Canadian Journal of
Zoology

Research Article

Coyotes take advantage of ungulate carrion subsidies as wolves recolonize Washington

Anna N. Malesis, **Rebecca M. Windell**, **Carmen M. Vanbianchi**, and **Laura R. Prugh**

School of Environmental and Forest Sciences, University of Washington, Seattle, WA 98195, USA

Corresponding author: **Anna N. Malesis** (email: annanm@uw.edu)

Abstract

Apex predators exert suppressive effects on mesocarnivores; however, they also provide important carrion subsidies. Optimal foraging theory predicts that individuals respond to resource competition by using high-value resources, while competition theory predicts that individuals respond by partitioning resources. This study investigated how the return of wolves (*Canis lupus* Linneas, 1758) to Washington state impacted the diet of a subordinate carnivore—the coyote (*Canis latrans* Say, 1823). We collected coyote scats from two areas of northern Washington with differing wolf densities and used traditional analysis of undigested remains to infer diet. We tested for differences in the volumes of prey categories, the proportion of ungulate prey that was scavenged, and diet diversity between seasons, study sites, and inside and outside of wolf pack territories. Coyote scats contained more adult ungulate remains inside of wolf pack territories (27%) compared to outside (14%), while seeds and berries were more commonly consumed outside of wolf pack territories (23%) than inside of wolf pack territories (4%). These findings suggest that coyotes are taking advantage of wolf kills to increase ungulate carrion consumption, as predicted by optimal foraging theory, which may substantially affect plant and wildlife communities as wolves continue to recover and coyote diets shift in response.

Key words: coyote, wolf, ungulate, scavenge, competition

Introduction

Apex predators can suppress populations of subordinate carnivores both directly and indirectly across wide geographic scales through behavioral changes, competition for resources, or mortality for the subordinate species (Letnic et al. 2011; Newsome et al. 2017), which can have important cascading effects on ecosystems (Prugh et al. 2009). However, these negative intraguild interactions, which can result in behavioral changes, competition for resources, or mortality for the subordinate species, can occur alongside positive associations, like facilitation. A global meta-analysis found that about one-third of mesocarnivore mortalities are attributed to large carnivores, yet mesocarnivores also rely on ungulate carrion for about one-third of their diet (Prugh and Sivy 2020). As a result, facilitation by way of carrion subsidies may partially offset the costs of negative interactions; however, the net effects of these positive and negative interactions between apex predator and mesocarnivore populations remain poorly understood.

Understanding how carnivores partition resources on the landscape and the extent to which apex predators provision carrion resources to mesocarnivores is central to untangling these positive and negative interactions. According to optimal foraging theory, individuals should respond to competition for resources by focusing use on resources with the highest net value (Macarthur and Pianka 1966). For example, fishers (*Pekania pennanti* (Erxleben, 1777)) and marten (*Martes americana* (Turton, 1806)) both use high-value carrion resources where sympatric despite the potential for intraguild predation (Kautz et al. 2021). Alternatively, competition theory suggests that individuals should respond to competition for limited resources by partitioning them (Schoener 1974; Sivy et al. 2018). For example, tigers (*Panthera tigris tigris* (Linnaeus, 1758)), leopards (*Panthera pardus* (Linnaeus, 1758)), and dholes (*Cuon alpinus* (Pallas, 1811)) in Central India have been found to partition resources to reduce the risk of intraguild competition by preying on ungulates of significantly different sex, age, and body size (Majumder et al. 2013). Examining the diet of mesocarnivore species in areas where apex predators are newly reestablished can provide a unique opportunity to investigate the relative contributions of optimal foraging and competition theories to understanding carnivore community dynamics.

The distribution of coyotes (*Canis latrans* Say, 1823) has expanded across North America following the near-extirpation of grey wolves (*Canis lupus* Linnaeus, 1758) from the American West by European settlers (Hody and Kays 2018). As wolf populations recover through reintroductions and natural recolonization, interactions between the two species have been of increasing interest. The body size ratio of wolves and coyotes, along with similarities in their morphology and diet, makes the risk of interference competition and interspecific killing particularly high (Donadio and Buskirk 2006; Prugh and Sivy 2020). Where wolves reach ecologically effective densities, coyote densities tend to decrease, and they may avoid wolves by changing their resource use and activity patterns (Atwood and Gese 2010; Ripple et al. 2013). However, coyotes coexist with and readily scavenge from wolf kills throughout much of their range, and considerable uncertainty remains regarding the nature of their interactions in areas of wolf recovery.

We investigated how the return of wolves to Washington state has affected coyote diet, taking advantage of this natural quasi-experiment to identify the key processes underlying resource use by a subordinate carnivore. Wolves were extirpated from Washington by the 1930s (Washington Department of Fish and Wildlife 2017*b*), just as coyotes began expanding into new areas of the state (Hody and Kays 2018). In 2008, the first breeding wolf pack in Washington since extirpation was discovered, and by the end of 2021, there were a minimum of 206 wolves and 33 packs in the state (Washington Department of Fish and Wildlife et al. 2022). A recent study found that coyotes strongly avoid core wolf home ranges in Washington (Prugh et al. 2023), but the impact of wolf recovery on resource use by coyotes remains poorly understood.

If coyotes respond to the presence of wolves according to optimal foraging theory, coyotes should increase their use of valuable resources like carrion from wolf-killed ungulates (Macarthur and Pianka 1966; Sivy et al. 2018). Coyotes effectively scavenge wolf kills (Arjo et al. 2002; Wilmers et al. 2003), and scavenging could be advantageous to coyotes because they face risk of injury, high energy expenditure, and low success rates when hunting ungulates (Atwood 2006). Further, in areas with wolves, coyote diet consists mainly of scavenged wolf-killed elk (*Cervus canadensis* Erxleben, 1777; Paquet 1992), and coyote diet consisted mainly of lagomorphs and plants before wolf recolonization in Montana and shifted to ungulates afterwards (Arjo and Pletscher 1999). These findings support the hypothesis that wolf recolonization increases the amount of ungulate carrion available to coyotes, which could ultimately bolster coyote populations (Arjo and Pletscher 1999; Wilmers 2004). Conversely, if coyotes respond according to competition theory, lagomorphs and other small prey items would be of increasing importance in coyote diet where wolves are present (Sivy et al. 2018). Ungulate population densities are also typically lower in the presence of wolves, resulting in a decrease in prey and winter-killed ungulate carrion for coyotes (Leopold et al. 1947; Ripple et al. 2011)—an effect that contributed to the loss of coyotes from Isle Royale (Krefting 1969). Scavenging large carnivore kills may also substantially increase risk of mortality for coyotes due to an increased chance of encountering dominant carnivores (Sivy et al. 2017; Klauder et al. 2021*a*; Ruprecht et al. 2021). Thus, competition with wolves could increase resource partitioning and reduce ungulate consumption by coyotes.

We collected coyote scats from two areas of northern Washington with differing wolf densities to quantify differences in coyote diet. We tested for differences in the volumes of prey categories and diet diversity between seasons, study sites, and inside and outside of wolf pack territories. We also identified ungulate prey items by species and age class to infer which ungulate prey were likely killed by coyotes and which were likely scavenged. If optimal foraging is the dominant process determining the diet of coyotes in the presence of wolves, we expect coyote scats collected inside of wolf pack territories and in the study site containing more wolf packs to have a greater frequency of ungulate remains compared to scats collected outside of wolf pack territories and in the study site containing fewer wolf packs. If resource partitioning is the dominant process, we expect scats collected inside of wolf pack territories and in the study site containing more wolf packs to have a lower frequency of ungulate remains and a higher diversity of dietary items compared to scats collected outside of wolf pack territories and in the study site containing fewer wolf packs. If wolf presence has minimal impact on coyote diet, we expect to find no differences in coyote diets between the two study sites or inside and outside of wolf pack territories.

