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Are inland wolf–ungulate systems influenced by marine subsidies of Pacific salmon?

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Abstract. Wolves (*Canis lupus*) in North America are considered obligate predators of ungulates with other food resources playing little role in wolf population dynamics or wolf–prey relations. However, spawning Pacific salmon (*Oncorhyncus* spp.) are common throughout wolf range in northwestern North America and may provide a marine subsidy affecting inland wolf–ungulate food webs far from the coast. We conducted stable-isotope analyses for nitrogen and carbon to evaluate the contribution of salmon to diets of wolves in Denali National Park and Preserve, 1200 river-km from tidewater in interior Alaska, USA. We analyzed bone collagen from 73 wolves equipped with radio collars during 1986–2002 and evaluated estimates of salmon in their diets relative to the availability of salmon and ungulates within their home ranges. We compared wolf densities and ungulate : wolf ratios among regions with differing salmon and ungulate availability to assess subsidizing effects of salmon on these wolf–ungulate systems. Wolves in the northwestern flats of the study area had access to spawning salmon but low ungulate availability and consumed more salmon (17% ± 7% [mean ± SD]) than in upland regions, where ungulates were sixfold more abundant and wolves did or did not have salmon spawning areas within their home ranges (8% ± 6% and 3% ± 3%, respectively). Wolves were only 17% less abundant on the northwestern flats compared to the remainder of the study area, even though ungulate densities were 78% lower. We estimated that biomass from fall runs of chum (*O. keta*) and coho (*O. kisutch*) salmon on the northwestern flats was comparable to the ungulate biomass there, and the contribution of salmon to wolf diets was similar to estimates reported for coastal wolves in southeast Alaska. Given the ubiquitous consumption of salmon by wolves on the northwestern flats and the abundance of salmon there, we conclude that wolf numbers in this region were enhanced by the allochthonous subsidy provided by salmon and discuss implications for wolf–ungulate relations.

Key words: allochthonous subsidies; apparent competition; Canis lupus; *$\delta^{13}C$; $\delta^{15}N$; Denali National Park and Preserve, Alaska, USA; marine-derived nutrients;* Oncorhynchus *spp.; Pacific salmon; predator–prey relations; ungulates; wolves.*

Introduction

Gaining insights into the relationships between wolves (*Canis lupus*; see Plate 1) and their prey is essential to guide the complex management of wolves, as well as inform the contentious scientific and public debates on the role of wolves in ecosystems they inhabit (National Research Council 1997, Fritts et al. 2003). Throughout North America, wolves are viewed as obligate predators of ungulates with other prey contributing little to wolf diets (Peterson and Ciucci 2003). Thus, little effort has been expended to consider the role of non-ungulate prey in the dynamics and ecosystem effects of wolf populations, even though wolves are known to consume a wide array of other prey (Peterson and Ciucci 2003). Recently, Pacific salmon (*Oncorhynchus* spp.) have been recognized as an important diet constituent for coastal wolf populations (Szepanski et al. 1999, Darimont and Reimchen 2002, Darimont et al. 2003, 2008). Although the potential for salmon to be important to inland wolves has been suggested (Darimont and Reimchen 2002, Darimont et al. 2008), salmon have largely been ignored as a food source for inland wolves (Peterson and Ciucci 2003).

Most tissue of individual salmon accrues during growth at sea and this marine-derived biomass is delivered to freshwater systems where salmon spawn and die (Willson et al. 2004). Considerable attention has been given to the marine-derived nutrient inputs provided by anadromous Pacific salmon to freshwater and terrestrial ecosystems (Cederholm et al. 1999, Gende

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et al. 2004, Willson et al. 2004, Merz and Moyle 2006) and the importance of salmon to a variety of terrestrial carnivores (Ben-David et al. 1997*a*, *b*, Hilderbrand et al. 1999, Szepanski et al. 1999, Belant et al. 2006). Influences of salmon-derived nutrients have been investigated almost entirely in coastal or near-coastal (<100 river-km from tidewater) regions; we are aware of only one published account on the topic at greater distances from the ocean (Belant et al. 2006). However, Pacific salmon are seasonally abundant and widely distributed far inland. For example, the Yukon River Basin, the largest drainage within the North American range of Pacific salmon, encompasses 845 000 km^2 of Alaska, Yukon Territory, and northern British Columbia (Brabets et al. 2000). On average, over 2.5 million salmon migrate each summer into the Yukon River system, dispersing to spawning areas as far as 3000 km by river from tidewater (Joint Technical Committee of the Yukon River US/Canada Panel [JTC] 2007*a*, *b*). Marine ecosystems are substantially more productive than terrestrial ecosystems at high latitudes (35–70° N; Gross et al. 1988, Erlandson et al. 2007); thus, Pacific salmon constitute a nutrient subsidy originating in a productive marine environment with great potential to influence comparatively depauperate terrestrial food webs that are far inland.

Where spawning salmon occur, wolves would be expected to consume them extensively because, as a meat source, they are: (1) available for several months during spawning in summer and fall and as carrion long after; (2) predictably clumped and locally abundant at spawning areas; and (3) less risky or costly to acquire than dangerous or fleet ungulate prey. Further, in Alaska and the Yukon Territory, ungulate densities are quite low over vast regions (Gasaway et al. 1992); thus salmon could provide a particularly important food resource for wolves in this portion of their North American range.

