



Exploitation of marine resources by wolves in southwestern Alaska

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Predation by large carnivores is a dominant factor shaping wildlife communities and an understanding of local foraging strategies of predators is central to the management of wildlife populations. Information on local foraging strategies is particularly important where carnivores might exploit alternate resources that could influence predator–prey interactions, carnivore population dynamics, and a variety of interactions at lower trophic levels. We used carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) values in serially sampled wolf (*Canis lupus*) vibrissae to quantify relative resource use and dietary variation among wolves ($n = 115$) from 4 areas in southwestern Alaska that differed in the availability of terrestrial and marine resources. Mean vibrissae isotope values varied by $\sim 8\text{‰}$ for $\delta^{13}\text{C}$ and $\sim 12\text{‰}$ for $\delta^{15}\text{N}$ and showed high levels of spatial, seasonal, and individual variation. While results showed that ungulates were the principal prey for wolves in all 4 areas, wolves also exploited a variety of alternate marine resources that represented an important component of wolf diets in some areas. Estimated dietary contributions from marine resources ranged from 28% to 56% among areas and use of these resources varied both spatially and seasonally. Dietary variation and use of marine resources increased from northeast to southwest along the Alaska Peninsula with increasing access to coastal areas and decreasing ungulate abundance. Seasonal shifts in resource use were also evident with dietary variation being highest during summer and fall when wolves consumed more alternate resources than during winter. Our findings suggest that use of marine resources and local variation in foraging strategies of wolves might, through a variety of pathways, have broad implications for the management of wolf–ungulate communities in southwestern Alaska.

Key words: *Canis lupus*, diet, marine resources, stable isotopes, vibrissae, wolves

Predation by large carnivores is a dominant factor shaping the structure and function of ecological communities (McLaren and Peterson 1994; Berger et al. 2001; Ripple and Beschta 2004; Ray et al. 2005). Accordingly, an understanding of carnivore foraging strategies and related top-down effects is central to the management of wildlife populations. For generalist carnivores, use of alternate resources may influence population dynamics and could, through trophic cascades, influence prey abundance, diversity, and a variety of interactions at lower trophic levels (Berger et al. 2001, 2008; Ripple et al. 2001; Estes et al. 2011). Contingent on the response of carnivore populations, alternate resources could influence carnivore–prey relationships in 2 basic ways. First, if increased resource availability fails to yield a numerical response among carnivores, apparent mutualism may lead to increased prey abundance as carnivores exploit alternate resources and reduce predation on primary prey (Abrams and Matsuda 1996). Conversely, where a

numerical response is realized, increased carnivore abundance could reduce prey abundance through apparent competition, especially where carnivores show preference for specific prey (Holt 1977; Abrams et al. 1998). Further, if alternate resources occur seasonally or in pulses, exploitation of such resources may satiate carnivores and reduce predation on primary prey for short periods. The long-term effect, however, could be increased survival or recruitment among carnivores and an overall increase in annual predation rates that reduce survival in primary prey populations.

Wolves are important to community structure and function and may regulate or limit their prey populations (Van Ballenberghe and Ballard 1994; Ballard et al. 1997; Bergerud and Elliot 1998; Ripple and Beschta 2004). Considerable evidence suggests that wolf population dynamics are closely linked to the abundance and availability of ungulate prey (Fuller et al. 2003; Paquet and Carbyn 2003; Peterson and Ciucci 2003).

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In North America, wolves are generally considered obligate predators of ungulates (primary prey) with non-ungulate (alternate) prey having little influence on population dynamics (Fuller et al. 2003; Peterson and Ciucci 2003). Nonetheless, wolves are opportunistic generalist carnivores and exhibit considerable dietary plasticity both among and within populations (Peterson and Ciucci 2003; Newsome et al. 2016). Exploitation of specific prey is influenced by local availability, encounter and success rates, risk of injury, learned behaviors, and other factors that can vary considerably among areas and through time. Prey use may also vary seasonally with changes in prey availability (e.g., seasonal prey migrations) or vulnerability (e.g., decreased ungulate body condition during winter—Peterson 1977; Jędrzejewski et al. 2002; Sand et al. 2008; Metz et al. 2012).

Ungulate abundance has declined throughout much of southwestern Alaska during the past 30 years. The migratory Northern Alaska Peninsula (NAP) and Mulchatna caribou (*Rangifer tarandus*) herds have declined by roughly 88% and 85% since their respective peaks in the 1980s and 1990s (Peterson 2013a). Decreased habitat quality and associated poor productivity and survival are considered to be the primary causal factors for these population declines (Peterson 2013a; Woolington 2013). The Southern Alaska Peninsula (SAP) caribou herd has declined by ~80% since its last peak in 2002 (Peterson 2013b). The Unimak Island caribou herd has also declined by ~70% since the population last peaked in 2005 (Peterson 2013c). Little information is available regarding causal factors for these declines but predation has been suggested as a factor retarding herd recovery (Peterson 2013b, 2013c). Because caribou abundance was low during our study, the study area was closed to caribou hunting and human harvest was not considered to be a limiting factor for caribou. Moose (*Alces alces*) also occurred at moderate-to-low densities on the Alaska Peninsula during our study and moose abundance had declined by ~60% since the 1960–1970s (Riley 2012). Decreased habitat quality and associated poor productivity and survival are considered to be the primary cause of moose population declines but predation, primarily by brown bears, has also been suggested as a primary factor limiting moose abundance in southwestern Alaska (Riley 2012). Because predation by wolves is a dominant factor influencing ungulate population dynamics, current management strategies in our study area are designed to reduce wolf abundance through liberal harvest limits, extended hunting and trapping seasons, and wolf control programs. The intent of these strategies is to reduce wolf abundance and predation on ungulates, particularly neonates, and increase ungulate survival and recruitment. However, little is known about resource use by wolves or how a variety of locally available alternate resources might influence wolf population dynamics or wolf–ungulate interactions in this region.

During periods of low ungulate availability, alternate prey may become locally or seasonally important (Spaulding et al. 1998; Mech 2007; Adams et al. 2010). Previous studies show that wolves will exploit a wide variety of alternate resources including lagomorphs, birds, beavers (*Castor canadensis*),

small rodents, and carrion (Forbes and Theberge 1992; Meiklejohn 1994; Peterson and Ciucci 2003; Watts et al. 2010). Pacific salmon (*Oncorhynchus* spp.) may also be an important seasonal resource for some wolf populations (Szepanski et al. 1999; Darimont and Reimchen 2002; Adams et al. 2010). In southwestern Alaska, salmon are ubiquitous and represent a high-quality, abundant, and predictable seasonal resource. Wolves in this region actively hunt salmon, often carrying carcasses to pups at dens and rendezvous sites that are commonly located near spawning streams (D. E. Watts, pers. obs.). The abundance of salmon in spawning streams has increased markedly throughout southwestern Alaska since the 1970s (Eggers and Irvine 2007; Hartill and Murphy 2011). Interestingly, such increases in the availability of salmon and other marine resources have occurred in concert with regional ungulate population declines.

Quantification of diets of large carnivores is difficult and expensive using traditional methods (e.g., direct observation, scat- and stomach-content analyses), particularly for cryptic species that occur at low densities or in remote regions. Carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope values of carnivore tissues reflect those of their prey and, through the application of trophic discrimination factors (TDFs), can be used to quantify carnivore diet composition using mixing models (Parnell et al. 2010; Philips 2012). In addition, isotope analysis of different tissues provides time-integrated information on diet composition over different temporal scales (Martínez del Río et al. 2009). Vibrissae are metabolically inert tissues that can be subsampled to provide a chronological record of an individual's dietary history during the period of growth (Lewis et al. 2006; Cherel et al. 2009; Newsome et al. 2009, 2015). For mammalian carnivores, vibrissae-derived isotopic records represent several months to years of dietary information (Cherel et al. 2009; Robertson et al. 2013; Tyrrell et al. 2013), which helps compensate for ephemeral diet shifts and biases related to prey size and digestibility, problems inherent in traditional diet proxies such as scat- and stomach-content analysis.

Our objective was to quantify wolf diets in southwestern Alaska and document any spatial or seasonal variation in resource use. Based on observations, we predicted that wolf isotope values would show use of several marine resources and that exploitation of these resources would vary spatially and seasonally with availability. We also predicted that coastal wolves would show higher dietary variation in response to increased resource diversity and availability along the coast. To investigate these hypotheses, we examined $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in serially sampled wolf vibrissae and tissues from local resources. This study is an important first step toward the characterization of wolf diets in southwestern Alaska and illuminates the diverse and complex role that wolves might play in community structure and function in the region.