Materials and methods

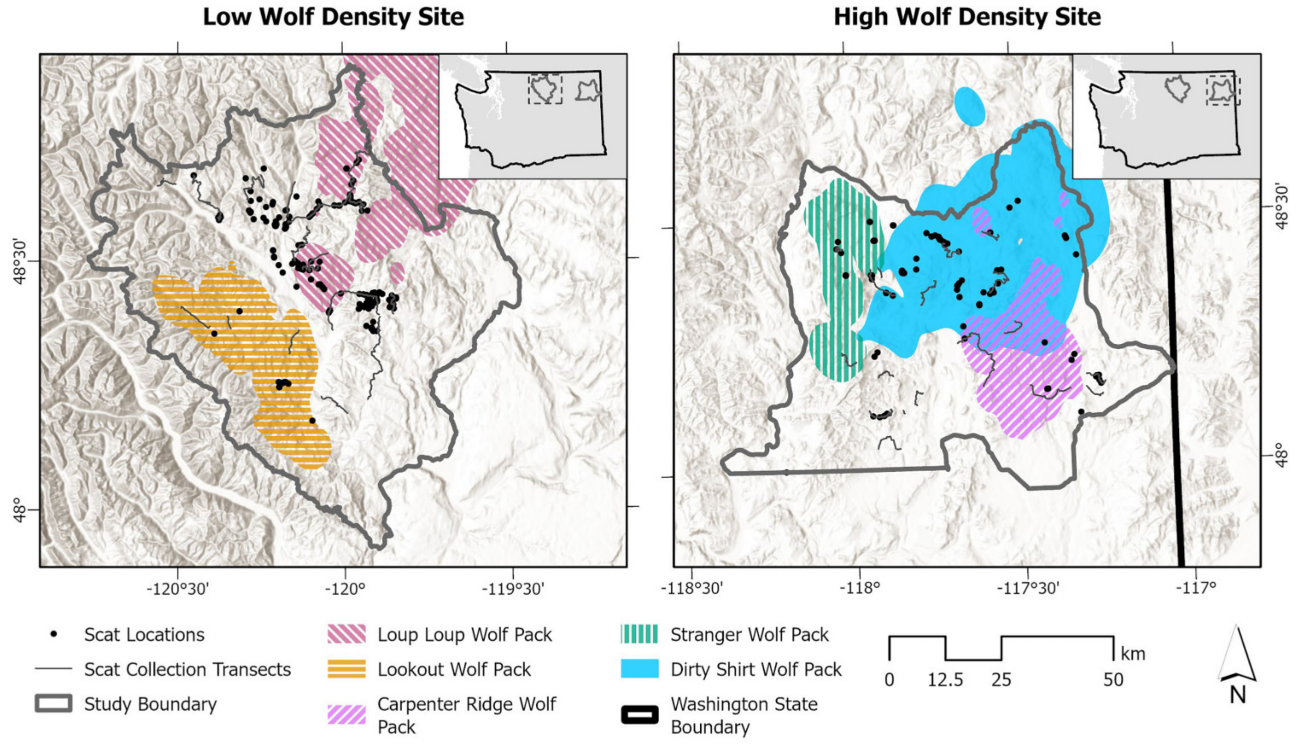
Study area

This study took place in two large study areas (each ~5000 km^2) in northern Washington as part of the Washington Predator Prey Project (Fig. 1). The first site (hereafter, high wolf density site) centered around Chewelah, WA, in northeastern Washington (48.2763, −117.7155) and was dominated by managed montane conifer forests at higher elevations above around 600 m, and agricultural lands along valley floors. The second site (hereafter, low wolf density site) centered around Winthrop, WA, in north-central Washington (48.4779, −120.1862) included a mix of shrub-steppe and coniferous forest habitat above elevations of around 600 m, with residential and agricultural development along valley floors. The high and low wolf density sites have very similar weather patterns for average highs (29 and 28 °C, respectively), lows (−8 and −9 °C, respectively), and annual precipitation (52 and 57 cm, respectively) (U.S. Climate Data 2023). The high wolf density site had an average of 0.62 km of road per km^2, while the low wolf density site had an average of 0.36 km per km^2 (WSDOT Online Map Center 2015), but both sites had similar population densities (4.9 people per km^2 at the high wolf density site and 4.1 people per km^2 at the low wolf density site; U.S. Census Bureau 2020). Both sites were also home to 48 mammal species from the orders Cetartiodactyla, Carnivora, Eulipotyphla, Lagomorpha, and Rodentia (Lester 1997; Verts and Carraway 1998), while an additional eight species occurred only in the low wolf density site and four species occurred only in the high wolf density site[1]. Ungulate species found in both sites consisted of mule deer (*Odocoileus hemionus* (Rafinesque, 1817)), white-tailed deer (*Odocoileus virginianus* (Zimmermann, 1780)), and moose (*Alces alces* (Linnaeus, 1758)). Elk occurred only in the high wolf density site, whereas mountain goats (*Oreamnos americanus* (Blainville, 1816)) and bighorn sheep (*Ovis canadensis* Shaw,

---

[1] See Table S1 in Supplementary Materials.

Fig. 1. Locations of collected coyote (*Canis latrans*) scats, study site boundaries, scat collection transects, and the territories of collared wolf (*Canis lupus*) packs in Washington State, USA, during the study periods in 2018 and 2019. Wolf pack territories are represented as 95% utilization distributions for each pack during each season using package "adehabitatHR" in program R Version 4.3.2 (Calenge 2006). This map shows the summer and winter territories overlaid together for all packs. Figure was created in ArcGIS Pro Version 3.0.2 (Esri Inc. 2022) using the following data sources: study area boundary from the Washington Department of Fish and Wildlife (2017*a*), Washington State boundary from the Washington Department of Natural Resources (2017), hillshade from Esri Inc. (2018), and polygon of North America from the United States Department of State Office of the Geographer (2013).



1804) occurred only in the low wolf density site (Lester 1997). Deer (mule deer and/or white-tailed deer) were by far the most common ungulates across both sites, with all other species being less abundant (Bassing et al. 2023). Differences in the densities of other species between sites are not known. Both sites are also home to other large carnivores: black bears (*Ursus americanus* Pallas, 1780) and cougars (*Puma concolor* (Linnaeus, 1771)), with cougars widely distributed across both sites (Bassing et al. 2023).

Wolf density was over four times higher at the high wolf density site, with an average minimum density of 0.58 wolves/100 km^2, than the low wolf density site, which had an average minimum density of 0.14 wolves/100 km^2. The low wolf density site overlapped with the territories of two wolf packs during the period of scat collection, Loup Loup (minimum of two wolves in December 2017 and five wolves in December 2018) and Lookout (minimum of three wolves in December 2017 and five wolves in December 2018) (Fig. 1). Meanwhile, the high wolf density site overlapped with the territories of four packs: Stranger (minimum of three wolves in December 2017 and four wolves in December 2018), Dirty Shirt (minimum of seven wolves in December 2017 and three wolves in December 2018), Huckleberry (minimum of six wolves in both years), and Carpenter Ridge (minimum of 13 wolves in December 2017 and 11 wolves in December 2018) (Washington Department of Fish and Wildlife et al. 2018, 2019). All packs contained collared individuals, but Huckleberry was not included in the analysis because no transects were sampled in the Huckleberry wolf pack range. While it is possible that lone or dispersing wolves passed through the study sites, lone wolves are thought to make up a small proportion of the population (Washington Department of Fish and Wildlife et al. 2018).

Scat collection and preparation

Scats were primarily collected from transects that were surveyed monthly (Fig. 1), with additional scats collected opportunistically at both sites during winter (January–March) 2018, summer (mid-June to mid-September) 2018, and winter (January–March) 2019. Transects were selected to provide coverage of the whole study area, both inside and outside of wolf pack territories, using areas that were publicly accessible, such as Forest Service roads, or where landowners granted permission. Scats were stored frozen, sterilized at −80 °C for 2 weeks, and then we determined species of origin by molecular analysis of mitochondrial DNA, as described in Ganz et al. (2022*b*). Scats attributed to coyotes were washed until only undigested remains were left and allowed to air dry (Prugh et al. 2008).

Prey identification

To identify diet items, we placed each scat in a tray, and sorted the contents—such as hairs, bones, teeth, exoskeletons, seeds, leaves, and rocks—into piles based on apparent similarity in color, length, thickness, or other identifying features. These piles were considered one prey "item" unless further analysis revealed the need for subdivision or combination of piles. We compared hair, bones, teeth, or claws to a reference collection of skins, skulls, and hairs of all mammal species occurring in the study area, as well as to identification guides (Moore et al. 1974). Identifying prey species from hair is possible because the structure of animal hair remains intact after digestion (Smith 1958; Tintner et al. 2020), and the majority of the hairs were complete. We examined multiple hairs from each pile to confirm prey identity, but only complete hairs with visible follicles and tips were used for measurements or for comparing characteristics that may vary along the length of the hair. Hairs were placed on slides and viewed under a microscope to discern medulla patterns, and scale casts were taken when necessary by placing hairs on a slide cover coated in clear nail polish. Once the nail polish was dry, the hair was removed, leaving an impression of the scale pattern, which was used to help identify the species of origin (Brunner and Coman 1974). We also used hair length, color pattern, and diameter, which we measured at the midpoint of the hairs with the Nurugo Micro Smartphone Microscope (Nurugo, Seoul, Republic of Korea), to help identify species of origin. Nearly all items were identifiable through these methods, and we grouped any remaining items into the "other" category (Table 1).

After taxonomic identification, we identified ungulate hairs from summer scats as either adult or juvenile, resulting in four species- and aged-based categories of ungulate prey: deer (adult deer), elk (adult elk), moose (adult moose), and juvenile ungulates (summer hair attributed to moose calves, elk calves, or deer fawns). Juvenile ungulates were not categorized by species due to the difficulty of accurately determining species from these hairs where deer and elk ranges overlapped. Differentiation between age classes was informed in part by differences in diameter. Deer hairs with diameters under 100 μm were considered juvenile, while deer hairs with diameters over 100 μm were considered adult (Calhoun et al. 2019). We confirmed this threshold with reference samples from radio-collared fawns and adults in the study area. Comparison of elk calf and adult elk reference samples, as well as hair diameter ranges from Moore et al. (1974), showed that a cutoff of approximately 125 μm differentiated adult and juvenile elk, but diameter alone was not sufficient to determine age class where elk and deer coexist because of the possibility for overlap in diameter ranges between different ungulate species and age classes. Observation revealed that both fawn and elk calf hairs shared a distinct color pattern—a dark tip blending into orange–brown, blending into white toward the follicle—that could also be used to identify juveniles for both species. Color pattern was important because juvenile elk and adult deer hair could have similar diameters. However, due to the similar color patterns and lengths, as well as the possibility for overlapping diameter, we could not reliably distinguish deer fawn hairs from elk calf hairs where their ranges overlapped. Moose calf and adult deer hairs also shared similar diameters and color patterns, so they were differentiated by length, with hairs less than 8 cm long classified as adult deer (Moore et al. 1974). Ungulate hairs collected in winter could not be identified to age class because hair diameter cannot be used to discern age class after the first molt (Calhoun et al. 2019). Thus, ungulate age class was determined for summer-collected scats only.

Once all items in the scat had been identified and sorted, we estimated the percent volume of each prey item pile to the nearest percent. This estimate was primarily based on the volume of hair present because the amount of bones recovered relative to the amount consumed can be highly variable, while the amount of hair recovered was found to be much less variable (Kelly and Garton 1997). Trace items under 1% of volume were omitted since they could represent contamination from the ground. The total volume of all items summed to 100% for each scat (calculated excluding trace items). We recorded the volume of each item because using multiple methods to describe diet—frequency of consumption and volume consumed—balances the importance of items eaten frequently with items eaten in large volumes (Zabala and Zuberogoitia 2003).

