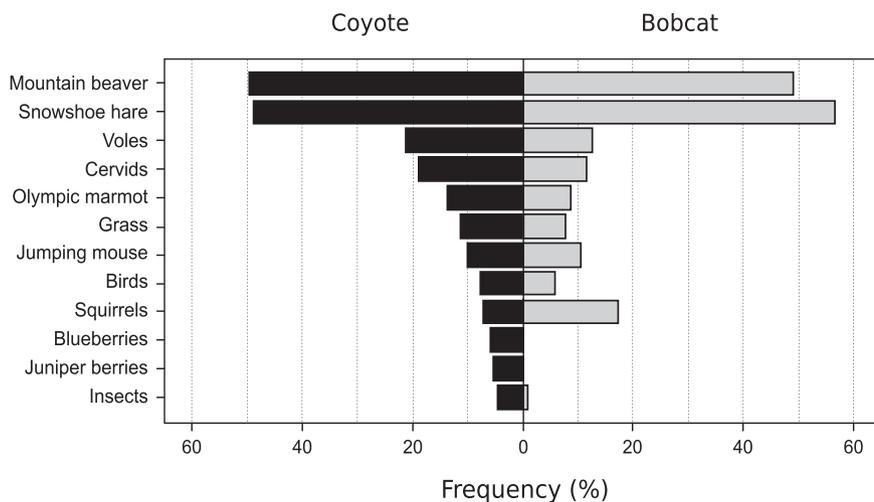


Figure 1 Frequency of occurrence of prey items in coyote *Canis latrans* (black bars, $n = 260$) and bobcat *Lynx rufus* (gray bars, $n = 104$) scats collected in Olympic National Park, Washington (May–September 2005–2006). Category ‘Squirrels’ includes *Tamiasciurus*, *Tamias* and *Glaucomys*.

with <10% differences in frequency of occurrence for all prey categories (Fig. 1). For both carnivores, two medium-sized mammals predominated in the diet: mountain beaver *Aplodontia rufa* and snowshoe hare *Lepus americanus*, each occurring in about 50% of analyzed scats. Other relatively frequent preys (10–20%) were cervids (primarily black-tailed deer *Odocoileus hemionus*), voles (*Arvicolinae*), Olympic marmot and Pacific jumping mouse *Zapus trinotatus*. The main difference in the carnivore diet was the presence of plant food [blueberries (*Vaccinium* sp.) and juniper berries *Juniperus communis*] exclusively in coyote scats. Undigested grass, by some authors assumed to serve as a purgative for an accumulation of parasites within the digestive tract (Toweill, 1986), was found in 11% of coyote and 8% of bobcat scats. For both species, there were no significant differences between frequency of occurrence of prey categories from scats collected on trail versus off trail, nor scats collected in different habitats (see Supporting Information Tables S1 and S2).

Dietary niche breadth expressed as the inverse of Simpson’s index was 6.14 for coyote and 4.75 for bobcat. Greater niche breadth value of coyote resulted mainly from the use of plant food by this species. The plot of mean value of the index against sample size (number of scats analyzed) indicated that sample sizes were sufficient for describing diet of both predators (curves reached asymptotes, Fig. 2).

Variability in diet across months was relatively low for both carnivores, except for a lack of insects and hibernating rodents (marmot, jumping mouse) in May and presence of blueberries (*Vaccinium* sp.) in coyote scats only from August and September. Although hare and mountain beaver predominated in scats of both carnivores during the whole period studied, the frequencies of snowshoe hare decreased from spring (May–June) toward September (from ≈ 70 to 30%), whereas use of mountain beaver increased (from ≈ 40 to 60%). Simpson index calculated separately for each month of the study period show increase of diet diversity from May to September for bobcat (from 4.58 in May to 5.43 in September) and especially for coyote (from 4.34 to 7.88). Monthly Pianka’s index values

