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Author(s): Julia Witzuk , Stanisław Pagacz , and L. Scott Mills

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Disproportionate predation on endemic marmots by invasive coyotes

JULIA WITCZUK,* STANISŁAW PAGACZ, AND L. SCOTT MILLS

Wildlife Biology Program, College of Forestry and Conservation, University of Montana, Missoula, MT 59812, USA (JW, LSM)

Museum and Institute of Zoology, Polish Academy of Sciences, Wilcza 64, 00-679 Warszawa, Poland (JW, SP)

* Correspondent: juliawit@miiz.eu

We investigated predation by nonnative coyotes (*Canis latrans*) on endemic Olympic marmots (*Marmota olympus*) in Olympic National Park, Washington, in 2005 and 2006. Although nearly the entire marmot range is protected within the park, declines and local extirpations of the species have been documented. Through analyses of carnivore scat across the range of the Olympic marmot we determined the distribution and relative density of coyotes and characterized the extent to which coyotes and native carnivores preyed on marmots. We used mitochondrial DNA analysis of scats to determine carnivore species, and microsatellite markers for individual coyote identification. Scat analysis indicated that invasive coyotes are widespread and the numerically dominant carnivore on sampled trails within the Olympic highlands—71% (301 of 426) of all scats verified to species arose from coyote. Out of all carnivore scats collected, 11.6% (111 of 958) contained marmot remains. For 85% of the samples with marmots, coyotes were confirmed as the predator. The remainder arose from bobcat (13%) and cougar (2%). Coyotes were the predominant marmot predator across all months and in most regions of the park. Twelve out of 13 coyote individuals identified with genetic markers preyed on marmots. Marmots ranked 5th in frequency of coyote diet items, after snowshoe hares (*Lepus americanus*), mountain beavers (*Aplodontia rufa*), voles, and cervids. Scat analysis indicated that in the Olympic Mountains, the coyote as an invasive generalist predator is subsidized by abundant multiple prey, and appears to be the primary terrestrial predator on the endemic Olympic marmot. We conclude that predation by coyotes on marmots is widespread and substantial across the marmot's species range, and therefore likely driving observed marmot declines and extinctions.

Key words: bobcat, *Canis latrans*, decline, diet, food habits, *Lynx rufus*, *Marmota olympus*, Olympic marmot, Olympic National Park, scat analysis

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Effects of predators on population dynamics of prey are greatest when the number of prey killed is high, prey numbers are small, and prey defense behaviors are minimal. All these conditions tend to be fulfilled when the predator is an invasive generalist encountering prey species limited in distribution and naïve to predation pressure from the predator. For example, island systems such as New Zealand, Hawaii, and Guam have suffered devastating results from generalized predators such as rats, cats, and brown tree snakes encountering naïve and often endemic prey (Fritts and Rodda 1998; Wiles et al. 2003).

In North America, the coyote (*Canis latrans*) is a generalist, opportunistic predator that has recently spread throughout most of the continent (Gompper 2002a; Moore and Parker 1992). Coyote predation has been linked to increased extinction risk for several endangered species including black-footed ferrets (*Mustela nigripes*), San Joaquin kit foxes (*Vulpes macrotis mutica*), whooping cranes (*Grus americana*), and caribou

(*Rangifer tarandus*—Boisjoly et al. 2010; Goodrich and Buskirk 1995).

For an endemic prey species the consequence of coyote predation relative to native carnivores will depend on predation rates and prey numbers. We investigate these dynamics for predation by coyotes on endemic marmots, found almost entirely within Olympic National Park. Coyotes likely invaded the Olympic Peninsula of western Washington State early in the 20th century, initially at low-elevation logged areas (Scheffer 1995). By the 1940s the 1st coyotes were reported at higher elevations of the Olympic Mountains (Schwartz and Mitchell 1945).

One of the potential prey coyotes encountered in the park, the Olympic marmot (*Marmota olympus*), has the most



restricted range and limited numbers among all marmots in the United States. The species is genetically and morphologically distinct from related species such as the hoary marmot (*M. caligata*) and Vancouver Island marmot (*M. vancouverensis*—Hoffmann et al. 1979; Rausch and Rausch 1971). More than 90% of the Olympic marmot's habitat is within Olympic National Park, and the species is restricted to high-elevation alpine and subalpine meadows (>1,400 m—Griffin et al. 2009a).

Olympic marmots appear to have suffered severe declines and local extirpations in recent years. More than one-half of the 25 colonies periodically documented since the 1950s are now extinct, abandoned burrow complexes are common throughout the park, and no known colonizations of new areas have been observed (Griffin et al. 2008). The best estimate of abundance for the species (approximately 1,000) is less than one-half that estimated in the late 1960s (Barash 1989; Griffin et al. 2008).

Tourist pressure, direct climate-change effects, disease, and inbreeding depression do not appear to be primary drivers of the marmot declines (Griffin et al. 2007, 2008); however, a viable likely driver remains predation by invasive coyotes. Coyotes are known to be effective predators on marmots in other systems, accounting for at least 47% of mortality in the yellow-bellied marmot (*Marmota flaviventris*) in Colorado (van Vuren 2001). Olympic marmots experience high mortality of nonjuveniles, with coyotes the cause in 33–90% of the deaths at different sites and years (Griffin et al. 2008, 2009b). These previous studies on Olympic marmots tended to be in areas of high visitor use. Because coyotes are known to be opportunistic generalists that thrive at the human interface (Fedriani et al. 2001; Gompper 2002b; Markovchick-Nicholls et al. 2008), predation might be expected to be higher in those areas than throughout the park. If true, then the overall predation rate on marmots by coyotes would be less than if coyotes were killing marmots throughout the park.

Our primary objective was to understand the distribution of coyotes across the range of Olympic marmots, and characterize the extent to which coyotes and native carnivores preyed on marmots. We sampled trails throughout most of the range of the endemic marmot species, with focal areas of high and low tourist density to test whether coyotes were subsidized in certain areas compared to others. We used DNA analysis of collected carnivore scats to determine predator species and the minimum number and distribution of individual coyotes. In addition, we evaluated diets of Olympic coyotes as well as other sympatric carnivores that might affect marmot dynamics.