Anadromous salmon are an example of nutrient transport across ecosystem boundaries; the implications of such allochthonous subsidies for the structure and dynamics of recipient food webs are well recognized (Polis et al. 1997, Huxel et al. 2004, Loreau and Holt 2004). If sufficient in magnitude, ecosystem subsidies to predators commonly result in increased predator numbers and increased predation pressure on resident prey through a top-down process analogous to apparent competition (Holt 1977, Polis et al. 1997). This outcome is particularly likely if resident prey are rare (Polis et al. 1997, Estes et al. 2001) or the predator exhibits a strong numerical response to increased food availability (Estes et al. 2001). Alternatively, predation on resident prey can be relaxed if the predator feeds mainly on the allochthonous resource (Huxel et al. 2004). As a consequence of either outcome, allochthonous subsidies commonly lead to food web dynamics that are inconsistent with models based only on local resource and consumer conditions (Polis et al. 1997).

We employed stable-isotope analyses to assess consumption of salmon by wolves in Denali National Park and Preserve (DNPP) in central Alaska, 1200 km via the Yukon River and its tributaries from the Bering Sea coast. Stable isotopes have been used with success to apportion diets between marine and terrestrial sources owing to predictable differences in isotopic composition of materials of marine or terrestrial origin (Chisholm et al. 1982, Gannes et al. 1998, Kelly 2000). Further, because stable isotope approaches estimate contributions of food items that are assimilated into consumer tissues, biases relative to prey size and digestibility inherent in other methods used to estimate wolf diets are not an issue (Hilderbrand et al. 1996, Gannes et al. 1998).

Research on wolf population dynamics in DNPP during 1986–2002 (Mech et al. 1998; L. G. Adams, *unpublished data*) provided a unique opportunity to investigate the use of salmon by wolves relative to the distribution of spawning salmon and ungulates on the landscape. In addition to documenting wolf distribution and abundance via radiotelemetry, skeletal remains of most wolves that were equipped with radio collars and subsequently died in or near the study area were regularly archived. Measurement of stable carbon (C) and nitrogen (N) isotope ratios of bone collagen allowed for appraisal of the long-term assimilation of food resources by these wolves. Bone collagen is remodeled at a rate such that isotope measurements are thought to reflect diets integrated over a period ranging from a few years (Gannes et al. 1998, Bocherens and Drucker 2007) to an individual's entire life (Braune et al. 2005). Because we knew the spatial distribution of home ranges of wolves we sampled, we could assess the contribution of salmon to wolf diets relative to the availability of salmon and ungulates across the Denali landscape. Finally, with data on the sizes and home ranges of nearly all wolf packs in the study area during this 16-year period, we could evaluate evidence of effects of salmon availability on wolf abundance. We hypothesized that where ungulate abundance was low and salmon were widely available, salmon would be well-represented in diets of wolves and that wolf numbers would be higher than expected from ungulate availability alone.

METHODS

Study area

The study area (15 400 km^2; 63° N, 151° W) included the portion of DNPP north of the Alaska Range crest <1830 m in elevation (Fig. 1). Populations of wolves and ungulates were little affected by human harvests within our study area (Mech et al. 1998). During 1986–2002, wolf densities averaged 5.3 and 6.9 wolves/1000 km^2 in mid-March and early October, respectively (Mech et al. 1998; L. G. Adams, *unpublished data*). Wolves were distributed throughout the area in packs that averaged 6.1 and 7.6 wolves (2–29 wolves/pack) in late winter and fall, respectively, and maintained

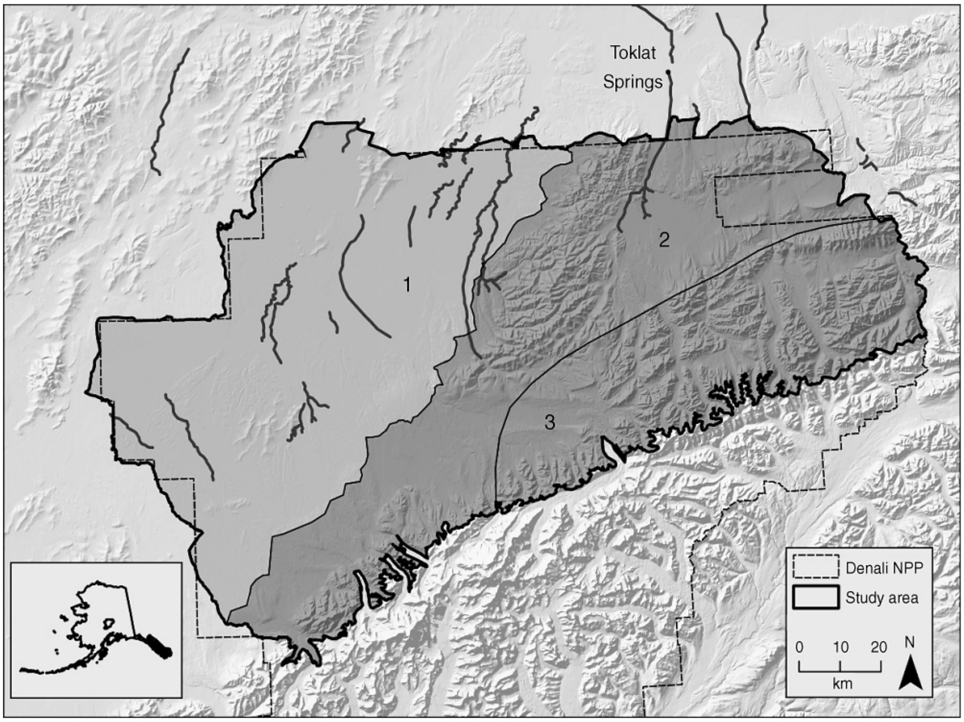

FIG. 1. Study area for investigations of wolf population dynamics during 1986–2002, Denali National Park and Preserve (NPP), Alaska, USA. Regional ungulate densities (light gray, 70 moose equivalents/1000 km^2; dark gray, 320 moose equivalents/1000 km^2), known and suspected salmon spawning areas (dark gray stream segments), and resulting categories of ungulate and salmon availability (1, salmon present, low ungulate density; 2, salmon present, high ungulate density; and 3, no salmon, high ungulate density) are depicted.

