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Salmon-supported bears, seed dispersal, and extensive resource subsidies to granivores

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Abstract. In salmon-rich environments, which once spanned much of the Northern Hemisphere, bears occur at exceptionally high densities. Salmon, by growing bear populations, have the potential to exert wide-ranging effects on ecosystem processes. Salmon-supported bears provide seed dispersal services to plants, and bear scats containing thousands of seeds may then be efficient nutritional resources for granivorous small mammals that also function as secondary seed dispersers while hoarding seeds for winter. We taxonomically identified and enumerated seeds in individual bear scats to characterize patterns of bear frugivory. We then combined estimates of seed abundance and digestible energy content to quantify the energy available to granivorous small mammals, and we quantified the proportion of the mouse population that could be supported by locally abundant bear populations in lowland salmon systems. We additionally monitored seed-filled bear scats with remote cameras to quantify small mammal visitation rates, and live-trapped small mammals seasonally to determine whether rodents visited bear scats proportional to their densities or whether some species preferentially selected for bear scats, and to assess whether seasonal variation in scat visitation was driven by density or selection. Bears were an important initial dispersal agent for 12 species of fruit, particularly devil's club (*Oplopanax horridus*) and blueberry (*Vaccinium* spp.), which occurred in 80% (5839 seeds/scat) and 50% (10,719 seeds/scat) of scats, respectively. Seeds in bear scats were intensively utilized and dispersed by small mammals, primarily scatter-hoarding northwestern deer mice (*Peromyscus keeni*; 8.5 visits per day/4295 total visits) and larder-hoarding northern red-backed voles (*Myodes rutilus*; 2.2 visits per day/1099 total visits), with visitation rates proportional to the seasonal density of each species. Small mammals likely incurred significant nutritional benefits from seeds deposited in bear scats (kcal/scat, mean = 114, n = 71). In coastal Alaska riparian areas, bears are potentially capable of indirectly subsidizing the energy needs of 45–65% of local deer mouse populations. Thus, this work helps elucidate the role that salmon, by supporting abundant bears, plays in ecological communities via influencing seed dispersal and resource subsidies to the small mammals that compose the base of the food web.

Key words: brown bear; diplochory; *Myodes rutilus;* northern red-backed vole; northwestern deer mouse; *Peromyscus keeni;* scatter-hoarding; seed dispersal; seed-filled bear scat; *Ursus arctos.*

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INTRODUCTION

The direct and indirect effects of top carnivores on ecosystems have been widely documented (Crooks and Soulé 1999, Ritchie and Johnson 2009, Estes et al. 2011, Levi and Wilmers 2012), but little is known about the community-level effects of large omnivores. Historically, high-density brown bear (*Ursus arctos*) populations were supported by anadromous fish throughout much of the Northern Hemisphere, including Europe, Asia, and in Western North America from Alaska to Mexico (Rausch 1963, Servheen 1990, McLellan 1998). Marine subsidies coupled with the ability of bears to hibernate when resources are scarce allow for brown bear biomass two orders of magnitude higher than in systems without anadromous fish (Hilderbrand et al. 1999*b*). Black bears (*Ursus americanus*) can also reach high densities when brown bears are absent and anadromous fish are present (Peacock 2004).

Previous research has focused on the role of bears in distributing marine-derived nutrients from salmon to terrestrial plants, insects, and vertebrate scavengers (Willson and Halupka 1995, Hilderbrand et al. 1999*a*) and fertilizing riparian systems with up to a quarter of their nitrogen budget (Helfield and Naiman 2006, Hocking and Reynolds 2011). However, high levels of bear biomass in salmon systems could have wide-ranging effects on ecosystem processes (Schoen et al. 1986, Miller et al. 1997, Hilderbrand et al. 1999*b*, Gende et al. 2002). In particular, the abundant bears in salmon-rich ecosystems provide important seed dispersal services with potential consequences for plant community composition (Willson and Gende 2004). Even in the presence of abundant salmon, brown bears extensively consume fruit to diversify macronutrients and maximize weight gain (Rode et al. 2006, Erlenbach et al. 2014). Seeds within fruit are able to successfully germinate after gut passage (Willson 1993, Traveset and Willson 1997, Alves-Costa and Eterovick 2007), and seeds that remain in bear scats have improved germination success and seedling growth rates (Traveset et al. 2001).