MATERIALS AND METHODS

Study area.—The study was conducted in the high country of the Olympic Mountains within Olympic National Park (Olympic Peninsula, northwestern Washington). The Olympic Mountains of the Olympic Peninsula are geographically isolated from other mountains, surrounded by the waters of the Puget Sound and by the Puget lowlands (Houston et al. 1994). The terrain is rugged with the highest peak reaching an

elevation of 2,427 m. Climate of the peninsula is characterized by a steep west–east precipitation gradient, as well as wet winters and dry summers. On the wet western slopes mean rainfall per year exceeds 400 cm, whereas the eastern part is relatively dry because it lies in a rain shadow (annual precipitation at high elevations averages about 100 cm). Eighty percent of the annual precipitation falls from October to March and only 5% falls in July and August (Houston and Schreiner 1994a). High-elevation areas are characterized by harsh climate and a short growing season.

This study was concentrated within 3 upper (>1,000 m) vegetation zones: montane, subalpine, and alpine. Montane forests at midelevations are predominantly silver fir (*Abies amabilis*), western hemlock (*Tsuga heterophylla*), and Douglas-fir (*Pseudotsuga menziesii*). Patches of subalpine forests at higher elevations are composed of subalpine fir (*Abies lasiocarpa*) and mountain hemlock (*Tsuga mertensiana*). Alpine meadows occur above 1,500 m and are composed of forbs, sedges, grasses, ericaceous shrubs, and spreading phlox (*Phlox diffusa*—Fonda and Bliss 1969; Houston and Schreiner 1994a).

Primary native predators expected to prey on marmots in the park include golden eagle (*Aquila chrysaetos*) and cougar (*Puma concolor*). Both species have been observed preying on Olympic marmots (Barash 1973; Griffin 2007), and are known to prey on marmots elsewhere (Barash 1989; Bryant and Page 2005; Marr and Knight 1983). Bobcats (*Lynx rufus*) are present in the park, have been documented to prey on Olympic marmots (S. Griffin, Port Angeles, Washington, pers. comm.), and also are known to prey on woodchucks (*M. monax*—Fox and Fox 1982; Fritts and Sealander 1978). Black bears (*Ursus americanus*), occasional predators of other marmot species in other regions (van Vuren 2001), also are present in the park; however, no evidence of bear predation on Olympic marmots was detected in 4 years of intensive study by Griffin (2007), and marmots and bears in Olympic National Park appear indifferent to each others' presence (J. Witczuk, pers. obs.). Although foxes (*Vulpes vulpes*) are present on the Olympic Peninsula (Aubry 1984; National Park Service 2012) they are not native and are unlikely to be in the park highlands (P. Happe, Olympic National Park Wildlife Branch Chief, pers. comm.). Mustelids and smaller raptors would not be expected to kill adult marmots (Barash 1989).

Scat collection.—We collected scats in 2005 and 2006 during the summer (May–September) when marmots were not hibernating. We conducted systematic monthly collection along 12 transects of varying length totaling 125 km, placed along park hiking trails and roads mainly in areas with relatively high marmot densities (Fig. 1). Where spring snow conditions prevented access to some transects, the 1st sampling period was postponed until June. All transects were located within an elevation range of 1,000–2,000 m (except for transect Lena starting at 750 m). Approximately 60% of the total length of transects traversed alpine meadows and mixed meadow–forest habitats, whereas the remainder led through montane forests. Three transects (Hurricane, Obstruction, and Royal)

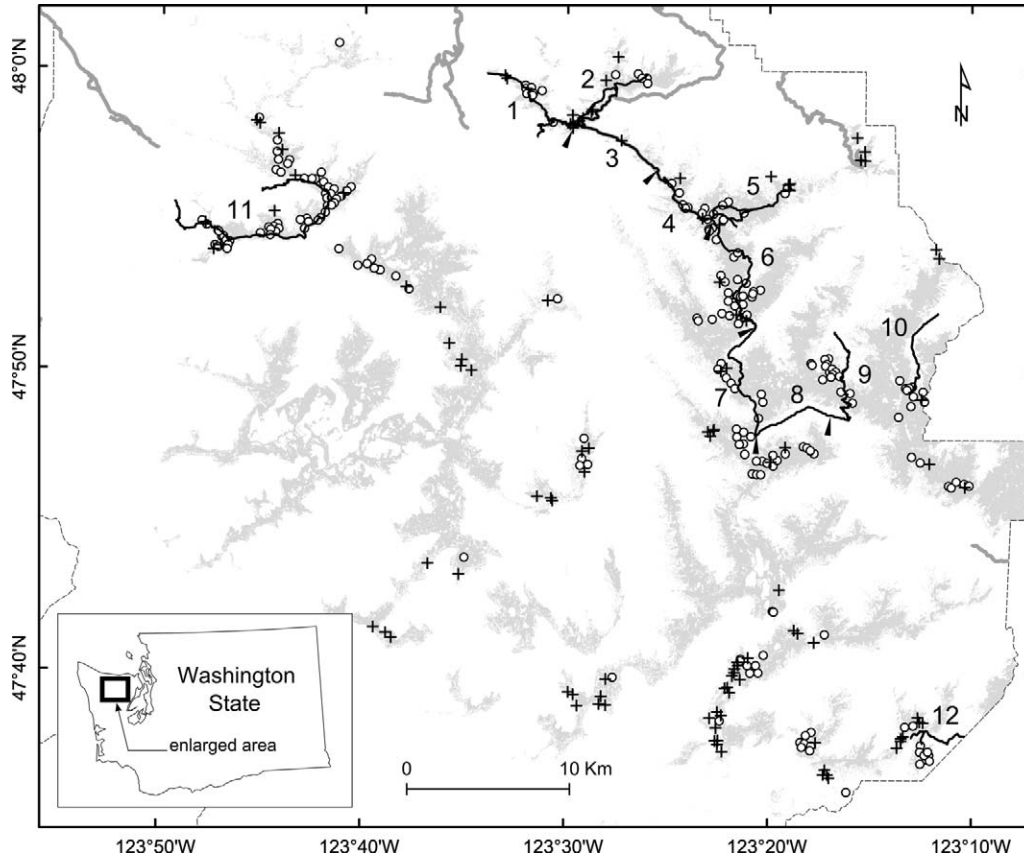


FIG. 1.—Sample transects (thin black lines) for systematic scat collection for this study (Olympic National Park, Washington; summers 2005 and 2006): 1—Hurricane, 2—Klahhane, 3—Steeple, 4—Obstruction, 5—Badger, 6—Grand, 7—Cameron, 8—Dosewallips, 9—Gray Wolf, 10—Royal, 11—Seven Lakes, 12—Lena; open circles indicate locations of active marmot colonies and crosses indicate locations of extinct marmot colonies in Olympic National Park recorded during surveys in 2002–2006 (Griffin et al. 2008); gray area—alpine zone; thick gray lines—roads.

were located in the areas containing intensively studied sites with marked marmots whose vital rates were monitored annually from 2002 to 2006 by Griffin et al. (2008); these transects (plus Steeple) were traveled more frequently than once a month (usually twice a month) in the course of other marmot project activities, and scats were collected whenever they were encountered. We also collected some scats (11% of total) opportunistically during transit and the course of other activities.