distinct, but overlapping, home ranges (Mech et al. 1998; L. G. Adams, *unpublished data*). Moose (*Alces alces*), caribou (*Rangifer tarandus*), and Dall's sheep (*Ovis dalli*) constituted the ungulate prey available to wolves in DNPP. In early winter, (ca. 1 November) ~2000 moose occurred within the study area, at densities of 200 moose/1000 km^2 in the mountains and foothills and 50 moose/1000 km^2 in the northwestern lowland spruce flats (U.S. National Park Service [NPS], *unpublished manuscripts*). The study area encompassed most of the range of the Denali caribou herd (averaging 2300 caribou in autumn during the study; Adams 2005) and the Tonzona caribou herd's (~1000 caribou; NPS, *unpublished manuscripts*) range overlapped the western periphery. Caribou mainly utilized open habitats in the mountains and foothills, with limited seasonal use of forested lowlands (L. G. Adams, *unpublished data*). Approximately 2000 Dall's sheep occurred primarily in the eastern mountains of the study area (NPS, *unpublished manuscripts*). Given each species' numbers and distribution throughout the year, ungulates were substantially more abundant in the open, upland habitats along the Alaska Range and eastern foothills of the study area (320 moose equivalents/1000 km^2; 1 moose equivalent = 1 moose, 3 caribou, or 6 sheep, following Keith [1983] and Fuller [1989]) than in the lowland, spruce-covered flats to the northwest (70 moose equivalents/1000 km^2; Fig. 1). Wolves also occasionally preyed on beaver (*Castor canadensis*), snowshoe hares (*Lepus americanus*), Arctic ground squirrels (*Spermophilus parryii*), hoary marmots (*Marmota caligata*), and various birds (Mech et al. 1998). Further, wolves in the study area have been observed consuming salmon on occasion (Mech et al. 1998; D. C. Miller, *personal observations*).

Three species of salmon occurred within the study area. Chinook salmon (*O. tshawytscha*), the largest of the three species (averaging 8.5 kg vs. 3.1 and 2.7 kg for chum [*O. keta*] and coho [*O. kisutch*], respectively; Alaska Department of Fish and Game [ADFG] 2006), arrived first in early July followed shortly by a summer run of chum salmon in mid-July. A second run of chum salmon reached the area in late August and spawned into November. Coho salmon arrived last in a run slightly later but overlapping the fall chum run.

The Kantishna River drained most of the study area (78%); the Nenana River and the Swift Fork of the Kuskokwim River drained the eastern and western margins, and all three river systems supported spawning salmon. Whereas information on the magnitude of salmon runs within the Denali region was limited, there was substantial information on fall chum salmon in the Kantishna River system. Since 1974, counts of spawning fall chums at Toklat Springs, 15 km north of the study area (Fig. 1), have been conducted annually to index population trends (Bue et al. 2006). During 1999–2005, fall chum population estimates in the Kantishna drainage were derived annually via mark–recapture methods, ranging from 21 500 to 107 700 salmon (Cleary and Hamazaki 2006). Based on these data, we estimated that an average of ~73 000 fall chums spawned annually during 1986–2002 within the Kantishna River drainage and annual runs may have varied by more than an order of magnitude, from 21 000 to 240 000 salmon. Little information existed on abundance of the other three salmon populations in the Kantishna system. Coho were probably second in number to fall chums, averaging about 5000 annually (P. M. Cleary, *personal communication*). Chinook and summer chums were less common, with each averaging $\leq$2000 salmon per year (Eiler et al. 2004, JTC 2007*a*; B. M. Borba, *personal communication*; T. R. Spencer, *personal communication*). All three salmon species also spawned in the Swift Fork and Nenana River portions of the study area, but salmon numbers there were unknown.

Wolf distribution and abundance

Investigations of wolf population dynamics at DNPP have been described in detail elsewhere (Mech et al. 1998). In brief, the distribution and sizes of wolf packs were monitored by equipping two to three wolves per pack with radio collars via helicopter darting and then locating them approximately every two weeks from light aircraft, with additional observations in late September–early October and March to obtain fall and late-winter pack counts, respectively. Home ranges of wolf packs were determined by the minimum convex polygon method with locations accumulated over two-year periods to ensure adequate sample sizes (Burch et al. 2005). We categorized wolves sampled for isotope analyses relative to salmon and ungulate availability within home ranges of their packs. We compared pack sizes in fall (ca. 1 October) and late winter (ca. 15 March), home range sizes of wolf packs, within-pack wolf densities (pack size/home range size), and ungulate : wolf ratios relative to salmon and ungulate distribution in the study area. We limited analyses of home range sizes to those based on $\geq$40 radiolocations to reduce sample size effects on home range estimates (Burch et al. 2005). We used within-pack densities rather than densities calculated for regions of the study area because the numbers of packs within regions were often small enough to bias density estimates (fewer than six packs; Burch et al. 2005), and average within-pack densities were strongly correlated with population-wide estimates of wolf density across North American studies ($r = 0.95$, $n = 30$, $P < 0.001$; data from Fuller et al. 2003:165–174).

Sample collection

During 1986–2002, we obtained samples of bone from 73 wolves that were equipped with radio collars and monitored as part of the DNPP research and that died in or near the study area. These wolves were $\geq$9 months old when initially captured and were radiotracked for an average of 761 days (range 19–2665 days). We categorized each wolf based on whether spawning salmon were likely to occur within the home range of its pack and whether its pack lived predominantly on the northwestern flats where ungulate abundance was low, yielding three groups: (1) salmon present, low ungulate density; (2) salmon present, high ungulate density; and (3) no salmon, high ungulate density (Fig. 1).

