

M.M. Szepanski · M. Ben-David · V. Van Ballenberghe

Assessment of anadromous salmon resources in the diet of the Alexander Archipelago wolf using stable isotope analysis

Received: 1 July 1998 / Accepted: 23 February 1999

Abstract The Alexander Archipelago wolf (*Canis lupus ligoni*) is unique to southeast Alaska, occurring on islands south of Frederick Sound and along the mainland between Dixon Entrance and Yakutat Bay. Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) are an important prey species for wolves across the southern part of the region. Spawning salmon (*Onchorynchus* sp.) are seasonally available but their presence in wolf diets has not previously been quantified. We examined the range of bone collagen $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for wolves throughout southeast ($n = 163$) and interior ($n = 50$) Alaska and used a dual-isotope mixing model to determine the relative contribution of salmon-derived marine protein in the diet. Southeast Alaska wolves consumed significantly more salmon (mean \pm SE: $18.3 \pm 1.2\%$) than did wolves from interior Alaska ($9.1 \pm 0.6\%$, $P < 0.001$). Wolves on the southeast Alaska mainland appeared to have higher marine isotopic signatures than island wolves, although this difference was not significant. Variation among individual wolf diets was higher for southeast than for interior Alaska wolves, and variation was highest in coastal mainland wolf diets ($P < 0.001$). Marine resources may augment the diet of southeast Alaska wolves during seasonal or annual fluctuations in the availability of deer, particularly in

those areas on the mainland where densities of terrestrial ungulates are relatively low.

Key words Alexander Archipelago · *Canis lupus ligoni* · Marine resources · Salmon · Stable isotopes

Introduction

Throughout their range in North America, wolf (*Canis lupus*) populations are closely linked to ungulate populations. Available data for wolves in southeast Alaska indicate that Sitka black-tailed deer are their primary prey on islands and portions of the coastal mainland (Kohira 1997; Person et al. 1996). Deer density varies across the region, with densities higher on islands than on the coastal mainland (Kirchhoff 1996), and wolf densities appear to parallel those of deer. As logging reduces old-growth forests and habitat carrying capacity for black-tailed deer in southeast Alaska, wolf abundance is predicted to decline (Person et al. 1996). Although human-caused mortality is expected, loss of primary prey is predicted to be an important risk to long-term viability and distribution of wolves in this region (Person et al. 1996).

Alternative prey resources may augment wolf diets when abundance of primary prey is low. Beaver (*Castor canadensis*), waterfowl, and other non-ungulate species often supplement wolf diets when ungulate prey are not readily available (Scott and Shackleton 1982). Southeast Alaska has a unique array of terrestrial and aquatic prey species available to terrestrial carnivores. In particular, anadromous salmon have been widely shown to supplement diets of terrestrial predators and may play an integral role as a keystone species within north Pacific coastal ecosystems (Willson and Halupka 1995). As adult salmon migrate from the ocean into freshwater to spawn, they deliver marine nutrients to aquatic and adjacent riparian communities and provide a rich supply of protein and nutrients for terrestrial consumers

M.M. Szepanski (✉)¹
Department of Fish and Wildlife Resources,
University of Idaho,
Moscow, ID 83844, USA

M. Ben-David
Institute of Arctic Biology,
University of Alaska,
Fairbanks, AK 99775, USA

V. Van Ballenberghe
Pacific Northwest Research Station,
3301C Street, Suite 200, Anchorage,
AK 99503, USA

Present address:
¹P.O. Box 222231,
Anchorage, AK 99522

(Ben-David et al. 1997a, 1997b; Hilderbrand et al. 1996; Kline et al. 1990). Of the many species that capitalize on this resource in southeast Alaska, wolves use salmon when they become seasonally available. Salmon runs exist in over 2000 streams regionwide (Sugai and Burrell 1984) and may last from August until January, providing an extensive seasonal food resource. Despite observations of wolves consuming salmon (Kohira 1997), little is known about use of fish by wolves and it is unclear if this phenomenon is widespread among wolf populations.

Using stable isotope techniques on wolf bone collagen, we investigated the incorporation of marine-derived (salmon) protein and dietary variation in southeast Alaska wolf diets. Stable isotope methodology for diet studies is based on the premise that carbon ($^{13}\text{C}/^{12}\text{C}$) and nitrogen ($^{15}\text{N}/^{14}\text{N}$) stable isotope ratios in animal tissue reflect those of their diet (DeNiro and Epstein 1981). Changes in the ratios of these isotopes (i.e., fractionation) occur via metabolism, protein synthesis, and deamination, which cause the 'lighter' isotope to be preferentially lost and the 'heavier' isotope to be retained. Hence, the stable isotope ratios of a consumer are indicative of and heavier than that of their prey; animal ^{13}C is enriched relative to the diet by about 1‰ and ^{15}N by about 3‰ (DeNiro and Epstein 1978, 1981). Distinct differences in stable carbon isotope ratios exist between marine and terrestrial systems, while ^{15}N increases with trophic level (Ben-David et al. 1997a, 1997b; Hobson and Sealy 1991). Although $\delta^{13}\text{C}$ values alone are often used to distinguish marine versus terrestrial diets, the unique combination of carbon and nitrogen stable isotope ratios can more effectively be used to discriminate between such foods in the diet.

Stable isotope analysis avoids bias inherent in other diet techniques often used for analyzing wolf diets. Differential digestibility of certain prey items can confound scat analysis interpretations of the relative contribution of prey items in the diet (Floyd et al. 1978). Specifically, analysis of scat could underestimate salmon consumption because fish may be more thoroughly digested and not easily detected (Carnes et al. 1996). Measuring stable isotope ratios not only ascertains assimilated foods but also provides relatively long-term diet information when tissues such as hair, toenails, or bone collagen are used. A predator's bone collagen is derived primarily from the protein of its prey (Krueger and Sullivan 1984) and because of its long metabolic turnover rate, it can be a useful indicator of the assimilation of food items over the lifetime of an animal (Tieszen et al. 1983). We expected that direct consumption of salmon tissues by wolves would result in simultaneous $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ enrichment in wolf bone collagen.

