

Seasonal foraging strategies of Alaskan gray wolves (*Canis lupus*) in an ecosystem subsidized by Pacific salmon (*Oncorhynchus* spp.)

Ashley E. Stanek, Nathan Wolf, Grant V. Hilderbrand, Buck Mangipane, Douglas Causey, and Jeffrey M. Welker

Abstract: Despite frequent observations of gray wolves (*Canis lupus* L., 1758) using nonungulate prey, the seasonal and interannual variation in the use and relative importance of alternative prey sources to gray wolf diets have not been studied at the individual scale. We used stable isotope analysis ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of guard hair and blood components (clot and serum) collected over 4 years to examine the occurrence, extent, and temporal variation of Pacific salmon (genus *Oncorhynchus* Suckley, 1861) as a food resource by both individual wolves and social groups in Lake Clark National Park and Preserve in southwestern Alaska, USA. Our results demonstrate substantial variability in the use of salmon over time. During summer, diets of five wolves consisted of at least 50% salmon, while the diets of 17 wolves consisted of primarily terrestrial prey. Over 3 years, one group of wolves consistently consumed salmon in summer and switched to terrestrial prey in winter. Prey choices were generally similar within social groups; however, the degree to which individuals consumed salmon was highly variable. The use of salmon as exhibited by wolves in Lake Clark is likely widespread where salmon are abundant and this finding should be taken into consideration in the conservation and management of wolves and their prey.

Key words: gray wolf, *Canis lupus*, *Oncorhynchus* spp., individual specialization, stable isotope analysis, predator–prey interactions.

Résumé : Même s'il est fréquent d'observer des loups (*Canis lupus* L., 1758) utiliser des proies non ongulées, les variations saisonnières et interannuelles de l'utilisation de différentes sources de proies et de leur importance relative dans le régime alimentaire des loups gris n'ont pas été étudiées à l'échelle de l'individu. Nous avons utilisé l'analyse d'isotopes stables ($\delta^{13}\text{C}$ et $\delta^{15}\text{N}$) de jarres et de composants du sang (coagulums et sérum) prélevés pendant 4 ans pour examiner la présence, l'étendue et les variations temporelles de saumons du Pacifique (genre *Oncorhynchus* Suckley, 1861) comme ressource alimentaire pour des loups individuels et des groupes sociaux dans le Parc national et la réserve faunique de Lake Clark, dans le sud-ouest de l'Alaska (États-Unis). Nos résultats démontrent une variabilité temporelle considérable de l'utilisation de saumons. En été, les régimes alimentaires de cinq loups comprenaient au moins 50 % de saumons, alors que ceux de 17 loups comprenaient principalement des proies terrestres. Sur 3 ans, un groupe de loup consommait uniformément des saumons en été pour passer à des proies terrestres en hiver. Les choix de proies étaient généralement semblables au sein d'un même groupe social; cependant, la mesure dans laquelle les individus consommaient des saumons était très variable. L'utilisation de saumons telle qu'elle est observée chez les loups du parc de Lake Clark est vraisemblablement répandue là où les saumons sont abondants, et cette constatation devrait être prise en considération dans les efforts de conservation et de gestion des loups et de leurs proies. [Traduit par la Rédaction]

Mots-clés : loup gris, *Canis lupus*, *Oncorhynchus* spp., spécialisation individuelle, analyse d'isotopes stables, interactions prédateur–proie.

Introduction

Intrapopulation variation in prey selection is recognized as a central aspect of the foraging ecology of animal populations and is most frequently attributed to dietary differences between sexes or ontogenic stages (Polis 1984; Bolnick et al. 2003; Bryan et al. 2006; Kim et al. 2012). Variations in population-level foraging ecology resulting from differences in the foraging strategies of known individuals, however, have received far less attention (Tinker et al.

2008). Broadly, the foraging ecology of a population can be described by the combined dietary niche width of its constituent individuals. A population that has a broad dietary niche may be composed of individuals either with similar generalist foraging strategies or of individuals with different specialized foraging strategies (Newsome et al. 2009; Matich et al. 2011). Conversely, a population with a narrow dietary niche can only consist of individuals with similar specialized foraging strategies. This discrep-

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ancy highlights the importance of variation in individual foraging strategies as a primary component determining the total population dietary niche width (Van Valen 1965), and consequently, the foraging ecology of a population.

The extent that individuals develop foraging specialization is driven primarily by the degree of resource competition (Araujo et al. 2011), either through changes in food availability (Tinker et al. 2008) or consumer densities (Bolnick et al. 2010). Prey switching by individuals in response to temporal or spatial changes in resource availability can drive variability in population-level diet (van Baalen et al. 2001); this process is complex and remains relatively unexplored.

Gray wolf (*Canis lupus* L., 1758) (henceforth, wolf) and ungulate systems in Alaska, USA, are an example of a multiple-prey system where variation in prey selection among individual consumers may strongly influence population-level predator-prey interactions. Although the foraging ecology of wolf packs is relatively well understood, the foraging ecology of individual pack members and the influence that this variation has on niche width of wolf populations remains relatively unstudied (Metz et al. 2011).

The techniques most commonly used to study wolf diets include scat and kill-site analyses, which make use of prey remains to assess the presence or absence and relative contributions of different prey types to wolf diets. Scat analyses focus on the remains found in fecal matter, whereas kill-site analyses examine the remains of large animal kills for signs of wolf activity. Although useful for assessing the diets of groups, significant efforts are required to assign scat or kill sites to individual wolves. As a result, an inherent assumption with kill-site and scat analyses is that wolf packs are a homogenous foraging unit and that individuals within a pack have the same (or similar) diets. Individual wolves are adept predators (Thurber and Peterson 1993; Mech and Boitani 2003) and, like other predators (e.g., Newsome et al. 2009; Edwards et al. 2011; Giroux et al. 2012; Kim et al. 2012), have the potential to exhibit different foraging strategies (Urton and Hobson 2005), even within the same pack. Without significant labor-intensive tracking efforts, however, kill-site and scat analyses cannot be used to assign a temporal component to individual dietary resource use. Furthermore, movements inferred by tracking wolves through snow has resulted in a seasonal bias of wolf foraging ecology studies towards winter (Mech and Peterson 2003), and seasonal variations in the vulnerability to predation and availability of prey species may play a large role in influencing the use of specific prey. Consequently, due to the seasonal bias among studies of wolf diets, the use of multiple prey types is not addressed equally across seasons (Jędrzejewski et al. 2002; Peterson and Ciucci 2003; Metz et al. 2012).

Stable isotope analysis presents a potential method by which the composition and temporal changes in diets of individual wolves can be studied (Dalerum and Angerbjörn 2005; Martínez del Rio et al. 2009a, 2009b; Newsome et al. 2012) without the difficulties in individual and temporal assignment of dietary inputs associated with scat and kill-site analyses. By measuring the carbon and nitrogen stable isotope values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively) of multiple tissues from an individual wolf, changes in an animal's diet over time can be inferred (Dalerum and Angerbjörn 2005). Metabolically inert tissues, such as hair and claws, incorporate dietary stable isotopes during growth and remain isotopically unaltered afterwards (Dalerum and Angerbjörn 2005). For example, wolves have one annual molt in the early summer (Young and Goldman 1944), thus wolf hair reflects isotope values of prey during summer and fall (Darimont et al. 2003). By contrast, blood components (such as the clot and serum) continuously incorporate the stable isotopes of dietary items as they are resynthesized. Thus, these tissues can be used to estimate diet during a period of weeks to months preceding sampling (Milakovic and Parker 2011).