MATERIALS AND METHODS

Study area.—The Alaska Peninsula is located in southwestern Alaska (Fig. 1). The study area (~4,000 km²) is situated

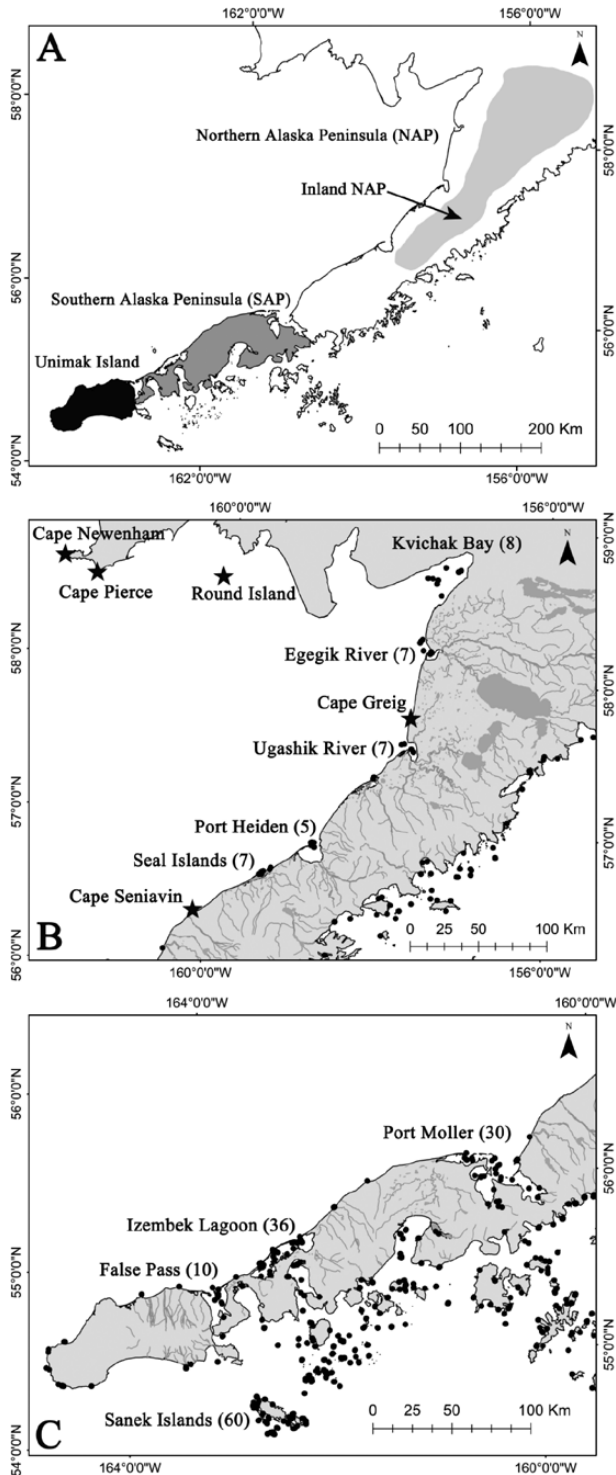


Fig. 1.—Maps depicting the study area on the Alaska Peninsula including A) 4 areas that differ in the availability of terrestrial and marine resources, and locations of marine mammal haulout concentrations along the B) Northern Alaska Peninsula and C) Southern Alaska Peninsula and surrounding islands. The number of haulouts at each concentration location is noted in parentheses. Stars in panel B indicate major walrus haulouts at Cape Newenham, Cape Pierce, Round Island, Cape Greig, and Cape Seniavin.

along the Alaska Peninsula and is directly adjacent to Bristol Bay, one of the most productive marine ecosystems in the world. Potential terrestrial prey include moose, caribou, hares

(*Lepus* sp.), beavers, porcupines (*Erethizon dorsatum*), arctic ground squirrels (*Spermophilus parryi*), small rodents, nesting waterfowl, eggs, and several species of mesocarnivores. Five species of Pacific salmon (*Oncorhynchus kisutch*, *O. nerka*, *O. keta*, *O. gorbuscha*, *O. tshawytscha*) spawn in the region with sockeye (*O. nerka*) and coho (*O. kisutch*) being the most abundant species. The distribution and abundance of salmon varies considerably among drainages both seasonally and among years (Schindler et al. 2013). Marine mammal carcasses including Pacific walrus (*Odobenus rosmarus divergens*), belugas (*Delphina pterus leucas*), harbor seals (*Phoca vitulina*), sea otters (*Enhydra lutris*), and gray whales (*Eschrichtius robustus*) regularly wash ashore and are exploited by wolves when available (Watts et al. 2010). Several large walrus haulouts and numerous harbor seal haulouts occur within the study area (Fig. 1). Seal abundance has largely remained stable or increased during the past 30 years with the number and magnitude of haulouts generally increasing from northeast to southwest along the Alaska Peninsula (Fig. 1; Small 2001; D. Withrow, NOAA Fisheries, pers. comm.).

Sample collection.—During 2006–2013, we chemically immobilized wolves using aerial darting methods, attached radiocollars, and clipped vibrissae at the base. Vibrissae were also collected opportunistically from wolves harvested by hunters, trappers, and wolf control programs. Muscle tissue samples of sockeye and coho were collected from angler-harvested salmon. Tissues (hair and muscle) samples of ungulate and other non-ungulate prey were collected during capture operations, from hunter and trapper harvests, and from wolf kill-sites. We used bone collagen isotope data for Bering Sea harbor seals reported in Hiron et al. (2001) and tooth dentin collagen isotope values for Bering Sea walrus derived from teeth archived at the University of Alaska Museum (UAM 111915, 111918, 111926, 111927, 111932, 111934, 111939, 111942, 111946). Wolf capture and sampling procedures followed ASM guidelines (Sikes et al. 2011) and were approved by the Alaska Department of Fish and Game Animal Care and Use Committee (Protocol Number 06-19).

Stable isotope analysis.—Wolf vibrissae and prey hair samples were rinsed in 2:1 chloroform:methanol solution to remove surface contaminants and air-dried. Vibrissae were serially subsampled into ~0.2–0.3 mg segments, the lowest weight for which carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope values could be reliably measured with our mass spectrometer system, in order to maximize the number of segments obtained for each individual wolf. Prey hair samples were cut into (~2–3 mm) pieces with surgical scissors and homogenized. Muscle samples were lipid-extracted via 3 sequential 24-h soaks in 2:1 chloroform:methanol, repeatedly rinsed in distilled water, and freeze-dried (Ben-David et al. 1997b). Tooth dentin was demineralized in 0.5N hydrochloric acid at 5°C for 24h, rinsed in distilled water, and freeze-dried. Wolf vibrissae segments and ~0.5–0.6 mg of each prey tissue sample were sealed in tin capsules for isotope analysis. Sample $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were determined using a Carlo Erba NC 2500 (Milan, Italy) or Costech 4010 (Valencia, California) elemental analyzer interfaced with a Thermo-Finnigan Delta Plus

XL mass spectrometer at the University of Wyoming Stable Isotope Facility (Laramie, Wyoming). Isotope values are expressed as delta (δ) values in parts per thousand (‰) relative to internationally accepted standards and defined as $\delta^{13}\text{C}$ or $\delta^{15}\text{N} = 1,000 \times [(R_{\text{sample}} - R_{\text{standard}})/R_{\text{standard}}]$, where R represents the corresponding ratio of $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$. International standards were Vienna Pee Dee Belemnite (V-PDB) for carbon and atmospheric N_2 for nitrogen. Within-run SD of organic internal reference materials was $\leq 0.2\text{‰}$ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values.

We grouped wolves into 4 categories based on geographic area and prey availability: 1) inland NAP, 2) coastal NAP, 3) SAP, and 4) Unimak Island (Fig. 1). The NAP included lands from the Naknek River south to Port Moller and the range of the NAP caribou herd. The NAP had relatively high moose and caribou abundance, while beavers and hares were also relatively common in this area. Because not all NAP wolves had access to marine mammal carcasses along the coast, we divided NAP wolves into inland and coastal groups based on known spatial use and pack territories derived from multiple years of wolf location data (D. E. Watts, pers. obs.). The SAP included lands from Port Moller to False Pass, the range of the SAP caribou herd, and areas where Alaska hares are present at low abundance but beavers and snowshoe hares are absent. Moose abundance in the SAP was limited by a general lack of quality habitat in this area (Riley 2012). Unimak Island included the range of the Unimak caribou herd, an area that is devoid of moose, hares, and beavers.