To detect the extent of salmon utilization by Alexander Archipelago wolves, we compared their diets to those of northern interior Alaska wolves. We hypothesized that southeast Alaska wolves would have significantly more elevated marine isotopic signatures, and

more variation among individual wolf diets, than those wolves occupying an ecosystem with limited marine input. We also hypothesized that individual southeast Alaska mainland wolves would incorporate more salmon in their diet, and have more variable diets overall, than island wolves. Occupying areas of low or fluctuating deer density, such as the coastal mainland, may necessitate a more varied diet and greater reliance on salmon resources. If mainland wolves extensively utilize alternative foods, it may be possible to assess the fate of island wolves in light of predicted declines in deer populations. Subsidies of alternative resources, particularly salmon, could influence wolf/prey dynamics in southeast Alaska by reducing the vulnerability of wolves to a numerical decline when deer numbers decrease. Thus, our ability to detect alternative prey resources such as salmon in wolf diets will enhance our knowledge of predator-prey relationships for wolves in southeast Alaska. Given their restricted distribution and apparent vulnerability to continued logging practices, this information will be important for managing wolf populations that are currently harvested.

Methods

Study area

Wolves inhabit most of southeast Alaska, from Icy Bay (59°45'N latitude, north of Yakutat) to Dixon Entrance (54°30'N latitude, southern end of Prince of Wales Island; Fig. 1), except for Admiralty, Baranof, and Chichagof Islands. The region is a naturally fragmented mosaic of forested islands (the Alexander Archipelago), mountains, and glaciers (MacDonald and Cook 1996). A maritime climate produces cool, wet summers and mild winters (~150–400 cm annual precipitation). Vegetation at lower elevations is typically old-growth western hemlock (*Tsuga heterophylla*) and Sitka spruce (*Picea sitchensis*) with dense understory (Alaback 1982). Muskeg is common in poorly drained areas and alpine tundra predominates at higher elevations. Southeast Alaska has approximately 16,000 km of shoreline (MacDonald and Cook 1996), consisting of rocky intertidal beaches and estuaries. In addition to thousands of smaller streams, several large mainland rivers are important habitat for anadromous and freshwater fish. Annual runs of spawning Pacific salmon last from late June to late November. Unlike anadromous fish in the Pacific northwest, salmon returning to British Columbia and southeast Alaska streams do not harbor the rickettsia-like parasite (*Neorickettsia helminthoeca*) known to be fatal in canids (Knapp and Millemann 1970). Thus, the condition known as 'salmon poisoning' does not affect wolves in the study area. Eulachon (*Thaleichthys pacificus*) are also anadromous and spawn from February to May in large, mainland rivers (Hart 1973). Potential mammalian prey species for wolves include Sitka black-tailed deer, beaver, mountain goats (*Oreamnos americanus*), moose, harbor seals (*Phoca vitulina*), mustelids (*Lutra canadensis*, *Mustela* spp.), and small rodents (*Microtus* spp., *Peromyscus* spp.).

Sample collection and preparation

We examined bone collagen stable isotope values from wolf skulls obtained from the University of Alaska Museum and from trappers. Skulls were chosen based upon year trapped, gender, age (juvenile or adult), and area. To test for temporal differences in diet

and to increase sample size, skulls from the 1960s and 1990s were analyzed. Isotope analysis indicated that males did not significantly differ from females (MANOVA, $P > 0.10$) and these two groups were subsequently pooled. Juveniles were defined as those wolves trapped during their first winter, and were identified by the lack of fused skull and leg bones (Rausch 1967). We initially separated juvenile and adult wolves to test for age effects because the ^{15}N -enriched milk diet of young animals might confound the interpretation of individual stable isotope ratios (Bocherens et al. 1994). Bone collagen of young animals tends to reflect diet primarily during the growth phase and is likely to be biased toward a shorter period of relative dietary integration than in adults (Hobson and Sease 1998). We selected samples from four geographic locations among which we expected to find significant dietary differences due to ungulate prey availability (Fig. 1). Because wolves occupy large home ranges (Person et al. 1996) and the spatial distribution of salmon streams in southeast Alaska is rather uniform (Alaska Department of Fish and Game 1994), we assumed that southeast Alaska wolves had equal access to anadromous salmon throughout that area. On the other hand, deer densities differ markedly across the region. In areas inhabited by wolves, relative deer density is high on Prince of Wales Island, moderate on Kupreanof Island, and low on the coastal mainland (Kirchhoff 1996). Hence, we chose southeast Alaska locations with distinct geographical or habitat variation and known differences in deer density. Wolves from northern interior Alaska ($n = 50$) had limited access to anadromous fish and were hypothesized to show a typical 'terrestrial' isotopic signature. Bone material from southeast Alaska deer ($n = 14$), moose ($n = 5$), beaver ($n = 8$), and mountain goat ($n = 5$) was also obtained from the University of Alaska Museum and analyzed. Prey species subsequently modeled for southeast Alaska wolves included deer, moose, beaver, mountain goat, voles, and salmon. Prey species considered for interior Alaska wolves were moose, caribou (*Rangifer tarandus*), and salmon. Northern Alaska caribou stable isotope data were compiled from Barnett (1994) and vole and salmon data from Ben-David (1996).

Skull samples had been previously defleshed by dermestid beetle larvae or boiled. A thin, rectangular piece ($1 \times 1/2 \times 1/8$ inch, 500–600 mg) of bone material was cut from the inner-right mandible of each skull (one sample per skull) using a Dremel tool and clean-cut wheel. Cleaning and collagen extraction procedures followed Stafford et al. (1988) and Matheus (1997). Bones were thoroughly scraped and sonicated in distilled water to remove soft tissue residue and contaminants, and were washed with acetone, methanol, and chloroform (8 h/wash) in precombusted (550°C) culture tubes to remove glues, shellacs, and lipids. Bone apatite was removed by demineralization in weak HCl (1N) at 5°C for 5–7 days. The collagen was gelatinized in HCl (pH 3–4) under N_2 gas at 101°C for 2–4 h. The solution was centrifuged and filtered through a $0.45\text{-}\mu\text{m}$ PTFE syringe filter to remove remaining contaminants. The supernatant solution was then lyophilized and weighed (1.5–2.0 mg) into miniature tin cups (4×6 mm) for analysis.

Stable isotope ratio analysis

The natural abundance of ^{13}C and ^{15}N stable isotopes in wolf and prey bone collagen was measured using a Europa C/N continuous-flow ratio mass spectrometer (CFIRMS). Analytical error was $\pm 0.1\text{‰}$ for both carbon and nitrogen. Stable isotope ratios were expressed in δ notation as the proportional deviation (in parts per thousand, ‰) of the sample isotope ratio from that of a standard:

$$\delta X = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1000$$

where X is ^{13}C or ^{15}N , R is $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$, and the appropriate standards were Pee Dee belemnite marine limestone and atmospheric nitrogen for carbon and nitrogen, respectively.