Previous studies using stable isotopes to examine the diets of wolves have shown that Pacific salmon (genus *Oncorhynchus* Suckley,

1861) (henceforth, salmon) is an important prey resource in both coastal (Szepanski et al. 1999; Darimont et al. 2003) and interior (Adams et al. 2010) systems of Alaska and British Columbia (Canada). The degree to which the proportion of salmon consumed by wolves changes throughout a year, however, has not yet been examined quantitatively. Although these studies present a summarized value describing a group of animals, calculated from measurements of individuals, they did not address patterns of variation among individuals within groups. Here we report the results of an investigation analyzing $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ to develop a quantitative estimate of the degree and timing with which individual wolves in Lake Clark National Park and Preserve in southwest Alaska used salmon as a food resource. Our study addressed the following four questions. (1) Do individual wolves in the Lake Clark region exhibit a generalist foraging strategy or do some individuals specialize on certain prey? (2) Are foraging strategies similar between individuals from the same social group? (3) Are there differences in foraging strategies between seasons? (4) Does differentiation in foraging strategies correspond with an increased use of salmon by wolves? We designed this study to gain novel insight on the intra-annual use of terrestrial and marine resources by individual wolves and to provide baseline information on the dietary habits of a previously unstudied population of wolves.

Materials and methods

Study area

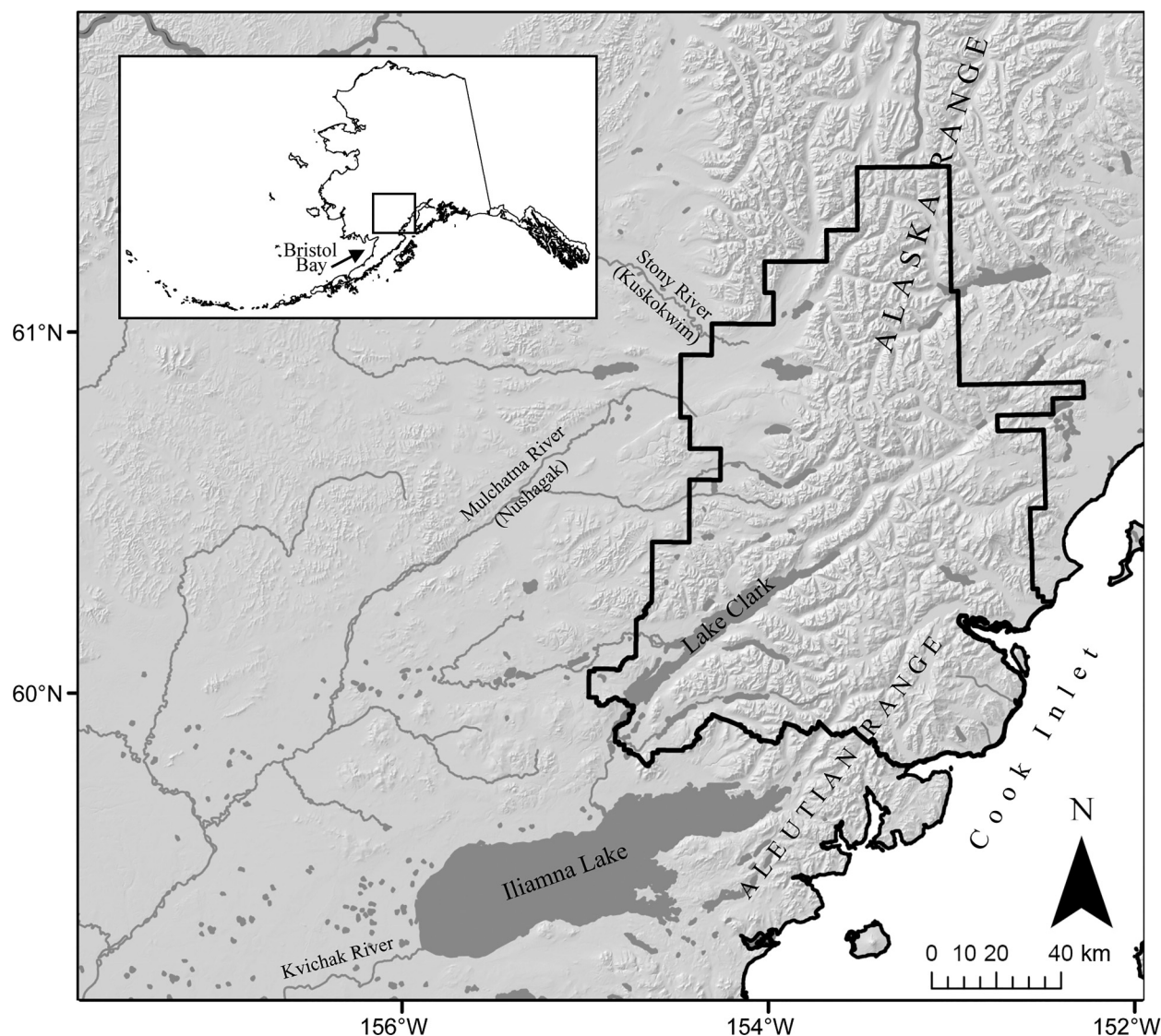
Lake Clark National Park and Preserve (LACL) encompasses 16 309 km² of southwest Alaska, at the intersection of the Alaska and Aleutian mountain ranges (Fig. 1). The Chigmit Mountains and Alaska Mountain Range bisect LACL into coastal (east) and inland (west) regions. This study focuses on wolves inhabiting the inland portion of the park and preserve. The Lake Clark region supports multiple ungulate species including caribou (*Rangifer tarandus* (L., 1758)), Dall's sheep (*Ovis dalli* Nelson, 1884), and moose (*Alces alces* (L., 1758)), each at relatively low densities. The Mulchatna caribou herd has traditionally used wintering and calving grounds near LACL and was potentially an important prey resource for wolves in the region (Woolington 2011). Considerable declines in the Mulchatna herd population (peak of ~200 000 individuals in 1996 to ~30 000 individuals in 2008) and shifts in their range away from LACL (Woolington 2011) have likely altered the availability of caribou as prey to wolves in the region. Consequently, if caribou have historically been an important resource for wolves, changes in the population size and range of the Mulchatna herd may have influenced the degree to which wolves are dependent on other prey. In addition to gray wolves, other predators in the region include brown bears (*Ursus arctos* L., 1758), black bears (*Ursus americanus* Pallas, 1780), lynx (*Lynx canadensis* Kerr, 1792), coyotes (*Canis latrans* Say, 1823), and wolverines (*Gulo gulo* (L., 1758)) (Bennett et al. 2006).

