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Role of brown bears (*Ursus arctos*) in the flow of marine nitrogen into a terrestrial ecosystem

Received: 11 February 1999 / Accepted: 7 July 1999

Abstract We quantified the amount, spatial distribution, and importance of salmon (*Oncorhynchus* spp.)-derived nitrogen (N) by brown bears (*Ursus arctos*) on the Kenai Peninsula, Alaska. We tested and confirmed the hypothesis that the stable isotope signature ($\delta^{15}\text{N}$) of N in foliage of white spruce (*Picea glauca*) was inversely proportional to the distance from salmon-spawning streams ($r=-0.99$ and $P<0.05$ in two separate watersheds). Locations of radio-collared brown bears, relative to their distance from a stream, were highly correlated with $\delta^{15}\text{N}$ depletion of foliage across the same gradient ($r=-0.98$ and -0.96 and $P<0.05$ in the same two separate watersheds). Mean rates of redistribution of salmon-derived N by adult female brown bears were 37.2 ± 2.9 kg/year per bear (range 23.1–56.3), of which 96% (35.7 ± 2.7 kg/year per bear) was excreted in urine, 3% (1.1 ± 0.1 kg/year per bear) was excreted in feces, and $<1\%$ (0.3 ± 0.1 kg/year per bear) was retained in the body. On an area basis, salmon-N redistribution rates were as high as 5.1 ± 0.7 mg/m² per year per bear within 500 m of the stream but dropped off greatly with increasing distance. We estimated that 15.5–17.8% of the total N in spruce foliage within 500 m of the stream was derived from salmon. Of that, bears had distributed 83–84%. Thus, brown bears can be an important vector of salmon-derived N in-

to riparian ecosystems, but their effects are highly variable spatially and a function of bear density.

Key words Bear · Nitrogen · Nutrient flow · Salmon · Spruce

Introduction

Nutrient inputs and their cycling are key processes controlling the productivity of ecosystems. Nitrogen (N) is frequently a limiting nutrient in northern forests (Chapin et al. 1986). Its principal sources of input are from atmospheric deposition and N-fixing plants (Van Cleve and Alexander 1981). However, freshwater and riparian ecosystems may also benefit from marine-derived N from the bodies of Pacific salmon (*Oncorhynchus* spp.) returning to their natal freshwater streams to spawn (Mathisen et al. 1988; Kline et al. 1990). Recent studies of stable isotope ratios of N ($\delta^{15}\text{N}$; Nadelhoffer and Fry 1994) of riparian vegetation have indicated that salmon-derived N may be an important source of N to the nearby terrestrial environment (Bilby et al. 1996; Ben-David et al. 1998). Redistribution of salmon carcasses by floods is expected to be a major route from the aquatic to the terrestrial environment in addition to piscivory and scavenging by terrestrial vertebrates (Ben-David et al. 1998). Bears (*Ursus* spp.) may be an important vector of salmon-N to the terrestrial system in ecosystems where bears and salmon are common (Willson et al. 1998). The implications of animal-distributed N from fish to the forest are widespread throughout food webs (Ben-David et al. 1998; Willson et al. 1998).

Although bears are known to consume large quantities of salmon when available (Troyer and Hensel 1969; Walker and Aumiller 1993; Hilderbrand et al. 1996, 1999, in press), their redistribution of salmon-derived N has never been quantified, especially in terms of its spatial distribution across the landscape. Because approximately 80% of the mass gained by bears feeding on salmon is lipid (Hilderbrand 1998), much of the N ingested as

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salmon is excreted in urine and feces. Knowledge of salmon consumption rates, excretion rates, and spatial patterns of habitat use by bears can provide the basis for quantifying the role of bears in redistributing salmon-derived N to the terrestrial ecosystem. The objectives of our study were to quantify the amount, spatial distribution, and importance of salmon-derived N by brown bears (*Ursus arctos*) on the landscape of our study areas on the Kenai Peninsula, Alaska, and to estimate the importance of this transport mechanism to the N budget of riparian ecosystems.