Two separated focal areas highly contrasting in human use level were selected among other study transects for comparative assessment of coyote use and predation on marmots. The Gray Wolf focal area (transect 9; Fig. 1) is in the remote backcountry, with very low visitor use, whereas the Obstruction–Badger focal area (transects 4 and 5; Fig. 1) is near the road and experiences high visitor use in summer months. These focal areas were within 10 air km (11.5 km overland) of each other.

All carnivore scats (except bear, scats of which are easily distinguishable from other carnivores and which was not considered a marmot predator) were collected from sample transects. For each scat a 1-cm-long segment of scat was stored with silica gel for genetic analysis, and the remainder saved in a plastic bag for diet analysis. Field collectors recorded

estimated species identity based on scat physical characteristics (Elbroch 2003; Murie 1954) and estimates of approximate age of the scat: fresh (dark coloration, glossy, soft, and smelly), medium (dark but dry and hard), and old (bright coloration and partially decomposed).

Based on approximate age of scat recorded, for the monthly analysis of carnivore diet we assigned each sample to the most likely date of deposit. Fresh scats were always assigned to the month of collection. Scats recorded as old or medium were assigned to the month of collection if collected after the 10th day of the month, and to the previous month if collected in the first 10 days of the month. Old scats collected away from the sample transects were removed from monthly analysis because the date of deposit was impossible to determine.

Genetic analysis of carnivore species and coyote individuals.—Because scats of coyote, bobcat, cougar, juvenile bear, fox, and domestic dog could be confused based on field identities (Davison et al. 2002; Farrell et al. 2000; Reed et al. 2004), we verified field-based species identification using mitochondrial DNA (mtDNA) analysis for about one-half (453 of 958) of all collected scats stratified by each of the 12 transects. Additionally species identification was verified for all the remaining scats containing marmot ($n = 45$).

Approximately 0.20 g of material scraped from the scat surface was used for extraction. We used QIAamp DNA Stool Mini Kits (Qiagen Inc., Valencia, California) to extract DNA from the samples. Extraction and amplification of DNA were processed in separate buildings at Mills' University of Montana laboratories to reduce the risk of contaminations of low-quantity–low-quality fecal DNA with polymerase chain reaction (PCR) products.

We used PCR and primers CanidL1 and HCarn200 (Bidlack et al. 2007; Paxinos et al. 1997) to amplify a short (196-base pairs) fragment of the cytochrome-*b* region of mtDNA for species identification. Twenty-microliter PCRs contained 4 μ l of DNA extract, 0.5 \times reaction buffer, 0.4 mM of each deoxynucleoside triphosphate, 0.5 μ M of each primer, 0.75 mM of MgCl₂, and 0.8 units of Platinum Taq (Life Technologies, Grand Island, New York). The PCR profile was initial denaturation at 95°C for 2 min, then 40 cycles with 95°C for 1 min, 54°C for 1 min, and 72°C for 2 min. We used 2 negative controls (water) and 4 positive controls from tissue samples of known coyote, bobcat, cougar, and black bear in each PCR. Five microliters of the PCR products was used to check for the presence of the sample on a 2% agarose gel and to check for contamination. A 2:3 dilution of cleaned PCR product was sequenced with use of the CanidL1 primer (3 pM) and processed by High-Throughput Genomics Center (Seattle, Washington). The resulting sequences were assigned to species by comparison to sequences in GenBank (Benson et al. 2012).

We identified individual coyotes based on nuclear microsatellite markers, analyzing all coyote scats with marmot remains, as well as a random subset of approximately 50% of coyote scats that did not contain marmots and that were found in 1 of the 2 focal areas with vastly different levels of human use. To avoid confounding factors associated with population turnover for the subset we used scats collected only during the 1st year of the study (2005).

We amplified 6 microsatellite loci (FH2137, FH2159, FH2140, FH2235, FH2096, and FH2001—Prugh et al. 2005) in 2 optimized multiplex PCRs for coyote individual identification. The 1st mix included loci FH2096, FH2235, and FH2137 and contained 2.5 μ l of DNA extract, 1 \times Qiagen Multiplex PCR Mix, 1 \times primer mix (each primer at 0.2 μ M), bovine serum albumin at a final concentration of 1 μ g/ μ l, and 0.5 \times Q-solution. The 2nd mix for loci FH2140, FH2001, and FH2159 was identical except Q-solution was not used. The final volume of reaction was 10 μ l in both cases. A touch-down PCR was performed with initial denaturation at 95°C for 5 min, followed by 20 cycles with 94°C denaturation for 30 s, 1 min annealing starting at 62°C and stepping down 0.5°C per cycle, and 1 min extension at 72°C and then an additional 25 cycles at 52°C annealing temperature with an additional final extension cycle of 5 min at 72°C. Genotypes were visualized using fragment analysis on a capillary automated DNA sequencer (Applied Biosystems, Foster City, California) and analyzed with GeneMapper software version 3.7 (Applied Biosystems). To minimize genotyping errors we adopted the comparative multiple tubes approach (Frantz et al. 2003). For each locus up

to 7 positive PCRs were run until an allele was observed twice for heterozygote loci and 3 times for homozygote loci. Samples that did not give consensus genotypes after 7 PCRs were discarded from further analysis. We used program GIMLET (Valiere 2002) to group genotypes and to estimate probability of identity (PI_{unbiased}).

Diet analysis.—All collected scat samples were autoclaved, soaked in water with detergent for 24 h, washed through a sieve, and air dried. Undigested prey items (hair, bone fragments, etc.) were manually separated. All samples were searched macroscopically for marmot remains: teeth, bone fragments, and hair. If the hair mass constituting a sample contained potential marmot hairs (based on characteristics such as length, thickness, and color) we conducted microscopic examination to confirm if it was marmot. Complete analysis of the diet was conducted on a random sample of approximately 50% of collected scats (the same 453 samples subjected to molecular identification of the predator species). Prey species were distinguished macroscopically and by microscopic examination, using comparison with specimens housed at the University of Montana Zoological Museum and a hair identification key (Moore et al. 1974).