A series of large lakes abutting the Alaska Mountain Range serves as headwaters for three major river drainages of southwest Alaska (the Kvichak, Nushagak, and Kuskokwim) and supports the Bristol Bay sockeye salmon (*Oncorhynchus nerka* (Walbaum in Arctedi, 1792)) fisheries. These salmon runs are an important nutrient resource for the region both as live fish and as carcasses, as well as decomposed nutrients at the base of the food web (Kline et al. 1993).

Sample collection

We collected samples of wolf guard hair, blood clot, and blood serum from each of 22 wolves from nine social groups during five capture events over four winters (2009–2012). Because we lack detailed information on the social structure of these groups, here we use the more general term “social group” rather than “pack”. Capture events occurred in December 2008, February 2009, February 2010, February–March 2011, and February 2012. Wolves captured

Fig. 1. The Lake Clark region in southwest Alaska, USA, with Lake Clark National Park and Preserve outlined in black.



in December 2008 and February 2009 were considered to be captured in the same season (winter 2009). Wolves that were captured or observed together were considered members of the same social group. Relevant group names or individual identifiers are provided in the results. Animal handling protocols were approved by U.S. Fish and Wildlife Service and University of Alaska Anchorage Institution Animal Care and Use committees (protocol Nos. 2008023 and 243626-1, respectively).

Wolves were anesthetized with Telazol (500 mg, Tiletamine-Zolazepam; Fort Dodge Animal Health, Fort Dodge, Iowa, USA) by aerial darting from a helicopter. Individuals were fitted with GPS collars (Telonics Inc., Mesa, Arizona, USA) that were programmed to record locations every 11 or 15 h. To determine whether variation in foraging strategies was potentially related to changes in location, we used GPS data from recaptured individuals to assess the general areas occupied by individual wolves.

At the time of capture, we collected guard hair and blood samples from each wolf. Guard hairs were collected from the base of the dorsal side of the neck and stored in paper envelopes. Blood samples were drawn into red top serum tubes (BD Vacutainers; BD Diagnostics, Franklin Lakes, New Jersey, USA). Immediately after collection, whole blood was centrifuged to separate serum and clot components that were then stored separately at -80°C . We

selected these tissues because their isotopic characteristics reflect diet over different time frames. Wolf guard hair incorporates dietary stable isotope values as it grows throughout the summer and fall (Young and Goldman 1944; Darimont and Reimchen 2002); thus, hair samples that we collected in the winter represent wolf diets during the preceding summer (Dalerum and Angerbjörn 2005). Blood clot and serum continuously incorporate dietary stable isotope values and represent diet over specific temporal periods up to the time of collection (Hobson and Clark 1993). To inform our diet investigation, we determined average residence times (Martínez del Río and Anderson-Sprecher 2008) of ^{13}C and ^{15}N in a captive wolf population fed a marine diet (100% salmon) and maintained at the Alaska Zoo (Anchorage, Alaska; Stanek 2014). Serum ^{13}C and ^{15}N mean average residence time was 19.5 days, allowing us to infer diet over the previous 3–4 weeks. Blood clot did not fully incorporate the marine diet within the 70 day study, so it likely reflects diet over at least the previous 3–4 months.

Muscle samples of potential wolf prey items were collected from the Lake Clark region (caribou: $n = 2$; Dall's sheep: $n = 3$; moose: $n = 10$; salmon: $n = 12$) and were stored frozen at -20°C prior to analysis. Prey samples were collected by National Park Service staff and donated by local hunters.

Table 1. Diet-to-tissue discrimination values used to estimate gray wolf (*Canis lupus*) diets.

Diet (prey)	Tissue	$\Delta^{13}\text{C}$ (‰; mean $\pm$ SD)	$\Delta^{15}\text{N}$ (‰; mean $\pm$ SD)	Source
Terrestrial	Hair	2.6 $\pm$ 0.2	3.4 $\pm$ 0.3	Roth and Hobson 2000: red fox, <i>Vulpes vulpes</i> (L., 1758)
	Clot	0.7 $\pm$ 0.2	2.6 $\pm$ 0.3	Roth and Hobson 2000: red fox
	Serum	0.6 $\pm$ 0.2	4.2 $\pm$ 0.3	Roth and Hobson 2000: red fox
Marine	Hair	6.05 $\pm$ 0.40	−0.49 $\pm$ 0.40	Stanek 2014: gray wolf
	Clot	0.24 $\pm$ 0.16	0.38 $\pm$ 0.16	Lecomte et al. 2011: arctic fox, <i>Vulpes lagopus</i> (L., 1758)
	Serum	2.57 $\pm$ 0.15	3.68 $\pm$ 0.40	Stanek 2014: gray wolf

Blood components were freeze-dried for at least 48 h and ground to a fine powder with a bead beater (BioSpec Products, Inc., Bartlesville, Oklahoma, USA). Prey muscle samples were also freeze-dried, then ground to a fine powder with a mortar and pestle. To remove surface oils and debris, whole guard hairs were cleaned in a 2:1 chloroform:methanol solution for 24 h and rinsed with Nanopure™ water (Darimont et al. 2007). Cleaned and dried guard hairs were ground to a fine powder using a Freezer/Mill® (SPEX SamplePrep, Metuchen, New Jersey, USA).

Approximately 1.0 mg of each ground tissue was weighed into tin cups (Costech Analytical Technologies, Inc., Valencia, California, USA) for analysis. Analysis was performed using an elemental analyzer (Costech Analytical Technologies, Inc., Valencia, California, USA) coupled to a Delta Plus XP continuous-flow isotope ratio mass spectrometer (Thermo Scientific, Waltham, Massachusetts, USA) at the University of Alaska Anchorage Environment and Natural Resources Institute (UAA ENRI) Stable Isotope Laboratory. Stable isotope values are reported in delta (δ) notation, relative to international standards (atmospheric nitrogen for $\delta^{15}\text{N}$ and Vienna Pee Dee Belemnite for $\delta^{13}\text{C}$). Internal standards (NIST 1547, bowhead whale (*Balaena mysticetus* L., 1758) baleen, acetanilide, and chicken feathers) were used to determine an accuracy of $\pm 0.1\%$ for carbon and $\pm 0.2\%$ for nitrogen.

Statistical analyses

If all individual wolves in a population were using a single foraging strategy, then we would have expected the natural variation of stable isotope values of a tissue to be normally distributed at a population level. If individuals in the population, however, were using multiple strategies (i.e., consuming different combinations of prey), then we would have expected to see multiple distributions at a population level, with each distribution representing a different foraging strategy. To detect whether our data came from one or multiple distributions (Barnett and Lewis 1978), we used a one-tailed Dixon’s Q test, which is designed for use with data sets with small sample sizes from unknown distributions (Dean and Dixon 1951; Rorabacher 1991). Dixon’s Q test evaluates whether a gap between sequentially ordered values is significantly larger than what would be expected if the values were from a single homogeneous distribution. We tested the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from each of the three tissue types, separately, in each year for the presence of significant gaps that may be a result of a heterogeneous distribution of values. If no significant gaps in stable isotope values were detected, then we inferred that individuals foraged from the same set of resources, which may contain both terrestrial and marine prey. If a significant gap was detected, then we inferred that the values reflected distinct foraging strategies within the sample population. The groups of values on either side of the significant gap were referred to as the “enriched group” or the “depleted group” as appropriate.