We calculated the marine and terrestrial diet component for each wolf from the combined values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in a dual-isotope, multiple-source mixing model (Ben-David et al. 1997a, 1997b). The model assumes that isotopic values of all prey items are

significantly different from each other and that an individual wolf consumes all available prey items. Proportions of rarely consumed prey may be overestimated, and commonly used prey may be underestimated. Therefore, the mixing model provides only an indication of relative prey consumption. Because collagen is derived from dietary protein, lipids and carbohydrates (i.e., fats and plant material) are often under-represented in the analysis of bone collagen (Hobson and Stirling 1997). Because any plant material in wolf diets was likely incidental (Kohira 1997), it would have little influence on collagen isotope values. We assumed the values observed in wolf collagen were indicative of an average, whole-prey value (e.g., muscle and bone). Both environmental and metabolic effects can influence stable isotope ratios of prey and predator, but fractionation was assumed to be constant with diet among individuals. Additionally, we assumed that changes in plant isotope values, and therefore prey values, did not occur between years. Only prey items that were frequently used were introduced into the mixing model, and fractionation values for terrestrial and marine prey were based upon feeding experiments on captive carnivores fed known diets (Ben-David 1996; Hilderbrand et al. 1996).

Statistical analysis

We assessed differences in stable isotopic values among prey (deer, moose, mountain goats, beaver, voles, caribou, and salmon) using a K nearest-neighbor randomization test (Rosing et al. 1998) prior

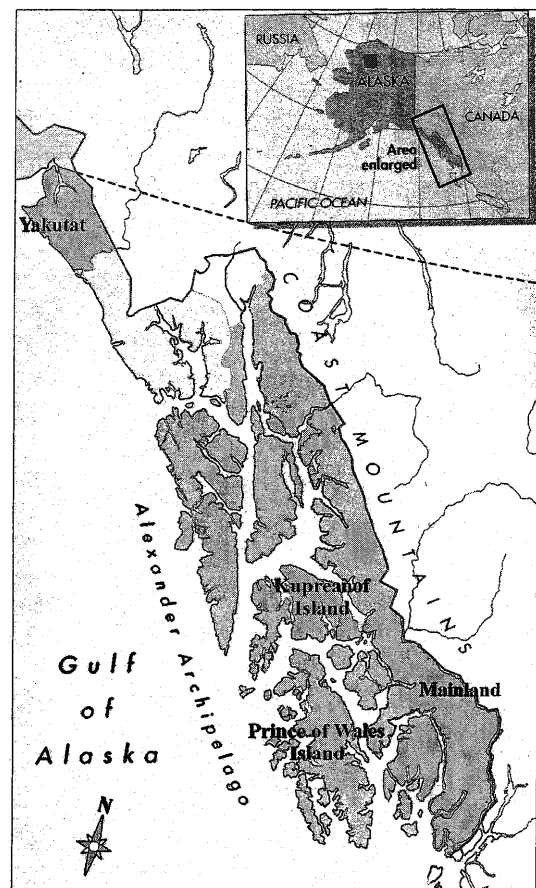


Fig. 1 Alexander Archipelago wolves occur on Kupreanof and Prince of Wales Islands, and along the mainland corridor. Wolf samples were selected from these southeast Alaska locations and from northern interior Alaska (square in inset). Map modified from Kirchhoff (1994)

to their incorporation into the dual-isotope mixing model. Moose, beaver, mountain goats, and voles were subsequently grouped together and labeled 'other herbivores' because they were not isotopically distinct ($P > 0.05$), and could not be measured independently in wolf diets. Birds, squirrels, berries, and marine invertebrates were not included in the K nearest-neighbor test for southeast Alaska wolves because their incidence in the diet may be limited (Kohira 1997). Likewise, ground squirrels (*Spermophilus undulatus*), beaver and snowshoe hares (*Lepus americanus*) were excluded for interior Alaska wolves (Stephenson and James 1982). We plotted $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ means from distinct prey items in the mixing model, calculated the percentage of each prey in the wolf diet, and determined the mean (\pm SE) salmon contribution for individual wolves. Salmon proportions were transformed using an arcsine transformation in order to use parametric statistical tests (Krebs 1989).

We tested the null hypothesis that there was no difference in use of salmon between southeast and interior Alaska wolves using an F -test on the transformed proportions (SAS 1985). To test the hypothesis that there were no differences in salmon diet among wolves across southeast Alaska, we incorporated age, year, and area factors into analyses of variance (ANOVA) on the transformed proportions. We explored variation among individual wolf diets using Levene's test of homogeneity by calculating the average deviation from the mean of each observation by area ($\sqrt{(\bar{x} - x^2)}$), and using a one-way ANOVA with multiple comparisons to investigate significant differences in variation among areas (SPSS 1996).

Results

Stable isotope values for wolves in southeast Alaska ($n = 163$) reflected a broad range of terrestrial and marine signatures (Fig. 2). Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (\pm SE) for southeast Alaska wolves were $-22.2 \pm 0.1\text{‰}$ and $7.6 \pm 0.1\text{‰}$, respectively. The mean $\delta^{13}\text{C}$ value for island wolves ($n = 101$) was $-22.7 \pm 0.1\text{‰}$; the mean $\delta^{15}\text{N}$ value was $7.5 \pm 0.1\text{‰}$. Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for wolves on the southeast Alaska coastal mainland ($n = 62$) were $-21.4 \pm 0.3\text{‰}$ and $7.6 \pm 0.3\text{‰}$, respec-

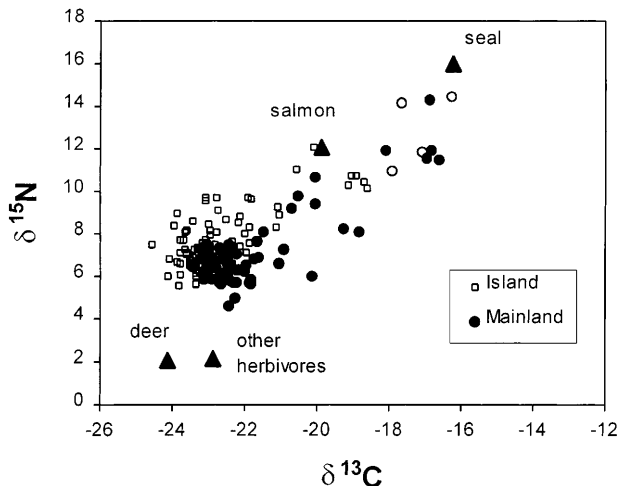


Fig. 2 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for wolves in southeast Alaska. Open circles indicate wolves ($n = 4$) from Yakutat, northern mainland. Mean stable isotope values are given for deer ($n = 14$), other herbivores (moose, voles, mountain goat, beaver; $n = 46$), and salmon ($n = 42$); harbor seal value from Smith et al. (1996)

tively. Yakutat wolves, within the coastal mainland group, showed the most enriched mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values ($-17.2 \pm 0.4\text{‰}$ and $12.9 \pm 0.9\text{‰}$, respectively; $n = 4$). Interior Alaska wolf values ($n = 50$; Fig. 3) averaged $-19.6 \pm 0.1\text{‰}$ for carbon, and $6.4 \pm 0.1\text{‰}$ for nitrogen.