The isotopic composition of ungulate prey was determined from blood samples collected in fall (late September–early November) and late winter (mid- to late March) during studies of moose and caribou in DNPP (Adams and Dale 1998; L. G. Adams, *unpublished data*) and blood samples and hair collected in mid-March from Dall's sheep 60 km east of our study area (Arthur 2003). Red blood cells from fall and late winter were assumed to represent isotopic composition of these ungulates during the three months prior to collection (mid-summer to fall and mid- to late winter for fall and late-winter collections, respectively; Hilderbrand et al. 1996, Ben-David et al. 2001), whereas sheep hair samples provided estimates during summer and fall when the hair was produced (Hilderbrand et al. 1996, Darimont and Reimchen 2002). Isotope composition of salmon was determined from recently spawned fall chums collected in mid-October from the Toklat Springs spawning area. All ungulate and salmon samples were kept frozen until processed for isotopic analyses.

Sample preparation and isotopic analysis

Wolf bones were initially cleaned of soft tissues in hot water and detergent, then broken into small chunks, washed in a weak detergent solution, thoroughly rinsed in deionized water, and dried. Next, samples were ground in a cryomill and lipids were extracted by washing three times in a 2:1 chloroform : methanol mixture. Approximately 0.5 g of resulting powder was washed three times with 10 mL 0.25 mol/L HCl and air-dried. Collagen was extracted from bone as described by Chisholm et al. (1983), then freeze-dried and ground. Red blood cells collected from ungulate prey were freeze-dried, then ground to a fine powder. Sheep hair samples were washed in a mild detergent solution, rinsed several times in distilled water, washed three times in a 2:1 chloroform : methanol solvent, allowed to air-dry, then finely chopped. Salmon tissue samples were freeze-dried, then ground to a fine powder in a cryomill. Approximately 2.0 mg of each of the resulting samples were loaded into tin capsules for isotopic analyses.

Prepared samples were analyzed for stable C and N isotopes by continuous-flow isotope ratio mass spectrometry using an elemental analyzer coupled to a mass spectrometer (Fry et al. 1992). Results are reported in δ notation as deviations in parts per thousand (‰) relative to a standard (Vienna PeeDee Belemnite [VPDB] and air

PLATE. 1. A wolf (*Canis lupus*) in Denali National Park and Preserve, Alaska (USA). Photo credit: Tom Meier, U.S. National Park Service.

for $\delta^{13}C$ and $\delta^{15}N$, respectively) calculated as follows:

$$\delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 10^3$$

where X is ^{13}C or ^{15}N and R is the appropriate ^{13}C:^{12}C or ^{15}N:^{14}N ratio. Analytical sequences included laboratory standards, and reproducibility of results was generally better than ±0.2‰ based on repeated analyses of standards and samples.

Isotopic ratios commonly change as dietary constituents are assimilated via differential retention of isotopes during metabolism and tissue synthesis; these processes generally enrich tissues in ^{13}C and ^{15}N (Hilderbrand et al. 1996, Kelly 2000). To account for diet tissue discrimination, we used values for enrichment from diet to blood cells in captive red foxes (*Vulpes vulpes*; +0.6‰ and +2.6‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively; Roth and Hobson 2000) and added adjustments for enrichment we noted from wolf red blood cells to bone collagen (+2.6‰ and +0.8‰, respectively; L. G. Adams, *unpublished data*); thus, prey signatures were adjusted by +3.2‰ and +3.4‰ to account for diet to bone collagen discrimination of ^{13}C and ^{15}N, respectively.

TABLE 1. Wolf diet analysis: $\delta^{13}C$ and $\delta^{15}N$ from bone collagen and estimated salmon (*Oncorhyncus* spp.) consumption by wolves (*Canis lupus*) categorized by the presence or absence of spawning salmon and ungulate abundance (low or high) within their home ranges, Denali National Park and Preserve, Alaska, USA, 1986–2002.

		$\delta^{13}C$ (‰)			$\delta^{15}N$ (‰)			Salmon in diet (%)		
Wolf group	*n*	Mean	SD	Range	Mean	SD	Range	Mean	SD	Range
1) Salmon, low ungulate	27	−20.1	0.54	−21.2 to −19.1	7.1	0.80	6.1–8.9	17	7.3	8–34
2) Salmon, high ungulate	29	−19.7	0.57	−20.8 to −18.7	6.1	0.64	5.1–7.3	8	5.7	0–19
3) High ungulate only	17	−19.8	0.67	−21.2 to −18.7	5.4	0.45	4.8–6.3	3	3.0	0–10
Combined	73	−19.9	0.61	−21.2 to −18.7	6.3	0.94	4.8–8.9	10	8.2	0–34