To correct for diet-to-tissue discrimination, we used discrimination values measured from captive wolves on a marine diet, i.e., 100% salmon (Table 1). For blood clot and terrestrial diet items, we applied discrimination values from the literature for other canids (Table 1) (Roth and Hobson 2000; Lecomte et al. 2011; Stanek 2014).

We used the Bayesian mixing model SIARSolo (Stable Isotope Analysis in R; Parnell et al. 2010) to estimate the relative proportion of each prey species in the diet of each wolf sampled. SIAR-Solo uses a Bayesian framework to estimate the contribution of resources to consumer tissues. This model incorporates variation in prey $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and diet-to-tissue discrimination values to generate a probability distribution of the contribution of each resource to the diet of an individual during the time period represented by each tissue. We present the most likely proportion (mode) of prey in the diet of each wolf as calculated from each tissue.

Results

Salmon were markedly enriched in ^{13}C and ^{15}N relative to terrestrial prey. By comparison, moose were the most depleted in carbon, Dall’s sheep were the most depleted in nitrogen, and caribou were enriched in both carbon and nitrogen relative to moose and Dall’s sheep. Due to small sample sizes of caribou and Dall’s sheep, we could not adequately distinguish among terrestrial prey; therefore, we group moose, Dall’s sheep, and caribou into “terrestrial prey” for the remaining results and discussion. Terrestrial prey ($n = 15$) values ranged from -26.77% to -22.65% for $\delta^{13}\text{C}$ ($-25.19\% \pm 0.95\%$, mean $\pm$ SD) and 0.81% to 4.46% for $\delta^{15}\text{N}$ ($2.10\% \pm 1.02\%$, mean $\pm$ SD). Salmon ($n = 12$) were significantly enriched in both ^{13}C (Welch’s t test: $t = 16.54$, $P < 0.001$) and ^{15}N ($t = 36.56$, $P < 0.001$) relative to terrestrial prey. Salmon $\delta^{13}\text{C}$ values ranged from -21.50% to -20.15% ($-20.67\% \pm 0.12\%$, mean $\pm$ SD) and $\delta^{15}\text{N}$ from 11.98% to 13.06% ($12.43\% \pm 0.10\%$, mean $\pm$ SD).

Stable isotope values of wolf tissues varied within and between years (Fig. 2). We found separate distributions in values in 8 of the 12 samples analyzed (3 tissues $\times$ 4 years) (Fig. 2). Samples that showed significant gaps in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values ($P < 0.05$) were 2009 serum, 2011 hair, and 2012 hair. The same individuals were enriched in both isotopes in these cases. Five samples had significant gaps in either $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ values. For $\delta^{13}\text{C}$ values, samples included 2009 hair ($P < 0.05$), 2009 blood clot ($P < 0.10$), and 2012 blood clot ($P < 0.10$), whereas for $\delta^{15}\text{N}$ values, samples included 2010 serum ($P < 0.05$) and 2011 blood clot ($P < 0.10$).

Of the 22 individuals sampled throughout the study, we focus the discussion on 11 individuals which had at least one tissue that was significantly enriched in ^{13}C or ^{15}N ($P < 0.10$) relative to the same tissue in other individuals, resulting in separate distributions in stable isotope values for a particular tissue-year combination (Fig. 2). These 11 individuals came from four social groups: Chekok, Nikabuna, Telaquana, and Tela2. In 2009, 2010, and 2011, members of the same social group were in the same distribution. In 2012, however, two social groups (Tela2 and Nikabuna, each comprised two individuals) had a much different pattern. Hair $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from both social groups were significantly different ($P < 0.05$) from their respective group member, and thus from a different distribution.

The results from SIARSolo (Fig. 3) indicated that the most likely proportion (mode) of salmon consumed varied (1%–89%) among individual wolves and at the time periods reflected by different tissues. The proportion of salmon in the diets of individuals during each summer consistently ranged from 1% to over 50% (Fig. 3),

Fig. 2. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of gray wolf (*Canis lupus*) tissues, with each plot showing a single tissue (columns) collected in each of four winters (rows). Mean values of prey are included as reference points (caribou, *Rangifer tarandus* (C); moose, *Alces alces* (M); Dall's sheep, *Ovis dalli* (D); Pacific salmon, *Oncorhynchus* spp. (S)) and have been adjusted for diet-to-tissue discrimination (Table 1). Individuals from the same social group have the same symbol (Chekok: $\square$; Nikabuna: $\circ$; Telaquana: $\triangle$; Tela2: $\diamond$) and other individuals not associated with these social groups are identified by $\bullet$. Gray lines show where a significant gap (solid: $P \leq 0.05$; dashed: $P \leq 0.10$) in $\delta^{13}\text{C}$ (vertical lines) or $\delta^{15}\text{N}$ (horizontal lines) was present.