Data analysis

We used a permutational analysis of variance (PERMANOVA) to investigate the impact of season, study site, and wolf presence on coyote diet. To approximate the territories of wolf packs during the study, we created 95% utilization distributions for each pack during each season using package "adehabitatHR" in program R Version 4.3.2 (Calenge 2006). The size and location of territories varied between seasons as wolves moved between winter and summer ranges. We used locations provided by the Washington Department of Fish and Wildlife from GPS-collared wolves in each pack to generate the distributions, spanning from 1 month before scat collection began to when scat collection finished for the season. On average, there were 1.5 collared wolves per pack statewide, and most wolves collared in 2017 and 2018 were adults (Washington Department of Fish and Wildlife et al. 2018, 2019). We mapped the scats collected along with the pack distributions from the corresponding season to determine whether each scat was collected inside or outside of a wolf pack territory.

To prepare the diet data for PERMANOVA tests, we divided prey items into groups based primarily on taxonomy, resulting in 13 categories (Table 1). Leporids and small mammals were grouped separately to allow for comparison of the role of leporids in coyote diet with previous studies. We excluded items that occurred in less than 5% of scats (trash, reptiles, and other)—or made up less than 2.5% of the diet by volume (birds, carnivores, domestic cattle, insects, and sciurids)—from the PERMANOVA and related tests because such rare

Table 1. All prey items, their frequency of occurrence (the number of scats in which they appeared), and the percent volume of the overall diet from coyote (*Canis latrans*) scats ($n = 284$) collected in northern Washington, USA.

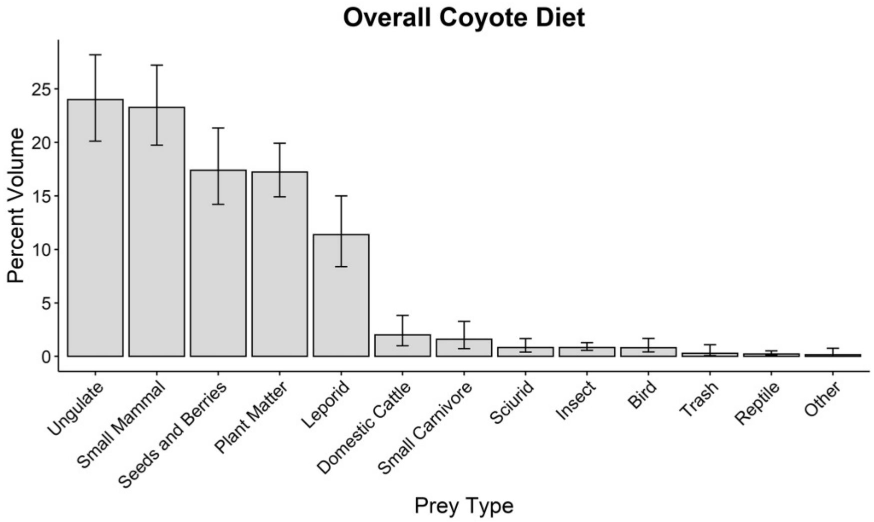
Prey category	Frequency of occurrence	Percent volume
Plant matter	247	17.2
Seeds and berries	116	17.4
Carnivore	16	1.6
Raccoon (*Procyon lotor* (Linnaeus, 1758))	4	0.5
Black bear (*Ursus americanus*)	1	0.3
Striped skunk (*Mephitis mephitis* (Schreber, 1776))	5	0.6
General carnivore	6	0.3
Leporid	54	11.4
Snowshoe hare (*Lepus americanus*)	17	3.4
Nuttall's cottontail (*Sylvilagus nuttalii* (Bachman, 1837))	1	0.09
General leporid	36	7.9
Sciurid	17	0.92
Chipmunk (*Tamias* spp.)	1	0.09
Tree squirrel	5	0.31
Small ground squirrel	6	0.29
Columbian ground squirrel (*Urocitellus columbianus* (Ord, 1815))	3	0.046
Marmot (*Marmota* spp.)	2	0.19
Small mammal	174	23.2
Small rodent	22	2.2
Mouse	5	0.7
Western jumping mouse (*Zapus princeps* J. A. Allen, 1893)	1	0.1
Great Basin pocket mouse (*Perognathus parvus* (Peale, 1848))	1	0.1
Vole	62	10.5
Red-backed vole (*Clethrionomys gapperi* (Vigors, 1830))	2	0.2
Northern pocket gopher (*Thomomys talpoides* (Richardson, 1828))	23	2.8
Bushy-tailed woodrat (*Neotima cinerea* (Ord, 1815))	4	1.0
Shrew (*Sorex* spp.)	3	0.2
General small mammal	51	5.4
Ungulate	145	24.0
Moose (*Alces alces*)	6	1.5
Elk (*Cervus elaphus*)	15	2.9
Deer (*Odocoileus* spp.)	103	16.0
General ungulate	21	3.6
Domestic cattle	18	2.0
Reptile	8	0.2
Bird	29	0.8
Insect	54	0.8
Trash	7	0.3
Other	3	0.2

Note: The percent volume was estimated to the nearest percent based primarily on the volume of hair present in each scat. Trace items under 1% of volume were disregarded since they could represent contamination from the ground or the washing process. The total volume of all items summed to 100% for each scat (calculated excluding trace items).

items are of limited interest when examining changes in primary coyote diet items (McCune et al. 2002). All items were included for the analyses of diet diversity.

We used the "vegan" package in program R to conduct community analyses based on Bray–Curtis matrices, which are recommended for ecological data with a high proportion of 0 abundances (McCune et al. 2002; Oksanen et al. 2019). We conducted a PERMANOVA to test for the effects of *season* (if the scat was collected in summer or winter), *site* (if the scat was collected from the low wolf density or high wolf density site), and *pack* (if the scat was collected from inside or outside of a wolf pack territory) on coyote diet. Results were visualized by creating nonmetric dimensional scaling (NMDS) plots with stress < 0.2, using a maximum of 200 iterations (Clarke 1993). Plots were overlaid with dispersion ellipses visualizing one standard deviation of the diet for each level of the covariate specified (Hill et al. 2015). We investigated any significant results with a similarity percentage analysis (SIMPER) with permutation tests,

Fig. 2. Overall percent volume of coyote (*Canis latrans*) diet (n = 284) attributed to each prey type, including 95% confidence intervals. Ungulate, small mammal, seeds and berries, plant matter, and leporid were the five most important prey items overall, while all other prey items each made up less than 5% of the diet by volume. Percent volume was estimated to the nearest percent based primarily on the volume of hair present in each scat. Trace items under 1% of volume were disregarded since they could represent contamination from the ground or the washing process. The total volume of all items summed to 100% for each scat (calculated excluding trace items). Confidence intervals were generated using bootstrapping resampling (n = 10 000) and the adjusted bootstrap percentile (BC_a) method (Efron 1987; DiCiccio and Efron 1996; Manly 2006).



which allowed us to attribute the dissimilarity in diet detected in the PERMANOVA to specific prey categories (Clarke 1993).

We also calculated means and 95% confidence intervals for percent volume of all 13 prey categories for the overall coyote diet, as well as for each covariate category (summer, winter, the high wolf density site, the low wolf density site, inside of wolf packs, and outside of wolf packs). We generated confidence intervals using bootstrapping resampling (n = 10 000) and the adjusted bootstrap percentile (BC_a) method (Efron 1987; DiCiccio and Efron 1996; Manly 2006). To facilitate comparison with other studies, means and confidence intervals for overall diet were also calculated using percent occurrence, instead of occurrence weighted by percent volume.

Lastly, we compared diet diversity between summer and winter, the high and low wolf density sites, and inside and outside of wolf pack territories. We calculated Shannon's diversity index (H) for each of these covariate categories and compared the diversity of the diets using t tests (Arjo et al. 2002; Zar 2010).