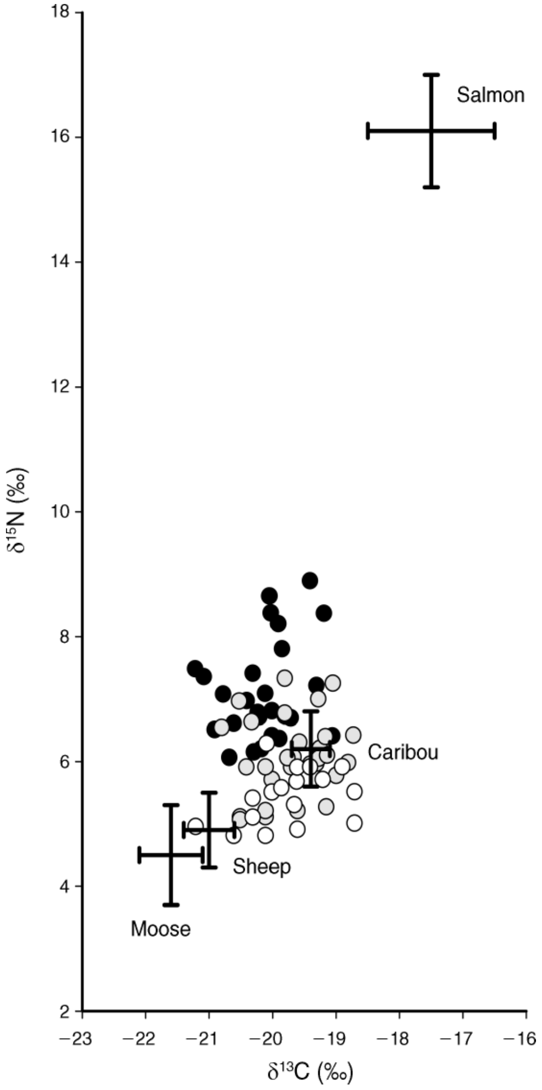

FIG. 2. Values of δ^{13}C and δ^{15}N from bone collagen of wolves ($n = 73$), Denali National Park and Preserve, Alaska. Wolves were categorized by salmon and ungulate availability within their home ranges: solid circles, group 1 (salmon, low ungulate abundance); gray circles, group 2 (salmon, high ungulate abundance); and open circles, group 3 (no salmon, high ungulate abundance). Mean values ± SD are indicated for ungulate prey and salmon (Table 2) adjusted to account for trophic enrichment (+3.2‰ and +3.4‰ for δ^{13}C and δ^{15}N, respectively).

Data analysis

We employed *K* nearest neighbors randomization tests (KNNRT; Rosing et al. 1998) to evaluate differences in isotopic composition among the three groups of wolves, seasonal isotope values for ungulate prey, and isotopic signatures among the three ungulate prey and salmon. Because of differences noted in seasonal isotopic composition of moose and caribou, we averaged seasonal values to derive a year-round estimate for each ungulate species.

Because we were primarily interested in the proportion of salmon in assimilated wolf diets and differences between N isotope ratios of salmon and ungulates were substantially greater than those of C (see *Results*), coupled with serious concerns recently raised regarding the use of C isotope ratios in estimating diets (Felicetti et al. 2003), we used a simple dual-source mixing model (Hobson et al. 2000) based on N isotope values to estimate the salmon contribution to the diet of each wolf we sampled:

$$P_{\text{sal}} = \frac{\delta^{15}\text{N}_{\text{wlf}} - (\delta^{15}\text{N}_{\text{ung}} + 3.4‰)}{\delta^{15}\text{N}_{\text{sal}} - \delta^{15}\text{N}_{\text{ung}}}$$

where P_{sal} was the proportion of a wolf's diet derived from salmon, $\delta^{15}\text{N}_{\text{wlf}}$ was the isotopic value for that wolf, $\delta^{15}\text{N}_{\text{ung}}$ was the combined isotopic value for all ungulates in the diet, and $\delta^{15}\text{N}_{\text{sal}}$ was the isotopic value of salmon. To determine the ungulate end member, $\delta^{15}\text{N}_{\text{ung}}$, we used the proportions of ungulate kills observed while radiotracking or snowtracking wolves during 1986–1993 (Mech et al. 1998; L. G. Adams, *unpublished data*) as approximations of the proportional biomass of each species consumed by the wolves (Mech et al. 1998). Because the composition and abundance of ungulates available in the northwestern flats differed from the remainder of our study area, we estimated the ungulate composition of wolf diets separately for each region (northwestern flats, 39% caribou, 61% moose [$n = 145$ kills]; remainder, 39% caribou, 43% moose, 18% sheep [$n = 371$ kills]). We assumed that prey other than ungulates and salmon (beaver, snowshoe hares, Arctic ground squirrels, hoary marmots, etc.) made up a small portion of wolf diets and were similar isotopically to the ungulates (Szepanski et al. 1999, Urton and Hobson 2005). Small negative estimates of salmon consumption (greater than or equal to -3.7%; $n = 9$) were considered to indicate no salmon in the diet of those wolves (Phillips 2001). We tested for differences in salmon consumption among the three wolf groups with one-way ANOVA procedures. For all tests, we considered $P \leq 0.05$ to be indicative of a significant result.

RESULTS

Isotopic values of bone collagen varied widely among the 73 wolves we sampled (Table 1, Fig. 2), but a clear pattern emerged when stratified by their home range locations relative to salmon and ungulate availability. Wolves belonging to group 1 (salmon present, low ungulate density) exhibited isotope ratios that were different from those of groups 2 and 3 (KNNRT, $P < 0.001$), primarily because of δ^{15}N values that averaged >1‰ higher (Table 1). Isotope signatures of wolves in groups 2 (salmon present, high ungulate density) and 3 (no salmon, high ungulate density) did not differ significantly (KNNRT, $P = 0.076$; Table 1), but group

Table 2. Isotope signatures (mean ± SD) for ungulates and salmon available to wolves in Denali National Park and Preserve, Alaska.

Sample type and period collected	n	δ^{13}C	δ^{15}N	K nearest neighbors test†	Annual estimate δ^{13}C	Annual estimate δ^{15}N
Caribou						
Fall RBC (late Sep/early Nov)	30	−23.0 ± 0.33	3.0 ± 0.51	$P < 0.001$	−22.6 ± 0.31	2.8 ± 0.56
Late winter RBC (mid/late Mar)	28	−22.3 ± 0.30	2.7 ± 0.60			
Moose						
Fall RBC (early Nov)	29	−24.9 ± 0.63	0.7 ± 0.84	$P < 0.001$	−24.8 ± 0.53	1.1 ± 0.80
Late winter RBC (mid-Mar)	30	−24.6 ± 0.40	1.4 ± 0.75			
Sheep						
Late winter RBC (mid-Mar)	21	−24.1 ± 0.31	1.5 ± 0.72	$P = 0.267$	−24.2 ± 0.39	1.5 ± 0.59
Hair (mid-Mar)	15	−24.2 ± 0.49	1.5 ± 0.33			
Salmon						
Skin/meat/bone (Oct)	27	−20.7 ± 1.01	12.7 ± 0.88			

Notes: Seasonal isotope ratios were averaged to arrive at an annual estimate for each ungulate species. RBC stands for red blood cells.