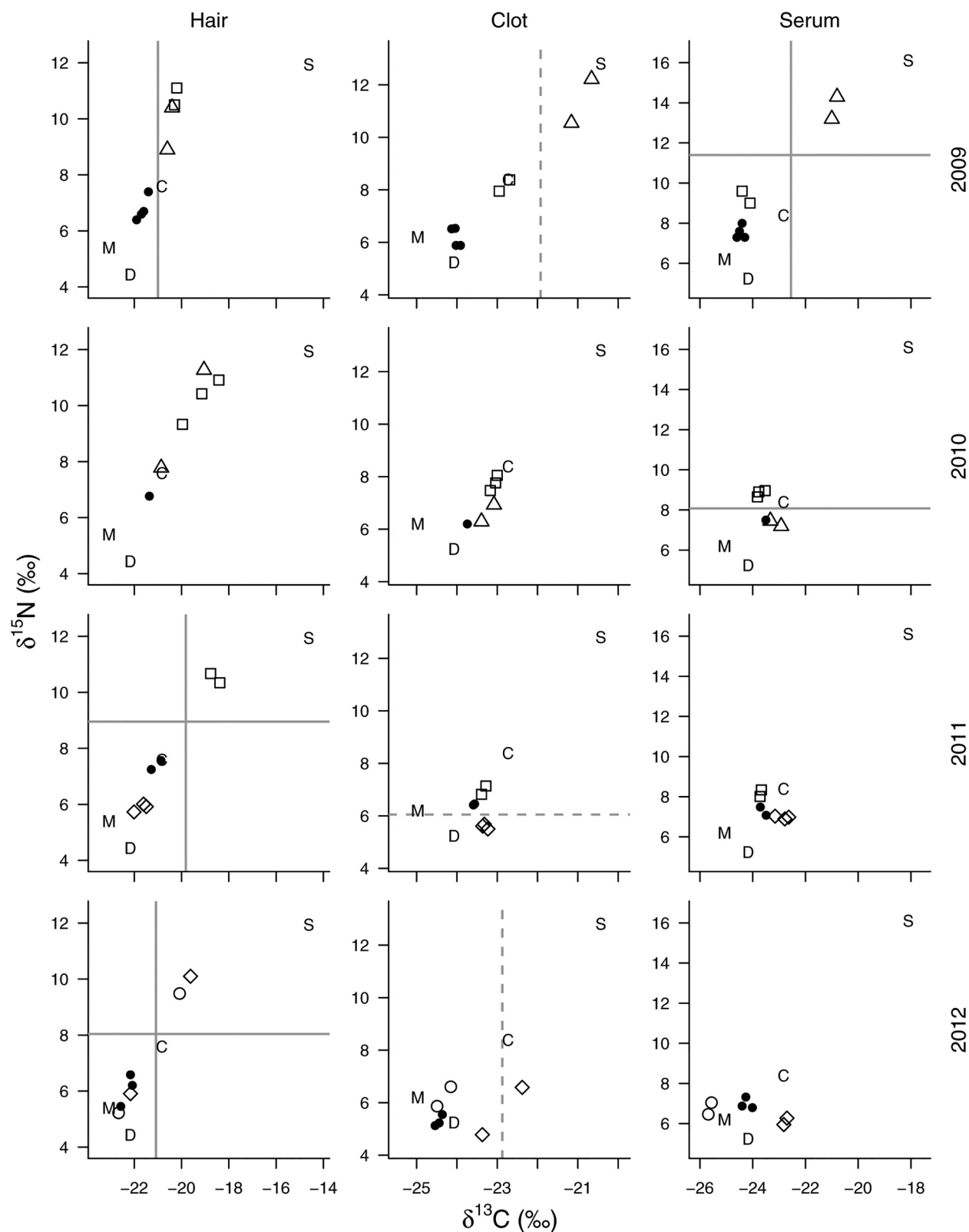
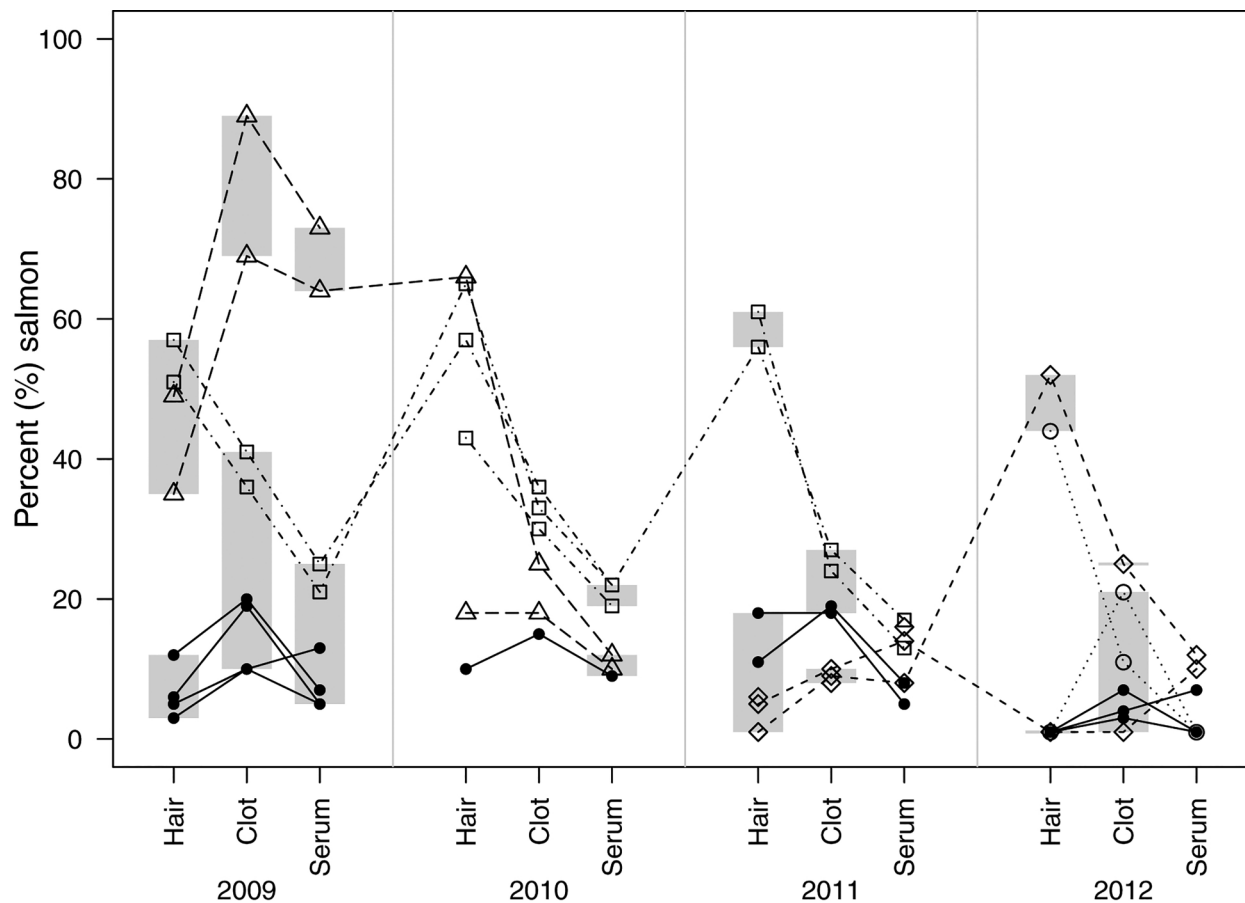


Fig. 3. Estimates (mode) of the proportion of Pacific salmon (*Oncorhynchus* spp.) in the diet of Lake Clark wolves (*Canis lupus*) from three tissues collected in each of four winters. Values from an individual are connected by lines, and individuals from the same social group have the same symbol and line pattern (Chekok: □ with dot-dashed lines; Nikabuna: ○ with dotted lines; Telaquana: △ with long-dashed lines; Tela2: ◇ with short-dashed lines). Other individuals not associated with these social groups are identified by ● and solid lines. Gray bars indicate a significant gap ($P \leq 0.10$) in $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ (Fig. 2). Note that hair collected in winter reflect the diet consumed in the preceding summer (e.g., 2010 hair reflects diet from summer 2009). Blood components represent shorter temporal periods up to the time of collection (e.g., clot reflects diet over the 3–4 months prior to collection and serum reflects diet over the 3–4 weeks prior to collection).



as estimated from hair stable isotope values. In winters 2010, 2011, and 2012, salmon was a smaller component of diet (less than 40%) than in summers. Estimates from winter 2009, however, indicated diets of the Telaquana wolves (LC0801 and LC0802) consisted primarily of salmon. The proportion of salmon ranged from 64% to 89% using values of blood clot and serum from both individuals.

We observed different overall patterns in diet constituents when multiple distributions occurred in both isotopes ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$), rather than when distributions of only one isotope ($\delta^{13}\text{C}$ or $\delta^{15}\text{N}$) were distinct. The difference between the ranges of percent salmon consumed by wolves in the enriched and depleted groups was greater when the carbon and nitrogen values were both indicative of multiple distributions (i.e., there was a significant gap in values of both isotopes for 2009 serum, 2011 hair, and 2012 hair) than when only one isotope was indicative of multiple distributions. For example, the smallest gap between distributions that occurred in both isotopes (2011 hair) reflected the difference between consuming 18% salmon and 56% salmon (Fig. 3). Hair and blood clot from 2009 were enriched in ^{13}C only, and also indicated salmon was a large component of the diets of some individuals. The difference in diet composition between enriched and depleted distributions, however, was not as great (hair: 12% salmon vs. 35% salmon; clot: 41% salmon vs. 69% salmon) compared with samples with enriched outliers in both isotopes.