The high density of seeds deposited in bear scats can result in increased seedling competition (Chavez-Ramirez and Slack 1993, Zhou et al. 2011). Secondary dispersal by scatter-hoarding rodents has the potential to reduce negative density dependence by distributing seeds in small caches to a variety of subterranean microsites (Vander Wall 2008). In North America, the deer mouse (*Peromyscus maniculatus*) is a scatter-hoarding rodent that has been documented to consume and disperse seeds found in black bear scats (Enders and Vander Wall 2012). There are multiple species of *Peromycus* (*maniculatus, boylii, truei, californicus, leucopus*) that have been documented to scatter hoard seeds (Borchert 2004, Pearson and Theimer 2004, Beck and Vander Wall 2010, Enders and Vander Wall 2012, Niederhauser and Matlack 2017), making the behavior widespread. In Southeast Alaska, the range of the deer mouse (*P. maniculatus*) transitions into the range of the closely related northwestern deer mouse (*Peromyscus keeni*; Hogan et al. 1997, Lucid and Cook 2007), which we presume is an ecologically equivalent scatter-hoarder. In contrast, we presume the northern red-backed voles to be strictly seed predators because a closely related species, the gray red-backed vole (*Myodes rufocanus*) has been documented to only larder hoard seeds (Zhang et al. 2013). Since most food sources during the summer and fall are ephemeral, storing food sources such as seeds is essential to small mammal overwinter survival (Wolff 1996). Consequently, dense aggregations of seeds found in bear scats likely represent a significant and efficiently utilized foraging resource for small mammals, and removal of fruit from plants and subsequent deposition of seeds on the forest floor can substantially expand the phenology of seed availability to small mammals by making seeds available on the forest floor prior to senescence of fruit.

Here, we (1) taxonomically identified and enumerated seeds in individual bear scats to characterize patterns of bear frugivory. We then (2) combined estimates of seed abundance and digestible energy (DE) content to quantify the energy available to granivorous small mammals, and (3) we quantified the proportion of the mouse population that could be supported by locally abundant bear populations in lowland salmon systems. We additionally (4) monitored seed-filled bear scats with remote cameras to quantify small mammal visitation rates, and (5) live-trapped small mammals during summer to determine whether mice and voles visited bear scats proportional to their densities or whether one or the other species preferentially selected for bear scats, and to assess whether visitation to bear scats varied seasonally beyond seasonal variation in density (Fig. 1).

MATERIALS AND METHODS

Study area

We studied ecological relationships between bears, fruit, and small mammals in the Upper Chilkat Valley, located 30 miles north of Haines (N 59.52779, W 136.08700), Alaska, USA, during