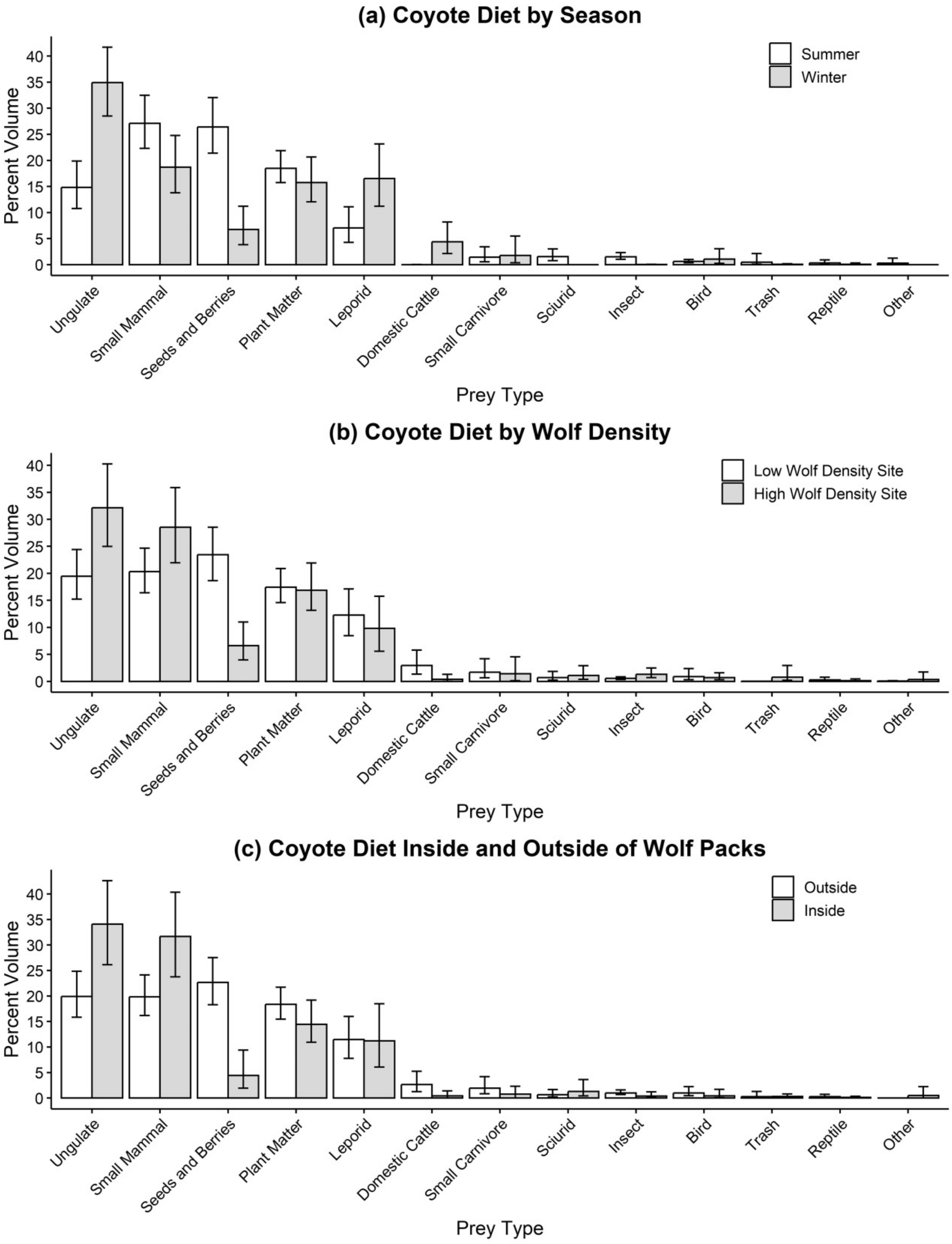
Ungulate consumption

Using the same methods as for the main diet analysis, we calculated means and 95% confidence intervals for the percent volume for deer, elk, moose, and juvenile ungulates consumed overall, as well as for each covariate category. We divided the ungulates consumed into two groups: likely predated (juvenile) and likely scavenged (adult). While coyotes have occasionally been documented killing adult deer in the western United States (Arjo et al. 2002), coyotes were responsible for only 0.4% of adult mule deer mortalities in southeastern Idaho, yet they caused 12.8% of neonate mortalities (Hurley et al. 2011). Patterns were similar in our study sites: coyotes caused 2.3% of collared adult deer mortalities, no adult elk mortalities, 13.5% of collared juvenile deer, and 3.3% of elk calf mortalities (Ganz et al. 2022*a*). It is unlikely that any consumption of juveniles could be scavenged from wolf kills because wolves tend to leave little behind when they predate deer fawns (Homkes 2021). We calculated means and 95% confidence intervals for percent volume likely scavenged for the high wolf density site, the low wolf density site, inside of wolf packs, and outside of wolf packs.

Results

We used 284 coyote scats in the diet analysis, with 154 (54%) collected in the summer and 130 (46%) in the winter. Of the 284 scats, 102 (36%) were from the high wolf density site and 182 (64%) were from the low wolf density site, and wolf utilization distributions revealed that 82 scats (29%) had been collected inside of wolf pack territories and 202 (71%) had been collected outside of wolf pack territories (Fig. 1). Of the 82 scats collected inside of wolf pack territories, 57 (70%) were from the high wolf density site and 25 (30%) were from the low wolf density site, and for the 202 scats collected outside of wolf pack territories, 45 (22%) were from the high wolf density site and 157 (78%) were from the low wolf density site. Five items made up over 90% of the coyote diet by volume: ungulate (24%), small mammal (23%), seeds and berries (17%), plant matter (17%), and leporids (11%) (n = 284). Each of the remaining categories made up less than 2.5% of the overall diet (Table 1), and they were excluded from the PERMANOVA (Fig. 2).

Fig. 3. Percent volume of coyote (*Canis latrans*) diets attributed to each prey type, with 95% confidence intervals, in (*a*) summer (n = 154) and winter (n = 130), (*b*) the high wolf (*Canis lupus*) density (n = 102) and low wolf density sites (n = 182), and (*c*) inside (n = 82) and outside of wolf pack territories (n = 202). Ungulates and leporids made up a larger part of coyote diet in the winter, while small mammals, seeds and berries, and plant matter making up a larger part in the summer. Ungulates and small mammals were consumed at higher volumes at the high wolf density site than at the low wolf density site.



More ungulate remains were found in scats collected in the high wolf density site (32%, 95% CI [25%–40%], n = 102) than in the low wolf density site (20%, 95% CI [15%–25%], n = 182; Fig. 3*b*). Similarly, more ungulate remains were found in scats collected inside of wolf pack territories (34%, 95% CI [26%–43%], n = 82) than outside of wolf pack territories (20%, 95% CI [16%–25%], n = 202; Fig. 3*c*). Across both sites, ungulate remains were the primary diet item consumed in the winter (35%; 95% CI [28%–42%], n = 130; Fig. 3*a*), while small mammal was the primary diet item

Table 2. Results of permutational analysis of variance testing for the effect of *site* (high wolf (*Canis lupus*) density site vs. low wolf density site), *season* (summer vs. winter), and *pack* (inside or outside of wolf pack territories) on coyote (*Canis latrans*) diet composition from scats collected in northern Washington, USA.

Source	df	Sum of squares	R^2	F	$p_r(>F)$
Season	1	5.56	0.0649	20.3	0.001
Site	1	2.82	0.0329	10.3	0.001
Pack	1	0.667	0.00779	2.44	0.042
Residuals	280	76.6	0.894		
Total	283	85.6	1.00		

consumed in the summer (27%; 95% CI [22%–33%], $n = 154$; Fig. 3*a*).

Factors affecting diet composition

Season, *site*, and *pack* all contributed significantly to variability in coyote diet, together accounting for 10.6% of overall variability (PERMANOVA; Table 2). NMDS ordination axes of coyote diet showed the most divergence in diet between seasons (Fig. 4*a*); diets overlapped in ordination space around plant matter, but summer diet was clustered around small mammals near seeds and berries, while winter diet was more diffuse and located closer to ungulates. There was major overlap between the high and low wolf density sites in ordination space around small mammals and plant matter, but the dispersion ellipse representing diet at the high wolf density site pointed closer to ungulates, while the low wolf density site ellipse was closer to seeds and berries (Fig. 4*b*). The pattern of differences in coyote diet inside and outside of wolf pack territories was very similar to the differences between the high and low wolf density sites, with the diet inside of wolf pack territories oriented closer to ungulates and the diet outside oriented closer to seeds and berries (Fig. 4*c*).

Prey items contributing to diet variability

Ungulates, small mammals, seeds and berries, plant matter, and leporids all made significant contributions to the difference in coyote diet between winter ($n = 130$) and summer ($n = 154$) (SIMPER analysis; Table 3). Together, these prey categories accounted for 75.7% of the difference in diet between seasons, with ungulates and leporids making up 51% of coyote diet in the winter and small mammals, seeds and berries, and plant matter making up 72% in the summer (Fig. 3*a*). Ungulates and small mammals contributed significantly to the difference in diet between the study sites, together accounting for 38.0% of the variation in diet (Table 4). Both were consumed at higher volumes at the high wolf density site than at the low wolf density site (Fig. 3*b*). Similarly, ungulates and small mammals contributed significantly to the difference in diet inside and outside of wolf pack territories. They accounted for 39.3% of the variation in diet (Table 5), and both were consumed at higher volumes at the high wolf density site than at the low wolf density site (Fig. 3*b*).

Diet diversity

Diet diversity did not differ significantly between seasons (Shannon diversity index $H' = 1.33$ in winter and $H' = 1.29$ in summer; $t = 0.214$, df = 272, $p = 0.83$), study sites ($H' = 1.44$ at the high wolf density site and $H' = 1.49$ at the low wolf density site; $t = -0.361$, df = 257, $p = 0.72$), or within versus outside wolf territories ($H' = 1.36$ inside of wolf packs and $H' = 1.53$ outside of wolf packs; $t = 1.13$, df = 234, $p = 0.26$).

Ungulate prey consumption and scavenging

Of the 284 scats used in the diet analysis, 145 contained ungulate prey and were used in the ungulate consumption sub-analysis. Most of the volume of ungulates consumed during the study was made up of adult deer (60.0%), followed by juvenile ungulates (25.0%), adult elk (8.62%), and adult moose (6.32%; Fig. 5). The order of importance of the ungulate categories was the same at both sites (omitting elk at the low wolf density site where they were not present). In the summer, juvenile ungulates were consumed at volumes over 4 times higher than any other category of ungulate (75% of ungulate remains consumed, $n = 57$), and in the winter, adult deer were consumed at volumes over 8 times higher than any other ungulate species (82% of ungulate remains consumed, $n = 88$; Fig. 5).

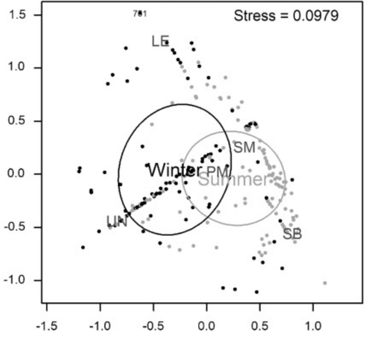
While ungulates made up 24% of the coyote diet, adult ungulate made up 18% (95% CI [15%–22%]), indicating the majority of ungulate consumed was likely scavenged ($n = 284$). Across both seasons, adult ungulates contributed more to the diet inside of wolf territories (27%, 95% CI [20%–36%], $n = 82$) than outside (14%, 95% CI = [10%−19%], $n = 202$), suggesting higher rates of scavenging inside of wolf pack territories. Conversely, confidence intervals for adult ungulate prevalence in the overall diet at the high (20%, 95% CI [13%–27%], $n = 102$) and low (17%, 95% CI [13%–22%], $n = 182$) wolf density sites overlapped (Fig. 5). During winter, adult ungulates tended to be more prevalent in the diet inside wolf territories (43%, 95% CI [32% – 54%], $n = 47$) than outside (31%, 95% CI [23% – 39%], $n = 83$), and also more prevalent in the high density site (48%, 95% CI [34% – 62%], $n = 37$) than the low density site (30%, 95% CI [23% – 38%], $n = 93$).