Using the randomly selected scats for which complete prey identity was conducted, we calculated frequency of occurrence for each prey species by month, transect, and predator species. Differences in frequency of prey types were assessed with Pearson's chi-square test with Yates' continuity correction (Zar 2010). Also, we calculated annual overlap of diets among carnivore species using Pianka's equation (Pianka 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 the diet of predator p , and q_i is the proportion of food item i in the diet of predator q . An index value of 1 indicates complete similarity, whereas 0 indicates complete dissimilarity of the diet.

RESULTS

Carnivore scat densities and distribution.—A total of 958 scats were collected during the 2-year study, with 89% (857 of 958) collected on the sample transects (see Appendix I). The average rate of encounter per year was 3.4 scats per 1 km of transect. Of the 11% (101 of 958) of scats collected opportunistically, only 27 (3% of total) were collected more than 1 km from the sample transects. The number of scats collected was similar between years (428 in 2005 and 530 in 2006), and scats were pooled for all analyses.

We observed considerable differences in density of scats among different transects, ranging from 2.4 to 13.2 scats/km (Fig. 2A), indicating either differences in relative abundance of carnivores or differential use of trails. Although relative scat densities also could be affected by sampling intensities (4 transects [Hurricane, Steeple, Obstruction, and Royal] were traveled more frequently than once a month) or by tourist foot traffic destroying scats, we think these factors are minimal. Scat densities were not systematically higher on transects

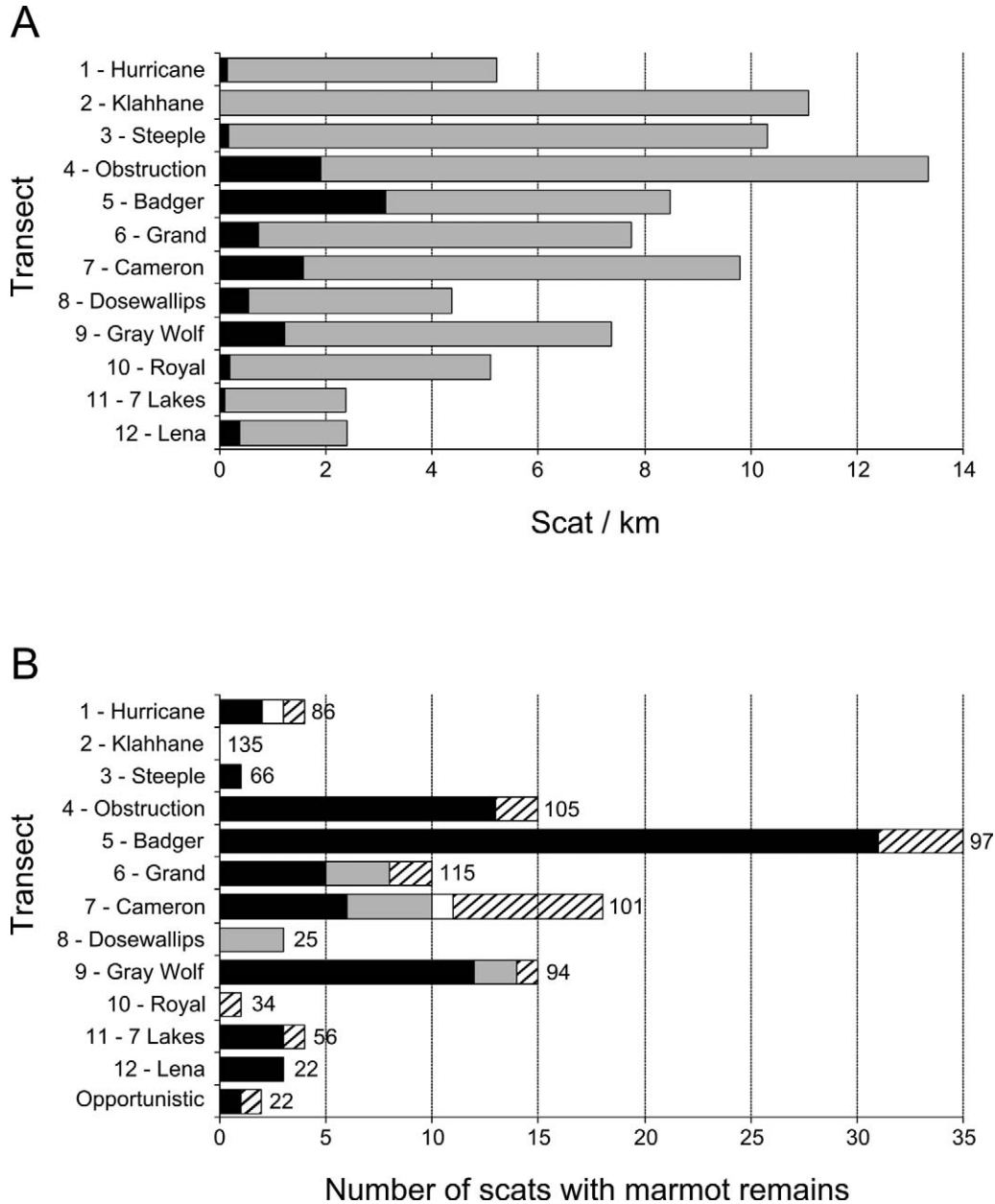


FIG. 2.—A) Number of scats (total for 2005 and 2006) that contain Olympic marmot (*Marmota olympus*) remains (black bars) or lack them (gray bars) per kilometer of transect in Olympic National Park, Washington. B) Number of scats with Olympic marmot remains collected at different transects and in their vicinity (<2 km from transects); “opportunistic” denotes scats from other park areas. Different shadings represent predator species identified with mitochondrial DNA: black—coyote (*Canis latrans*), gray—bobcat (*Lynx rufus*), white—cougar (*Puma concolor*), dashed—predator species not identified. Sample sizes are to right of bars.

sampled more often (Fig. 2A), nor did we observe an inverse relationship between tourist use intensity of a given trail and scat number. For example, the Klahhane transect had a high rate of scats discovered and also is one of the most popular trails in the park.

Genetic species identification.—Overall amplification success for species identification was 86% (426 of 498). Among the scats for which predator species was confirmed with mtDNA, the majority were identified as coyote (71%, 301 of 426) and the remainder as bobcat (25%, 107 of 426) and cougar (4%, 18 of 426; see Appendix I). Coyote scats

constituted the majority collected in all months of study (63–74%), and along all except 2 transects (felid scats predominated only at Dosewallips and Cameron transects, mainly along deep river valleys). Among 426 scats verified to species, 38 scats were found off transect (off trail). Also in this subset, coyote scats constituted the highest proportion (79%, 30 of 38).