Significant differences in stable isotope ratios were found among prey types using the K nearest-neighbor test ($P < 0.05$; Table 1). Caribou, moose, and salmon – interior Alaska prey species – were isotopically distinct ($P = 0.000$; Fig. 3). Deer, salmon, and other herbivores were isotopically separate prey species for southeast Alaska wolves (Fig. 2). The 'salmon' group ($n = 42$) reflects the mean isotopic signature of coho (*O. kisutch*, $n = 18$), pink (*O. gorbuscha*, $n = 21$) and chum (*O. keta*, $n = 3$) salmon. Although pink and chum salmon were isotopically different from coho salmon ($P = 0.036$), we combined them to allow for wolf diet comparisons between areas (three prey groups per area). All three species exist in southeast Alaska, but coho salmon are not found in interior Alaska rivers. Violating the mixing model assumption of separate prey groups might not be severe in this case since the three salmon species have close isotopic values that are significantly different from all other prey, and can be considered one functional group representing 'marine' diet.

Southeast Alaska wolves relied significantly more on salmon ($18.3 \pm 1.2\%$, $n = 163$) than did wolves in interior Alaska ($9.1 \pm 0.6\%$, $n = 50$, $P < 0.001$, Fig. 4, Table 1). Likewise, variation among individual wolf diets was higher for southeast Alaska wolves ($SD = 15.5$) than for interior Alaska wolves ($SD = 4.5$, Levene's test of homogeneity, $P < 0.001$; Fig. 5). Relative salmon content ranged from 1.7 to 88.8% in southeast Alaska wolf diets, and only 1.5–26.8% in interior Alaska wolf diets.

A significant three-way interaction among area, year, and age (ANOVA, $P < 0.001$) precluded the demonstration of significant differences in percent salmon

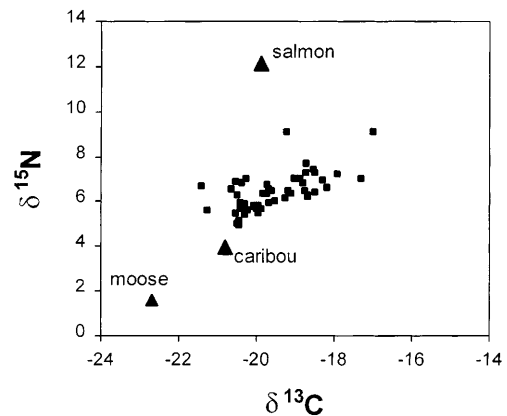


Fig. 3 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for wolves in northern interior Alaska. Mean stable isotope values are given for caribou ($n = 41$; Barnett 1994), moose ($n = 5$), and salmon ($n = 42$; Ben-David 1996)

Table 1 Mean (\pm SE) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for and relative contribution of prey items to southeast and interior Alaska wolf diets. Percentages of prey in the diet were calculated by the dual-isotope mixing model

Species	<i>n</i>	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	Relative contribution in wolf diet (% mean \pm SE)			
				Kupreanof (<i>n</i> = 50)	Mainland (<i>n</i> = 62)	P.O.W. (<i>n</i> = 51)	Interior Alaska (<i>n</i> = 50)
Deer	14	-24.1 ± 0.2	2.1 ± 0.3	49.0 ± 1.2	48.7 ± 1.9	44.7 ± 1.2	
Other herbivores	46	-22.9 ± 0.2	2.2 ± 0.3	35.7 ± 0.4	34.4 ± 1.1	36.2 ± 0.5	
Salmon	42	-19.9 ± 0.3	12.1 ± 0.2	15.3 ± 1.3	20.0 ± 2.7	19.1 ± 1.5	9.1 ± 0.6
Caribou	41	-20.8 ± 0.0	4.0 ± 0.1				55.2 ± 3.0
Moose	5	-22.7 ± 0.8	1.6 ± 0.4				35.7 ± 2.9

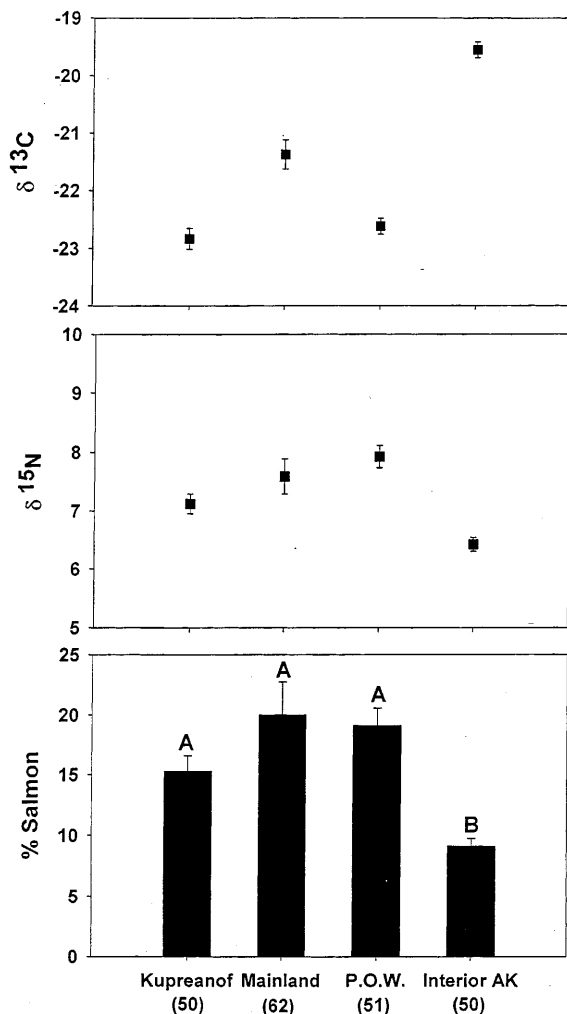


Fig. 4 Mean (\pm SE) stable isotope and % *Salmon* values for wolves from southeast and interior Alaska. Different letters indicate significant differences at $\alpha = 0.05$ (*F*-test on arcsine-transformed proportions). Sample sizes are given below bars

among all southeast Alaska areas. However, effects of year and age on diet were apparent for some areas. Wolves on Kupreanof Island had a significantly higher marine signature during the 1990s (20.4%, $n = 50$, $P = 0.031$; Table 2) but there were no dietary differences due to age ($P = 0.764$). Year and age significantly interacted for coastal mainland wolves ($P = 0.012$). A