Seasonal analysis.—Because wolves were more intensively sampled within the NAP, it was possible to examine seasonal diet variation in this area. Inland and coastal NAP wolves were grouped by season of sample collection: 1) vibrissae collected during late spring were assumed to represent diet during winter and early spring (winter diet), and 2) vibrissae collected during late fall were assumed to represent diet during summer and fall (summer diet); see “Discussion” for a detailed description of growth rates of mammalian carnivore vibrissae. We did not conduct seasonal analyses for SAP or Unimak wolves because sample sizes were too small for different seasons.

Statistics.—A fundamental assumption of stable isotope analysis is that the isotopic composition of potential prey types is distinct (Bearhop et al. 2004). Marine resources generally have higher $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope values compared

to terrestrial prey (Angerbjörn et al. 1994; Ben-David et al. 1997b). Terrestrial prey may also have distinct isotope values that permit quantification of their relative contributions to carnivore diets (Adams et al. 2010; Milakovic and Parker 2011). We grouped potential prey species into 7 prey types based on similar isotopic compositions: hares, beavers, caribou, moose, salmon, seals, and walruses (Table 1; Fig. 2). We used Kruskal–Wallis and pairwise Mann–Whitney U -tests between similar groups to determine if prey types were significantly different and, thus, appropriate for use as distinct prey in mixing models. We used a Spearman rank-order correlation to test mean individual $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for correlation and Mann–Whitney U -tests to compare mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ between seasons.

Isotope mixing models.—We used the Bayesian-based Stable Isotope Analysis in R (SIAR) to quantify resource use among wolves (Parnell et al. 2010; R Core Development Team 2012). Mixing model inputs included wolf and prey type isotope values, associated TDFs, and estimates of variance (SD) for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ TDFs (Table 1). We used $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ TDF values reported for captive wolves and considered both trophic and tissue-specific discrimination for comparing wolf keratin (vibrissae) to the keratin (hair), muscle, and collagen (bone and tooth dentin) of potential prey (Derbridge et al. 2015; Table 1). To correct wolf data for $\delta^{13}\text{C}$ trophic discrimination, we used 2.0‰ for hair, 2.0‰ for muscle, and 1.0‰ for collagen. We used the same TDF value for hair and muscle (2.0‰) because these tissues had similar $\delta^{13}\text{C}$ values (Table 1). Previous studies have also shown that ungulate hair and muscle tissues have similar $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (Tieszen and Boutton 1989; Derbridge et al. 2015). To correct for $\delta^{15}\text{N}$ trophic discrimination, we used 3.0‰ for all tissues because little $\delta^{15}\text{N}$ discrimination occurs among the different tissues we analyzed (Roth and Hobson 2000; Derbridge et al. 2015). To account for variation in TDFs, we used a SD of 0.5‰ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in mixing models.

An important assumption of mixing models is that all resources utilized by consumers are included in models. Accordingly, mixing models must reflect the availability of different prey types, which may vary among different areas. We constructed area-specific mixing models for the 4 areas described above to reflect locally available

Table 1.—Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and associated variation (SD) of primary prey types available to wolves in southwestern Alaska during 2006–2013.

Prey type	Species	Tissue	n	Mean $\delta^{13}\text{C}$ (SD)	Mean $\delta^{15}\text{N}$ (SD)
Hares ^a	<i>Lepus americanus</i> , <i>L. othus</i>	Hair	9	−26.2 (0.5)	2.7 (1.4)
Beavers	<i>Castor canadensis</i>	Hair	9	−24.9 (0.4)	4.9 (1.4)
Caribou	<i>Rangifer tarandus</i>	Hair	60	−23.6 (0.7)	2.2 (1.6)
Moose	<i>Alces alces</i>	Hair	24	−24.7 (0.4)	3.1 (0.9)
Moose	<i>Alces alces</i>	Muscle	11	−24.4 (0.2)	3.1 (0.0)
Salmon ^a	<i>Oncorhynchus nerka</i> , <i>O. kisutch</i>	Muscle	25	−19.6 (0.5)	12.4 (0.8)
Seals ^b	<i>Phoca vitulina</i>	Collagen	15	−14.3 (0.7)	17.6 (2.1)
Walruses	<i>Odobenus rosmarus</i>	Collagen	10	−13.4 (0.3)	15.7 (0.5)

^aMultiple species that exhibited similar isotope values were included.

^bIsotope values for harbor seals from the Bering Sea obtained from Hirons et al. (2001).

resources. Although wolves also had access to other prey (e.g., waterfowl, sciurids, small rodents, porcupines, bird eggs), we assumed that such prey made relatively negligible dietary contributions and did not include them in models in order to improve model accuracy for principal prey (see “Discussion”). To summarize mixing model outputs for each area, we generated mean individual proportional contributions and averaged these mean diet proportions for all wolves in a given area (Table 2).

RESULTS

Prey types showed a wide range in mean isotope values, from -26.3‰ to -13.7‰ for $\delta^{13}\text{C}$ and 2.0‰ to 17.4‰ for $\delta^{15}\text{N}$ (Table 1). Variation within prey types ($SDs = 0.5\text{--}2.0\text{‰}$) was small compared to variation between prey types; Kruskal–Wallis tests of $\delta^{15}\text{N}$ ($P \leq 0.00$) and $\delta^{13}\text{C}$ ($P \leq 0.00$) and pairwise Mann–Whitney U -tests between similar groups indicated that prey types were significantly different from each other

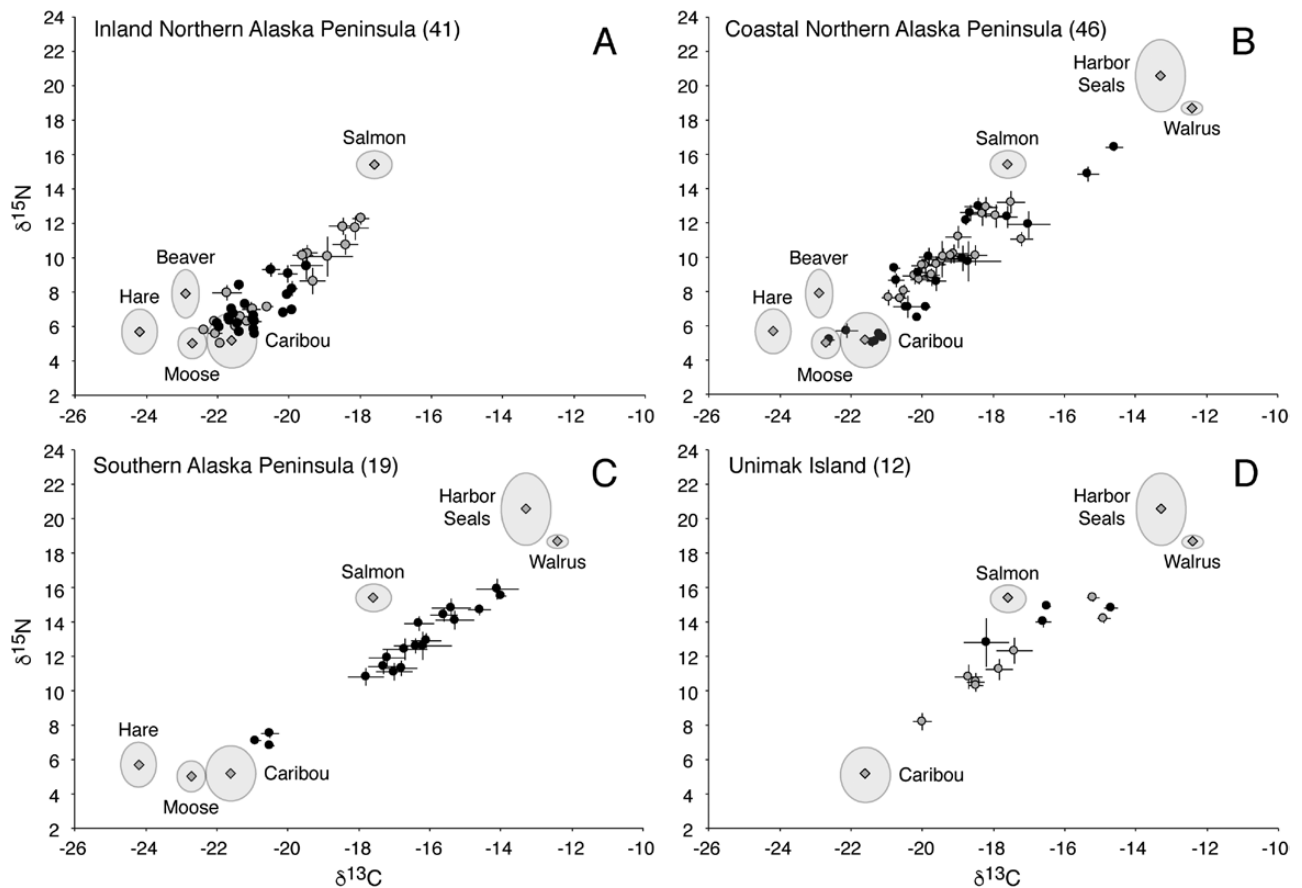


Fig. 2.—Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values ($\pm SD$) from serially sampled vibrissae for individual wolves from the Alaska Peninsula, during 2006–2013. Circles are mean values for individual wolves grouped by season where black circles represent winter diet and gray circles represent diet during summer and fall. Shaded diamonds are mean $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ values for potential wolf prey collected from the Alaska Peninsula; ellipses represent SD . Refer to Table 1 for scientific names, sample sizes, and mean isotope values ($\pm SD$) of prey species. Prey $\delta^{13}\text{C}$ isotope values have been corrected for trophic discrimination by adding 2.0‰ for hair keratin and muscle and 1.0‰ for bone and dentin collagen. Prey $\delta^{15}\text{N}$ isotope values have been corrected for trophic discrimination by adding 3.0‰ to all tissue types.