Materials and methods

Gradients in ^{15}N concentrations in vegetation

We hypothesized that plant foliage in riparian forests would have a decreasing $\delta^{15}\text{N}$ signature with increasing distance from salmon spawning streams because salmon are relatively rich sources of ^{15}N [Ben-David et al. 1998; ^{15}N of Kenai salmon = 13.2 ± 0.4 (SE), Jacoby et al. 1999]. We also hypothesized that if salmon are an important source of nitrogen to the terrestrial ecosystem, the $\delta^{15}\text{N}$ signature of plants should reach an asymptotic, minimal baseline some distance from the stream where salmon-derived nitrogen no longer occurs in significant amounts. We used foliage samples from white spruce (*Picea glauca*) for measures of ^{15}N concentrations because white spruce is the dominant tree species in our riparian forest and is known to root shallowly and preferentially take up N in its inorganic ammonium and nitrate forms (Schulze et al. 1994).

Spruce needles were collected in June 1998 from trees located near four current or historic salmon-spawning streams: Mystery Creek, Killey River, Russian River, and Cooper Creek. At each site, two transects were run perpendicular to the stream. Five needles from each of the previous 5 years growth were collected from the nearest spruce every 25 m. Transects were continued for 3000 m or until spruce were no longer encountered. Samples from each transect were composited by distance categories, freeze-dried, ground to a powder, and analyzed for their ^{15}N concentration (expressed as $\delta^{15}\text{N}$, Hilderbrand et al. 1996). Means and variances were calculated by distance category for the two transects at each site. Two additional 500-m transects were run parallel to Mystery Creek to measure variation in ^{15}N concentration at given distances (5 and 50 m) from the stream.

The four study streams provided useful contrasts. Mystery Creek and Killey River both had runs of several salmon species and were heavily used by brown bears. Russian River had abundant salmon but few bears and Cooper Creek had few bears and little to no salmon. Russian River had early and late runs of sockeye salmon (*Oncorhynchus nerka*) that were heavily used by sport fishermen 24 h per day throughout their seasons of availability. Bears were excluded by these human activities. Cooper Creek historically supported a run of sockeye salmon, but that run was made nearly extinct by the damming of Cooper Lake for hydroelectric development in 1961.

Mystery Creek and Killey River are located in areas with extensive spruce forest, so spruce samples were composited into 500-m categories of distances from stream to coincide with distance categories for bear locations (see below). In contrast, Russian River and Cooper Creek are located in narrow valleys with spruce ranging only 300–500 m from the stream, so their samples were composited into 100-m categories. Another important difference among watersheds is that only Russian River and Cooper Creek had extensive hillside stands of Sitka alder (*Alnus sinuata*) occurring in bands above the spruce forests. Because alder is a N-fixing species with high $\delta^{15}\text{N}$ values (Kohl and Shearer 1980), baseline $\delta^{15}\text{N}$ values of spruce from Russian River and Cooper Creek watersheds were not expected to be directly comparable to those from Mystery Creek and Killey River. Rather, our inquiry

focused on patterns of change in $\delta^{15}\text{N}$ in relation to distance from each stream, relative to the unique baseline of each watershed.

Redistribution of salmon-derived N by bears

Total salmon-derived N intake (kg) per bear was estimated by multiplying the mean annual salmon intake per adult female brown bear on the Kenai Peninsula (Hilderbrand et al., in press) by the mean N concentration of Chinook salmon (*O. tshawytscha*, Hilderbrand et al. 1996). Although both brown and black bears (*U. americanus*) occur on the Kenai Peninsula, black bears consume little to no salmon in areas where brown bears are abundant and where this study was undertaken (Jacoby et al. 1999).

Terrestrial deposition of salmon-derived N by bears occurs in three major ways: (1) urinary N, (2) fecal N, and (3) body tissue N that eventually becomes available through tissue turnover or upon bear death. Fecal N was estimated as the product of total salmon-derived N intake (kg) and the indigestible fraction of salmon protein (3%; S.D. Farley and C.T. Robbins, unpublished data from captive-bear feeding trials). Body tissue N was estimated as the product of change in lean body mass (kg) attributable to salmon consumption (Hilderbrand et al., 1999) and N concentration of lean body mass (13.3% of dry matter; Robbins 1993; Farley and Robbins 1994). Urinary N was calculated by subtracting the sum of fecal N and body tissue N from total salmon-derived N intake. Urinary nitrogen was determined by difference because it is not a constant proportion of intake or excretion and biologically is defined as that portion of the nitrogen that is absorbed but not retained. Estimates of N deposition (kg) are reported as means $\pm$ SEs.