Discussion

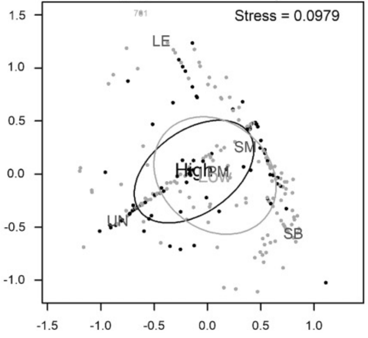
We found more ungulate remains in coyote scats inside wolf territories than outside of wolf territories, and un-

Fig. 4. The results of PERMANOVA analysis testing for the impact of *season* (if the scat was collected in summer ($n = 154$) or winter ($n = 130$)), *site* (if the scat was collected from the low wolf (*Canis lupus*) density ($n = 182$) or high wolf density site ($n = 102$)), and *pack* (if the scat was collected from inside ($n = 82$) or outside of a wolf pack territory ($n = 202$)) on the relative percent volume of prey items in coyote (*Canis latrans*) diet were visualized by creating nonmetric dimensional scaling (NMDS) plots with stress < 0.2, using a maximum of 200 iterations (Clarke 1993). Plots were overlaid with dispersion ellipses visualizing one standard deviation of the diet for each level of the covariate specified (Hill et al. 2015). Prey items are shown on the plots as UN (ungulate), LE (leporid), SM (small mammals), PM (plant matter), and SB (seeds and berries). NMDS ordination axes of coyote diet showed the most divergence in diet between seasons (*a*). There was major overlap between the high and low wolf density sites (*b*) in ordination space around small mammals and plant matter, and the plot of differences in coyote diet inside and outside of wolf pack territories (*c*) was very similar to the plot comparing the high and low wolf density sites, with the diet inside of wolf pack territories oriented closer to ungulates and the diet outside oriented closer to seeds and berries.

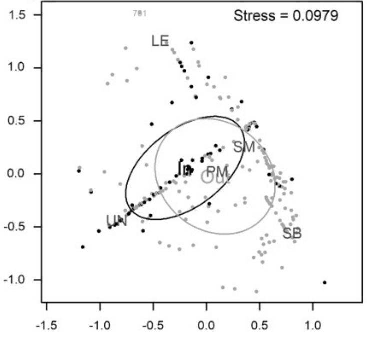
(a) Season



(b) Wolf Density



(c) Inside or Outside of Wolf Pack



gulate was a significant contributor to differences in diet between scats collected inside and outside of wolf pack territories. Scats from inside of wolf pack territories indicated increased ungulate consumption—particularly of adult ungulates—across all analyses. These results suggest that, as predicted by optimal foraging theory, coyotes are consuming more ungulate in the presence of wolves (Sivy et al. 2018). These findings are supported by a meta-analysis of coyote diet (Jensen et al. 2022) and suggest that coyotes are taking advantage of wolf kills as a high-quality resource despite the inherent risks involved (Macarthur and Pianka 1966; Arjo and Pletscher 1999; Wilmers 2004; Sivy et al. 2018).

The importance of carrion subsidies from wolves is supported by our analysis of scavenged ungulates in the coyote diet. The percent volume of likely scavenged ungulates consumed inside of wolf pack territories was 1.9 times higher than outside of wolf pack territories. This pattern suggests that coyotes increase consumption of ungulate carrion inside of wolf pack territories. Comparing the locations of scats, wolf pack territories, and seasonal deer ranges does not suggest any correlation between wolf pack territories and deer availability (Bassing et al. 2023), meaning differences in ungulate consumption inside and outside wolf pack territories are unlikely to be caused by differences in the availability of winter-killed ungulates (i.e., deer that died from other causes in winter). While the percent volume of likely scavenged (i.e., adult) ungulates in coyote diet did not differ among study sites, this result could be due to the overrepresentation of summer scats at the high wolf density site (64% of scats collected, compared to 50% at the low wolf density site), which could deflate the relative importance of ungulate in overall diet, as well as inflate importance of juvenile ungulates relative to other ungulate prey (Fig. 5). While confidence intervals for the amount adult ungulate consumed in the winter inside and outside of wolf pack territories, as well as at the high and low wolf density sites, overlapped, this finding was likely limited by small sample sizes. The large differences in means, with trends toward increased ungulate consumption inside of wolf pack territories and at the high wolf density site, suggest the importance of scavenging from wolf kills over the winter. Overall, our findings indicate that inside of wolf pack territories, coyotes in Washington appear to be taking advantage of ungulate carrion subsidies from wolves, consistent with optimal foraging theory. While coyotes also scavenge from ungulate carrion provided by other large carnivores, other carnivore kills would not contribute to differences in scavenging inside and outside of wolf pack territories: cougars were widespread across both study areas (Bassing et al. 2023), and black bears are much more likely to steal kills and consume them completely than provide carrion (Prugh and Sivy 2020).

This increase in ungulate carrion provisioned by recolonizing wolves could ultimately benefit coyotes in Washington. Because wolves spread the availability of carrion resources over the winter—in contrast to a pulse of elk mortality at the end of winter in wolves' absence—scavenger populations may benefit (Wilmers 2004). Similarly, coyote group size increased as wolves recolonized northwestern Montana, suggesting that subsidies from wolf kills increased the amount

Table 3. Results of similarity percentage analysis to determine which prey categories made significant contributions to the difference in coyote (*Canis latrans*) diet between scats collected in northern Washington, USA, during the winter ($n = 130$) and during the summer ($n = 154$).

Prey item	Winter	Summer	Contribution	SD	*p*
Ungulates	34.9	14.8	0.198	0.194	0.01
Small mammal	18.7	27.1	0.177	0.179	0.05
Seeds and berries	6.75	26.4	0.154	0.184	0.01
Plant matter	15.7	18.5	0.118	0.122	0.01
Leporids	16.5	7.04	0.111	0.191	0.01

Note: The Winter and Summer columns show the percent volume of each diet item during each season. The following three columns show each prey item's contribution to the average dissimilarity between seasons, the standard deviation of the contribution, and whether the contribution is significant.

Table 4. Results of similarity percentage analysis to determine which prey categories made significant contributions to the difference in coyote (*Canis latrans*) diet between scats collected in the high wolf (*Canis lupus*) density ($n = 102$) and low wolf density sites ($n = 182$) in northern Washington, USA.

Prey item	Low wolf density	High wolf density	Contribution	SD	*p*
Ungulates	19.5	32.1	0.197	0.197	0.01
Small mammal	20.3	28.5	0.183	0.182	0.03
Seeds and berries	23.5	6.60	0.137	0.174	1.00
Plant matter	17.4	16.9	0.113	0.124	0.56
Leporids	12.3	9.79	0.103	0.183	0.83

Note: The Low wolf density and High wolf density columns show the percent volume of each diet item at each site. The following three columns show each prey item's contribution to the average dissimilarity between sites, the standard deviation of the contribution, and whether the contribution is significant.

Table 5. Results of similarity percentage analysis to determine which prey categories made significant contributions to the difference in coyote (*Canis latrans*) diet between scats collected in inside of wolf (*Canis lupus*) pack territories ($n = 82$) and outside of wolf pack territories ($n = 202$) in northern Washington, USA.

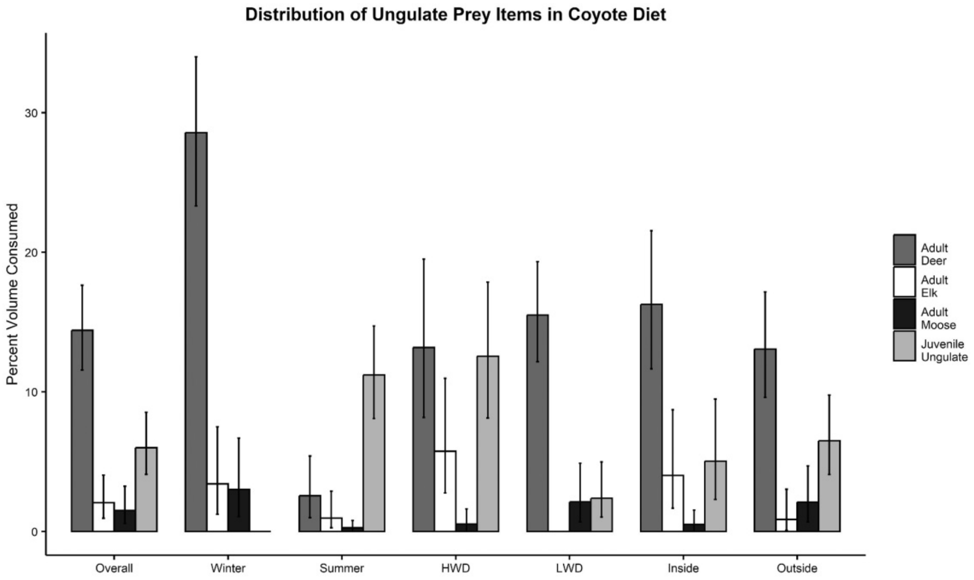
Prey item	Outside	Inside	Contribution	SD	*p*
Ungulates	19.9	34.1	0.202	0.196	0.01
Small mammal	19.9	31.7	0.191	0.184	0.01
Seeds and berries	22.7	4.4	0.128	0.171	1.00
Plant matter	18.4	14.4	0.109	0.117	0.95
Leporids	11.5	11.2	0.105	0.182	0.63

Note: The Inside and Outside columns show the percent volume of each diet item inside and outside of wolf pack territories. The following three columns show each prey item's contribution to the average dissimilarity between inside and outside of wolf pack territories, the standard deviation of the contribution, and whether the contribution is significant.

of food available to coyotes, allowing juvenile coyotes to stay longer in their natal territories (Arjo and Pletscher 1999). Overlap between coyote and wolf home ranges has also been shown to increase during the winter (Arjo and Pletscher 1999), where coyotes select for areas frequently used by wolves and increase their proximity to wolves (Klauder et al. 2021*a*). This seasonal pattern suggests that coyotes benefit most from the presence of wolves during the winter, when resources are relatively scarce, and is supported by our finding of increased ungulate remains in winter coyote scats (Fig. 3).