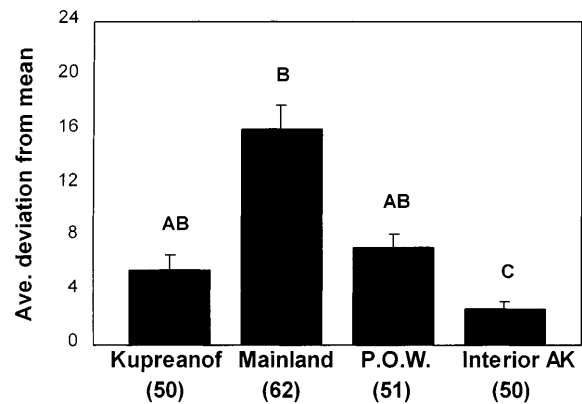


Fig. 5 Mean (\pm SE) differences in variation among southeast and interior Alaska wolves. Different letters indicate significant differences at $\alpha = 0.05$ (Levene's test of homogeneity and one-way ANOVA with Bonferroni multiple comparisons). Sample sizes are given in parentheses

subsequent one-way ANOVA indicated that mainland adult and juvenile diets did not differ ($P = 0.785$) but wolves of both age cohorts in 1990 had diets higher in salmon content than in 1960 ($P = 0.001$; Table 2). No differences in year or age were observed for wolves on Prince of Wales Island or in interior Alaska ($P > 0.100$). The relative contribution of salmon in wolf diets varied significantly among the four areas (Levene's test of homogeneity, $P < 0.001$; Fig. 5). Bonferroni multiple comparisons revealed that variation among individual wolf diets on the southeast Alaska mainland was higher than in other areas ($P < 0.001$). Variance between juveniles and adults, and between years, was not significantly different.

Discussion

Causes of stable isotopic variation among areas

Regardless of the extent of salmon resources in southeast Alaska, it was entirely possible that wolves in this region did not significantly utilize them. Wolf populations in southeast Alaska were purported to have a strong preference for deer, similar to that of interior Alaska wolves for caribou. However, we found that salmon significantly

Table 2 Relative contribution (mean \pm SE) of salmon in the diet of wolves by area, year, and age. Percentages were calculated using the dual-isotope mixing model

Area	1960						1990					
	Adult			Juvenile			Adult			Juvenile		
	%	SE	<i>n</i>	%	SE	<i>n</i>	%	SE	<i>n</i>	%	SE	<i>n</i>
Kupreanof Island	13.2	1.7	20	13.9	1.0	5	19.9	6.9	17	20.6	5.1	8
Coastal mainland	8.9	0.5	17	17.9	2.9	6	55.2	10.2	32	26.2	12.9	7
Prince of Wales Island	20.9	3.9	9	20.6	4.4	17	14.1	1.2	11	22.8	2.5	14
Interior Alaska	9.9	1.5	13	7.9	1.8	12	8.7	0.8	13	9.8	0.7	12

augmented diets of southeast Alaska wolves compared to diets of their counterparts in interior Alaska. We were able to reject the hypothesis of no difference in constancy of wolf diet between regions, demonstrating that individual wolves in southeast Alaska do significantly expand their diet to include salmon. Hence, diets of wolves in this region overall were more opportunistic and showed less specialization to a uniformly deer diet. Comparisons between coastal and inland coyotes in Baja, California, showed similar patterns of expanded dietary breadth in coastal individuals (Rose and Polis 1998). Diets of coyotes along the coast were more varied and the trophic diversity of scat contents at coastal study sites was significantly broader than inland site scat contents. Although interior Alaska wolf samples were selected over the entire northern Alaska region during two time periods, they showed little isotopic variation. Angerbjorn et al. (1994) similarly reported that arctic foxes from the coast of Iceland had significantly higher variance in $\delta^{13}\text{C}$ values than inland fox samples collected throughout the island. Higher variation among individual wolf diets in southeast Alaska may have been due to the inclusion of marine prey items other than salmon in some wolf diets. Eulachon smelt, common in large mainland rivers, spawn in the spring when other food resources tend to be limited (Willson and Halupka 1995). Additionally, mussels, crabs, and other marine invertebrates are readily accessible in the intertidal zone. These marine resources, though not analyzed in this study, are available year-round and may have contributed to the more enriched stable isotope values of southeast Alaska wolves.

Although wolves in northern interior Alaska have access to several terrestrial and some fish prey items, their greater reliance on caribou was evident from stable isotope analysis. This conclusion was supported by Ballard et al. (1997), who showed the importance of caribou in wolf diets despite the presence of ground squirrels, hares, and moose. Stephenson and James (1982) also reported dietary specialization of caribou within northern interior Alaska wolf diets. We found most stable isotope values for interior wolves resided near the mean caribou value (Fig. 4). The scatter of enriched wolf values paralleled the varied stable isotope values of caribou (Barnett 1994) and was probably a reflection of the forb/shrub/lichen diet of caribou.