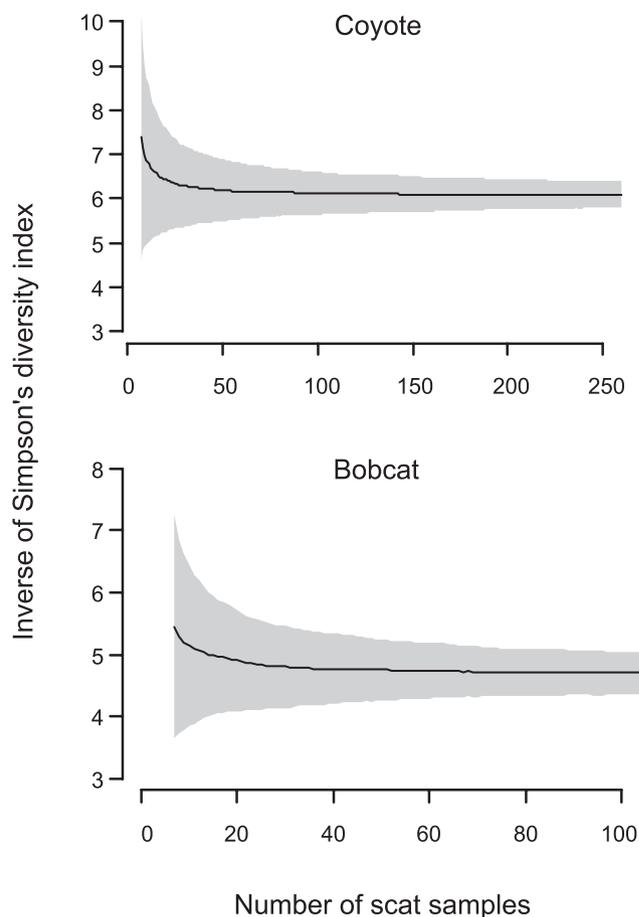


Figure 2 Mean and standard deviation of the diet diversity index (obtained by sampling with replacement 1000 times) for coyote *Canis latrans* and bobcat *Lynx rufus* scat samples collected in Olympic National Park, Washington (May–September 2005–2006).

show slight decrease of the dietary overlap between coyote and bobcat, from 0.97 in May to 0.80 in September.

Habitat use

Scats of both species were found within all three major habitat types, but with different proportions in the alpine and forest zones. The highest proportion of bobcat scats (63%; $n = 104$) was found in the forest, often along deep river valleys (see Supporting Information Fig. S1), and only 19% in the alpine, while 33% ($n = 260$) of coyote scats were discovered in the forest and 43% in the alpine zone.

Habitat selection based on scat distribution relative to availability of different habitat types along transects indicated strong selectivity by bobcat [$\chi^2 = 23.28$; degrees of freedom (d.f.) = 2; $P < 0.001$] and less pronounced selectivity for coyote ($\chi^2 = 6.06$; d.f. = 2; $P = 0.048$). Manly's selectivity index w (Fig. 3) supported a strong selectivity by bobcat for forest cover ($w = 1.53$) and avoidance of the alpine zone ($w = 0.50$), while for coyotes the index indicated weaker selection for alpine zone ($w = 1.10$) and against forest ($w = 0.82$).

Discussion

Analysis of scats collected throughout the highlands of Olympic National Park and rigorously assigned to carnivore species using DNA testing indicates lack of food partitioning between the invasive coyote and native bobcat. Instead, we observed a high degree of dietary overlap – both carnivores used the same prey in very similar proportions (dietary overlap 97%). Such high dietary similarity between coyote and bobcat in Olympics suggests the potential for interspecific competition for mammalian prey.