Despite the potential benefits gained from scavenging wolf kills, wolves can negatively impact coyotes through interference competition, interspecific killing, and fear effects (Smith et al. 2003; Ripple et al. 2011; Suraci et al. 2016; Prugh and Sivy 2020; Klauder et al. 2021*a*). The benefits of subsidies from wolf-killed ungulates may not overcome the negative effects of risk of death and interference competition from wolves (Smith et al. 2003; Ripple et al. 2011), and carrion subsidies provided by large carnivores could serve as an ecological trap and ultimately lead to the suppression of mesocarnivore populations at a large scale (Sivy et al. 2017). In addition to suppression through killing, fear of large carnivores can both reduce foraging behavior in mesocarnivores (Suraci et al. 2016) and decrease coyote use of carcasses in areas with higher long-term use by wolves (Klauder et al. 2021*a*). For example, no collared coyotes in our study areas were confirmed to have been killed by wolves, but strong avoidance of wolves and cougars led coyotes to increase use of human-impacted areas, where human-caused mortality rates were high (Prugh

Fig. 5. The distribution of ungulate prey types within 95% confidence intervals in coyote (*Canis latrans*) diet overall ($n = 145$), in the winter ($n = 88$), in the summer ($n = 57$), at the high wolf (*Canis lupus*) density site (HWD) ($n = 57$), at the low wolf density site (LWD) ($n = 88$), inside of wolf pack territories ($n = 38$), and outside of wolf pack territories ($n = 107$). Ungulate prey were sorted into four species- and aged-based categories: deer (adult deer; *Odocoileus virginianus* and *Odocoileus hemionus*), elk (adult elk; *Cervus canadensis*), moose (adult moose; *Alces alces*), and juvenile ungulates (summer hair attributed to moose and elk calves and deer fawns). Juvenile ungulates were not categorized by species due to the difficulty of accurately determining species from these hairs.



et al. 2023). However, it remains unclear if coyote densities at our study sites were suppressed by wolves, and whether suppressive effects may increase over time as wolf populations continue to recover: wolves may need to reach ecologically effective densities to suppress coyote abundance (Newsome et al. 2017). Our findings indicate the coyotes that remain in areas occupied by wolves do take advantage of increased scavenging opportunities, especially in winter.

Increased reliance on scavenging wolf kills could reduce consumption of other items. We found that ungulates, small mammals, seeds and berries, plant matter, and leporids were the most important items in coyote diet across both study sites (Fig. 2), and deer were the most important ungulate prey item overall (Fig. 5). These diet patterns were similar to those reported in other areas of the northwestern contiguous United States (Arjo and Pletscher 1999; Dowd and Gese 2012; Jensen et al. 2022). At 11.4% of the diet by volume, the relative importance of leporids may appear low, given they have been frequently documented as the coyote's prey of choice (Ripple et al. 2013; Hinton et al. 2017). However, this level of importance was consistent with previous studies in the northwest continental United States (Arjo and Pletscher 1999; Dowd and Gese 2012; Jensen et al. 2022), with higher proportions documented in boreal ecosystems where snowshoe hare (*Lepus americanus* Erxleben, 1777) populations can reach high levels (O'Donoghue et al. 1998; Prugh 2005; Jensen et al. 2022). Coyotes also rely more heavily on leporid prey in the American Southwest, where the abundance of black-tailed jackrabbits (*Lepus californicus* Gray, 1837) impacts coyote population dynamics (Mills and Knowlton 1991; Stoddart et al. 2001; Jensen et al. 2022). By diverting foraging activity of coyotes from lagomorphs to carrion, wolves may indirectly reduce coyote predation on this key prey species, which could in turn benefit other avian and mammalian predators that rely heavily on lagomorphs, such as threatened populations of Canada lynx (*Lynx canadensis* Kerr, 1792; Ripple et al. 2011). However, in this study, small mammal consumption tended to be higher inside of wolf pack territories and at the high wolf density site, and seeds and berries were the only diet item that was significantly more important outside of wolf pack territories or at the low wolf density site than inside of wolf pack territories or at the high wolf density site (Fig. 3).

The relative importance of seeds, berries, and plant matter in coyote diet was higher than previously found in the northwestern contiguous United States. Across a 5-year study in northern Montana, the percent occurrence of plants in coyote scats ranged from 0% to 17% (Arjo and Pletscher 1999), and plants occurred at a rate of 13.9% in northwestern Wyoming (Dowd and Gese 2012). We found that, when combined, seeds, berries, and plant matter made up 34.7% of the diet by volume (Fig. 2)—which was more consistent with diet studies in the American South or Southwest (Bowyer et al. 1983; Andelt et al. 1987; Young et al. 2006; Albers 2012). In the summer, seeds and berries were the second most common diet item, at 26.4%. Although previous studies measured the percent occurrence of diet items (Arjo and Pletscher 1999; Dowd and Gese 2012), while we measured percent volume, analyzing our data as percent occurrence only inflated the importance of seeds, berries, and plant matter to 42.0% (Table 1). Precipitation was lower than average at both sites in 2018 (86% of average at the low wolf density site and 91% of average for the 8 months with available data at the high wolf density site) (U.S. Climate Data 2023), which means the high importance of berries is unlikely to have been caused by above-average berry production (Holden et al. 2012). These results suggest that plants could be a more important part of coyote diet in Washington, supporting recent findings that coyotes and other carnivores may be important seed dispersers (Draper et al. 2022).

The seasonal differences in coyote diet that our study documented support previous findings that coyotes consume more ungulates during the winter and more small mammals and plants during the summer (Arjo et al. 2002; Dowd and Gese 2012; Jensen et al. 2022). Coyotes consume more ungulate biomass in the winter both in areas where deer are susceptible to winterkill and across snowy landscapes where predators are more successful as snow deepens and deer condition decreases (Gese and Grothe 1995; Gese et al. 2008). During the summer, the diversity of available resources increases with the emergence of small mammals from under the snowpack and availability of plants and berries (Bowyer et al. 1983; Arjo et al. 2002). However, in addition to ungulate, seeds and berries, small mammal, and plant matter, we found that increased leporid consumption during the winter significantly contributed to the dietary difference we observed between seasons (Table 3). Other results from similar latitudes have been less clear, with leporid consumption peaking during the winter in some years and during the summer in others (Arjo et al. 2002). There was no significant difference in the seasonal consumption of snowshoe hares in Riding Mountain National Park, Manitoba (Meleshko 1986), but in northwest Wyoming, hare consumption was highest in fall and decreased through the winter, suggesting that as snow depth increased, coyotes switched to more readily available prey, such as ungulate carcasses (Dowd and Gese 2012). Given the variation in results across studies, more research is needed to understand the predator–prey dynamics between coyotes and leporids at these latitudes.

Our study provides a baseline for coyote diet in Washington, and sheds light on how coyotes are impacted by wolf recolonization. We found that coyotes increased their consumption of ungulate prey inside of wolf pack territories, suggesting that continued wolf recovery in Washington may benefit coyotes and other scavenger populations (Arjo and Pletscher 1999; Wilmers 2004). Additional work is needed to determine whether coyotes in our study sites were susceptible to suppression by wolves despite the benefits of carrion provisioning or whether suppression may increase over time as wolves enter new territories. Mesopredator suppression may be more likely to occur where top predators are at higher densities (Newsome et al. 2017). Overall, our results suggest that coyotes are responding to competition with wolves according to optimal foraging theory by increasing their use of, and access to, high-value ungulate prey. This shift in resource use by an abundant, generalist predator may have substantial cascading effects throughout the food web in areas of wolf recovery, potentially benefitting small mammal populations and competing mesopredators through an among-predator cascade (Levi and Wilmers 2012). A better understanding of these dynamics may help to resolve the multi-faceted roles of large carnivores in ecosystems where their populations are recovering.

Acknowledgements

Funding was provided by a NSF CAREER grant to LRP (DEB-1652420). We thank J. Bradley at the Burke Museum for loaning reference specimens needed to accurately identify prey items. E. Reese supervised and conducted genetic labwork to identify coyote scats. Invaluable assistance with scat collection was provided by A. Machowicz, A. Van Scoyoc, L. Satterfield, K. Orlofsky, J. Roughgarden, M. Danielson, B. Bernhardt, K. West, N. Klopmeier, L. Saldo, L. Redmond, Z. Wardle, C. Horton, and S. Shiver. We are grateful to B. Kertson at the Washington Department of Fish and Wildlife for facilitating access to wolf location data.

Article information

History dates

Received: 29 January 2024
Accepted: 4 June 2024
Accepted manuscript online: 8 June 2024
Version of record online: 17 September 2024

Copyright

Data availability

Data generated during this study are available in the Dryad repository, DOI: 10.5061/dryad.v9s4mw73d.