Spatial patterns of N deposition were determined by quantifying the spatial distribution of bear locations during the period of salmon availability (July 15–October 15). From 1996 through 1998, 59 adult female brown bears were captured and fitted with radio collars of very high frequency (VHF; $n=22$) or with both VHF and global positioning system (GPS; $n=37$) capabilities (Telonics, Mesa, Ariz.). Schwartz and Arthur (in press) report that 95% of locations collected by GPS collars at two test sites on the Kenai Peninsula were within 143 and 248 m of the true location. Bears fitted with VHF collars were located from fixed-winged aircraft once every 1–2 weeks. GPS collars were programmed to collect one location every 5.75 h or every 11.5 h (i.e., two or four locations every 23 h) to reflect movement patterns throughout the day. The success rate of obtaining locations via GPS collars may be affected by habitat condition, geographic features, and bear activity, particularly movement (Schwartz and Arthur, in press). Thus, locations were not obtained at every scheduled GPS fix. Bear locations (>5000) were mapped on a Geographic Information System (GIS) database (ESRI, Redlands, Calif.). Frequency distributions of bear locations in relation to distance from salmon stream (500-m categories) were calculated for each bear, and means ($\pm$ SE) were calculated across bears for each distance category. Areas (m^2) within each distance category were calculated for streams along their salmon-spawning reaches (G.V. Hilderbrand, personal observations). Values of N deposition per bear (kg) were converted to N deposition per bear per m^2 (mg/m^2) by multiplying the former values by the relative proportion of time spent in each distance category and by dividing that product by the respective area of each distance category. We assumed that bear spatial occupancy patterns are synonymous with bear nitrogen excretion pattern as there is no way to quantify excretion, particularly urination, of wild bears.

Simple correlation analyses ($\alpha=0.05$) were used to test two null hypotheses in relation to distance from spawning streams: (1) $\delta^{15}\text{N}$ values of spruce needles does not decrease, and (2) the relative proportion of bear locations is not positively related to $\delta^{15}\text{N}$ values of spruce needles.

Results

Spruce needles exhibited the expected gradient of decreasing $\delta^{15}\text{N}$ value with increasing distance from a stream

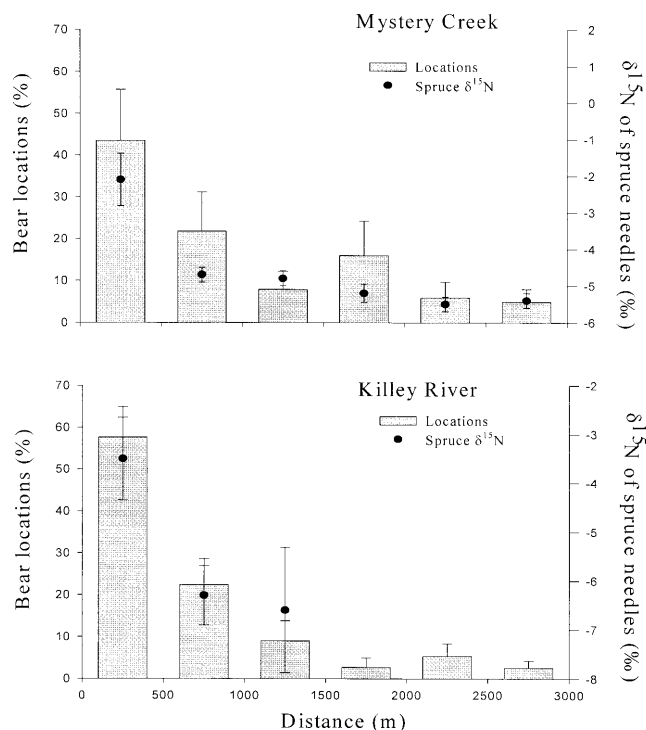


Fig. 1a,b Spatial patterns of $\delta^{15}\text{N}$ signatures of spruce needles (mean $\pm$ SE) and adult female brown bear locations (mean $\pm$ SE) in relation to distance from a stream, Kenai Peninsula, Alaska. No spruce were encountered along transects beyond 1500 m of the Killey River