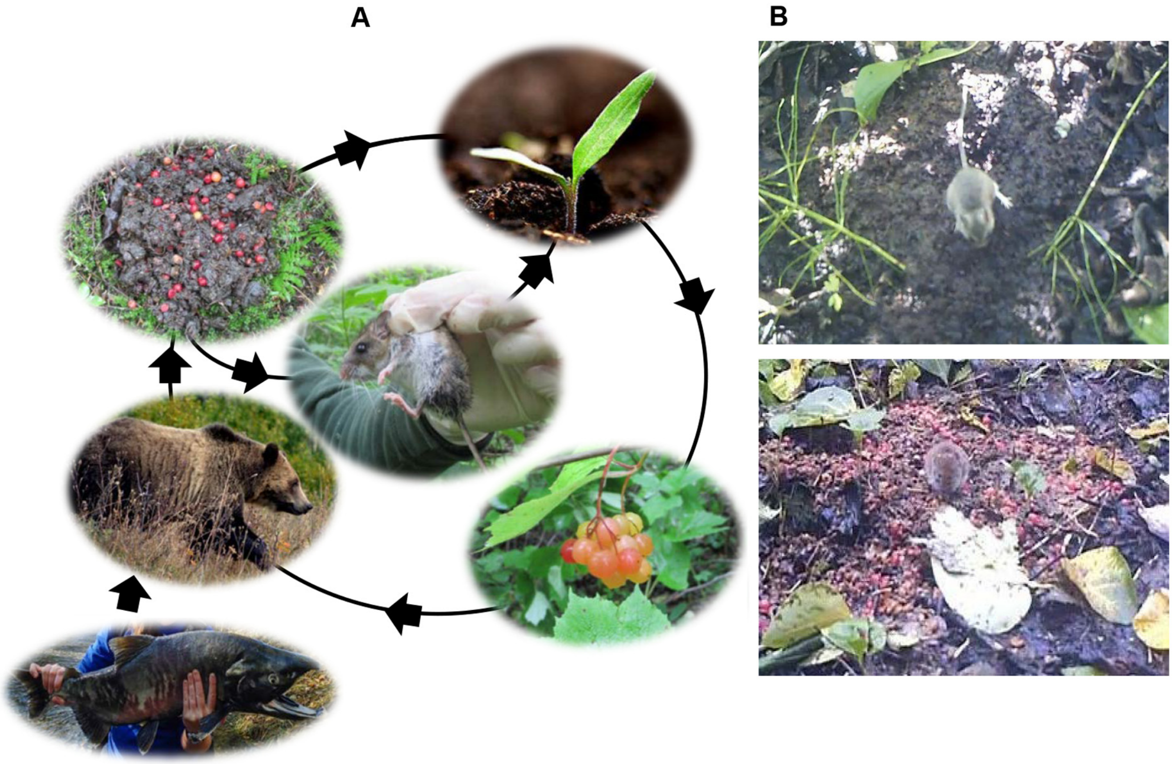

Fig. 1. (A) The diplochory cycle involving salmon, brown bears, fruit, and northwestern deer mice. The northern red-backed vole (not shown) is a larder-hoarder and is not expected to significantly aid in seed dispersal of fruiting plants. (B) Two more common small mammals in our Haines, Alaska study area, the northwestern deer mouse (top) and the northern red-backed vole (bottom), feeding on seeds in bear scats.

June–October 2014–2015. We established a study area located at the confluence of the Chilkat and Kelsall Rivers to collect fine-scale data on small mammals (Appendix S1: Fig. S1). At this site, we established two 1.56-ha grids for small mammal trapping. One grid was placed in a dense second growth Sitka spruce (*Picea sitchensis*) and western hemlock (*Tsuga heterophylla*) forest, while the second grid was established in a riparian black cottonwood (*Populus trichocarpa*) forest.

Study approach

We collected bear scats during the summer berry fruiting season to characterize patterns of frugivory by bears at a relatively broad spatial scale. Bear scats were genetically identified to species (Appendix S2) and manually sorted in the laboratory by hand to determine the abundance of fruits consumed by bears and the number of seeds subsequently available to granivores. We retained a subsample of bear scats and used motion-detecting remote cameras to record small mammal visitation to seed-filled bear scats. Since it was not possible to verify which seed species small mammals are collecting from bear scats, we conducted a modified cafeteria-style feeding experiment to (1) verify that small mammals were actually feeding on seeds (as opposed to bear fecal material) and (2) assess whether certain seeds were selected more than others, given equal availability. To determine whether patterns in visitation to bear scats were driven by changes in selection or changes in the population density of granivorous rodents, we additionally conducted a small mammal mark–recapture study to estimate densities of the two key species in the study area, northwestern deer mice and northern red-backed voles. Samples of fruit and seeds consumed by bears and small mammals were also analyzed to characterize nutritional quality and infer the extent to which seeds in bear scats nutritionally subsidize small mammal populations.

Bear scat collection, seed identification, and nutritional analyses

We opportunistically collected bear scats on roads and trails within our study area during July–September 2014–2015 in order to characterize patterns of bear frugivory over the course of the berry fruiting season. All scats were swabbed for DNA, and genetic analyses were conducted to identify the species of bear (Appendix S2). Each scat was washed of fecal material, dried at 50°C, weighed, and manually homogenized. We then subsampled 10% of the total mass of each scat and counted and identified each seed to genus/species (subsampling was necessary to effectively enumerate tiny blueberry [*Vaccinium* spp.] seeds, which can exceed 100,000 seeds in individual scats). We then calculated the density of seeds by species for each bear scat by extrapolating the number of seeds counted in the subsample to the total weight of the bear scat (Willson and Gende 2004, Di Domenico et al. 2012). For example, if a dried bear scat weighed 120 g and there were 800 blueberry seeds in the 10% subsample, the density of blueberry seeds in that scat was 8000 seeds (i.e., 800 × 10).