Table 2.—SIAR results of area-specific and seasonal models for estimated mean proportional contributions to wolf diets of prey types and associated variation (SD) from the Alaska Peninsula, Alaska, during 2006–2013. NA denotes that the prey type was not available in the area. Species names are provided in Table 1. NAP = Northern Alaska Peninsula; SAP = Southern Alaska Peninsula; SIAR = Stable Isotope Analysis in R.

Area (n)	Hares	Beavers	Caribou	Moose	Salmon	Seals	Walrus
Inland NAP (37)	0.10 (0.05)	0.11 (0.04)	0.32 (0.11)	0.19 (0.06)	0.28 (0.20)	NA	NA
Coastal NAP (47)	0.13 (0.05)	0.12 (0.03)	0.23 (0.10)	0.17 (0.05)	0.10 (0.04)	0.11 (0.07)	0.14 (0.08)
SAP (19)	0.09 (0.05)	NA	0.21 (0.09)	0.14 (0.07)	0.09 (0.02)	0.20 (0.08)	0.27 (0.11)
Unimak Island (12)	NA	NA	0.45 (0.17)	NA	0.22 (0.08)	0.16 (0.08)	0.18 (0.10)
Inland NAP–winter (18)	0.10 (0.04)	0.11 (0.04)	0.38 (0.08)	0.21 (0.04)	0.20 (0.10)	NA	NA
Inland NAP–summer (19)	0.10 (0.06)	0.11 (0.04)	0.26 (0.07)	0.17 (0.07)	0.36 (0.24)	NA	NA
Coastal NAP–winter (27)	0.14 (0.06)	0.12 (0.04)	0.24 (0.12)	0.18 (0.06)	0.09 (0.05)	0.11 (0.08)	0.12 (0.10)
Coastal NAP–summer (20)	0.13 (0.03)	0.12 (0.03)	0.20 (0.06)	0.17 (0.04)	0.11 (0.03)	0.12 (0.06)	0.15 (0.06)

and appropriate for our analysis. We collected vibrissae from 115 wolves during 2006–2013. The number of segments analyzed per wolf varied with vibrissae length ($\bar{x}(\text{length}) = 6.2$ cm, $SD = 1.2$ cm; $\bar{x}(\text{number of segments per individual}) = 14$, $SD = 5$). Mean wolf $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were positively correlated (Spearman rank-order correlation, $r_s = 0.94$, $P < 0.000$). Mean vibrissa values varied widely, ranging from 5.0‰ to 16.4‰ for $\delta^{15}\text{N}$ and -22.8 ‰ to -14.6 ‰ for $\delta^{13}\text{C}$ in the NAP, 6.8‰ to 15.9‰ for $\delta^{15}\text{N}$ and -20.9 ‰ to -14.0 ‰ for $\delta^{13}\text{C}$ in the SAP, and 8.2‰ to 15.4‰ for $\delta^{15}\text{N}$ and -14.7 ‰ to -20.0 ‰ for $\delta^{13}\text{C}$ on Unimak Island (Fig. 2). Wolves showed considerable between-individual isotopic variation and occupied most of the available isotopic diet space (Fig. 2). In the NAP (inland and coastal), mean ($\pm SD$) population $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were -20.0 ‰ (± 1.7) and 8.7‰ (± 2.7), respectively. In the SAP, mean ($\pm SD$) population $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were -16.8 ‰ (± 2.0) and 12.2‰ (± 2.7), respectively. Unimak wolves had similar mean population $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of -17.2 ‰ (± 1.7) and 12.5‰ (± 2.3), respectively.

Prey contributions.—Mixing models showed that proportional contributions from prey varied among areas (Table 2). Ungulates generally made the largest contributions to wolf diets in all 4 areas. In the inland NAP, where ungulate abundance was relatively high, combined mean ($\pm SD$) proportional contributions from ungulates (caribou and moose) were $51 \pm 12\%$. Ungulates contributed $40 \pm 11\%$ in the coastal NAP where moose occurred at lower densities than farther inland. Similarly, ungulates contributed $35 \pm 11\%$ to SAP wolf diets where caribou are the primary ungulate available and moose occur at relatively low abundance. On Unimak Island, where alternate terrestrial prey was limited, the only ungulate available (caribou) contributed $45 \pm 17\%$ to wolf diets.

Although ungulates were the primary prey for wolves on the Alaska Peninsula, terrestrial and marine alternate prey were also exploited to varying degrees (Table 2). Mean ($\pm SD$)

proportional contributions from salmon ranged from $10 \pm 4\%$ in the coastal NAP to $28 \pm 20\%$ in the inland NAP where salmon availability is higher. Salmon were also an important resource on Unimak Island and contributed $22 \pm 8\%$ to wolf diets. Salmon contributions were low ($9 \pm 2\%$) among SAP wolves but use of salmon was probably underestimated for this area (see “Discussion”). Marine mammal carcasses also made important contributions (25–47%) to coastal wolf diets. Mean ($\pm SD$) contributions from combined marine resources (salmon and marine mammals) were $28 \pm 20\%$ in the inland NAP (salmon only), $35 \pm 11\%$ in the coastal NAP, $56 \pm 14\%$ in the SAP, and $55 \pm 15\%$ on Unimak Island and showed that exploitation of marine resources increased from northeast to southwest along the Alaska Peninsula (Fig. 1; Table 2).

Seasonal variation.—In the coastal NAP, ungulates contributed $42 \pm 14\%$ to wolf diets during winter and $37 \pm 7\%$ during summer. Ungulates also contributed more to wolf diets during winter ($59 \pm 9\%$) than during summer ($43 \pm 10\%$) in the inland NAP. Mean individual and vibrissae segment $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values generally showed higher use of marine resources during summer and fall (Fig. 3). Mean contributions from salmon ($\pm SD$) in the inland NAP increased from $20 \pm 11\%$ during winter to $36 \pm 23\%$ during summer. Contributions from salmon in the coastal NAP were relatively similar during winter ($9 \pm 5\%$) and summer ($11 \pm 3\%$). Marine mammals contributed $23 \pm 13\%$ during winter and $27 \pm 8\%$ during summer and may have collectively represented a reliable annual resource for coastal NAP wolves. Mean individual $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were significantly higher during summer than winter indicating greater use of marine resources during summer (Fig. 2; Mann–Whitney test, $P = 0.01$ for $\delta^{13}\text{C}$, $P < 0.00$ for $\delta^{15}\text{N}$). Mean individual $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for wolves in some coastal areas, however, showed relatively high use of marine resources during both seasons (e.g., Ilnik pack—Watts et al. 2010).