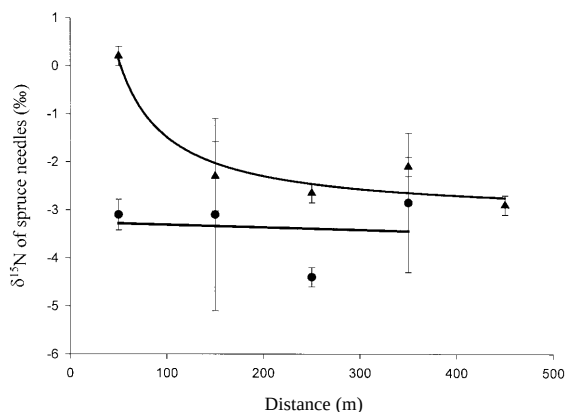


Fig. 2 Spatial patterns of $\delta^{15}\text{N}$ signatures of spruce needles (mean $\pm$ SE) at Cooper Creek (circles; $y = -3.25 - 0.00055x$, $r^2 = 0.01$) and Russian River [triangles; $y = -3.11 + (162.1/x)$, $r^2 = 0.93$] in relation to distance from the stream, Kenai Peninsula, Alaska. No spruce were encountered along transects beyond 400 m of Cooper Creek and 500 m of Russian River

near Mystery Creek ($r = -0.99$, $P < 0.01$) and the Killey River ($r = -0.99$, $P < 0.05$) (Fig. 1). A similar but weaker enrichment of ^{15}N occurred near the river at the low-bear site (Russian River) ($r = -0.96$, $P < 0.05$), whereas no gradient of enrichment occurred at the salmon-free site (Cooper Creek) ($r = -0.10$, $P > 0.25$) (Fig. 2). Variation in $\delta^{15}\text{N}$ values (SD) from the two transects run parallel to Mystery Creek was 0.74 at the 5-m distance and 0.89 at 50 m.

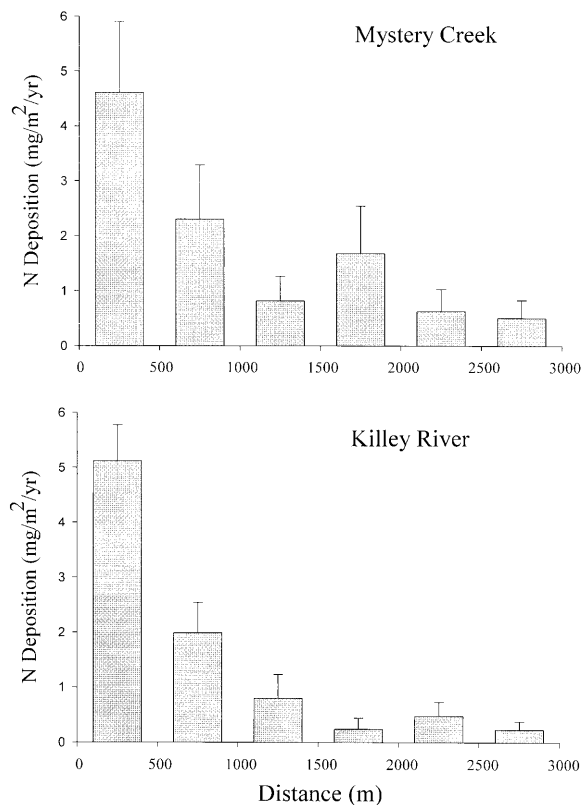


Fig. 3a,b Spatial patterns of N deposition (mean $\pm$ SE) by individual adult female brown bears in relation to distance from a stream, Kenai Peninsula, Alaska

Total annual salmon-derived N consumption per bear was 37.2 ± 2.9 kg/year, of which 96% (35.7 ± 2.7 kg/year per bear) was excreted in urine. Fecal salmon-N excretion was 1.1 ± 0.1 kg/year per bear (3% of annual salmon consumption), whereas 0.3 ± 0.1 kg/year per bear (<1% of annual salmon consumption) was retained in the body.

During the period of salmon availability, 77.6% of bear locations were within 1500 m of spawning streams. Gradients for bear location and $\delta^{15}\text{N}$ value of spruce needles were well correlated for both Mystery Creek ($r = -0.96$, $P < 0.01$) and Killey River ($r = -0.98$, $P < 0.05$) (Fig. 1). When expressed on an area basis, salmon-N redistribution rates by bears were as high as 4.6 ± 1.3 mg/m² per year (Mystery Creek) to 5.1 ± 0.7 mg/m² per year (Killey River) per bear within 500 m of the stream (Fig. 3).