In addition to diet, ecosystem variability likely contributed to observed differences between southeast and interior Alaska wolf isotope values. Stable isotope signatures have been shown to vary among biomes due to soil differences, water regimes, and plant types (Ambrose 1991; Cormie and Schwarcz 1994). For example, although $\delta^{13}\text{C}$ values from interior Alaska wolves were highly enriched and appear 'marine', $\delta^{15}\text{N}$ values were relatively low. This suggests those wolves, rather than having a marine diet, consume caribou subsisting on a shrub/lichen diet. Water-stressed lichens retain available water, assimilate more of the heavy isotope ^{13}C , and generally show more enriched $\delta^{13}\text{C}$ values (Barnett 1994). Mean $\delta^{13}\text{C}$ values for lichens in interior Alaska and the Yukon Territory were -23.3‰ (Barnett 1994) and -22.8‰ (M. Ben-David and D.S. Hik, unpublished data), respectively. This carbon enrichment would subsequently be incorporated into caribou tissues. Southeast Alaska understory plants, on the other hand, tend to show more depleted $\delta^{13}\text{C}$ values (Ben-David et al. 1998). Sitka black-tailed deer ^{13}C values appeared to be similarly depleted as their diet includes forbs and low-growing evergreen plants (Kirchhoff and Larson 1998). As a result, southeast Alaska wolves on a deer diet showed greater depletion in carbon values than interior Alaska wolves on an ungulate diet (Figs. 3, 4).

Salmon content (%) in wolf diets did not significantly differ among areas within southeast Alaska, but the simultaneous enrichment of carbon and nitrogen stable isotopes reflected the high use of salmon by southeast Alaska mainland wolves (Figs. 2, 4). The extreme 'marine' isotope values observed for north mainland (Yakutat) wolves were isotopically similar to values for black bears (*Ursus americanus*) and brown bears (*U. arctos*) on a salmon diet (Hilderbrand et al. 1996), and were closest to mean values obtained for harbor seals in Hudson Bay (Smith et al. 1996) and Alaska (Hobson et al. 1997). Although they were not included in the mixing model, seals may contribute to the diets of wolves in some areas. Harbor seals spend a substantial amount of time on shore at low tide (Terhune and Brillant 1996), where they would be particularly vulnerable to wolves. In Adams Inlet, Glacier Bay National Monument, seals (primarily pups) accounted for nearly one-third of summer wolf diet (Meiklejohn

1994). Although moose were also present in that study area, they were observed in only 5 of 155 wolf scats (3%). Harbor seals and other marine foods were also noted in the diet of wolves introduced on Coronation Island, southeast Alaska, particularly when deer numbers were low (Klein 1995).

Lack of simultaneous enrichment of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values suggests that wolves on islands in southeast Alaska had less marine contribution to their diets and relied more heavily on terrestrial food items (Fig. 4). Deer densities are relatively high on Kupreanof and Prince of Wales Islands, and scat analysis has confirmed a strong reliance of wolves on deer on the latter (Kohira 1997). Although their stable carbon isotope values were relatively depleted, $\delta^{15}\text{N}$ values imply that Prince of Wales Island wolves also foraged at a higher trophic level (Fig. 4). Consuming other carnivores would elevate wolf ^{15}N and, potentially, the ‘% salmon’ values derived from the mixing model. Black bear and mustelid remains have been found in wolf scats on Prince of Wales Island (Kohira 1997). Ligon (1926) noted ‘fatal conflicts’ between wolves and bears on this island, and wolf predation of black bears has been noted elsewhere (Horesji et al. 1984; Paquet and Carbyn 1986; Rogers and Mech 1981). Additionally, harvest of black bears is relatively high on Prince of Wales Island (D. Larsen, Alaska Department of Fish and Game, personal communication), and it seems reasonable to suspect that discarded bear carcasses could supplement wolf diet. Black bear do not occur in high numbers on the coastal mainland and their occurrence in wolf diets on Prince of Wales Island is perhaps unique.

More pronounced than isotopic differences of wolves among areas in southeast Alaska was the magnitude of diet variability; the proportion of salmon in wolf diets was more constant on islands than on the mainland (Fig. 5). Differential availability of ungulates (i.e., deer) may have necessitated a greater reliance on salmon and contributed to the higher dietary variation observed for mainland wolves, rather than differences in salmon availability. Keith (1981) and Marquard-Peterson (1998) suggested that when ungulate density and vulnerability vary, differences in wolf diets are likely to occur. Wolf densities are generally higher where deer are abundant (Van Ballenberghe et al. 1975; Weaver 1994; but see Peterson and Page 1988) and this pattern is evident on southeast Alaska islands (Person et al. 1996). Moose and mountain goat are the primary ungulate prey on the coastal mainland (Fox and Streveler 1986) but kill rates for wolves (and wolf densities) tend to be lower where these species prevail (Carnes et al. 1996; Dale et al. 1995; but see Hayes 1995). Consequently, wolves in southeast Alaska prey on deer when available but likely use more alternative resources where deer are absent or at low densities (i.e., on the coastal mainland). Because availability of ungulate prey may be limited, variation among individual wolf diets on the coastal mainland was higher.

Annual variation

During years of low deer abundance, encounter rates of wolves with deer would likely be reduced. Consequently, other prey items, such as salmon, should have increased importance and contribution in wolf diets. The proximity of Kupreanof Island wolf $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values to the mean deer value implied a diet dependent on deer, a dependency that appeared to have changed over time. After a decline in the deer population on Kupreanof Island during the 1970s (Olson 1979), wolves apparently incorporated more salmon in their diet (Table 2). Deer numbers similarly declined on the coastal mainland during the same time period and wolves showed increased use of salmon during the 1990s. In contrast, severe winter mortality of deer was not observed on Prince of Wales Island, and the range of $\delta^{13}\text{C}$ values for wolves suggested a terrestrial, predominantly deer diet during both the 1960s and 1990s. If isotope ratios of bone collagen, with lower resolution than other tissues, can discern such temporal changes in diet, actual dietary shifts of wolves over time due to fluctuating deer densities may be more extensive.

Implications for predator/prey dynamics

In this study, we found distinct patterns in the stable isotopic signatures of southeast Alaska wolves that suggest they make substantial use of anadromous salmon and, potentially, other marine resources. This may not be surprising considering that wolves are opportunistic predators and that other canids successfully utilize salmon and other marine foods (Andriashek et al. 1985; Rose and Polis 1998). Reviews of wolf food habits generally have not noted fish to be an important prey item (e.g., Mech 1970) but in coastal ecosystems, salmon may be relatively important in wolf diets. Anadromous fish are spatially constrained, relatively easy to capture, and more or less predictable (Willson and Halupka 1995). Additionally, fish and other marine resources in southeast Alaska are available for longer periods than are ungulate neonates, and are therefore less ‘seasonal’ in nature.