Author information

Author ORCIDs

Anna N. Malesis https://orcid.org/0009-0002-7989-597X
Rebecca M. Windell https://orcid.org/0000-0003-4142-7820
Carmen M. Vanbianchi https://orcid.org/0000-0002-1180-5774
Laura R. Prugh https://orcid.org/0000-0001-9045-3107

Author contributions

Conceptualization: LRP
Data curation: ANM
Formal analysis: ANM
Funding acquisition: LRP
Investigation: ANM, RMW, CMV
Methodology: LRP
Project administration: LRP
Supervision: LRP
Visualization: ANM
Writing – original draft: ANM
Writing – review & editing: RMW, CMV, LRP

Competing interests

The authors declare there are no competing interests.

Funding information

Funding was provided by a NSF CAREER grant to LRP (DEB-1652420).

Supplementary material

Supplementary data are available with the article at https://doi.org/10.1139/cjz-2024-0019.

References

Albers, G. 2012. Coyote diets in West Virginia. West Virginia University.

Andelt, W.F., Kie, J.G., Knowlton, F.F., and Cardwell, K. 1987. Variation in coyote diets associated with season and successional changes in vegetation. J. Wildl. Manage. **51**(2): 273–277. doi:10.2307/3801002.

Arjo, W.M., and Pletscher, D.H. 1999. Behavioral responses of coyotes to wolf recoloniation in northwestern Montana. IEEE Trans. Knowl. Data Eng. **32**: 1919–1927.

Arjo, W.M., Pletscher, D.H., and Ream, R.R. 2002. Dietary overlap between wolves and coyotes in northwestern Montana. J. Mammal. **83**(3): 754–766. doi:10.1644/1545-1542(2002)083⟨0754:dobwac⟩2.0.co;2.

Atwood, T.C. 2006. Behavioral interactions between coyotes, *Canis latrans*, and wolves, *Canis lupus*, at ungulate carcasses in southwestern Montana. West. North Am. Nat. **66**(3): 390–394. doi:10.3398/1527-0904(2006)66[390:BIBCCL]2.0.CO;2.

Atwood, T.C., and Gese, E.M. 2010. Importance of resource selection and social behavior to partitioning of hostile space by sympatric canids. J. Mammal. **91**(2): 490–499. doi:10.1644/09-MAMM-A-078.1.

Bassing, S.B., Devivo, M., Ganz, T.R., Kertson, B.N., Prugh, L.R., Roussin, T., et al. 2023. Are we telling the same story? Comparing inferences made from camera trap and telemetry data for wildlife monitoring. Ecol. Appl. **33**(1). doi:10.1002/eap.2745. PMID: 36107138.

Bowyer, R.T., Mckenna, S.A., and Shea, M.E. 1983. Seasonal changes in coyote food habits as determined by fecal analysis. Am. Midl. Nat. **109**(2): 266–273. doi:10.2307/2425406.

Brunner, H., and Coman, B. 1974. The identification of mammalian hair. 1st ed. Inkata Press, Melbourne.

Calenge, C. 2006. The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. Ecol. Modell. **197**: 516–519. doi:10.1016/j.ecolmodel.2006.03.017.

Calhoun, T., Kelly, M., Holcombe, B., Osborn, D., and D'Angelo, G. 2019. Splitting hairs: differentiating adult and fawn white-tailed deer hairs by width—implications for scat studies. *In* American Fisheries Society and The Wildife Society 2019 Joint Annual Conference, Reno. The Wildlife Society. Available from https://afs.confex.com/afs/2019/meetingapp.cgi/Paper/36758 [accessed June 2020].

Clarke, K.R. 1993. Non-paramteric multivariate analyses of changed in community structure. Aust. J. Ecol. **18**: 117–143. doi:10.1111/j.1442-9993.1993.tb00438.x.

DiCiccio, T.J., and Efron, B. 1996. Bootstrap confidence intervals. Stat. Sci. **11**(3): 189–228. doi:10.1007/978-3-319-01931-4_24.

Donadio, E., and Buskirk, S.W. 2006. Diet, morphology, and interspecific killing in carnivora. Am. Nat. **167**(4): 524–536. doi:10.1086/501033. PMID: 16670995.

Dowd, J.L.B., and Gese, E.M. 2012. Seasonal variation of coyote diet in northwestern wyoming : implications for dietary overlap with Canada lynx? Northwest Sci. **86**(4): 289–299. doi:10.3955/046.086.0405.

Draper, J.P., Young, J.K., Schupp, E.W., Beckman, N.G., and Atwood, T.B. 2022. Frugivory and seed dispersal by carnivorans. Front. Ecol. Evol. **10**: 864864. doi:10.3389/fevo.2022.864864.

Efron, B. 1987. Better bootstrap confidence intervaks. J. Am. Statist. Assoc. **82**(397): 171–185. doi:10.1080/01621459.1987.10478410.

Esri Inc 2018. World Hillshade. Arcgis.com.

Esri Inc. 2022 ArcGIS Pro. Environmental Systems Research Institute (Esri), Inc., Redlands, California.

Ganz, T.R., Devivo, M.T., Kertson, B.N., Roussin, T., Satterfield, L., Wirsing, A.J., and Prugh, L.R. 2022*a*. Interactive effects of wildfires, season and predator activity shape mule deer movements. J. Anim. Ecol. **91**(11): 2273–2288. doi:10.1111/1365-2656.13810. PMID: 36071537.

Ganz, T.R., Devivo, M.T., Reese, E.M., and Prugh, L.R. 2022*b*. Wildlife whodunnit: forensic identification of predators to inform wildlife management and conservation. Wildl. Soc. Bull. **47**. [Preprint]. doi:10.1002/wsb.1386.

Gese, E.M., and Grothe, S. 1995. Analysis of coyote predation on deer and elk during winter in Yellowstone National Park, Wyoming. Am. Midl. Nat. **133**(1): 36–43. doi:10.2307/2426345.

Gese, E.M., Ruff, R.L., and Crabtree, R.L. 2008. Foraging ecology of coyotes (*Canis latrans*): the influence of extrinsic factors and a dominance hierarchy. Can. J. Zool. **74**(5): 769–783. doi:10.1139/z96-089.

Hill, A.D., Daly, E.A., and Brodeur, R.D. 2015. Diet variability of forage fishes in the Northern California current ysstem. J. Mar. Syst. **146**: 121–130. doi:10.1016/j.jmarsys.2014.08.006.

Hinton, J.W., Ashley, A.K., Dellinger, J.A., Gittleman, J.L., Van Manen, F.T., and Chamberlain, M.J. 2017. Using diets of Canis breeding pairs to assess resource partitioning between sympatric red wolves and coyotes. J. Mammal. **98**(2): 475–488. doi:10.1093/jmammal/gyw233.

Hody, J.W., and Kays, R. 2018. Mapping the expansion of coyotes (*Canis latrans*) across North and Central America. ZooKeys, **759**: 81–97. doi:10.3897/zookeys.759.15149.

Holden, Z.A., Kasworm, W.F., Servheen, C., Hahn, B., and Dobrowski, S. 2012. Sensitivity of berry productivity to climatic variation in the Cabinet-Yaak Grizzly Bear Recovery Zone, Northwest United States, 1989-2010. Wildl. Soc. Bull. **36**(2): 226–231. doi:10.1002/wsb.128.

Homkes, A.T. 2021. Wolf selection of human-modified linear features and cover types when hunting and killing white-tailed deer fawns. Northern Michigan University.

Hurley, M.A., Unsworth, J.W., Zager, P., Hebblewhite, M., Garton, E.O., Montgomery, D.M., et al. 2011. Demographic response of mule deer to experimental reduction of coyotes and mountain lions in southeastern Idaho. Wildl. Monogr. **178**(178): 1–33. doi:10.1002/wmon.4.

Jensen, A.J., Marneweck, C.J., Kilgo, J.C., and Jachowski, D.S. 2022. Coyote diet in North America: geographic and ecological patterns during range expansion. Mamm. Rev. **52**(4): 480–496. doi:10.1111/mam.12299.

Kautz, T.M., Beyer, D.E., Farley, Z., Fowler, N.L., Kellner, K.F., Lutto, A.L., et al. 2021. American martens use vigilance and short-term avoidance to navigate a landscape of fear from fishers at artificial scavenging sites. Sci. Rep., **11**(1). doi:10.1038/s41598-021-91587-4.

Kelly, B.T., and Garton, E.O. 1997. Effects of prey size, meal size, meal composition, and daily frequency of feeding on the recovery of rodent remains from carnivore scats. Can. J. Zool. **75**(11): 1811–1817. doi:10.1139/z97-810.

Klauder, K., Borg, B.L., and Prugh, L.R. 2021. Living on the edge: spatial response of coyotes (*Canis Latrans*) to wolves (*Canis lupus*) in the subarctic. Can. J. Zool. **99**(4): 279–288. doi:10.1139/cjz-2020-0050.

Krefting, L.W. 1969. The rise and fall of the coyote on Isle Royale. Naturalist, **20**(4): 24–31.

Leopold, A., Sowls, L.K., and Spencer, D.L. 1947. A survey of overpopulated deer ranges in the United States. J. Wildl. Manage. **11**(2): 162–177.

Lester, D. 1997. Mammal Maps, NatureMapping Foundation. Available from http://naturemappingfoundation.org/natmap/maps/wa/#mammals [accessed 23 February 2018].

Letnic, M., Greenville, A., Denny, E., Dickman, C.R., Tischler, M., Gordon, C., and Koch, F. 2011. Does a top predator suppress the abundance of an invasive mesopredator at a continental scale?. Global Ecol. Biogeogr. **20**(2): 343–353. doi:10.1111/j.1466-8238.2010.00600.x.

Levi, T., and Wilmers, C.C. 2012. Wolves—coyotes—foxes: a cascade among carnivores. Ecology, **93**(4): 921–929. doi:10.1890/11-0165.1. PMID: 22690642.