Additional differences in foraging strategies as represented by significant gaps in values (such as in 2010 serum, 2011 clot, and 2012 clot) do not appear related to salmon consumption. The difference in isotope values within these samples represents minimal differences in the proportion of salmon consumed (e.g., 10% salmon vs. 18% salmon).

Discussion

The range in stable isotope values among individual tissue samples revealed substantial heterogeneity in diet composition within and between wolves in the Lake Clark region. The distribution of stable isotope values of each tissue from each year (Fig. 2) implied that not all wolves consume the same mixture of prey within a season or year. Although the diets of some wolves were rich in salmon, their diets shifted between seasons and years (Fig. 3). These dietary patterns are likely a function of the seasonal dynamics of prey availability, including salmon, and may also be a function of social interactions.

Variation in foraging strategies within social groups

When we detected multiple foraging strategies (as reflected by multiple distributions in stable isotope values) in 2009 (hair, clot, and serum), 2010 (hair), and 2011 (hair and clot) (Fig. 2), individuals in the same social group were also in the same distribution of

isotope values (either enriched or depleted group together), which we inferred to reflect shared foraging strategies within groups during the first 3 years of the study. In 2012, however, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of individuals from the Tela2 and Nikabuna social groups suggested different foraging strategies were used within these social groups. In both of these social groups, stable isotope values of hair revealed that one individual made considerable use of salmon during the summer, while the other individual consumed primarily terrestrial prey (Tela2: 52% salmon vs. 1% salmon; Nikabuna: 44% salmon vs. 1% salmon). Isotope values of tissues collected the previous year (winter 2011) from Tela2 wolves indicated that they had similar, primarily terrestrial, diets.

During the summer of 2011 (April 2011 to October 2011), location data showed that a geographical separation occurred between the two individuals of the Tela2 social group, and this geographical separation coincided with a separation in stable isotope values of hair collected in 2012. Following this separation, both wolves began traveling together throughout the fall and winter (October 2011 through February 2012). Stable isotope values corresponding to this later period (blood clot and serum collected in 2012) indicated that their diets became increasingly similar over the fall and winter. Hair values of wolf LC1119 were significantly enriched relative to wolf LC1118 at the 95% CI, blood clot at 90%, whereas serum values were not different from each other (Fig. 2). Hence, their isotope values implied that when these wolves were together, they were consuming similar prey, and when they were apart, they used different foraging strategies. Isotope values from the Nikabuna wolves suggested a similar pattern of behavior. The cohesiveness with which wolf social groups forage can vary between seasons, based on the age structure of the group, and sometimes depending on the size of available prey (Metz et al. 2012).

Despite the importance of individual foraging strategies to population-level foraging ecology, variation in prey selection among individuals within groups is rarely addressed and is generally assumed to be small. Our isotopic data from individuals within social groups during the first 3 years of our study supported this idea. The differences in summer diet by wolves in the Tela2 and Nikabuna groups suggested, however, that variation within groups can be significant. These differences in foraging behavior may not have been detected or incorporated in our assessment of predation patterns if we had only assessed diet using traditional techniques.

Seasonal patterns in foraging strategies

Ungulates are far less susceptible to wolf predation during the mid- to late summer, and wolves may need to increase their use of nonungulate prey at this time (Spaulding et al. 1998). In this study, we found notable differences in the use of marine versus terrestrial resources especially within summers. The stable isotope values of hair grown during summer were relatively high, indicating that salmon was an important resource to several individuals at that time (Fig. 2). For example, on average, over half (55%) of the diet of wolves in the Chekok group consisted of salmon in each of three summers. By contrast, blood clot and serum values indicated that they consumed primarily terrestrial diets throughout the winter (26% salmon). Within this social group, wolf LC0906 was captured in 3 years (2009, 2010, and 2011). The consistency in stable isotope values of each tissue between years implied a consistent diet within each season. Between seasons, however, this individual shifted from a diet rich in salmon during the summer to a primarily terrestrial diet during the winter. This consistency in overall diet is mirrored by a consistency in locations throughout each year.

Seasonal diet shifts may result from seasonal shifts in resource availability. In winter 2009, we detected the use of salmon by wolves in the Telaquana group (up to 89% of an individual's diet;

Fig. 3). We did not detect this strong use of salmon in subsequent years by individuals in the Telaquana social group. It is worth noting, however, that tissue samples were collected from the Telaquana wolves in December (2008), whereas those from other groups were collected later in the winter (February and (or) March) in all years. Consequently, values of blood clot and serum from Telaquana wolves represented diet over time periods earlier in the fall and winter compared with tissues collected later in the winter and thus potential differences in prey use within a winter. As snow depths increase throughout winter, ungulates become more vulnerable to predation, while salmon may become less available as winter progresses. After spawning, some carcasses can remain along lake shores throughout the fall and winter. Wolves may continue to consume salmon long after spawning has ended if carcasses remain available, even during the winter, and especially in years when snowfall is poor or in areas where lakes and rivers remain clear of ice. In the Lake Clark region, there are no late-winter runs of salmon, yet the Telaquana wolves were observed feeding on salmon carcasses frozen at lake shores throughout the fall and at the time of their capture in December.

Salmon as a food resource

The contribution of salmon to the diets of individual wolves was highly variable over the seasons represented by each sample. In some seasons, salmon contributed minimally (1%) to the diet of some individuals and substantially (89%) to others (Fig. 3). Wolves employed distinct marine and terrestrial foraging strategies in winter of 2009 and summers of 2010 and 2011 (as reflected by 2009 blood clot and serum, 2011 hair, and 2012 hair, respectively).

In previous studies conducted in coastal British Columbia (Darimont et al. 2008, 2009), southeast Alaska (Szepanski et al. 1999), and interior Alaska (Adams et al. 2010), the relative use of salmon was partially attributed to geographical differences in ungulate and (or) salmon availability. Given the widespread availability of salmon in inland waterways of the LACL region, we assumed that all wolves living in the Lake Clark region would have access to salmon, but data are incomplete. Social groups that remained in the study area with active collars (Chekok, Telaquana, and Tela2), and whose general territories could be assessed, appeared to make greater use of salmon than those who did not remain in the study area. The range of the relative contribution of salmon to the diets of Lake Clark wolves appears greater than has been reported for other regions (Szepanski et al. 1999; Darimont et al. 2009; Adams et al. 2010), but this may reflect the relatively short time periods for which we estimated diet. On an annual basis, salmon may be less important than terrestrial prey. Our results, however, indicated that salmon were likely an important or critical resource over short time periods or at times when availability of ungulates was potentially low.