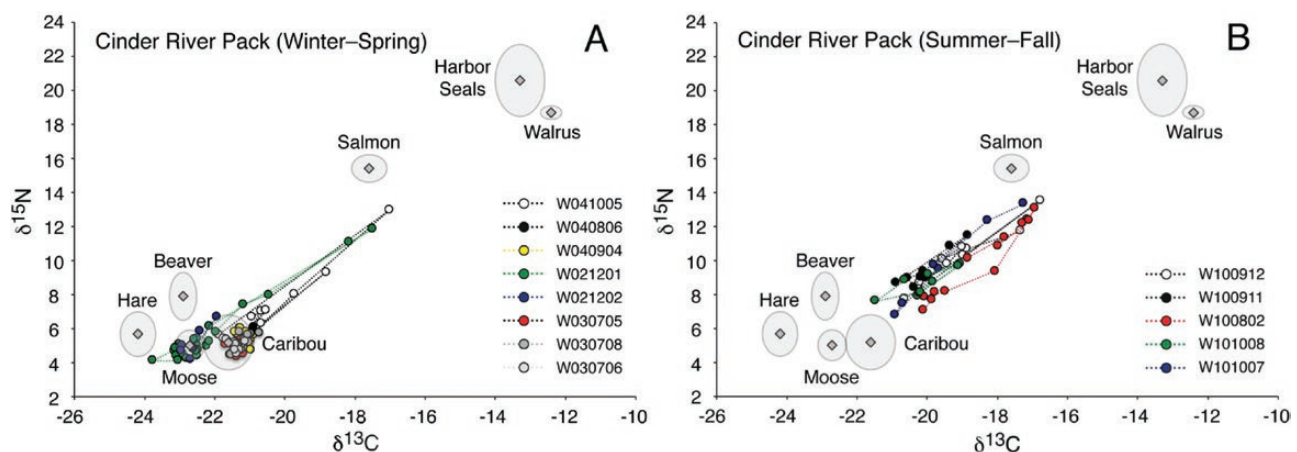


Fig. 3.—Comparison of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from serially sampled wolf vibrissae from the Cinder River pack in the coastal Northern Alaska Peninsula collected during February–April (A) representing diets during late fall through winter and vibrissae collected during October (B) representing diets during summer and fall. Lines connect sequential segments (dots) from each subsampled vibrissa. Note individuals W041005 and W021201 (A) still retain some older vibrissae segments with higher marine values from fall diets. In the case of W021201, this is probably due to a higher than average number of segments ($n = 23$) and sample collection earlier in winter (February) compared to other individuals collected later in the spring (March and April).

DISCUSSION

We used $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in vibrissae to examine diet composition and variation among wolves on the Alaska Peninsula. Mean vibrissae isotope values varied by $\sim 8\%$ for $\delta^{13}\text{C}$ and $\sim 12\%$ for $\delta^{15}\text{N}$ and showed considerable spatial and seasonal variation. Mean vibrissae values also showed substantial variation among individuals within specific areas suggesting that variation at the pack or individual levels may also be an important aspect of local wolf ecology that warrants further investigation. As expected, our data show that ungulates were the primary prey for wolves in our study area and contributed 35–51% to wolf diets. Caribou made relatively greater contributions to wolf diets (21–40%) than did moose (14–19%). While our results show that ungulates were the principal prey of wolves on the Alaska Peninsula, alternate resources also made important dietary contributions. Use of marine-derived resources increased from northeast to southwest along the Alaska Peninsula in accordance with increasing access to coastal areas and decreasing ungulate abundance. Seasonal shifts in resource use were also evident with dietary variation being highest during summer and fall when wolves consumed more alternate prey (terrestrial and marine) and expanded their niche breadth to exploit seasonally abundant resources such as salmon.

Because salmon represent a high-quality and seasonally abundant resource that requires little energetic investment (e.g., search and handling time) and decreased risk of injury compared to ungulate prey, optimal foraging theory predicts that wolves might select salmon whenever abundant (Pyke 1984). However, whether salmon represent a primary or alternate resource for wolf populations is a topic of debate. In interior Alaska, salmon contributed more to wolf diets in areas where salmon were more abundant and ungulate densities were low in comparison to areas where ungulates were more abundant (Adams et al. 2010). Szepanski et al. (1999) also suggested that exploitation of salmon by Alexander Archipelago wolves resulted from decreased availability of black-tailed deer (*Odocoileus hemionus sitkensis*). Conversely, Darimont et al. (2008) reported that salmon consumption in coastal British Columbia was correlated with the availability of salmon rather than the availability of deer, suggesting that salmon were selected over ungulates whenever abundant.

Our data show that wolves on the Alaska Peninsula made extensive use of salmon. As expected, use of salmon varied seasonally in accordance with increased availability during summer and fall (Table 2; Figs. 2 and 3). Data also suggested that some wolves may consume salmon carcasses during winter, a pattern supported by observations of wolves eating carcasses through late November (D. E. Watts, pers. obs.). In the coastal NAP, where availability of salmon was relatively limited, our results suggest that salmon were probably of limited importance (Table 2). Exploitation of salmon also varied spatially with overall contributions varying from $10 \pm 4\%$ in areas with relatively limited access to spawning streams (coastal NAP), to as much as $28 \pm 20\%$ (inland NAP) and $22 \pm 8\%$ (Unimak Island) where salmon were readily available (Table 2). Our

results show that salmon are an important resource for wolves in southwestern Alaska, particularly during periods of decreased ungulate availability as in our study. However, whether wolves in this region traditionally exploited salmon or if such high use represents a population-level response to ungulate population declines is not known. Ongoing research comparing data presented here with data from wolf tissues collected in the study area during historical periods of high ungulate abundance may shed light on this topic.

Previous studies report mean bone collagen and guard hair $\delta^{13}\text{C}$ values ranging between -19.9% and -22.3% and $\delta^{15}\text{N}$ values between 6.3% and 7.6% for coastal and inland wolf populations with access to marine resources (Szepanski et al. 1999; Darimont and Reimchen 2002; Adams et al. 2010). Population mean (\pm SD) $\delta^{13}\text{C}$ ($-20.0 \pm 1.7\%$) and $\delta^{15}\text{N}$ ($8.7 \pm 2.7\%$) values among NAP wolves (inland and coastal) in our study were similar to data reported in these previous studies. However, population isotope values in the SAP ($\delta^{13}\text{C} = -16.8 \pm 2.0\%$, $\delta^{15}\text{N} = 12.2 \pm 2.7\%$) and on Unimak Island ($\delta^{13}\text{C} = -17.2 \pm 1.7\%$, $\delta^{15}\text{N} = 12.5 \pm 2.3\%$) show that exploitation of marine resources in these areas far exceeded previously reported levels. In fact, after accounting for tissue-specific carbon isotope discrimination, mean $\delta^{13}\text{C}$ values for wolves in these areas more closely resembled values reported for polar bear (*Ursus maritimus*) bone collagen (Ramsay and Hobson 1991) than those previously reported for wolves. Collectively, marine resources contributed 28–56% to wolf diets on the Alaska Peninsula and Unimak Island, a range that exceeds estimates of 17–18% reported for other regions where wolves exploited marine resources (Szepanski et al. 1999; Adams et al. 2010). Our data also show that, in addition to salmon, wolves in southwestern Alaska exploit a variety of other marine resources including marine mammals. Use of these resources also increased from northeast to southwest along the Alaska Peninsula, a logical pattern given the increasing access to marine resources and decreasing ungulate diversity and abundance along this gradient (Fig. 1). These findings also demonstrate that wolves may increase their niche breadth with increasing availability of alternate resources, a behavior that could potentially influence wolf–ungulate interactions in some regions.

Study limitations.—Our study had several limitations common to isotope-based studies of carnivore diets. First, Bayesian-based isotope mixing models are sensitive to TDFs and use of inaccurate TDFs can influence estimated dietary proportions (Bond and Diamond 2011). For captive wolves fed an extremely lean-muscle diet, McLaren et al. (2015) estimated TDFs for keratin to be 4.3% and 3.1% for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively. For captive wolves that were fed a diet that more closely mimics the mixture of protein and lipids consumed by wild wolves, Derbridge et al. (2015) estimated $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ TDFs for keratin of 2.0% and 3.0% , respectively. This pattern is consistent with data for other wild carnivores in which TDFs for $\delta^{13}\text{C}$ decrease with increasing dietary lipid content (Newsome et al. 2010). We used TDFs of 2.0% for $\delta^{13}\text{C}$ and 3.0% for $\delta^{15}\text{N}$ (Derbridge et al. 2015) because we believe

these estimates more closely reflect the mixture of tissues consumed by wild wolves in our study area. Further, our estimates of marine versus terrestrial use were probably robust because SIAR accounts for variation in TDFs and because marine and terrestrial resources in our study area had distinct isotope values that differed by $\sim 8\%$ in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$.