Amplification was successful for 89% of scats estimated in the field to be fresh (135 of 151), 80% of scats classified as medium (186 of 232), and 91% of those categorized as old (105 of 115).

TABLE 1.—Accuracy of field identifications of carnivore scats to species, coyote (*Canis latrans*), bobcat (*Lynx rufus*), and cougar (*Puma concolor*), in Olympic National Park, Washington (2005–2006). Data are sample sizes with percentages given in parentheses; correct field assignments are shown in boldface type.

Genetic identification	Field assignment			Total
	Coyote	Bobcat	Cougar	
Coyote	230 (81)	3 (1)	52 (18)	285
Bobcat	54 (53)	10 (10)	37 (37)	101
Cougar	5 (28)	0 (0)	13 (72)	18
Total	289	13	102	404

Based on the 404 scats for which we had both field assignment of the species and the species confirmation with mtDNA (Table 1), overall accuracy in distinguishing carnivore species in the field was 63% (253 of 404). Even considerable size difference between cougar and other carnivores did not ensure reliable recognition of this species. Field identification was the most precise for coyote scats (81% correct field assignments; 230 of 285). Sparse scats of cougar were correctly identified in 72% of cases (13 of 18) and bobcat scats only 10% of the time (10 of 101). Field collectors noted as uncertain their identities of 12% of actual coyote samples, 17% of actual bobcat samples, and 22% of true cougar samples. Thus, uncertainty of the field assignments mostly reflected the actual error rates, except that error rate of bobcat (100% – 10% = 90%) was much higher than the uncertainty assessment made for this species by the field collectors.

Carnivore diet.—The 453 feces randomly selected for carnivore diet analysis and mtDNA identification of predator species revealed as primary prey 2 medium-size mammals: mountain beaver (*Aplodontia rufa*, 51% frequency of occurrence) and snowshoe hare (*Lepus americanus*, 48%). Other relatively frequent prey included voles (18%), cervids (17%), Olympic marmot (11%), and Pacific jumping mouse (*Zapus trinotatus*, 11%). Minor prey items observed in less than 10% of scats included sciurids (*Tamiasciurus douglasii*, *Glaucomys sabrinus*, and *Tamias* sp.), birds, insects, blueberries (*Vaccinium* sp.), and juniper berries (*Juniperus communis*). Sporadic prey (<1% scats) included other small mammal species (*Neotoma cinerea*, *Peromyscus* sp., *Thomomys mazama melanops*, and *Scapanus townsendii*). Additionally, some cases of intraguild predation were possible, because long-tailed weasel (*Mustela frenata*) and other unidentified small carnivore remains were found in several scats, as well as 3 scats containing bobcat claws (1 of the 3 scats was confirmed to be from a bobcat). Carnivore diet was relatively similar throughout the park. On each transect usually the same set of prey items was observed occurring in similar frequencies, with dominance of mountain beaver and hare (40–60%) and other prey categories rarely exceeding 20%. Seasonal variability in carnivore diet was not apparent, except for a lack of hibernating rodents (marmot and jumping mouse) and insects in May and presence of

blueberries (*Vaccinium* sp.) only in scats from August and September, as expected.

Only one-third of analyzed scats contained just 1 prey species. Most scats consisted of the remains of 2 or 3 different prey and sometimes more (up to 5). In a majority of samples the number of teeth, claws, and distinctive bone fragments indicated the presence of single individuals of a given species. In rare cases several voles, jumping mice, and insects of the order Orthoptera were observed in 1 sample.

Analysis of prey by individual carnivore species was based on the 381 samples that successfully amplified for diagnostic mtDNA species identification (Table 2); the small number of cougar scats ($n = 17$) limits quantitative comparison with the other 2 species. Diets of coyote and bobcat inferred from scat analysis ($n = 260$ for coyote and $n = 104$ for bobcat) show a high degree of similarity (Pianka's overlap index = 0.97), with differences in frequency of occurrence for all prey categories 10% or less. For both carnivore species the primary prey were mountain beaver and hare, each occurring in about 50% of analyzed scats. The main difference in the diet of these species was presence of blueberries and juniper berries exclusively in scats of coyote. Cougar diets lacked small rodents and had a higher frequency of cervids.

Predation on marmots.—Marmot remains were found in 11.6% (111 of 958) of all scats collected, with the proportion similar across years (13.6% in 2005 versus 10.0% in 2006). Marmot remains were found in scats from all transects studied except Klahhane (Fig. 2B). For 85% (77 of 91) of the samples with marmots that could be amplified for diagnostic mtDNA carnivore species determination, coyotes were confirmed as the predator. The remainder arose from bobcat (13%; 12 of 91) and cougar (2%, 2 of 91). Coyotes were the predominant marmot predator across all months (Fig. 3) and at all transects but 1 (Fig. 2B).

Although most scats with marmots came from coyotes, the overall occurrence of marmot in coyote scats (14%) was not significantly higher than in the scats of bobcat (9%, $\chi^2_{adj} = 1.07$, $d.f. = 1$, $P = 0.30$). Seasonal analysis of coyote diet (Fig. 4) indicated highest marmot consumption in late spring (June—20%) and in fall (September—31%), when marmot was consumed as much as the coyote's primary prey, mountain beaver, and hare.

Individual identification of coyotes with genetic markers.—Of scats identified to be from coyotes and analyzed for individual genotypes, 68% (80 of 117) successfully amplified at all 6 microsatellite loci, identifying a minimum of 13 different coyotes in the high country of Olympic National Park (Table 3). The unbiased estimate of the probability of identity was 1.328×10^{-6} . Most of the analyzed samples (82%, 96 of 117) came from the 2 focal areas chosen for comparative assessment of coyote densities in human visitation levels that were high (Obstruction–Badger, 44 scats containing marmot and 30 without) versus low (Gray Wolf, 11 scats with and 11 without marmot). The remaining 21 samples were scats containing marmots collected at other transects.

TABLE 2.—Frequency of occurrence of prey items in coyote (*Canis latrans*), bobcat (*Lynx rufus*), and cougar (*Puma concolor*) scats collected in Olympic National Park, Washington (2005–2006). Identity of all carnivore species was confirmed by mitochondrial DNA tests.