Dietary plasticity likely contributes more to the success of wolves in southeast Alaska than would be expected given their purported dependence on black-tailed deer. Results of the mixing model suggested prey items other than deer make up a large portion of wolf diet in all southeast Alaska areas. Even if the dual-isotope mixing model was not accurately assessing percentages of each prey item in wolf diets, the high ratio of deer : other prey is notable. Because wolves in southeast Alaska have the potential to use salmon resources when their primary ungulate prey is unavailable, switching to alternative prey (i.e., a functional response) could ameliorate long-term numerical declines in wolf populations. In southeast Alaska, the potential for marine resources to influence predator/prey relationships is substantial

and future research requires further clarification of the importance of marine diets to coastal wolf population dynamics (i.e., distribution, density, and reproduction).

Acknowledgements We thank the University of Alaska Museum and southeast Alaska wolf trappers for their generous contribution of wolf skulls. Special thanks to Dr. P. Matheus for extending isotopic tutoring and laboratory space, and to M. Kirchhoff and Drs. D. Schell, D. Person, T. Hanley, and K. Hobson for their insight and support. We are grateful to N. Haubenstock for mass spectrometer analysis, Dr. C. Williams for statistical support, and the University of Alaska Fairbanks Department of Biology and Wildlife for office space during data collection. Dr. J. Peek, G. Hilderbrand, Dr. C. Robbins, M. Weinstein, and Dr. D. Murray made helpful comments on earlier versions, and comments of two anonymous reviewers improved the manuscript. Funding for the project was provided by the Alaska Department of Fish and Game, USDA Forest Service, Pacific Northwest Research Station, and the University of Idaho.

References

- Alaback PB (1982) Dynamics of understory biomass in Sitka spruce-western hemlock forests of southeast Alaska. *Ecology* 63:1932–1948
- Alaska Department of Fish and Game (1994) Catalog of waters important for spawning, rearing or migration of anadromous fishes. ADFG, Habitat Division, Juneau, Alaska
- Ambrose SH (1991) Effects of diet, climate and physiology on nitrogen isotope abundances in terrestrial foodwebs. *J Archaeol Sci* 18:293–317
- Andriashek D, Kiliaan HPL, Taylor MK (1985) Observations on foxes, *Alopex lagopus* and *Vulpes vulpes*, and wolves, *Canis lupus*, on the off-shore sea ice of northern Labrador. *Can Field Nat* 99:86–89
- Angerbjorn A, Hersteinsson P, Liden K, Nelson E (1994) Dietary variation in arctic foxes (*Alopex lagopus*): an analysis of stable carbon isotopes. *Oecologia* 99:226–232
- Ballard WB, Ayres LA, Krausman PR, Reed DJ, Fancy SG (1997) Ecology of wolves in relation to a migratory caribou herd in northwest Alaska. *Wildl Monogr* 135
- Barnett BA (1994) Carbon and nitrogen isotope ratios of caribou tissues, vascular plants, and lichens from northern Alaska. MS thesis, University of Alaska, Fairbanks
- Ben-David M (1996) Seasonal diets of mink and martens: effects of spatial and temporal changes in resource abundance. PhD thesis, University of Alaska, Fairbanks
- Ben-David M, Flynn RW, Schell DM (1997a) Annual and seasonal changes in diets of martens: evidence from stable isotope analysis. *Oecologia* 111:280–291
- Ben-David M, Hanley TA, Klein DR, Schell DM (1997b) Seasonal changes in diets of coastal and riverine mink: the role of spawning Pacific salmon. *Can J Zool* 75:803–811
- Ben-David M, Hanley TA, Schell DM (1998) Fertilization of terrestrial vegetation by spawning Pacific salmon: the role of flooding and predator activity. *Oikos* 83:47–55
- Bocherens H, Fizet M, Mariotti A (1994) Diet, physiology and ecology of fossil mammals as inferred from stable carbon and nitrogen isotope biogeochemistry: implications for Pleistocene bears. *Palaeogeogr Palaeoclimatol Palaeoecol* 107:213–225
- Carnes J, Van Ballenberghe V, Peek JM (1996) Ecology of wolves on the Copper and Bering River Deltas, Alaska. Prog Rep US For Serv, PNW Research Station, Anchorage
- Cormie AB, Schwarcz HP (1994) Stable isotopes of nitrogen and carbon of North American white-tailed deer and implications for paleodietary and other food web studies. *Palaeogeogr Palaeoclimatol Palaeoecol* 107:227–241
- Dale BW, Adams LG, Bowyer RT (1995) Winter wolf predation in a multiple ungulate prey system, Gates of the Arctic National Park, Alaska. In: Carbyn LN, Fritts SH, Seip DR (eds) Ecology and conservation of wolves in a changing world. Canadian Circumpolar Institute, University Alberta, Edmonton, pp 223–230
- DeNiro MJ, Epstein S (1978) Influence of diet on the distribution of carbon isotopes in animals. *Geochim Cosmochim Acta* 42:495–506
- DeNiro MJ, Epstein S (1981) Influence of diet on the distribution of nitrogen isotopes in animals. *Geochim Cosmochim Acta* 45:341–351
- Floyd TJ, Mech LD, Jordan PA (1978) Relating wolf scat content to prey consumed. *J Wildl Manage* 42:528–532
- Fox JL, Streveler GP (1986) Wolf predation on mountain goats in southeastern Alaska. *J Mammal* 67:192–195
- Hart JL (1973) Pacific fishes of Canada. Fisheries Research Board of Canada, Ottawa
- Hayes RD (1995) Numerical and functional responses of wolves and regulation of moose in the Yukon. MS thesis, Simon Fraser University, British Columbia
- Hilderbrand GV, Farley SD, Robbins CT, Hanley TA, Titus K, Servheen C (1996) Use of stable isotopes to determine diets of living and extinct bears. *Can J Zool* 74:2080–2088
- Hobson KA, Sealy SG (1991) Marine protein contributions to the diet of northern saw-whet owls on the Queen Charlotte Islands: a stable-isotope approach. *Auk* 108:437–440
- Hobson KA, Sease JL (1998) Stable isotope analyses of tooth annuli reveal temporal dietary records: an example using Stellar sea lions. *Mar Mammal Sci* 14:116–129
- Hobson KA, Stirling I (1997) Low variation in blood $\delta^{13}\text{C}$ among Hudson Bay polar bears: implications for metabolism and tracing terrestrial foraging. *Mar Mammal Sci* 13:359–367
- Hobson KA, Sease JL, Merrick RL, Piatt JF (1997) Investigating trophic relationships of pinnipeds in Alaska and Washington using stable isotope ratios of nitrogen and carbon. *Mar Mammal Sci* 13:114–132
- Horejsi BL, Hornbeck GE, Raine RM (1984) Wolves, *Canis lupus*, kill female black bear, *Ursus americanus*, in Alberta. *Can Field Nat* 98:368–369
- Keith LB (1981) Population dynamics of wolves. In: Carbyn LN (ed) Wolves in Canada and Alaska: their status, biology, and management. *Can Wildlife Serv Rep Ser* 45:66–77
- Kirchhoff MD (1994) Rescue for a rainforest. *Defenders* 69:9–17
- Kirchhoff MJ (1996) Deer pellet-group surveys in southeast Alaska. Alaska Department of Fish and Game, Douglas
- Kirchhoff MD, Larsen DN (1998) Dietary overlap between native Sitka black-tailed deer and introduced elk in southeast Alaska. *J Wildl Manage* 62:236–242
- Klein DR (1995) The introduction, increase, and demise of wolves on Coronation Island, Alaska. In: Carbyn LN, Fritts SH, Seip DR (eds) Ecology and conservation of wolves in a changing world. Canadian Circumpolar Institute, University Alberta, Edmonton, pp 275–280
- Kline TC, Goering JJ, Mathisen OA, Poe PH (1990) Recycling of elements transported upstream by runs of Pacific salmon. I. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ evidence in Sashin Creek, southeastern Alaska. *Can J Fish Aquat Sci* 47:136–144
- Knapp SE, Millemann RE (1970) Salmon poisoning disease. In: Davis JW, Karstad LH, Trainer DO (eds) Infectious diseases of wild mammals. Iowa State University Press, Ames, pp 332–342
- Kohira M (1997) Diets of wolves, *Canis lupus*, in logged and unlogged forests of southeastern Alaska. *Can Field Nat* 111:429–435
- Krebs CJ (1989) Ecological methodology. Harper Collins, New York, NY
- Krueger HW, Sullivan CH (1984) Models for carbon isotope fractionation between diet and bone. In: Stable isotopes in nutrition. American Chemical Society, Washington, DC, pp 205–220
- Ligon JS (1926) When wolves forsake their ways. *Nat Mag* 7:156–159
- MacDonald SO, Cook JA (1996) The land mammal fauna of southeast Alaska. *Can Field Nat* 110:571–598
- Marquard-Peterson (1998) Food habits of arctic wolves in Greenland. *J Mammal* 79:236–244