In addition to being predictable and plentiful, salmon can also serve as an important source of lipids for young wolves that may increase survival (Robbins 1993). This pattern was noted by Bryan et al. (2006) in an analogous case in which harbor seals (*Phoca vitulina* L., 1758) constituted a greater component of the diets of young wolves (45.7%) than of adult wolves (23.9%). When prey with a high-fat content such as harbor seals are abundant, adults may selectively provision young with prey of higher fat content (Bryan et al. 2006). Because salmon have a relatively high lipid content compared with terrestrial prey sources, social groups of wolves that are provisioning young may be more likely to seek out a diet rich in salmon.

Our study indicates that diet switching in wolves may be more widespread than previously thought. Given the ubiquity of salmon across much of Alaska, wolves throughout the state may be using nonungulate resources, such as salmon, as predictable

alternatives, or even as a primary food source in some regions. A more in-depth examination of the influence of salmon on terrestrial predator–prey systems is warranted.

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References

- Adams, L.G., Farley, S.D., Stricker, C.A., Demma, D.J., Roffler, G.H., Miller, D.C., and Rye, R.O. 2010. Are inland wolf–ungulate systems influenced by marine subsidies of Pacific salmon? *Ecol. Appl.* **20**(1): 251–262. doi:10.1890/08-1437.1. PMID:20349845.
- Araujo, M.S., Bolnick, D.I., and Layman, C.A. 2011. The ecological causes of individual specialisation. *Ecol. Lett.* **14**(9): 948–958. doi:10.1111/j.1461-0248.2011.01662.x. PMID:21790933.
- Barnett, V., and Lewis, T. 1978. *Outliers in statistical data*. Wiley, New York.
- Bennett, A.J., Thompson, W.L., and Mortenson, D.C. 2006. Vital signs monitoring plan, Southwest Alaska Network. National Park Service, Anchorage, Alaska.
- Bolnick, D.I., Svanbäck, R., Fordyce, J.A., Yang, L.H., Davis, J.M., Hulse, C.D., and Forister, M.L. 2003. The ecology of individuals: incidence and implications of individual specialization. *Am. Nat.* **161**(1): 1–28. doi:10.1086/343878. PMID:12650459.
- Bolnick, D.I., Ingram, T., Stutz, W.E., Snowberg, L.K., Lau, O.L., and Paull, J.S. 2010. Ecological release from interspecific competition leads to decoupled changes in population and individual niche width. *Proc. R. Soc. B Biol. Sci.* **277**(1689): 1789–1797. doi:10.1098/rspb.2010.0018.
- Bryan, H.M., Darimont, C.T., Reimchen, T.E., and Paquet, P.C. 2006. Early ontogenetic diet in gray wolves, *Canis lupus*, of coastal British Columbia. *Can. Field-Nat.* **120**(1): 61–66. doi:10.22621/cfn.v120i1.247.
- Dalerum, F., and Angerbjörn, A. 2005. Resolving temporal variation in vertebrate diets using naturally occurring stable isotopes. *Oecologia*, **144**(4): 647–658. doi:10.1007/s00442-005-0118-0. PMID:16041545.
- Darimont, C.T., and Reimchen, T.E. 2002. Intra-hair stable isotope analysis implies seasonal shift to salmon in gray wolf diet. *Can. J. Zool.* **80**(9): 1638–1642. doi:10.1139/z02-149.
- Darimont, C.T., Reimchen, T.E., and Paquet, P. 2003. Foraging behaviour by gray wolves on salmon streams in coastal British Columbia. *Can. J. Zool.* **81**(2): 349–353. doi:10.1139/z02-246.
- Darimont, C.T., Paquet, P., and Reimchen, T.E. 2007. Stable isotopic niche predicts fitness of prey in a wolf–deer system. *Biol. J. Linn. Soc.* **90**(1): 125–138. doi:10.1111/j.1095-8312.2007.00716.x.
- Darimont, C.T., Paquet, P.C., and Reimchen, T.E. 2008. Spawning salmon disrupt trophic coupling between wolves and ungulate prey in coastal British Columbia. *BMC Ecol.* **8**: 14. doi:10.1186/1472-6785-8-14. PMID:18764930.
- Darimont, C.T., Paquet, P.C., and Reimchen, T.E. 2009. Landscape heterogeneity and marine subsidy generate extensive intrapopulation niche diversity in a large terrestrial vertebrate. *J. Anim. Ecol.* **78**(1): 126–133. doi:10.1111/j.1365-2656.2008.01473.x. PMID:19120600.
- Dean, R.B., and Dixon, W.J. 1951. Simplified statistics for small numbers of observations. *Anal. Chem.* **23**(4): 636–638. doi:10.1021/ac60052a025.
- Edwards, M.A., Derocher, A.E., Hobson, K.A., Branigan, M., and Nagy, J.A. 2011. Fast carnivores and slow herbivores: differential foraging strategies among grizzly bears in the Canadian Arctic. *Oecologia*, **165**(4): 877–889. doi:10.1007/s00442-010-1869-9. PMID:21153738.
- Giroux, M.-A., Berteaux, D., Lecomte, N., Gauthier, G., Szor, G., and Bêty, J. 2012. Benefiting from a migratory prey: spatio-temporal patterns in allochthonous subsidization of an arctic predator. *J. Anim. Ecol.* **81**(3): 533–542. doi:10.1111/j.1365-2656.2011.01944.x. PMID:22268371.
- Hobson, K.A., and Clark, R. 1993. Turnover of ^{13}C in cellular and plasma fractions of blood: implications for nondestructive sampling in avian dietary studies. *Auk*, **110**(3): 638–641. doi:10.2307/4088430.
- Jędrzejewski, W., Schmidt, K., Theuerkauf, J., Jędrzejewska, B., Selva, N., Zub, K., and Szymura, L. 2002. Kill rates and predation by wolves on ungulate populations in Białowieża Primeval Forest (Poland). *Ecology*, **83**(5): 1341–1356. doi:10.1890/0012-9658(2002)083[1341:KRABW]2.0.CO;2.
- Kim, S.L., Tinker, M.T., Estes, J.A., and Koch, P.L. 2012. Ontogenetic and among-individual variation in foraging strategies of northeast Pacific white sharks based on stable isotope analysis. *PLoS ONE*, **7**(9): e45068. doi:10.1371/journal.pone.0045068. PMID:23028766.
- Kline, T.C., Jr., Goering, J.J., Mathisen, O.A., Poe, P.H., Parker, P.L., and Scalani, R.S. 1993. Recycling of elements transported upstream by runs of Pacific salmon: II. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ evidence in the Kvichak River watershed, Bristol Bay, southwestern Alaska. *Can. J. Fish. Aquat. Sci.* **50**(11): 2350–2365. doi:10.1139/f93-259.
- Lecomte, N., Ahlström, Ø., Ehrich, D., Fuglei, E., Ims, R.A., and Yoccoz, N.G. 2011. Intrapopulation variability shaping isotope discrimination and turnover: experimental evidence in arctic foxes. *PLoS ONE*, **6**(6): e21357. doi:10.1371/journal.pone.0021357. PMID:21731715.
- Martínez del Río, C., and Anderson-Sprecher, R. 2008. Beyond the reaction progress variable: the meaning and significance of isotopic incorporation data. *Oecologia*, **156**(4): 765–772. doi:10.1007/s00442-008-1040-z. PMID:18446374.
- Martínez del Río, C., Sabat, P., Anderson-Sprecher, R., and Gonzalez, S.P. 2009a. Dietary and isotopic specialization: the isotopic niche of three *Cinclodes* ovenbirds. *Oecologia*, **161**(1): 149–159. doi:10.1007/s00442-009-1357-2. PMID:19424728.
- Martínez del Río, C., Wolf, N., Carleton, S.A., and Gannes, L.Z. 2009b. Isotopic ecology ten years after a call for more laboratory experiments. *Biol. Rev. Camb. Philos. Soc.* **84**(1): 91–111. doi:10.1111/j.1469-185X.2008.00064.x. PMID:19046398.
- Matich, P., Heithaus, M.R., and Layman, C.A. 2011. Contrasting patterns of individual specialization and trophic coupling in two marine apex predators. *J. Anim. Ecol.* **80**(1): 294–305. doi:10.1111/j.1365-2656.2010.01753.x. PMID:20831730.
- Mech, L.D., and Boitani, L. 2003. *Wolf social ecology*. In: *Wolves: behavior, ecology and conservation*. Edited by L.D. Mech and L. Boitani. University of Chicago Press, Chicago, Ill. pp. 1–34.
- Mech, L.D., and Peterson, R.O. 2003. Wolf–prey relations. In: *Wolves: behavior, ecology and conservation*. Edited by L.D. Mech and L. Boitani. University of Chicago Press, Chicago, Ill. pp. 131–160.
- Metz, M.C., Vucetich, J.A., Smith, D.W., Stahler, D.R., and Peterson, R.O. 2011. Effect of sociality and season on gray wolf (*Canis lupus*) foraging behavior: implications for estimating summer kill rate. *PLoS ONE*, **6**(3): e17332. doi:10.1371/journal.pone.0017332. PMID:21390256.
- Metz, M.C., Smith, D.W., Vucetich, J.A., Stahler, D.R., and Peterson, R.O. 2012. Seasonal patterns of predation for gray wolves in the multi-prey system of Yellowstone National Park. *J. Anim. Ecol.* **81**(3): 553–563. doi:10.1111/j.1365-2656.2011.01945.x. PMID:22260633.
- Milakovic, B., and Parker, K.L. 2011. Using stable isotopes to define diets of wolves in northern British Columbia, Canada. *J. Mammal.* **92**(2): 295–304. doi:10.1644/10-MAMM-A-038.1.
- Newsome, S.D., Tinker, M.T., Monson, D.H., Oftedal, O.T., Ralls, K., Staedler, M.M., Fogel, M.L., and Estes, J.A. 2009. Using stable isotopes to investigate individual diet specialization in California sea otters (*Enhydra lutris nereis*). *Ecology*, **90**(4): 961–974. doi:10.1890/07-1812.1. PMID:19449691.
- Newsome, S.D., Yeakel, J.D., Wheatley, P.V., and Tinker, M.T. 2012. Tools for quantifying isotopic niche space and dietary variation at the individual and population level. *J. Mammal.* **93**(2): 329–341. doi:10.1644/11-MAMM-S-187.1.
- Parnell, A.C., Inger, R., Bearhop, S., and Jackson, A.L. 2010. Source partitioning using stable isotopes: coping with too much variation. *PLoS ONE*, **5**(3): e9672. doi:10.1371/journal.pone.0009672. PMID:20300637.
- Peterson, R.O., and Ciucci, P. 2003. The wolf as a carnivore. In: *Wolves: behavior, ecology and conservation*. Edited by L.D. Mech and L. Boitani. University of Chicago Press, Chicago, Ill. pp. 104–130.
- Polis, G.A. 1984. Age structure component of niche width and intraspecific resource partitioning: can age groups function as ecological species? *Am. Nat.* **123**(4): 541–564. doi:10.1086/284221.
- Robbins, C.T. 1993. *Wildlife feeding and nutrition*. 2nd ed. Academic Press, San Diego, Calif.
- Rorabacher, D.B. 1991. Statistical treatment for rejection of deviant values: critical values of Dixon's "Q" parameter and related subrange ratios at the 95% confidence level. *Anal. Chem.* **63**(2): 139–146. doi:10.1021/ac00002a010.
- Roth, J.D., and Hobson, K.A. 2000. Stable carbon and nitrogen isotopic fractionation between diet and tissue of captive red fox: implications for dietary reconstruction. *Can. J. Zool.* **78**(5): 848–852. doi:10.1139/z00-008.
- Spaulding, R.L., Krausman, P.R., and Ballard, W.B. 1998. Summer diet of gray wolves, *Canis lupus*, in northwestern Alaska. *Can. Field-Nat.* **112**(2): 262–266.
- Staneck, A.E. 2014. Dietary ecology of Alaskan gray wolves: variation in seasonal foraging strategies in a salmon subsidized ecosystem. M.Sc. thesis, Department of Biological Sciences, University of Alaska Anchorage, Anchorage.
- Szepanski, M., Ben-David, M., and van Ballenberghe, V. 1999. Assessment of anadromous salmon resources in the diet of the Alexander Archipelago wolf using stable isotope analysis. *Oecologia*, **120**(3): 327–335. doi:10.1007/s004420050866. PMID:28308010.
- Thurber, J.M., and Peterson, R.O. 1993. Effects of population density and pack size on the foraging ecology of gray wolves. *J. Mammal.* **74**(4): 879–889. doi:10.2307/1382426.
- Tinker, M.T., Bentall, G., and Estes, J.A. 2008. Food limitation leads to behavioral diversification and dietary specialization in sea otters. *Proc. Natl. Acad. Sci. U.S.A.* **105**(2): 560–565. doi:10.1073/pnas.0709263105. PMID:18195370.