Seeds found in bear scats were identified and analyzed to determine nutritional characteristics including gross energy, and percent total dietary fiber (%TDF), crude protein, and crude fat (Wildlife Habitat and Nutrition Lab, Washington State University, Pullman, Washington, USA). We performed nutritional analysis on whole seeds and then subtracted the gross energy content of the fibrous husk, as well as fiber in the embryo, because a majority of seeds found in bear scats were too small to remove the husk without damaging or losing the embryo. We thus subtracted the gross energy due to fiber to estimate percent digestible energy (%DE) using the equation $\%\text{DE} = 96.6 - 0.96 \times \%\text{TDF}$ from Kienzle et al. (2006). We then estimated DE per seed by multiplying the gross energy by %DE. To the extent that seed husks contain DE, our estimates of DE will be biased high.

Small mammal density estimation

Small mammal trapping was conducted on two 1.56-ha grids (described above) to estimate small mammal densities. We placed baited Sherman live traps (7.62 × 8.89 × 22.86 cm; H. B. Sherman Traps, Tallahassee, Florida, USA; $n = 156$) at 10-m intervals in each 120 × 130-m grid. We conducted three trapping sessions (3–5 d each) during July–October 2014 and one session during June and July 2015. During trapping sessions, traps were opened at sunset and checked the following morning. Number of trapping days ranged from 3 to 5 d due to inclement weather and other logistic constraints.

All small mammals captured were taxonomically identified, sexed, and deployed with a passive integrated transponder tag under the skin to quickly identify recaptures using a radio-frequency identification reader during subsequent trapping events. Small mammal trapping was approved by the Institutional Animal Care and Use Committee at Oregon State University (ACUP #4557).

We used Program MARK (White and Burnham 1999, Cooch and White 2001) to estimate abundance and calculate density using the effective sampling area for northwestern deer mice and northern red-backed vole using Pollock's robust design; this method enabled us to optimally utilize all of our field data and assumed capture and recapture probabilities were constant and equal during trapping sessions (Fig. 2; Cormack 1964, Jolly 1965, Seber 1965, Kendall et al. 1995, 1997).

Small mammal utilization of seed-filled bear scats

The purpose of the video data was to determine whether seed-filled bear scats were being utilized by small mammals, which species visited most often, the corresponding relative frequency of use, and how this related to population density. In July 2014, we collected and evenly distributed 10 seed-filled bear scats (weight range = 800–2000 g) per grid. We placed a motion detection camera (Bushnell Trophy Cam; Bushnell, Overland Park, Kansas, USA) within 1 m of each scat to monitor small mammal and bird visitation rates. Cameras were set to record 20-s videos and used to determine timing, species, and behavior of animals that visited each bear scat. Camera data were analyzed to quantify the number of visits to bear scats per day by each small mammal and bird species. We averaged data across cameras for periods with at least five concurrent cameras (based on simulation analyses, this level of sampling ensured the