	Coyote (<i>n</i> = 260)		Bobcat (<i>n</i> = 104)		Cougar (<i>n</i> = 17)	
	Count	Frequency of occurrence	Count	Frequency of occurrence	Count	Frequency of occurrence
Mammals						
Rodentia (large)	165	63.5	60	57.7	11	64.7
<i>Aplodontia rufa</i>	129	49.6	51	49.0	10	58.8
<i>Marmota olympus</i>	36	13.8	9	8.7	1	5.9
Rodentia (small)	126	48.5	56	53.8	1	5.9
Arvicolinae	55	21.2	13	12.5	—	—
<i>Zapus trinotatus</i>	26	10.0	11	10.6	—	—
<i>Tamiasciurus</i> , <i>Tamias</i> , <i>Glaucomys</i>	19	7.3	18	17.3	1	5.9
Unidentified small rodents	26	10.0	14	13.5	—	—
Lagomorpha						
<i>Lepus americanus</i>	127	48.8	59	56.7	1	5.9
Artiodactyla						
Unidentified cervids	49	18.8	12	11.5	6	35.3
Birds						
Unidentified birds	20	7.7	6	5.8	—	—
Insects						
Unidentified insects	12	4.6	1	1.0	2	11.8
Fruits	29	11.2	—	—	—	—
<i>Vaccinium</i> sp.	15	5.8	—	—	—	—
<i>Juniperus communis</i>	14	5.4	—	—	—	—
Grass	29	11.2	8	7.7	8	47.1

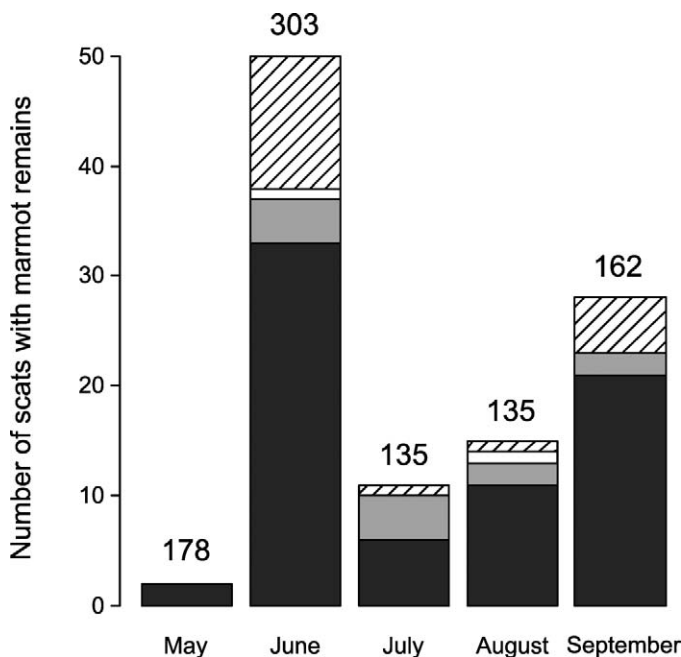


FIG. 3.—Number of scats with Olympic marmot (*Marmota olympus*) remains by month of scat deposit (*n* = 106; Olympic National Park, Washington; summers 2005 and 2006). Different shadings represent predator species identified with mitochondrial DNA: black—coyote (*Canis latrans*), gray—bobcat (*Lynx rufus*), white—cougar (*Puma concolor*), dashed—predator species not identified. Numbers above the bars indicate sample size (number of all scats collected for each month).

Because of the geographic and topographic distance between focal areas different coyote individuals were found to inhabit each region (Fig. 5). Four coyote individuals were detected in the high-use area (O1–O4 in Table 3), whereas in the low-use area 3 coyotes were found (GW1–GW3), translating to 2.3 and 2.5 coyote individuals per 10 km of transect in each area. Individual animals left variable numbers of detected scats (Table 3).

Marmot remains were found in scats of all but 1 of the 13 identified coyote individuals, with the exception being 1 individual in the high-use area (O4) represented by 1 scat. Except for this individual, all coyotes identified within the focal areas were detected in both years of study. Numerous individuals were identified from scats collected in consecutive months (2 individuals in all months from May to September and 2 individuals from June to September), implying that they were present in the high country throughout the whole study season.

DISCUSSION

Based on 958 carnivore scats collected over 2 years, we found invasive coyotes to be by far the predominant terrestrial predator on endemic and declining Olympic marmots. To ensure correct inferences on marmot predation, we coupled traditional diet analyses of scats with carnivore species identification and coyote individual identification using genetic markers. Overall, 86% (426 of 498) of scats could be amplified at mtDNA markers for carnivore species identification; of the samples confirmed to have come from coyotes, 68% (80 of 117) could be amplified at 6 microsatellite markers for

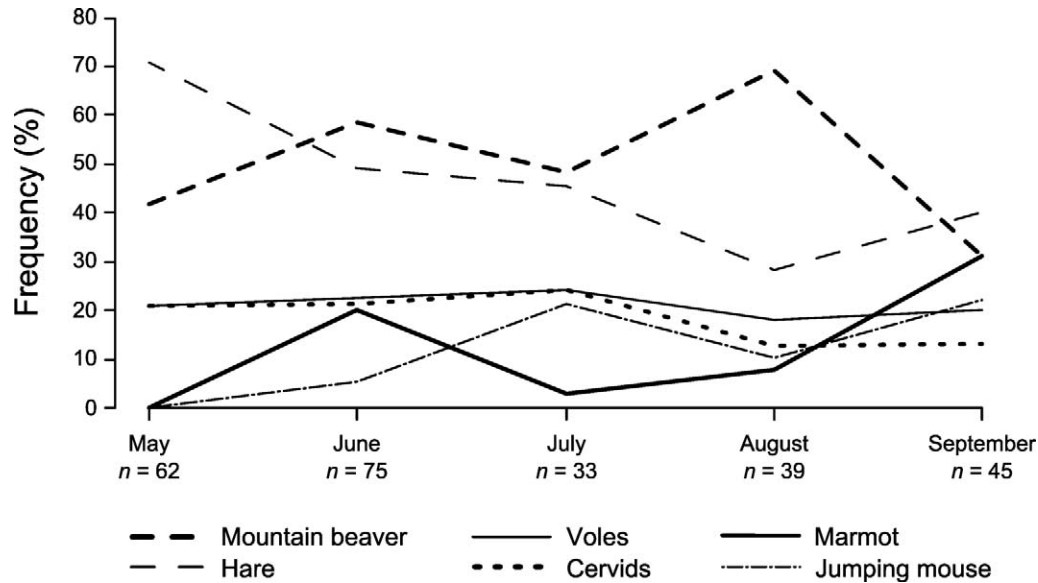


FIG. 4.—Temporal pattern of 6 major (overall frequency of occurrence greater than 10%) prey categories in coyote (*Canis latrans*) diet, from spring to fall 2005–2006 in Olympic National Park, Washington.

individual identification. Field assessment of putative age of the scat did not predict amplification success, because about the same fraction of samples could be amplified for species identification regardless of whether they were categorized as fresh, medium, or old. The molecular confirmation of species identification was an important step because overall accuracy in distinguishing carnivore species in the field was 63% (253 of 404). Field identification was the most precise for coyote scats (81% correct field assignments; 230 of 285). Collectively, these results underscore the importance of confirming carnivore species identity in diet studies based on scats (Kelly et al. 2012).