- Urton, E.J.M., and Hobson, K.A. 2005. Intrapopulation variation in gray wolf isotope ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) profiles: implications for the ecology of individuals. *Oecologia*, **145**(2): 317–326. doi:[10.1007/s00442-005-0124-2](https://doi.org/10.1007/s00442-005-0124-2). PMID:[15883848](https://pubmed.ncbi.nlm.nih.gov/15883848/).
- Van Valen, L. 1965. Morphological variation and width of ecological niche. *Am. Nat.* **99**(908): 377–390. doi:[10.1086/282379](https://doi.org/10.1086/282379).
- van Baalen, M., Křivan, V., van Rijn, P.C.J., and Sabelis, M.W. 2001. Alternative food, switching predators, and the persistence of predator–prey systems. *Am. Nat.* **157**(5): 512–524. doi:[10.1086/319933](https://doi.org/10.1086/319933). PMID:[18707259](https://pubmed.ncbi.nlm.nih.gov/18707259/).
- Woolington, J.D. 2011. Mulchatna caribou management report, Units 9B, 17, 18 south, 19A and 19B. *In* Caribou management report of survey and inventory activities 1 July 2009–30 June 2010. Edited by P. Harper. Alaska Department of Fish and Game, Juneau. pp. 11–32.
- Young, S.P., and Goldman, E.A. 1944. The wolves of North America. Dover Publications, New York.