† Seasonal isotopic values were compared via K nearest neighbors tests described by Rosing et al. (1998).

2 wolves had isotope values that were generally intermediate between groups 1 and 3 (Fig. 2).

The isotope signatures of the three ungulate species and salmon differed significantly in all pairwise comparisons (KNNRT, $P < 0.001$; Table 2, Fig. 2). Salmon isotopic values differed substantially from the ungulate values, exceeding caribou by 1.9‰ and 9.9‰ for δ^{13}C and δ^{15}N, respectively (Table 2).

Estimates of the salmon contribution to diets of individual wolves varied widely, ranging from 0 to 34% of their long-term assimilated diets (Table 1, Fig. 3). Estimates of salmon consumption varied significantly among the three wolf groups ($F_{2,70} = 36.4$, $P < 0.001$) and were consistent with expectations from prey availability; group 1 wolves averaged nearly three times as much salmon in their diets as wolves in the other groups combined (Table 1). All group 1 wolves had δ^{15}N values indicative of salmon consumption ≥8%, whereas nearly half (14 of 29) of the group 2 wolves fell below that level and only one wolf in group 3 exceeded 8% (Fig. 3). The ungulate endmembers ($\delta^{15}\mathrm{N}_{\mathrm{ung}}$) we calculated for regions of low and high ungulate abundance were identical (1.8‰), thus variation in estimates of salmon in the diets of individual wolves resulted entirely from the variation in their δ^{15}N values.

Ungulate densities were 78% lower in the northwestern flats compared to the remainder of our study area, but within-pack wolf densities were reduced by only about 17% (Table 3). As a result, ratios of ungulates to wolves differed widely between the two regions (12 and 44 moose equivalents/wolf in regions of low and high ungulate abundance, respectively). Differences in within-pack wolf densities between the two regions resulted from combined effects of slightly smaller pack sizes (9% and 5% in fall and late winter, respectively) and slightly larger home ranges (9%) for wolves inhabiting the low-ungulate area (Table 3).

Discussion

Although the wolves we studied lived ≥1200 river km from the coast, Pacific salmon were utilized to varying degrees by wolves throughout the Denali ecosystem. In particular, salmon contributed most to diets of wolves where salmon were abundant and ungulates occurred at low densities; all these wolves had N isotope ratios indicative of salmon constituting ≥8% of their diet and salmon made up ≥20% of the diet for one-third of them. Given that bone collagen provided isotopic values that were integrated over at least a few years (Gannes et al. 1998, Bocherens and Drucker 2007), these wolves included higher proportions of salmon in their diets during some years.

Isotopic values for wolves inhabiting Denali's northwestern flats were similar to those reported by Szepanski et al. (1999) for wolves in coastal southeast Alaska, and estimates of salmon in wolf diets were nearly identical (17% in this study vs. 18% for southeast Alaskan wolves). As noted by Szepanski et al. (1999), coastal wolves had several other marine foods available to them, including harbor seals (*Phoca vitulina*), various marine mammal carcasses, anadromous eulachon smelt (*Thaleichthys pacificus*), and marine invertebrates, which were not accounted for in their analyses of wolf diets. Thus, coastal wolves probably utilized other marine foods and the estimated contribution of salmon to their diets was likely inflated. Given that salmon was the only marine-derived food resource available to Denali wolves, salmon consumption by wolves in the northwestern region of DNPP may have actually exceeded that of the coastal wolves studied by Szepanski et al. (1999).

Wolves with home ranges in which ungulates were more abundant utilized salmon less on average than those with few ungulates available. However, six of 17 wolves we sampled with no spawning salmon within their home ranges exhibited δ^{15}N values indicative of