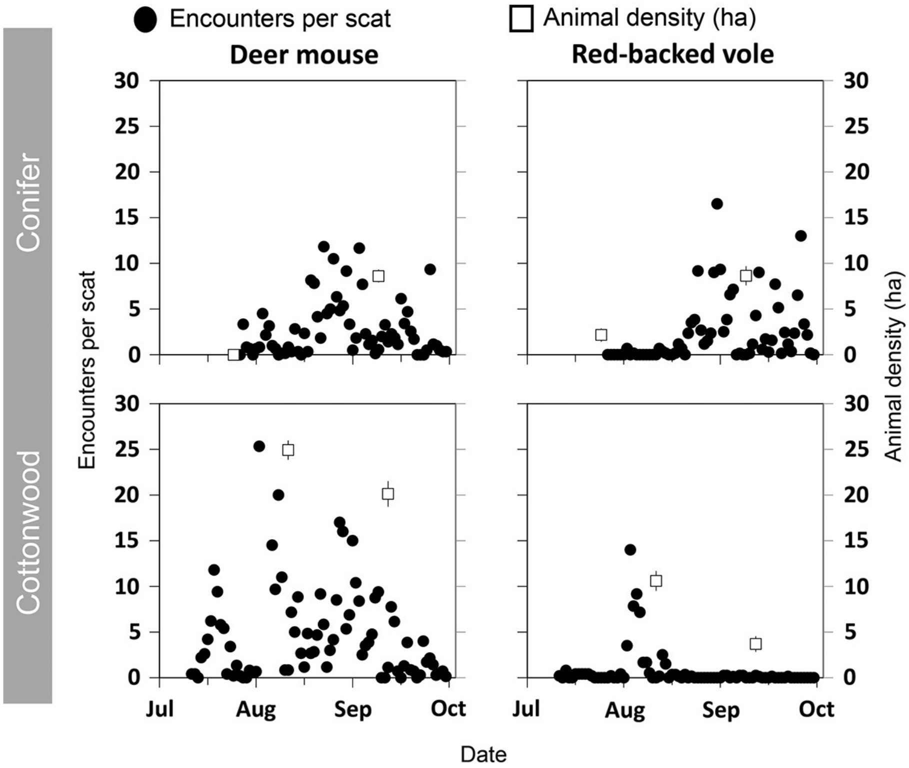

Fig. 2. Relationship between deer mice and red-backed voles density (ha) and seed-filled bear scat visitation in conifer and cottonwood habitat types during July–October 2014, near Haines, Alaska. Visitation rates (i.e., encounters/scat) were based on data collected using remote cameras. Small mammal density was estimated based on small mammal trapping and mark–recapture data analyses.

coefficient of variation of estimates was less than 0.20–0.30; Shakeri 2017).

Small mammal feeding experiments

In order to characterize seed foraging characteristics of northwestern deer mice and northern red-backed voles, we conducted a cafeteria-style feeding experiment. We also wanted to verify that northern red-backed voles, which are thought to be less granivorous (Banfield 1974, West 1982), were indeed eating seeds found in bear scats as opposed to bear fecal material. We baited live traps with a set quantity (n = 100) of seeds considered to be commonly consumed by bears including highbush cranberry (*Viburnum trilobum*), devil's club, bunchberry (*Cornus canadensis*) and elderberry (*Sambucus racemosa*) seeds. We ultimately determined that elderberry was not present in seed-filled bear scats in our study area, likely due to its patchy distribution, but is consumed by brown bears in other regions of Southeast Alaska (Hamilton and Bunnell 1987). We did not use blueberry seeds due to their very small size (i.e., 0.0002 g), which made it challenging to accurately account for all seeds in the trap; instead, we separately video-monitored petri dishes containing blueberry seeds to qualitatively determine whether they were consumed by small mammals. Traps were set inside bags to prevent seeds from being lost during the recovery of traps. All small mammals captured were taxonomically identified prior to release, and all seeds and husks were removed from the trap and counted to determine how many seeds of each species were consumed by each animal captured.

RESULTS

Berry consumption and seed provisioning by bears

Of the 71 scats collected, genetic analyses indicated 43 were deposited by brown bears and 6 by black bears; 22 could not be identified to bear