Discussion

The observed gradients in $\delta^{15}\text{N}$ values of spruce needles with increasing distance from a salmon stream (Mystery, Killey, and Russian River) were consistent with similar patterns in southeastern Alaska (Ben-David et al. 1998). The enrichment in $\delta^{15}\text{N}$ at the Russian River did not extend beyond 100 m from the stream and may be due to the effects of salmon-N distribution by sport-fisherman (carcasses) and smaller, less mobile consumers. The enrichment patterns at Mystery Creek and the Killey River extended 500–1000 m

from the stream. The absence of such an enrichment pattern at our salmon-free site (Cooper Creek) suggests that the $\delta^{15}\text{N}$ gradients at the other sites were caused by salmon-N rather than other potentially confounding influences. Such other influences could include, for example, anoxic soil conditions (Hedin et al. 1988; Nadelhoffer and Fry 1988), differences in spruce rooting depths (Schulze et al. 1994; Hogberg 1997), and interaction between different soil nitrogen pools (Handley and Scrimgeour 1997). Furthermore, spatial variation in $\delta^{15}\text{N}$ for the transects run parallel to Mystery Creek was the same for both distances from the stream (coefficient of variation=1.21 at 5 m distance and 1.27 at 50 m). The higher $\delta^{15}\text{N}$ baselines of the Russian River (~ 2.5 $\delta^{15}\text{N}$) and Cooper Creek (~ 3.2 $\delta^{15}\text{N}$) watersheds (Fig. 2) than those of Mystery Creek (~ 5.5 $\delta^{15}\text{N}$) and Killey River (~ 6.5 $\delta^{15}\text{N}$) (Fig. 1) may reflect the presence of alder in the former two systems.

Spatial patterns of bear activity almost exactly matched the patterns of $\delta^{15}\text{N}$ of spruce needles (Fig. 1); however, we cannot assume cause and effect. The absolute amounts of salmon-derived N that were redistributed by bears might seem high (37.2 kg/year per bear), but they were relatively low on an area basis (4.6–5.1 mg/m² per year per bear) within the first 500 m from the stream. Other natural rates of N input to spruce and birch (*Betula papyrifera*) forests at similar latitudes to our study area range from 126 to 130 mg/m² per year in precipitation and from 7 to 165 mg/m² per year in N fixation (Van Cleve and Alexander 1981). Thus, if similar rates of N input occurred in our study area, each bear might contribute 1.6–3.8% of the total N input to the forest occurring within 500 m of the stream. Redistribution of salmon-derived N by bears dropped off greatly beyond 500 m to near baseline levels beyond 1000 m.

Several factors, however, heighten the potential importance of the salmon-derived N redistributed by bears. First, because 96% of that N was distributed in urine, which rapidly converts to ammonium, it is a highly available form of N. Spruce readily take up ammonium (Schulze et al. 1994; Buckmann et al. 1995). Moreover, salmon-derived nitrogen could prime the microbial pool and enhance N mineralization (Hobbs 1996). The effect of N redistribution by bears, therefore, may be primarily through indirect effects on soil processes, and secondarily by way of direct N fertilization.

A second factor relating to the relative importance of N redistribution by bears is that our calculations were on a *per bear* basis. Bear home ranges may overlap greatly, and many bears may concentrate along spawning reaches of salmon streams. Greater bear density increases the bear-distributed N proportionally. As many as seven collared adult female brown bears have been located along spawning reaches of streams such as Mystery Creek and Killey River in a single year (G.V. Hilderbrand, personal observation). Thus, brown bear inputs might easily be 10–20 times the values calculated on a per bear basis. These would be significant inputs to the terrestrial ecosystem.

A third factor affecting the importance of salmon-N distributed by bears is that bear distributions are not uni-

form across the landscape, not even at constant distances from the stream. “Hot spots” of bear activity occur above favorite fishing areas where fish are most easily captured (i.e., at the base of steep stream stretches or along shallow-water riffles). For example, estimated N deposition within the area encompassing the most clustered 25% of each bear’s locations is 16.2 ± 3.0 mg/m² per year per bear. This uneven pattern of habitat use occurs at the levels of both the individual bear and the population. The interaction of favorite fishing spots and population density can in some cases result in large concentrations of salmon-feeding bears. The salmon-derived N input to the terrestrial ecosystem above such areas far exceeds the mean values.