Macarthur, R.H., and Pianka, E.R. 1966. On optimal use of a patchy environment. Am. Nat. **100**(916): 603–609.

Majumder, A., Sankar, K., Qureshi, Q., and Basu, S. 2013. Predation ecology of large sympatric carnivores as influenced by available wild ungulate prey in a tropical deciduous forest of Central India. J. Trop. Ecol. **29**(5): 417–426. doi:10.1017/S0266467413000473.

Manly, B.F.J. 2006. Randomization, bootstrap and Monte Carlo methods in biology. Chapman & Hall/CRC.

McCune, B., Grace, J.B., and Urban, D.L. 2002. Analysis of ecological communities. MjM Software Design, Gleneden Beach, Oregon.

Meleshko, D.W. 1986. Feeding habits of sympatric canids in an area of moderate ungulate density. University of Alberta. Available from https://era.library.ualberta.ca/files/9s1618379/ML30149.pdf [accessed June 2019].

Mills, L.S., and Knowlton, F.F. 1991. Coyote space use in relation to prey abundance. Can. J. Zool. **69**: 1516–1521. doi:10.1139/z91-212.

Moore, T.D., Spence, L.E., and Dugnolle, C.E. 1974. Identification of the dorsal guard hairs of some mammals of Wyoming. Wyoming Game and Fish Department, Laramie.

Newsome, T.M., Greenville, A.C., Ćirović, D., Dickman, C.R., Johnson, C.N., Krofel, M., et al. 2017. Top predators constrain mesopredator distributions. Nat. Commun. **8**. doi:10.1038/ncomms15469.

O'donoghue, M., Boutin, S., Krebs, C.J., Zuleta, G., Murray, D.L., and Hofer, E.J. 1998. Functional responses of coyotes and lynx to the snowshoe hare cycle. Ecology, **79**(4): 1193–1208. doi:10.1890/0012-9658(1998)079%5b1193:FROCAL%5d2.0.CO;2.

Oksanen, J., Simpson, G., Kindt, R., Legendre, P., Minchin, P., O'Hara, R., et al. 2019. vegan: Community ecology package. Available from https://cran.r-project.org/package=vegan [accessed June 2020].

Paquet, P.C. 1992. Prey use strategies of sympatric wolves and coyotes in Riding Mountain National Park, Manitoba. Am. Soc. Mammal. **73**(2): 337–343.

Prugh, L.R. 2005. Coyote prey selection and community stability during a decline in food supply. Oikos, **110**(2): 253–264. Available from https://about.jstor.org/terms [accessed January 2019].

Prugh, L.R., and Sivy, K.J. 2020. Enemies with benefits: integrating positive and negative interactions among terrestrial carnivores. Ecol. Lett. **23**. [Preprint]. doi:10.1111/ele.13489. PMID: 32185877.

Prugh, L.R., Arthur, S.M., and Ritland, C.E. 2008. Use of faecal genotyping to determine individual diet. Wildl. Biol. **14**(3): 318–330. doi:10.2981/0909-6396(2008)14[318:uofgtd]2.0.co;2.

Prugh, L.R., Stoner, C.J., Epps, C.W., Bean, W.T., Ripple, W.J., Laliberte, A.S., and Brashares, J.S. 2009. The rise of the mesopredator. Bioscience, **59**(9): 779–791. doi:10.1525/bio.2009.59.9.9.

Prugh, L.R., Cunningham, C.X., Windell, R.M., Kertson, B.N., Ganz, T.R., Walker, S.L., and Wirsing, A.J. 2023. Fear of large carnivores amplifies human-caused mortality for mesopredators. Science, **380**(6646): 754–758. doi:10.1126/science.adf2472. PMID: 37200434.

Ripple, W.J., Wirsing, A.J., Beschta, R.L., and Buskirk, S.W. 2011. Can restoring wolves aid in lynx recovery?. Wildl. Soc. Bull. **35**(4): 514–518. doi:10.1002/wsb.59.

Ripple, W.J., Wirsing, A.J., Wilmers, C.C., and Letnic, M. 2013. Widespread mesopredator effects after wolf extirpation. Biol. Conserv. **160**: 70–79. doi:10.1016/j.biocon.2012.12.033.

Ruprecht, J., Eriksson, C.E., Forrester, T.D., Spitz, D.B., Clark, D.A., Wisdom, M.J., et al. 2021. Variable strategies to solve risk–reward tradeoffs in carnivore communities. Proc. Natl. Acad. Sci. USA, **118**(35). doi:10.1073/pnas.2101614118.

Schoener, T.W. 1974. Resource partitioning in ecological communities. Science, **185**(4145): 27–39. doi:10.1126/science.185.4145.27. PMID: 17779277.

Sivy, K.J., Pozzanghera, C., Grace, J., and Prugh, L. 2017. Fatal Attraction? Intraguild facilitation and suppression among predators. Am. Nat. **190**(5): 663–679. doi:10.5061/dryad.tj590. PMID: 29053355.

Sivy, K.J., Pozzanghera, C.B., Colson, K.E., Mumma, M.A., and Prugh, L.R. 2018. Apex predators and the facilitation of resource partitioning among mesopredators. Oikos, **127**(4): 607–621. doi:10.1111/oik.04647.

Smith, D.W., Peterson, R.O., and Houston, D.B. 2003. Yellowstone after wolves. Bioscience, **53**(4): 330–340. doi:10.1641/0006-3568(2003)053[0330:YAW]2.0.CO;2.

Smith, F.R. 1958. The effect of natural and laboratory digestion on the microscopic appearance of certain animal hairs. J. Assoc. Off. Agric. Chem. **41**(2): 479–480.

Stoddart, L.C., Griffiths, R.E., and Knowlton, F.F. 2001. Coyote responses to changing jackrabbit abundance affect sheep predation. J. Range Manage. **54**(1): 15–20. doi:10.2307/4003521.

Suraci, J.P., Clinchy, M., Dill, L.M., Roberts, D., and Zanette, L.Y. 2016. Fear of large carnivores causes a trophic cascade. Nat. Commun. **7**. doi:10.1038/ncomms10698. PMID: 26906881.

Tintner, J., Hatlauf, J., Weber, H., and Lanszki, J. 2020. Molecular recalcitrance of hair passing the digestive system of a canid. Molecules, **25**(19): 4404. doi:10.3390/molecules25194404. PMID: 32992751.

United States Department of State Office of the Geographer 2013. Detailed World Polygons (LSIB), North America, 2013. United States Department of State Office of the Geographer Humanitarian Information Unit.

U.S. Census Bureau 2020. DECENNIALP12020. Data.census.gov.

U.S. Climate Data 2023. *US Climate Data*. Available from www.usclimatedata.com/climate/chewelah/washington/united-states/uswa0074 [accessed 21 December 2023].

Verts, B.J., and Carraway, L.N. 1998. Land mammals of Oregon. 1st ed. University of California Press, Berkeley.

Washington Department of Fish and Wildlife. 2017*a*. Game Management Units. Washington Geospatial Open Data Portal.

Washington Department of Fish and Wildlife. 2017*b*. Gray Wolf Conservation and Management, Washington Department of Fish and Wildlife. Available from https://wdfw.wa.gov/conservation/gray_wolf/packs/ [accessed January 2019].

Washington Department of Fish and Wildlife, Confederated Colville Tribes, Spokane Tribe of Indians, USDA-APHIS Wildlife Services, and U.S. Fish and Wildlife Service. 2018. Washington Gray Wolf Conservation and Management 2017 Annual Report. Washington Department of Fish and Wildlife, Ellensburg, WA.

Washington Department of Fish and Wildlife, Confederated Colville Tribes, Spokane Tribe of Indians, USDA-APHIS Wildlife Services, and U.S. Fish and Wildlife Service. 2019. Washington Gray Wolf Conservation and Management 2018 Annual Report. Washington Department of Fish and Wildlife, Ellensburg, WA. Available from https://www.boq.com.au/content/dam/boq/files/shareholder-centre/financial-results/2018/FY2018_Annual_Report.pdf%0Ahttps://contact.co.nz/-/media/contact/pdfs/…/annual-report-2018-contact-energy.ashx [accessed June 2020].

Washington Department of Fish and Wildlife, Confederated Tribes of the Colville Reservation, Spokane Tribe of Indians, USDA-APHIS Wildlife Services, and U.S. Fish and Wildlife Service. 2022. Washington Gray Wolf Conservation and Management 2021 Annual Report. Washington Department of Fish and Wildlife, Ellensburg, WA.

Washington Department of Natural Resources. 2017. CADASTRE.JURISDICTION. Washington Geospatial Open Data Portal.

Wilmers, C.C. 2004. The gray wolf—scavenger complex in Yellowstone National Park. University of California, Berkeley.

Wilmers, C.C., Stahler, D.R., Crabtree, R.L., Smith, D.W., and Getz, W.M. 2003. Resource dispersion and consumer dominance: scavenging at wolf- and hunter-killed carcasses in Greater Yellowstone, USA. Ecol. Lett. **6**, (6): 996–1003. doi:10.1046/j.1461-0248.2003.00522.x.

WSDOT Online Map Center. 2015. WSDOT—Public Roads. ArcGIS Hub.

Young, J.K., Andelt, W.F., Terletzky, P.A., and Shivik, J.A. 2006. A comparison of coyote ecology after 25 years: 1978 versus 2003. Can. J. Zool. **84**(4): 573–582. doi:10.1139/z06-030.

Zabala, J., and Zuberogoitia, I. 2003. Badger, *Meles meles* (Mustelidae, Carnivora), diet assessed through scat-analysis: a comparison and critique of different methods. Folia Zool. **52**(1): 23–30.

Zar, J.H. 2010. Biostatistical analysis. 5th ed. Prentice Hall, Upper Saddle River.