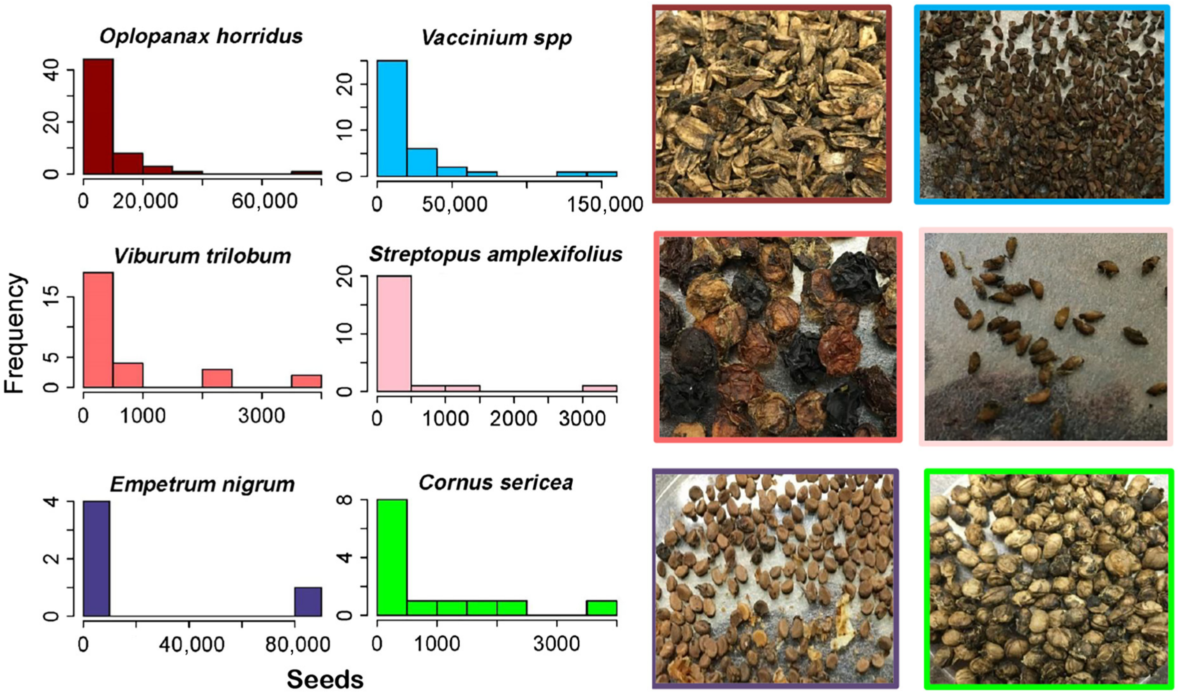

Fig. 3. Frequency distributions describing the variation in the number of seeds found in bear scats; only data for the six most commonly consumed plant species are presented. Accompanying photographs of the seeds for each species are presented in the right panel.

species and were classified as unknown bears because of poor-quality DNA. Due to the small number of black bear samples collected, we were unable to test for interspecific differences in berry consumption. For the ensuing analyses, we pooled all bear scat samples and assumed that our data predominantly represented brown bears (i.e., 43/49 known samples or 87%).

Table 1. Mean number of seeds and frequency of occurrence for 12 fruit species found in seed-filled bear scats (N = 71) in Haines Alaska, 2014–2015.

Species	Mean	SE	Freq.
Blueberry (*Vaccinium* spp.)	10,719.4	3136.9	0.50
Devil's Club (*Oplopanax horridus*)	5839.0	1256.4	0.80
Crowberry (*Empetrum nigrum*)	1438.4	1216.4	0.07
Soapberry (*Shepherdia canadensis*)	285.3	198.4	0.04
Highbush Cranberry (*Viburnum trilobum*)	281.7	91.6	0.39
Red-osier Dogwood (*Cornus sericea*)	144.5	67.5	0.18
Clasp-leaf twisted stalk (*Streptopus amplexifolius*)	125.1	50.2	0.32
Wild Rose (*Rosa nutkana*)	92.8	52.5	0.14
Black Currant (*Ribes lacustre*)	47.6	25.9	0.11
Bunchberry (*Cornus canadensis*)	10.5	7.2	0.04
Serviceberry (*Amelancheir alnifolia*)	7.6	5.5	0.11
Thimbleberry (*Rubus parviflorus*)	0.1	0.1	0.01

We identified 12 species of fruit in bear scats. The most common seed found in bear scats was devil's club, which was present in over 80% of bear scats collected (mean = 5839 ± 1256 per scat; Fig. 3, Table 1). Blueberry and highbush cranberry were also very prevalent in bear scats and found in 50% and 39% of scats, respectively (blueberry, mean ± standard error [SE] = 10,719 ± 3127 per scat; highbush cranberry, mean ± SE = 282 ± 92 per scat; Fig. 3, Table 1). Other berries that were frequently found in brown bear scats include clasp-leaf twisted stalk (*Streptopus amplexifolius*; 32%), red-osier dogwood (*Cornus sericea*; 18%), and wild rose (*Rosa nutkana*; 14%; Fig. 3, Table 1). Illustrative of the potentially long-distance seed dispersal provided by bears, there were two instances where crowberry (*Empetrum nigrum*), a common high-elevation alpine plant, was identified in bear scats in our lower-elevation study area (Fig. 3, Table 1). The frequency and number of seeds for each species also varied widely. Among the 57 bear scats containing devil's club, there was a range of 140–73,230 seeds. Of the 36 bear scats that contained blueberry seeds, the range was between 10 and 157,178. There were also 28 bear scats that had between 10 and 3933 highbush cranberry seeds (Fig. 3).