Finally, bears do not consume all the salmon they take from the stream. Partial consumption is the rule, and many salmon carcasses are left scattered throughout the forest (Willson et al. 1998). The N content of the uneaten carcasses is additional to the distribution rates calculated above. Thus, the relative input of salmon-derived nitrogen from bear urination, defecation, and transport and decay of salmon carcasses could potentially be 10–25% of the total nitrogen budget of riparian spruce forests.

Bilby et al. (1996) used the relative difference in $\delta^{15}\text{N}$ values of salmon and riparian vegetation along streams with and without salmon to estimate that 17.5% of the total N in vegetation along salmon streams in their study area was derived from salmon. Use of the same method, except substituting baseline $\delta^{15}\text{N}$ values for Killey River and Mystery Creek (because of the problem of between-site variation in baseline values), yields estimates of 15.5% (Killey River) to 17.8% (Mystery Creek) salmon-derived N in spruce needles within 500 m of our streams. By comparing the relative differences in $\delta^{15}\text{N}$ values of spruce needles above baseline levels of Killey River and Mystery Creek with those above baseline of the “low-bear” Russian River, we estimate that 83% (Killey) to 84% (Mystery) of the salmon-derived N occurring in the spruce needles within 500 m of the stream had been distributed by bears. These calculations assume that the impacts of other piscivorous vertebrates (e.g., marten, mink, otter, eagles) did not differ across sites.

Thus, there is general agreement between independent estimates of nitrogen inputs to spruce forests by bears consuming salmon. The first estimate was derived from nitrogen budgets and spatial distribution patterns of bears (10–25% of the total nitrogen input) and the second was derived from the magnitude of salmon-derived nitrogen in spruce trees estimated from $\delta^{15}\text{N}$ enrichments of spruce needles (15.5–17.8%).

Conclusions

Together, salmon and bears can play an important role in transfer of N from the marine to the terrestrial ecosystem. Although salmon-N may be widely distributed in the landscape, bears immediately distribute salmon-N

close to the salmon streams. Similar patterns of redistribution of other nutrients from salmon (e.g., phosphorus) are likely and could be important additions to riparian ecosystems. Salmon-derived nutrient input from bears is relatively consistent in its interannual timing, as salmon runs are consistent in their seasonality. However, the magnitude of input may vary greatly as a function of variations in both salmon and bear abundance. Moreover, the spatial pattern of nutrient distribution by bears is highly variable, in both lateral (distance from stream) and longitudinal (in relation to fishing-related hot spots in some stream reaches) directions.

Bear inputs from salmon-derived N for any particular ecosystem depend on several factors: salmon abundance, bear density and distribution, bear distribution of uneaten or partially eaten salmon carcasses, and bear distribution rates of urinary, fecal, and body tissue N (of which urinary N is the most important). The relationship between salmon abundance and bear intake of salmon is likely an asymptotic functional response, where moderate fluctuations in abundance may have only minor effects on intake (Stephens and Krebs 1986). Salmon abundance, bear density and distribution, and distribution of uneaten salmon carcasses may all be estimated by direct observation in the field. Distribution rates of urine, feces, and body tissue, however, cannot be estimated from field observations alone. Our estimates of these distribution values provide a basis for field workers to quantify the role of bears in salmon-N distribution within other ecosystems.

The interactions between salmon, bears, and their effects on terrestrial nutrient budgets and productivity are important factors in ecosystems that either historically had or currently have significant runs of spawning salmon.

Acknowledgements Biologists G. Del Frate, L. Lewis (Alaska Department of Fish and Game), E. Berg, R. Ernst, T. Bailey (United States Fish and Wildlife Service), S. Jenkins, E. Shochat (Washington State University) and D. Johnson and pilots T. Cambier, J. DeCreft, R. Johnston, J. Larivee, C. Lofstedt, V. Lofstedt, L. Nichols, L. Rogers, and K. Solloy assisted with data collection on the Kenai Peninsula. K. Kielland, R. Vadas Jr., and an anonymous reviewer provided valuable insight and comments that greatly improved this manuscript. Funding was provided by the United States Forest Service (Pacific Northwest Research Station and Chugach National Forest), United States Park Service (Kenai Fjords National Park), United States Fish and Wildlife Service (Kenai National Wildlife Refuge), Alaska Department of Fish and Game, National Fish and Wildlife Foundation, and the Raili Korkka Brown Bear Endowment. This study complied with the current laws of the United States of America.

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