Of the sampled carnivore scats that contained marmot remains, 85% (77 of 91) originated from coyotes. Coyote predation on marmots predominated across all months sampled (Fig. 3) and in most regions of the park (Fig. 2B), including where marmot colonies were very small and sparse.

The relative predation rate on marmots by coyotes compared to native carnivores depends on each predator’s relative numbers and functional response (per capita kill rate—Mills 2013). Although we cannot quantify these, examination of our data strongly indicates that both are highest for coyotes, implying that predation rate on marmots also is highest for coyotes. We found that 71% of all scats verified to species

TABLE 3.—Individual coyotes (*Canis latrans*) identified in the Olympic National Park (Washington) high country using microsatellite analysis in summers of 2005 and 2006. Individual symbols of coyotes in the high- or low-use focal areas are used on Fig. 5. All individuals were associated with marmot prey except for individual 4, with only 1 scat collected.

Individual no.	Individual coyote identification	No. scats associated with that individual		Transect	
		With marmot	Without marmot		
1	O1	○	25	13	Obstruction, Badger, Grand
2	O2	◇	5	2	Obstruction, Badger, Grand
3	O3	△	4	5	Obstruction, Badger
4	O4	◊	0	1	Obstruction
5	GW1	☆	6	1	Gray Wolf
6	GW2	□	3	3	Gray Wolf
7	GW3	●	4	0	Gray Wolf, Grand, Cameron
8	H1		1	0	Hurricane
9	H2		1	0	Hurricane
10	L1		2	0	Lena
11	7L1		2	0	Seven Lakes
12	7L2		1	0	Seven Lakes
13	A1		1	0	Anderson ^a
		Total	55	25	

^a Outside of study areas.

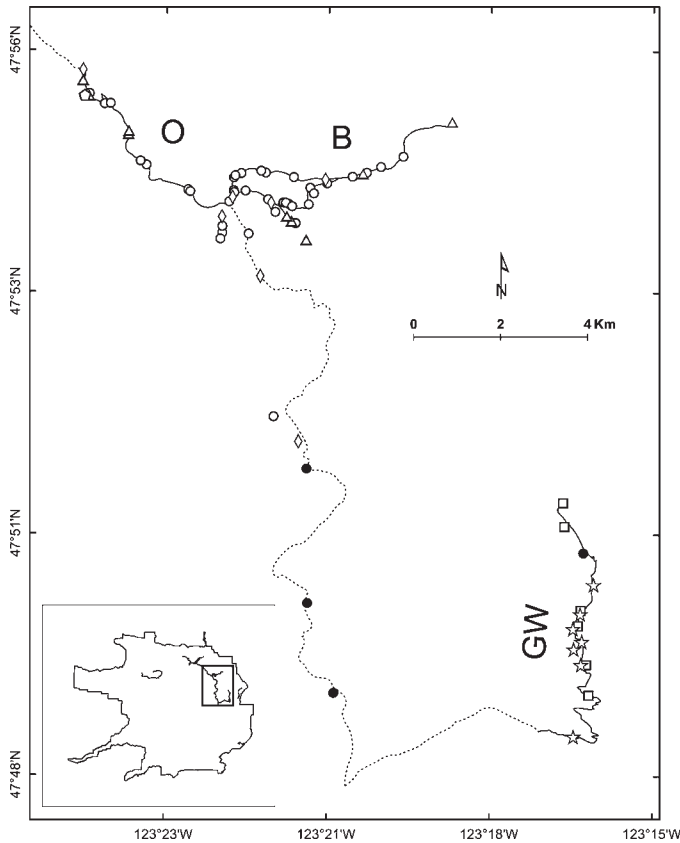


FIG. 5.—Locations of scats from 7 coyote (*Canis latrans*) individuals identified using microsatellites in 2 focal areas of Olympic National Park, Washington: high visitor use (along Obstruction [O] and Badger [B] transects) and low visitor use (along Gray Wolf transect [GW]). Solid lines—transects within focal areas, dashed line—other transects. Different symbols represent different coyote individuals (Table 3) detected across 2005 and 2006.

arose from coyote, implying that in the sampled areas coyotes were the numerically dominant predator. Furthermore, we definitively identified at least 13 individual coyotes, and found that 12 of those preyed on marmots. By contrast, the relative numbers of native predators appear considerably smaller than for coyotes. Only 25% of collected scats arose from bobcats and 4% from cougars, consistent with expectations from the literature that densities of bobcats and cougars—especially in subalpine zones—would be less than coyotes (Carbone and Gittleman 2002).

Likewise, functional responses on marmots (marmot kill rate per individual predator) for bobcats and cougars are likely less than coyotes, for 3 reasons. First, Olympic marmots evolved with bobcats and cougars and so would be expected to have better developed predator-defense strategies compared to their response to invasive coyotes; wolves (*Canis lupus*) previously in the park were likely limited to below 500 m (Ratti et al. 2004) and so were unlikely to have substantially encountered marmots. Second, cougars and bobcats are usually nocturnal or crepuscular and so are less likely to forage on marmots, which are exclusively diurnal. Also marmots live in open habitat with

an activity season coinciding with presence of human visitors, and visitor use may cause these felids to become even more nocturnal (George and Crooks 2006). Third and following from the first 2, we found that only 13% of the scats containing marmots originated from bobcats and 2% from cougars, much less than the 85% for coyotes. Collectively, it seems clear that invasive coyotes are imposing higher predation rates on Olympic marmots than the native carnivores.