Food niche partitioning between coyotes and sympatric bobcats observed in other studies resulted from use of different foods or the same foods in differing proportions. Coyotes, bigger than bobcats and with different hunting technique, often rely on larger prey (Litvaitis & Harrison, 1989; McKinney & Smith, 2007); for example, coyotes feed mainly on ungulates and fruits while bobcats prey on lagomorphs and rodents in California (Neale & Sacks, 2001) and Florida

(Thornton *et al.*, 2004). In these areas and others, dietary overlap between coyotes and bobcats tend to be lower than the 97% we computed in our study: 46% (McKinney & Smith, 2007), 49% (Thornton *et al.*, 2004), 62% (Neale & Sacks, 2001) and 47–76%, depending on season (Litvaitis & Harrison, 1989).

In Olympic highlands, both species rely on rodents and snowshoe hares, while ungulates (black-tailed deer) are secondary prey comprising scat frequencies of 19% for coyote and 12% for bobcat. Likewise, we did not find the pattern of seasonal separation of bobcat and coyote food niches arising from high fruit consumption by coyotes in summer, as has been observed in other studies (Toweill, 1986; Litvaitis & Harrison, 1989). The frequencies of blueberries and juniper berries in coyote scats in our study were only 6 and 5%, respectively (with the monthly values ranging from 0% in July to a maximum of 18% for blueberries in August–September and 13% for juniper berries in May). This suggests that fruits available in the Olympic highlands are not sufficient to either seasonally support coyote diet or to allow substantial dietary divergence between coyotes and bobcats.

High dietary overlap values between coyote and bobcat similar to our study were reported from Oregon's Coast Range (94–100%, depending on season; Witmer & Decalesta, 1986). However at that low-elevation location, lack of snow cover allowed for year-round access to abundant prey (primarily mountain beaver), and this superabundant resource was thought to decrease competition between the carnivores.

Competitive interactions between coyote and bobcat are expected to be more important in northern and mountainous areas of United States because harsh climates with severe winters may decrease the availability, diversity and seasonal stability of the prey base compared with mild, relatively stable climates of southern and west-coastal North America (Neale & Sacks, 2001). Indeed, year-round research of bobcat–coyote niche relationships conducted in harsh climates consistently report higher dietary overlap in winter versus summer months (Toweill, 1986; Major & Sherburne, 1987; Litvaitis & Harrison, 1989). Although we did not study winter dynamics, we believe that this idea of increased potential for competition in areas with harsh winters may be relevant to our study area,

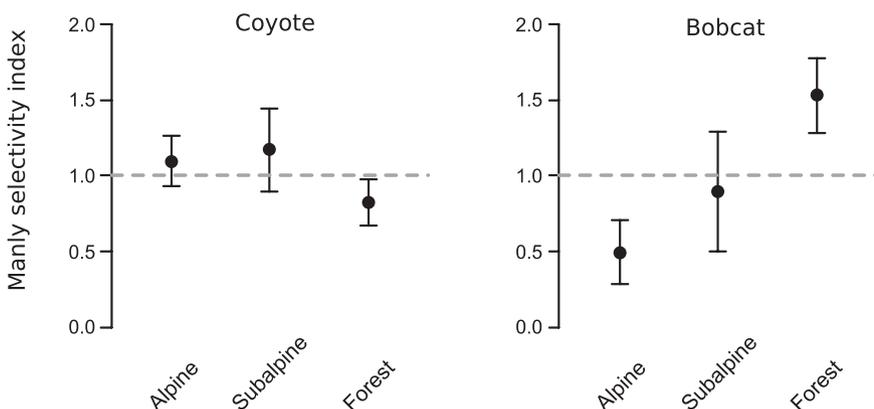


Figure 3 Coyote *Canis latrans* and bobcat *Lynx rufus* habitat selection determined with Manly's selectivity indices (w) for the three categories of cover in Olympic National Park highlands in May–September 2005–2006. The dashed line is the neutral value of the index, whereas values above the line indicate preference and below the line indicate avoidance. Confidence intervals (95%) were computed with Bonferroni correction $\alpha = 0.05/3 = 0.0167$.

because diet overlap would only be amplified in winter, when the only foods that distinguished coyote diets from bobcats (fruits such as blueberries and juniper berries) would be absent and because of limited access to mountain beaver and other rodents (hibernating or hidden by deep snow).