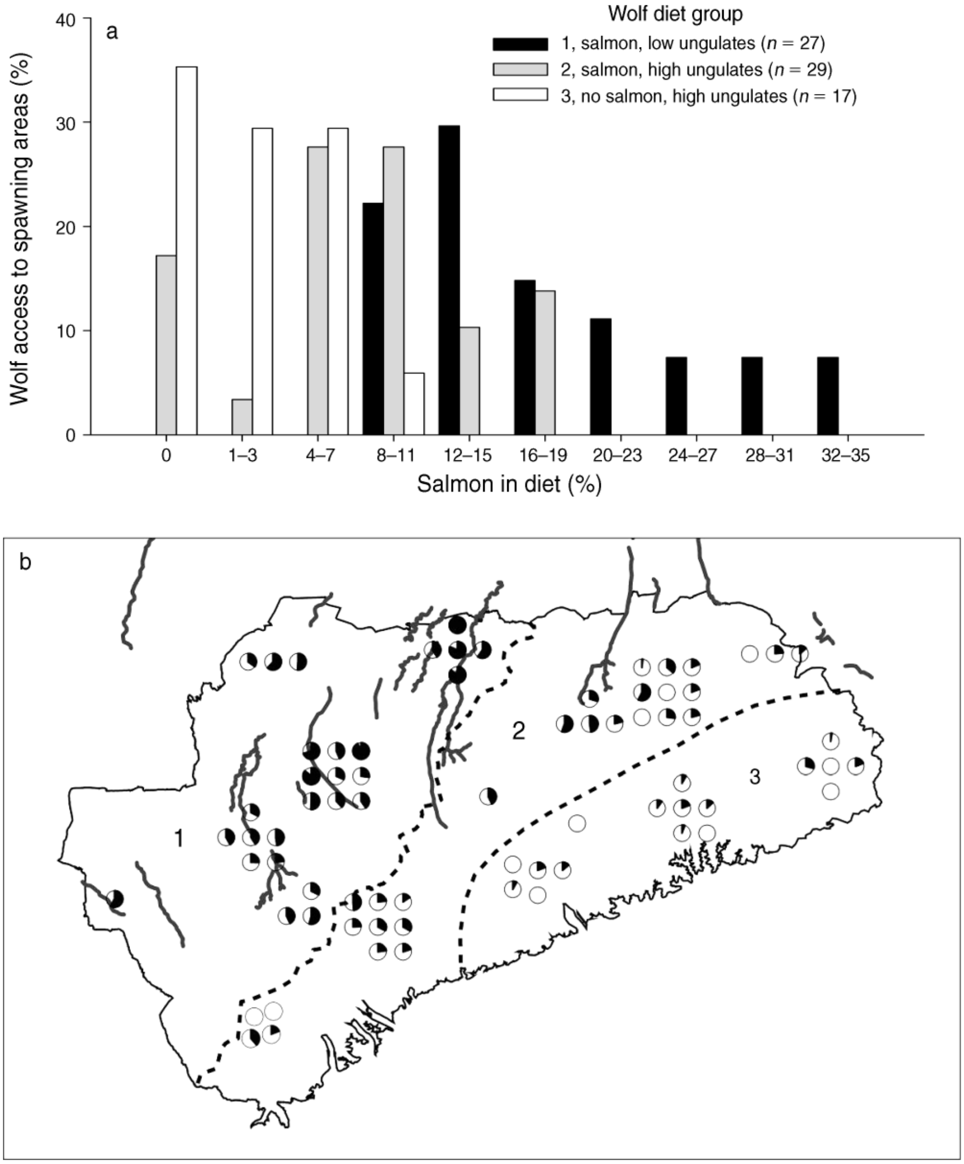

FIG. 3. Prevalence of salmon in the diets of wolves from Denali National Park and Preserve, Alaska (a) relative to percentage of wolves in each group with access to salmon spawning areas and ungulate availability and (b) as distributed on the landscape (circles indicate percentage of salmon in diet: 0%, solid white; 34%, solid black). Numbered areas in panel (b) correspond to wolf diet groups 1–3. Known and suspected salmon spawning areas are depicted as black stream segments.

salmon contributing 4–10% of their diets. Wolves are known to occasionally make long-distance forays outside of their territories, trespassing on neighboring wolf packs (Fuller 1989, Mech et al. 1998), and five of these wolves were radio-located on such forays within a few kilometers of spawning areas (L. G. Adams, *unpublished data*). Spawning areas would be attractive to trespassing wolves because of the predictable availability of easily obtained meat that could outweigh the risks associated with detection by resident wolves (Mech and Boitani 2003). Although spawning areas did not exist in several pack home ranges in our study area, spawning areas occurred within 20 km of these wolf pack range limits, well within distances regularly traveled by wolves (Mech and Boitani 2003).

Fall runs of chum and coho likely contributed most to wolf diets in the Denali region. These salmon were substantially more abundant than summer-spawning chum and chinook. Also, unlike summer-run salmon, those spawning in fall congregate in stream reaches that commonly remain ice-free throughout the winter due to upwelling of groundwater (JTC 2007*b*). Retention of salmon carcasses in Denali streams was probably very high because of high sinuosity, woody debris, and reduced base flows during winter (Cederholm et al. 1989, Gende et al. 2004). Further, decomposition of carcasses

TABLE 3. Population characteristics of wolves inhabiting regions of Denali National Park and Preserve with low ungulate abundance and spawning salmon (group 1; 70 moose equivalents/1000 km^2) vs. high ungulate abundance (groups 2 and 3; 320 moose equivalents/1000 km^2) during 1986–2002.

	Group 1				Groups 2 and 3			
Characteristic	*n*	Mean	SD	Range	*n*	Mean	SD	Range
Pack size (wolves/pack)								
Fall (1 Oct)	67	7.3	3.93	2–23	137	8.0	5.30	2–29
Late winter (15 Mar)	69	6.0	3.89	2–23	129	6.3	4.31	2–24
Home range size (km^2)	53	1567	812.1	482–4005	122	1420	759.1	226–4437
Within-pack density (wolves/1000 km^2)								
Fall (1 Oct)	49	5.8	3.74	1.1–16.6	116	7.2	4.95	0.6–20.2
Late winter (15 Mar)	53	4.4	2.35	1.2–11.3	119	5.2	3.27	0.6–13.4

Note: The sample size is pack-years. One moose equivalent = 1 moose, 3 caribou, or 6 sheep, following Keith (1983) and Fuller (1989).

of fish dying in late fall would be inhibited by cold winter temperatures. Thus fall-run salmon were probably available to wolves to some degree throughout winter.

Fall salmon runs of chum and coho constitute considerable biomass entering the study area. Given the magnitude of fall salmon runs and the distribution of spawning habitat within the Kantishna drainage, we estimated that salmon biomass on the northwestern flats of the study area averaged approximately 150 Mg annually, equivalent to ~70 moose/1000 km^2 (average moose = 350 kg; Franzmann et al. 1978; NPS, *unpublished manuscripts*) or equivalent to the ungulate biomass there. In the remainder of the study area, salmon constituted a small fraction of the available prey biomass because of markedly higher ungulate abundance and limited salmon spawning habitat (Fig. 1).