Of course, our inferences regarding predation rates of terrestrial carnivores on marmots assume that the sampled trails represent reasonable survey units for coyotes, bobcats, and cougars. Wild canids and felids are known to prefer trails and roads for travel, albeit at different rates across space and time (George and Crooks 2006; Harmsen et al. 2010; Macdonald 1980). Thus, we do not attempt to quantify predation rates for each species, recognizing the possibility that different species may differentially use trails. Nonetheless, nothing in the literature indicates aversion of trails by the other species in a park setting, so we find it highly unlikely that the preponderance of coyote scats, and percent of marmot remains found in coyote scats, could arise from vastly disparate trail use by the predator species. The fact that coyote scats also predominate among scats collected off trails suggests that observed pattern is rather due to the differences in carnivore densities.

Previous intensive demographic studies on Olympic marmots (Griffin 2007) recorded high coyote predation in several sites with easy road access and high, year-round visitor use. Our findings indicate that these areas were representative of dynamics in other areas of the Olympic marmot's range, including the backcountry. Our 2 focal areas chosen for highly contrasting relative access and visitor volume showed similar use by individual coyotes (~2 coyotes per 10 km of trail). Also, our park-wide scat analysis shows that the proportion of coyote scats with marmot observed at intensively studied sites (e.g., Obstruction transect: 23%) is similar to the levels detected in several other regions throughout the park, often deep into backcountry wilderness (e.g., >20% at Badger, Gray Wolf, Lena, and Seven Lakes transects). Thus, coyote predation is widespread across the range of Olympic marmots and coyote predation pressure is likely similarly high throughout the park.

Our study results were consistent with previous observed patterns of marmot mortality (Griffin et al. 2008). For example, marmots in the Royal area had been documented to have relatively high estimated annual survival (0.8 for adult females—Griffin et al. 2008), and at that transect we found a low number of scats and just 1 scat containing marmot. Conversely, our highest number of carnivore (mainly coyote) scats often containing marmots were collected on the Obstruction transect (Fig. 2A), previously documented as having very low marmot survival rates (0.62) as well as observed population declines (from 44 to 27 marmots—Griffin 2007). Similarly, our high number of scats collected along the Klahhane transect may well be linked to the high marmot colony extinctions (at least 5 colonies) that occurred 2–15 years

before this study (Griffin et al. 2008; Houston and Schreiner 1994b). The 3rd transect with very high number of scats observed was Steeple, where the marmot colony disappeared sometime in the 1989–2002 period (Griffin et al. 2008).

Different proportions of marmots in the diet of coyotes inhabiting different regions can be caused by differences in marmot density or behavioral differences between individual coyotes. Several authors reported coyote individuals differing in their diet preferences (Bekoff and Wells 1980; Fedriani and Kohn 2001; Prugh et al. 2008). However, we found that all or nearly all individual coyotes (at least 12 of 13 recognized individuals) did consume marmots.

Our study indicates that coyote predation on marmots is present through the whole period of marmot aboveground activity, with peaks in June and September (Fig. 4). The seasonal changes were consistent with previously documented patterns of carnivore predation on radiotagged Olympic marmots (Griffin 2007). Low predation is expected in May, because most marmots emerge from hibernation no earlier than the 2nd half of May, and some postpone emergence until June.

Being relatively rare and difficult to catch, marmots are not the primary prey of Olympic coyotes, 5th in frequency after snowshoe hares, mountain beavers, voles, and cervids. Bobcats showed similar diet patterns to coyotes (although coyotes also included berries). However, because coyotes are generalists subsidized by abundant multiple prey year-round, we can expect their numerical response to be decoupled from marmot numbers (including during hibernation), as reported for yellow-bellied marmots (van Vuren 1991). Fixed predator density independent of prey densities can create a situation where predation rate increases with declining prey density, thereby accelerating prey decline (destabilizing positive density dependence—Gascoigne and Lipcius 2004; Mills 2013). This could lead to a scenario where marmot colonies are driven to extinction with no consequence for the coyote population, as observed in other contexts with invasive predators supported by multiple alternate prey species (e.g., Mack et al. 2000; Prugh 2005).

One unknown but potentially important factor is the absence of gray wolves, extirpated from the Olympic Peninsula about 1930 (Scheffer 1995). In other systems, wolves effectively outcompete coyotes with potential to reduce coyote numbers (Berger and Conner 2008; Smith et al. 2003). Wolf introduction has been considered for Olympic National Park, and although wolves would likely spend most of their time below 500 m (Ratti et al. 2004), they may positively affect marmots by limiting colonization of additional coyotes from outside the peninsula.

Our analyses support and extend demographic studies (Griffin 2007) showing high predation pressure from coyotes on Olympic marmots. The fact that coyote predation appears to be widespread throughout the park highlands, and most coyote individuals kill marmots, implies that the problem would not be reduced by removing just a few “problem” coyotes.

If our results continue to hold, comprehensive control of the invasive coyote population in the high country may be the only

solution to maintain the endemic marmots in Olympic National Park.

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APPENDIX I

Number of scats collected at different transects in Olympic National Park, Washington (from May to September 2005–2006), and number of scats identified to coyote (*Canis latrans*), bobcat (*Lynx rufus*), and cougar (*Puma concolor*) with mitochondrial DNA (mtDNA) tests.

Transect	No. scats collected				Identified with mtDNA						Total
	On transect	Per kilometer of transect	Off transect ^a	Total	On transect			Off transect			
					Coyote	Bobcat	Cougar	Coyote	Bobcat	Cougar	
1 Hurricane	71	5.2	15	86	20	5	1	7	3	0	36
2 Klahhane	133	11.1	2	135	43	10	0	1	0	0	54
3 Steeple	65	10.3	1	66	18	1	3	0	0	0	22
4 Obstruction	84	13.2	21	105	25	4	1	8	2	1	41
5 Badger	95	8.5	2	97	61	2	2	2	0	0	67
6 Grand	97	7.8	18	115	25	18	0	4	0	0	47
7 Cameron	99	9.8	2	101	18	32	1	1	0	1	53
8 Dosewallips	24	4.4	1	25	5	5	3	0	0	0	13
9 Gray Wolf	90	7.4	4	94	29	16	4	1	0	0	50
10 Royal	27	5.1	7	34	9	2	1	2	0	0	14
11 Seven Lakes	53	2.4	3	56	9	6	0	2	0	0	17
12 Lena	19	2.4	3	22	9	0	0	1	0	0	10
Opportunistic ^b			22	22				1	1	0	2
Total	857	N/A	101	958	271	101	16	30	6	2	426

^a Scats collected opportunistically in vicinity of a given transect (<2 km from transect).

^b Scats collected opportunistically at other areas of the park.

N/A = Not applicable.