In our study, both carnivores preferred available and abundant medium-sized prey – snowshoe hare and mountain beaver (1–2 kg). High use of mountain beaver in local diets of coyote and bobcat has been widely reported in the Pacific Northwest including Oregon (>70% for each species; Witmer & Decalesta, 1986) and Washington (42% for bobcat; Knick *et al.*, 1984). In some areas of the region, densities of mountain beaver can be as high as 20/ha (Arjo, 2007).

Complete absence of plant food (blueberries, juniper berries) in bobcat scats confirm this felid as solely carnivorous (Fedriani *et al.*, 2000; Thornton *et al.*, 2004). Although some studies have described fruits in bobcat diet (e.g. Litvaitis, 1981; Litvaitis & Harrison, 1989; Neale & Sacks, 2001; McKinney & Smith, 2007), in instances where molecular tests were not used to verify carnivore species, fruit may have been misattributed to bobcats through misidentification of scats.

In contrast to the high similarities in diet, observed patterns of habitat use inferred from scat locations show differences in coyote and bobcat habitat preferences, implying some degree of habitat partitioning. Assuming that relative density of scats of a given species in different habitats reflects differences in their use, it can be concluded that coyote inhabits mainly alpine and subalpine zones compared with forest. This pattern of selectivity is not surprising given its evolutionary roots in open prairie ecosystems (Witmer & Decalesta, 1986; Major & Sherburne, 1987). For bobcat, our analysis shows significant preference of relatively dense montane forests (canopy cover >40%) at lower elevations, consistent with other studies of this species (Koehler & Hornocker, 1991; McDonald *et al.*, 2008). This habitat selection may arise through bobcat's preference to avoid people and use cover while hunting. On the other hand, the spatial separation may result at least in part from bobcat avoidance of areas intensively used by coyote – a dominant competitor (Case & Gilpin, 1974; Linnell & Strand, 2000; Wilson *et al.*, 2010). The observed habitat partitioning may alleviate foraging competition between coyote and bobcat and potentially decrease negative effects of coyote colonization on bobcat populations.

Coyotes, a strongly interacting species everywhere in its range, have been shown to exert strong effects when it invades new communities; in Olympic National Park these effects are apparent for a rare, endemic prey – Olympic marmot (Griffin, 2007; Witczuk *et al.*, 2013). The final outcome of competitive interactions between native bobcat and invasive coyote in the Olympic Mountains is difficult to predict. We have found that coyotes consume very similar foods to bobcats, a pre-condition of resource competition. We also found that coyotes and bobcats substantially segregate by habitat, which could be either a mechanism for reducing foraging competition, or an outcome of competitive displacement. At this point, we cannot reject the possibility that numerical increases in coyotes in the future could lead to negative competitive interactions of coyotes on bobcats. To resolve the question of

competitive displacement will require radiotelemetry studies of both species in sympatry over time.

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Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Figure S1. Locations of carnivore scats collected in the central part of the study area in Olympic National Park, Washington (May–September 2005–2006); carnivore species identified with mitochondrial DNA (bobcat $n = 76$, coyote $n = 150$, puma = 13). Inset in the upper right shows locations of all transects (black lines) and the extent of the enlarged area (red box).

Table S1. Frequency of occurrence (FO) of prey items in coyote *Canis latrans* and bobcat *Lynx rufus* scats collected on transects and opportunistically off-transect in Olympic National Park, Washington (May–September 2005–2006).

Table S2. Frequency of occurrence (FO) of prey items in coyote *Canis latrans* and bobcat *Lynx rufus* scats collected in major highland habitat types in Olympic National Park, Washington (May–September 2005–2006).