Wolf abundance in the northwestern flats was only slightly lower than in the remainder of the study area, even though ungulates occurred at substantially lower densities. We conclude that wolf abundance in this region was enhanced as a result of the allochthonous subsidy provided by salmon in that: (1) wolves are known to exhibit a strong numerical response to prey availability (Fuller 1989, Fuller et al. 2003); (2) salmon provide a food resource equal in magnitude to ungulate abundance; and (3) the use of salmon by wolves residing in the area was ubiquitous, accounting for 17% of their diets on average. Marine subsidies have been shown to increase abundance of other terrestrial predators across a wide array of taxa including spiders (Polis and Hurd 1996), lizards (Polis and Hurd 1996), Arctic foxes (*Alopex lagopus*; Roth 2003), coyotes (*Canis latrans*; Rose and Polis 1998), and brown bears (*Ursus arctos*; Hilderbrand et al. 1999).

Increased abundance of subsidized consumers generally results in increased predation pressure on local prey resources (Holt and Lawton 1994, Polis et al. 1997), particularly when prey subsidies occur at high levels (Huxel and McCann 1998, Estes et al. 2001). Although salmon constituted a sizable portion of the diet for wolves on the northwestern flats, ungulates still comprised an estimated 83% of the wolf diets, indicative of substantial predation pressure on ungulates, particularly given the low ratios of ungulates to wolves that occurred there. With information presented here (wolf diet composition, wolf densities, and ungulate densities) and estimates of consumption rates for wolves (Peterson and Ciucci 2003), we approximated winter predation rates (15 October–30 April; the period from when estimates of moose and caribou abundance were derived to immediately prior to the annual ungulate birth pulse), expressed as the proportion of moose equivalents in each region of our study area that were consumed by wolves. With the conservative assumption that all salmon consumption by wolves occurred during this period (differences in predation rates between regions increased with lower salmon consumption during the period), estimated predation rates on ungulates in the northwestern flats were approximately three times higher than those in the remainder of our study area (19% vs. 6%, respectively). These estimates are reasonable given survival patterns of moose and caribou in DNPP (L. G. Adams, *unpublished data*). More importantly, while the values of these rates will vary depending on the consumption rate used to calculate them, the relative difference between the two rates result solely from the differences in wolf and ungulate abundance and salmon contribution to wolf diets in the two regions of our study area, thus providing strong evidence that wolf predation rates were markedly higher on ungulates on the northwestern flats. Further, given the low ratio of ungulates to wolves on the northwestern flats, salmon would have to constitute ~40% of annual wolf diets there for predation rates on ungulates to be similar to the upland regions of the study area.

We conclude that salmon as an allochthonous subsidy to wolves probably contributed to low ungulate densities observed in northwestern DNPP. Moose comprised most of the ungulate biomass in the northwestern flats and occurred at densities approaching the lowest in North America (Gasaway et al. 1992, Messier 1994) while exhibiting body size and reproductive characteristics indicative of little nutritional constraint on their population dynamics (Boertje et al. 2007; L. G. Adams, *unpublished data*). Further, moose populations with moose : wolf ratios <20 generally occur at very low densities or exhibit population declines compared to areas where moose : wolf ratios are higher (Gasaway et al. 1983). With brown bears and American black bears (*Ursus americanus*) in the system, moose populations are even more strongly limited by the combined predation effects (Van Ballenberghe 1987, Ballard and Van Ballenberghe 1997). We speculate that Pacific salmon may play a similar role in other regions of northwestern North America where spawning salmon are abundant and ungulate densities are low.

In addition to effects on the long-term numerical relationships between wolves and ungulates, Pacific salmon probably invoke substantial variability in wolf–ungulate interactions from year to year. Returns of fall chum to the Kantishna drainage varied fivefold during 1999–2005 (Cleary and Hamazaki 2006) and index counts of fall chum salmon have varied by more than an order of magnitude during the last 35 years (Bue et al. 2006). Thus, the availability of salmon in northwestern DNPP has probably varied from less than one-third to more than three times the ungulate biomass there. Factors influencing annual run sizes for Pacific salmon are complex and include oceanographic and climatic patterns over the North Pacific (Downton and Miller 1998, Finney et al. 2002), salmon harvests on the high seas and within riverine systems (Holder and Senecal-Albrecht 1998, Schindler et al. 2005, JTC 2007*a*), and escapement of salmon to spawning areas in previous years (Holder and Senecal-Albrecht 1998, JTC 2007*a*). Thus, factors associated with distant marine environments and the complex management of salmon fisheries likely influence the subsidizing effects of salmon on inland wolf–ungulate systems.

Current understanding and management of wolf–ungulate systems is based on the assumption that effects of other prey resources are minimal (Messier 1994, Mech and Peterson 2003). That assumption may be reasonable where ungulate prey are abundant and alternative prey make up a small proportion of the prey biomass utilized by wolves. However, throughout the current range of wolves in North America, low-density wolf–ungulate systems are quite common (Gasaway et al. 1992, Fuller et al. 2003) and these systems are prone to be influenced by non-ungulate alternative prey (Dale et al. 1994). For example, Mech (2007) recently reported that trends of wolf abundance on Ellesmere Island in the Canadian Arctic Archipelago were correlated with Arctic hare (*Lepus arcticus*) abundance, but not with that of muskox (*Ovibos moschatus*), the predominant ungulate in the region.

Our findings indicate that Pacific salmon are an important food source for wolves well beyond coastal areas and can provide a substantial marine influence on wolf–prey systems far inland where ungulates occur at low densities. Because salmon are allochthonous subsidies in these wolf–prey systems, they can reduce ungulate : wolf ratios through numerical responses of wolves to salmon availability and heighten predation pressure on resident ungulates. Further, the abundance of spawning salmon varies widely among years, adding substantial variability in the realized effects of this subsidy on local wolf–ungulate communities. Thus, the spawning migrations of Pacific salmon provide a previously unrecognized and dynamic connection between inland wolf–ungulate communities in northwestern North America and distant marine ecosystems.

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