Accurate interpretation of isotopically derived dietary information from vibrissae requires an understanding of growth rates. If vibrissae grow continuously and at a constant rate (linearly), then equal length sections represent equal time periods. If wolves exhibit nonlinear growth, however, equal length sections could represent different periods of time, making interpretation more complex. Studies of captive wolves suggest that wolf vibrissae grow linearly but that growth may slow as vibrissae reach full length (Stanek 2014; McLaren et al. 2015). Based on these studies, we estimated that mean vibrissae growth rates for wild wolves were ~ 1.3 cm/month. Accordingly, mean (\pm SD) vibrissae length in our study (6.3 ± 1.1 cm) probably represented ~ 5 months but may range between 3 and 9 months because sampled vibrissae length was not uniform among individuals. Some degree of variation in growth rates would also be expected among individuals. Additionally, the timing of sample collections also probably influenced estimated contributions from salmon, particularly for areas where summer diet samples were limited. For example, most SAP vibrissae were collected in early summer and primarily represented wolf diets during winter, when salmon availability is low. Accordingly, results suggested that salmon contributed little ($9 \pm 2\%$) to SAP wolf diets compared to other areas (NAP) where sample timing better reflected all seasons. Overall use of salmon at a regional scale was, therefore, probably underestimated in our study.

Lastly, Bayesian-based isotope mixing models assume that all prey included are consumed and their proportional use must sum to 100%. As a result, they tend to overestimate contributions from rarely consumed prey and underestimate contributions from primary prey. Thus, inclusion of additional prey that are only rarely consumed (e.g., eggs, small rodents, mesocarnivores) would underestimate contributions from primary prey. We therefore excluded such prey from models to improve estimates of primary prey contributions. Accordingly, our estimates of non-ungulate terrestrial prey (hares and beavers) may have been inflated, particularly for areas where models included more prey types. We suggest that prey types contributing $\leq 10\%$ probably represented relatively minor dietary components. Similarly, where prey types made larger contributions (e.g., ungulates and salmon), reported proportions probably underestimated actual contributions. Matrix plots also indicated negative correlations between some prey types, which suggests that SIAR struggled when distinguishing between contributions from prey with more similar isotope values relative to other prey types (e.g., caribou versus moose, seals versus walrus). Some of SIAR's inability to distinguish between relatively similar prey types in our study may also have been exacerbated by the wide spread in isotope values among terrestrial and marine prey in our study. Thus, the proportional contributions of different resources are probably most useful

when viewed through post hoc groupings (e.g., ungulates versus marine mammals versus salmon) and some caution should be exercised when making direct comparisons between isotopically similar prey types or between area-specific models that include different prey.

Implications of marine resource use.—The conservation and management of wolf–ungulate communities is complicated by a variety of direct and indirect top-down influences that wolves exert within ecosystems (Berger et al. 2001, 2008; Ripple and Beschta 2004). Such influences cannot, however, be accurately predicted in multi-prey systems without an understanding of how wolves use locally available resources. This is particularly important where wolf–ungulate interactions are manipulated (e.g., wolf control) to achieve management goals such as increased ungulate abundance. Our data show that access to a variety of allochthonous marine-derived resources provides abundant and reliable food sources for wolves in southwestern Alaska that could have important implications for management.

Wolves are generally considered obligate predators of ungulates and are often managed under this paradigm, probably because evidence suggests that wolf abundance is primarily driven by the availability and abundance of ungulate prey (Fuller et al. 2003). Because information on use of alternate prey is difficult to obtain, it often receives little attention in management plans. Accordingly, the effects of multiple prey species and use of alternate resources on wolf population dynamics and wolf–ungulate interactions remain poorly understood (Fuller et al. 2003; Garrott et al. 2007). Increased resource availability or diversity could influence wolf–ungulate interactions in different ways depending on wolf population responses. Where wolves fail to show a numerical response to increased resource availability, apparent mutualism could lead to increased ungulate abundance as wolves exploit alternate resources and reduce predation on ungulates (Abrams and Matsuda 1996). Alternately, where a numerical response is realized, increased wolf abundance and predation could potentially reduce local ungulate abundance through apparent competition, especially where wolves show preference for ungulate prey (Holt 1977; Abrams et al. 1998; Fuller et al. 2003; Adams et al. 2010).

The population-level effects of marine resource use by wolves are not well documented. The influence of seasonally abundant resources like salmon probably also varies with the timing and extent of their availability. For example, wolf population dynamics are closely linked to pup survival and recruitment during summer and fall (Mech et al. 1998; Fuller et al. 2003). Because salmon are readily available and predictable during these seasons, exploitation of salmon might influence population dynamics through increased pup survival and recruitment. In our study system, the most likely scenario is probably a subsidizing effect because: 1) salmon are an exceptionally abundant resource, 2) the seasonal availability of salmon is predictable and reliable, and 3) salmon availability is probably not influenced by wolf predation. In addition, marine mammals are available year-round in many areas and provide coastal wolves with additional food sources that might influence the survival of lone wolves or subordinate individuals within packs

where competition for terrestrial resources would otherwise be greater. Given that 64% of the variation observed in wolf densities across North America can be directly accounted for by variation in prey biomass (Fuller et al. 2003), such resources might buffer wolves from decreased ungulate availability. In such a scenario, relatively high wolf:ungulate ratios might even chronically limit ungulate abundance for long periods, a situation referred to as a predator pit. This is most important in areas where small ungulate populations occur (e.g., Unimak Island) or where predation and other factors (e.g., poor habitat conditions or harsh winters) act synergistically to limit ungulate abundance.

Even in areas where alternate resources are exploited, wolves probably still prey primarily on ungulates and would still be expected to have strong influence on ungulate population dynamics, particularly where wolves exhibit a numerical response to alternate resources. For example, Adams et al. (2010) found that wolves in interior Alaska showed a positive numerical response to salmon and concluded that use of salmon resulted in relatively high wolf densities and a three-fold increase in predation rates in some areas. Rose and Polis (1998) also showed that while coastal coyotes (*Canis latrans*) occurred at higher densities and derived much of their diet from marine resources, use of terrestrial prey still remained high (~50%) and ultimately depressed terrestrial prey populations. Other large carnivores also exhibit higher reproductive rates and abundance where allochthonous marine resources are used (Zabel and Taggart 1989; Hilderbrand et al. 1999b; Wiesel 2006). Wolf densities prior to our study were unknown but anecdotal evidence (i.e., frequency of observations and harvest records) suggests that, despite extensive declines in ungulate abundance, wolf abundance may have remained stable or possibly increased during the past 20–30 years. Interestingly, the availability of both salmon and marine mammals in the region has increased during this same time period (Eggers and Irvine 2007; Hartill and Murphy 2011; D. Withrow, NOAA Fisheries, pers. comm.). Although recent declines in ungulate abundance on the Alaska Peninsula were primarily driven by poor habitat conditions, subsidized wolf populations could have exacerbated population declines or hindered ungulate population recovery.

Lastly, our study suggests that wolves might also play a more diverse and ecologically complex role in the region than previously recognized. The transfer and distribution of marine-derived nutrients by bears (*Ursus* spp.) is a key process influencing the productivity of freshwater and riparian ecosystems (Hilderbrand et al. 1999a; Helfield and Naiman 2006; Quinn et al. 2009). Wolves might serve a similar role in the transport of marine-derived carcasses and nutrients into terrestrial ecosystems, making them available to a variety of terrestrial consumers (Ben-David et al. 1997a, 1997b; Hocking and Reimchen 2006; Hocking et al. 2009). Further, use of marine mammal carcasses by wolves might also have unexpected but important ecological implications such as vectors for pathogens (e.g., *Toxoplasma gondii*, *Neospora caninum*) that affect ungulates and other terrestrial wildlife (Dubey et al. 2003; Watts and Benson 2016). Our study represents an important first step toward understanding the complex role that wolves play, not

only in regional ungulate population dynamics but also in community structure and function in southwestern Alaska. Lastly, our study highlights the complexity of how variation in foraging strategies at different scales, an often overlooked aspect of carnivore ecology, might shape wolf–ungulate interactions and have pronounced direct and indirect effects that shape the structure and function of terrestrial ecosystems (McLaren and Peterson 1994; Berger et al. 2001, 2008; Ripple and Beschta 2003, 2004; Ray et al. 2005).