- Matheus PE (1997) Paleo-ecology and ecomorphology of the giant short-faced bear in east Beringia. PhD thesis, University of Alaska, Fairbanks
- Mech LD (1970) The wolf: the ecology and behavior of an endangered species. Doubleday/Natural History, Garden City, NY
- Meiklejohn BA (1994) Ecology and sensitivity to human disturbance of a wolf pack at Glacier Bay National Park and Preserve, Alaska. Unpublished report, Field Naturalist Prog, University of Vermont, Burlington
- Olson ST (1979) The life and times of the black-tailed deer in southeast Alaska. In: Wallmo OC, Schoen JW (eds) Sitka black-tailed deer: proceedings of a conference in Juneau. US Department of Agriculture, US Forest Service, Alaska Region, ser no R10-48, pp 160-168
- Paquet PC, Carbyn LN (1986) Wolves, *Canis lupus*, killing denning black bears, *Ursus americanus*, in the Riding Mountain National Park area. *Can Field Nat* 100:371-372
- Person DK, Kirchhoff MD, VanBallenberghe V, Iverson GC, Grossman E (1996) The Alexander Archipelago wolf: a conservation assessment. Gen Tech Rep PNW-GTR-384, Portland, Ore
- Peterson RO, Page RE (1988) The rise and fall of Isle Royale wolves, 1975-1986. *J Mammal* 69:89-99
- Rausch RA (1967) Some aspects of the population ecology of wolves, Alaska. *Am Zool* 7:253-265
- Rogers LL, Mech LD (1981) Interactions of wolves and black bears in northeastern Minnesota. *J Mammal* 62:434-436
- Rose MD, Polis GA (1998) The distribution and abundance of coyotes: the effects of allochthonous food subsidies from the sea. *Ecology* 79:998-1007
- Rosing MN, Ben-David M, Barry RP (1998) Analysis of stable isotope data: a k nearest-neighbors randomization test. *J Wildl Manage* 62:380-388
- SAS (1985) SAS user's guide. SAS Institute, Cary, NC
- Scott BM, Shackleton DM (1982) A preliminary study of the social organization of the Vancouver Island wolf. In: Harrington FH, Paquet PC (eds) *Wolves of the world*. Noyes, Park Ridge, NJ, pp 13-25
- Smith RJ, Hobson KA, Koopman HN, Lavigne DM (1996) Distinguishing between populations of fresh- and salt-water harbour seals (*Phoca vitulina*) using stable-isotope ratios and fatty acid profiles. *Can J Fish Aquat Sci* 53:272-279
- SPSS (1996) SPSS for Windows. SPSS, Chicago
- Stafford TW, Brendel K, Duhamel R (1988) Radiocarbon ^{13}C and ^{15}N analysis of fossil bone: removal of humates with XAD-2 resin. *Geochim Cosmochim Acta* 52:2257-2267
- Stephenson RO, James D (1982) Wolf movements and food habits in northwest Alaska. In: Harrington FH, Paquet PC (eds) *Wolves of the world*. Noyes, Park Ridge, NJ, pp 26-42
- Sugai SF, Burrell DC (1984) Transport of dissolved organic carbon, nutrients, and trace metals from the Wilson and Blossom Rivers to Smeaton Bay, southeast Alaska. *Can J Fish Aquat Sci* 41:180-190
- Terhune JM, Brillant SW (1996) Harbour seal vigilance decreases over time since haul out. *Anim Behav* 51:757-763
- Tieszen LL, Boutton TW, Tesdahl KG, Slade NA (1983) Fractionation and turnover of stable carbon isotopes in animal tissues: implications for $\delta^{13}\text{C}$ analysis of diet. *Oecologia* 57:32-37
- Van Ballenberghe V, Erickson AW, Byman D (1975) Ecology of the timber wolf in northeastern Minnesota. *Wildl Monogr* 43:1-43
- Weaver JL (1994) Ecology of wolf predation amidst high ungulate diversity in Jasper National Park, Alberta. PhD thesis, University of Montana, Missoula
- Willson MF, Halupka KC (1995) Anadromous fish as keystone species in vertebrate communities. *Conserv Biol* 9:489-497