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LITERATURE CITED

- ABRAMS, P. A., R. D. HOLT, AND J. D. ROTH. 1998. Apparent competition or apparent mutualism? Shared predation when populations cycle. *Ecology* 79:201–212.
- ABRAMS, P. A., AND H. MATSUDA. 1996. Positive indirect effects between prey species that share predators. *Ecology* 77:610–616.
- ADAMS, L. G., ET AL. 2010. Are inland wolf-ungulate systems influenced by marine subsidies of Pacific salmon? *Ecological Applications* 20:251–262.
- ANGERBJÖRN A, P. HERSTEINSSON, K. LIDÉN, AND E. NELSON. 1994. Dietary variation in arctic foxes (*Alopex lagopus*) - an analysis of stable carbon isotopes. *Oecologia* 99:226–232.
- BALLARD, W. B., L. A. AYRES, P. R. KRAUSMAN, D. J. REED, AND S. G. FANCY. 1997. Ecology of wolves in relation to a migratory caribou herd in northwest Alaska. *Wildlife Monographs* 135:1–47.
- BEARHOP, S., C. E. ADAMS, S. WALDRON, R. A. FULLER, AND H. MACLEOD. 2004. Determining trophic niche width: a novel approach using stable isotope analysis. *Journal of Animal Ecology* 73:1007–1012.
- BEN-DAVID, M., R. W. FLYNN, AND D. M. SCHELL. 1997a. Annual and seasonal changes in diets of martens: evidence from stable isotope analysis. *Oecologia* 111:80–291.
- BEN-DAVID, M., T. A. HANLEY, D. R. KLEIN, AND D. M. SCHELL. 1997b. Seasonal changes in diets of coastal and riverine mink: the role of spawning Pacific salmon. *Canadian Journal of Zoology* 75:803–811.
- BERGER, K. M., E. M. GESE, AND J. BERGER. 2008. Indirect effects and traditional trophic cascades: a test involving wolves, coyotes, and pronghorn. *Ecology* 89:818–828.
- BERGER, J., P. B. STACEY, L. BELLIS, AND M. P. JOHNSON. 2001. A mammalian predator-prey imbalance: grizzly bears and wolf extinction affect avian Neotropical migrants. *Ecological Applications* 11:947–960.
- BERGERUD, A. T., AND J. P. ELLIOT. 1998. Wolf predation in a multiple-ungulate system in northern British Columbia. *Canadian Journal of Zoology* 76:1551–1569.
- BOND, A. L., AND A. W. DIAMOND. 2011. Recent Bayesian stable-isotope mixing models are highly sensitive to variation in discrimination factors. *Ecological Applications* 21:1017–1023.

- CHEREL, Y., L. KERNALÉGUEN, P. RICHARD, AND C. GUINET. 2009. Whisker isotopic signature depicts migration patterns and multi-year intra- and inter-individual foraging strategies in fur seals. *Biology Letters* 5:830–832.
- DARIMONT, C. T., P. C. PAQUET, AND T. E. REIMCHEN. 2008. Spawning salmon disrupt trophic coupling between wolves and ungulate prey in coastal British Columbia. *BMC Ecology* 8:14.
- DARIMONT, C. T., AND T. E. REIMCHEN. 2002. Intra-hair stable isotope analysis implies seasonal shift to salmon in gray wolf diet. *Canadian Journal of Zoology* 80:1638–1642.
- DERBRIDGE, J. J., ET AL. 2015. Experimentally derived $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ discrimination factors for gray wolves and the impact of prior information in Bayesian mixing models. *PLoS ONE* 10:e0119940.
- DUBEY, J. P., ET AL. 2003. *Toxoplasma gondii*, *Neospora caninum*, *Sarcocystis neurona*, and *Sarcosystis canis-like infections* in marine mammals. *Veterinary Parasitology* 116:275–296.
- EGGERS, D. M., AND J. R. IRVINE. 2007. Trends in abundance and biological characteristics for north Pacific sockeye salmon. *North Pacific Anadromous Fish Commission Bulletin* 4:53–75.
- ESTES, J. A., ET AL. 2011. Trophic downgrading of planet Earth. *Science* 333: 301–306
- FORBES, G. J., AND J. B. THEBERGE. 1992. Importance of scavenging on moose by wolves in Algonquin Park, Ontario. *Alces* 28:235–241.
- FULLER, T. K., L. D. MECH, AND J. F. COCHRANE. 2003. Wolf population dynamics. Pp. 161–191 in *Wolves: behavior, ecology, and conservation* (L. D. Mech and L. Boitani, eds.). University of Chicago Press, Chicago, Illinois.
- GARROTT, R. A., J. E. BRUGGEMAN, M. S. BECKER, S. T. KALINOWSKI, AND P. J. WHITE. 2007. Evaluating prey switching in wolf-ungulate systems. *Ecological Applications* 17:1588–1597.
- HARTILL, T. G., AND R. L. MURPHY. 2011. North Alaska Peninsula commercial salmon annual management report 2010. *Fishery Management Report Number 11-07*. Alaska Department of Fish and Game, Anchorage.
- HELFIELD, J. M., AND R. J. NAIMAN. 2006. Keystone interactions: salmon and bear in riparian forests of Alaska. *Ecosystems* 9:167–180.
- HILDERBRAND, G. V., T. A. HANLEY, C. T. ROBBINS, AND C. C. SCHWARTZ. 1999a. Role of brown bears (*Ursus arctos*) in the flow of marine nitrogen into a terrestrial ecosystem. *Oecologia* 121:546–550.
- HILDERBRAND, G. V., ET AL. 1999b. The importance of meat, particularly salmon, to body size, population productivity, and conservation of North American brown bears. *Canadian Journal of Zoology* 77:132–138.
- HIRONS, A. C., D. M. SCHELL, AND B. P. FINNEY. 2001. Temporal records of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in North Pacific pinnipeds: inferences regarding environmental change and diet. *Oecologia* 129:591–601.
- HOCKING, M. D., AND T. E. REIMCHEN. 2006. Consumption and distribution of salmon (*Oncorhynchus* spp.) nutrients and energy by terrestrial flies. *Canadian Journal of Fisheries and Aquatic Sciences* 63:2076–2086.
- HOCKING, M. D., R. A. RING, AND T. E. REIMCHEN. 2009. The ecology of terrestrial invertebrates on Pacific salmon carcasses. *Ecological Research* 24:1091–1100.
- HOLT, R. D. 1977. Predation, apparent competition, and the structure of prey communities. *Theoretical Population Biology* 12:197–229.
- JEDRZEJEWSKI, W., K. SCHMIDT, J. THEUERKAUF, B. JEDRZEJEWSKA, N. SELVA, K. ZUB, AND L. SZYMURA. 2002. Kill rates and predation by wolves on ungulate populations in Bialowieza primeval forest (Poland). *Ecology* 83:1341–1356.
- LEWIS, R., T. C. O'CONNELL, M. LEWIS, C. CAMPAGNA, AND A. R. HOELZEL. 2006. Sex-specific foraging strategies and resource partitioning in the southern elephant seal (*Mirounga leonine*). *Proceedings of the Royal Society of London, B. Biological Sciences* 273:2901–2907.
- MARTÍNEZ DEL RIO, C., N. WOLF, S. A. CARLETON, AND L. Z. GANNES. 2009. Isotopic ecology ten years after a call for more laboratory experiments. *Biological Reviews* 84:91–111.
- MCLAREN, A. A. D., G. J. CRAWSHAW, AND B. R. PATTERSON. 2015. Carbon and nitrogen discrimination factors of wolves and accuracy of diet inferences using stable isotope analysis. *Wildlife Society Bulletin* 39:788–796.
- MCLAREN, B. E., AND R. O. PETERSON. 1994. Wolves, moose, and tree rings on Isle Royale. *Science* 266:1555–1558.
- MECH, L. D. 2007. Annual arctic wolf pack size related to arctic hare numbers. *Arctic* 60:309–311.
- MECH, L. D., L. G. ADAMS, T. J. MEIER, J. W. BURCH, AND B. W. DALE. 1998. *The wolves of Denali*. University of Minnesota Press, Minneapolis.
- MEIKLEJOHN, B. A. 1994. Ecology and sensitivity to human disturbance of a wolf pack at Glacier Bay National Park and Preserve, Alaska. National Park Service, Glacier Bay, Alaska.
- METZ, M. C., D. W. DOUGLAS, J. A. VUCETICH, D. R. STAHLER, AND R. O. PETERSON. 2012. Seasonal patterns of predation for gray wolves in the multi-prey system of Yellowstone National Park. *Journal of Animal Ecology* 81:553–563.
- MILAKOVIC, B., AND K. L. PARKER. 2011. Using stable isotopes to define diets of wolves in northern British Columbia, Canada. *Journal of Mammalogy* 92:295–304.
- NEWSOME, S. D., ET AL. 2009. Using stable isotopes to investigate individual diet specialization in California sea otters (*Enhydra lutris nereis*). *Ecology* 90:961–974.
- NEWSOME, S. D., H. M. GARBE, E. C. WILSON, AND S. D. GEHRT. 2015. Individual variation in anthropogenic resource use in an urban carnivore. *Oecologia* 178:115–128.
- NEWSOME, S. D., K. RALLS, C. VAN HORN JOB, M. L. FOGEL, AND B. L. CYPHER. 2010. Stable isotopes evaluate exploitation of anthropogenic foods by the endangered San Joaquin kit fox (*Vulpes macrotis mutica*). *Journal of Mammalogy* 91:1313–1321.
- NEWSOME, T. M., ET AL. 2016. Food habits of the world's grey wolves. *Mammal Review*. doi: 10.1111/mam.12067.
- PARNELL, A. C., R. INGER, S. BEARHOP, AND A. L. JACKSON. 2010. Source partitioning using stable isotopes: coping with too much variation. *PLoS ONE* 5:e9672.
- PAQUET, P. C., AND L. N. CARBYN. 2003. Gray wolf. Pp 482–510 in *Wild mammals of North America: biology, management, and conservation* (G. A. Feldhammer, B. C. Thompson, and J. A. Chapman, eds.). 2nd ed. Johns Hopkins University Press, Baltimore, Maryland.
- PETERSON, C. 2013a. Units 9C and 9E caribou management report. Pp. 46–56 in *Caribou management report of survey and inventory activities 01 July 2010–30 June 2012* (P. Harper, ed.). Alaska Department of Fish and Game, Species Management Report, ADF&G/DWC/SMR-2013-3, Juneau.
- PETERSON, C. 2013b. Units 9D caribou management report. Pp. 57–67 in *Caribou management report of survey and inventory activities 01 July 2010–30 June 2012* (P. Harper, ed.). Alaska Department of Fish and Game, Species Management Report, ADF&G/DWC/SMR-2013-3, Juneau.
- PETERSON, C. 2013c. Units 10 caribou management report. Pp. 68–75 in *Caribou management report of survey and inventory activities 01 July 2010–30 June 2012* (P. Harper, ed.). Alaska Department of Fish and Game, Species Management Report, ADF&G/DWC/SMR-2013-3, Juneau.

- PETERSON, R. O. 1977. Wolf ecology and prey relationships on Isle Royale. National Park Service scientific monograph 11. U.S. Government Printing Office, Washington, D.C.
- PETERSON, R. O., AND P. CIUCCI. 2003. The wolf as a carnivore. Pp. 104–130 in *Wolves: behavior, ecology, and conservation* (L. D. Mech and L. Boitani, eds.). University of Chicago Press, Chicago, Illinois.
- PHILIPS, D. L. 2012. Converting isotope values to diet composition: the use of mixing models. *Journal of Mammalogy* 93:342–352.
- PYKE, G. H. 1984. Optimal foraging theory: a critical review. *Annual Review of Ecology, Evolution, and Systematics* 15:523–575.
- QUINN, T. P., S. M. CARLSON, S. M. GENDE, AND H. B. RICH, JR. 2009. Transportation of Pacific salmon carcasses from streams to riparian forest by bears. *Canadian Journal of Zoology* 87:195–203.
- RAY, J. C., K. H. REDFORD, R. S. STENECK, J. BERGER. 2005. Large carnivores and the conservation of biodiversity. Island Press, Washington, D.C.
- RILEY, M. D. 2012. Unit 9 moose management report. Pp. 108–116 in *Moose management report of survey and inventory activities 01 July 2009–30 June 2011* (P. Harper, ed.). Alaska Department of Fish and Game, Species Management Report, ADF&G/SMR/DWC-2012-5, Juneau.
- RIPPLE, W. J., AND R. L. BESCHTA. 2003. Wolf reintroduction, predation risk, and cottonwood recovery in Yellowstone National Park. *Forest Ecology and Management* 184:299–313.
- RIPPLE, W. J., AND R. L. BESCHTA. 2004. Wolves and the ecology of fear: can predation risk structure ecosystems? *BioScience* 54:755–766.
- RIPPLE, W. J., E. J. LARSEN, R. A. RENKIN, AND D. W. SMITH. 2001. Trophic cascades among wolves, elk and aspen on Yellowstone National Park's northern range. *Biological Conservation* 102:227–234.
- R DEVELOPMENT CORE TEAM. 2012. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. www.R-project.org. Accessed January 2016.
- RAMSAY, M. A., AND K. A. HOBSON. 1991. Polar bears make little use of terrestrial food webs: evidence from stable-carbon isotope analysis. *Oecologia* 86:597–600.
- ROBERTSON, A., R. A. McDONALD, R. J. DELAHAY, S. D. KELLY, AND S. BEARHOP. 2013. Whisker growth in wild Eurasian badgers *Meles meles*: implications for stable isotope and bait marking studies. *European Journal of Wildlife Research* 59:341–350.
- ROSE, M. D., AND G. A. POLIS. 1998. The distribution and abundance of coyotes: the effects of allochthonous food subsidies from the sea. *Ecology* 79:998–1007.
- ROTH, J. D., AND K. A. HOBSON. 2000. Stable carbon and nitrogen isotopic fractionation between diet and tissue of captive red fox: implications for dietary reconstruction. *Canadian Journal of Zoology* 78:848–852.
- SAND, H., P. WABAKKEN, B. ZIMMERMANN, Ö. JOHANSSON, H. C. PEDERSEN, AND O. LIBERG. 2008. Summer kill rates and predation pattern in a wolf-moose system: can we rely on winter estimates? *Oecologia* 156:53–64.
- SCHINDLER, D. E., J. B. ARMSTRONG, K. T. BENTLEY, K. J. JANKOWSKI, P. J. LISI, AND L. X. PAYNE. 2013. Riding the crimson tide: mobile terrestrial consumers track phenological variation in spawning of an anadromous fish. *Biology Letters* 9: 20130048.
- SIKES, R. S., W. L. GANNON, AND THE ANIMAL CARE AND USE COMMITTEE OF THE AMERICAN SOCIETY OF MAMMALOGISTS. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy* 92:235–253.
- SMALL, R. J. 2001. Aerial surveys of harbor seals in Southern Bristol Bay, Alaska, 1998–1999. Pp. 71–83 in *Harbor Seal Investigation in Alaska Annual Report NOAA Grant NA87FX0300*. Alaska Department of Fish and Game, Anchorage.
- SPAULDING, R. L., P. R. KRAUSMAN, AND W. B. BALLARD. 1998. Summer diet of gray wolves, *Canis lupus*, in northwestern Alaska. *Canadian Field-Naturalist* 112:262–266.
- STANEK, A. E. 2014. Dietary ecology of Alaskan grey wolves: variation in seasonal foraging strategies in a salmon subsidized ecosystem. M.S. thesis, University of Alaska Anchorage, Anchorage.
- SZEPANSKI, M. M., M. BEN-DAVID, AND V. VAN BELLENBERGHE. 1999. Assessment of salmon resources in the diet of the Alexander Archipelago wolf using stable isotope analysis. *Oecologia* 120:327–335.
- TIESZEN, L. L., AND T. W. BOUTTON. 1989. Stable carbon isotopes in terrestrial ecosystem research. Pp. 167–195 in *Stable isotopes in ecological research* (P. W. Rundel, J. R. Ehleringer, and K. A. Nagy, eds.). Springer-Verlag, Berlin, Germany.
- TYRRELL L., S. D. NEWSOME, M. L. FOGEL, M. VIENS, R. BOWDEN, AND M. J. MURRAY. 2013. Vibrissae growth rates and trophic discrimination factors in captive southern sea otters (*Enhydra lutris nereis*). *Journal of Mammalogy* 94:331–338.
- VAN BALLEMBERGHE, V., AND W. B. BALLARD. 1994. Limitation and regulation of moose populations: the role of predation. *Canadian Journal of Zoology* 72:2071–2077.
- WATTS, D. E., AND A. M. BENSON. 2016. Prevalence of antibodies for selected canine pathogens among wolves from the Alaska Peninsula. *Journal of Wildlife Diseases* 52:506–515.
- WATTS, D. E., L. G. BUTLER, B. W. DALE, AND R. D. COX. 2010. The Ilnik wolf *Canis lupus* pack: use of marine mammals and offshore sea ice. *Wildlife Biology* 16:144–149.
- WIESEL, I. 2006. Predatory and foraging behavior of brown hyenas (*Parahyaena brunnea* Thunberg 1820) at Cape fur seal (*Arctocephalus pusillus pusillus* Schreber 1776) colonies. Ph.D. dissertation, University of Hamburg, Germany.
- WOOLINGTON, J. D. 2013. Mulchatna caribou management report, Units 9B, 17, 18 south, 19A & 19B. Pp. 23–45 in *Caribou management report of survey and inventory activities 01 July 2010–30 June 2012* (P. Harper, ed.). Alaska Department of Fish and Game, Species Management Report, ADF&G/DWC/SMR-2013-3, Juneau.
- ZABEL, C. J., AND S. J. TAGGART. 1989. Shift in red fox, *Vulpes vulpes*, mating system associated with El Nino in the Bearing Sea. *Animal Behavior* 38:830–838.

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