Nutritional characteristics of whole seeds and bear scats

Digestible energy of seeds varied between species (Table 2). For example, red-osier dogwood (1.0 kcal/g) and bunchberry (1.1 kcal/g) had the lowest DE concentration and constituted 58% of the DE concentration of blueberry (1.7 kcal/g), devil's club (1.7 kcal/g), and highbush cranberry (1.7 kcal/g; Table 2). Based on the data above and given the variation observed in the species-specific composition and abundance of seeds in individual bear scats, we determined that seed-based DE concentration varied between 3 and 989 kcal per bear scat (Fig. 4).

Small mammal density and utilization of seed-filled bear scats

We trapped small mammals over 31 d resulting in 4836 trap nights of effort. Overall, we captured 109 individual northwestern deer mice and 48 northern red-backed voles. Our mark–recapture analyses revealed that small mammal densities varied between species, trapping session, and habitat type. Northwestern deer mouse and northern red-backed vole densities were similar in conifer forest (Appendix S3: Table S1). In the conifer forest grid, northwestern deer mice were absent during our August trapping session, but in September, we estimated 8.6 ± 0.7 northwestern deer mice per 1.56-ha grid. We estimated 2.2 ± 0.7 and 8.6 ± 1.1 northern red-backed voles on the conifer grid during August and September, respectively. Both species increased in densities on the conifer forest grid from August through September. Overall, northwestern deer mice were more abundant in the cottonwood than the conifer forest. On the cottonwood forest grid, we had an estimate of 24.9 ± 0.7 northwestern deer mice in August and 20.1 ± 1.4 in September. Northern red-backed vole densities on the cottonwood grid started out at 10.6 ± 1.1 in August and dropped to 3.7 ± 0.9 by September.

Seed-filled bear scats (scats monitored/d, mean = 6.3) were intensively utilized by small mammals, primarily northwestern deer mice (*Peromyscus keeni*; visits/scat per day = 8.5, total visits = 4295) and northern red-backed voles (*Myodes rutilus*; 2.2 visits/scat per day, 1099 total visits; Table 3). At the conifer forest site, 47% (*n* = 1103) of visits were northwestern deer mice,

Table 2. The nutritional characteristics of different species of fruit and seeds found in seed-filled bear scats, near Haines, Alaska, USA.

Species†	Average weight (g)	Gross energy (kcal/g)	Crude fat (%)	Crude protein (%)	Total dietary fiber (%)	Energy digestibility‡ (%)	Digestible energy (kcal/g)
Vaccinium spp.							
Whole fruit	0.2900	3.9	4.42	6.24	23.9	73.65	2.8
Seed	0.0002	5.6	23.29	18.58	68.1	31.22	1.7
Cornus canadensis							
Whole fruit	0.2800	4.1	8.37	7.33	47.6	50.90	2.1
Seed	0.0072	5.3	11.85	8.36	78.0	21.72	1.1
Oplopanax horridus							
Whole fruit	0.1700	5.0	26.94	8.49	42.9	55.4	2.8
Seed	0.0079	5.6	23.35	12.33	69.1	30.26	1.7
Viburum trilobum							
Whole fruit	0.5300	4.4	7.75	4.83	38.5	59.64	2.6
Seed	0.0233	5.7	20.03	10.75	69.2	30.17	1.7
Cornus sericea							
Whole fruit	0.3200	5.4	27.36	6.97	48.1	50.42	2.7
Seed	0.0254	5.2	11.50	7.81	80.6	19.24	1.0

Note: Samples were collected during the peak of the fruiting season (August 2014).

† Number of seeds per fruit: *Vaccinium* spp. = 40, *C. canadensis* = 1, *O. horridus* = 2, *V. trilobum* = 2, *C. sericea* = 1.

‡ Based on equation in Kienzle et al. (2006).

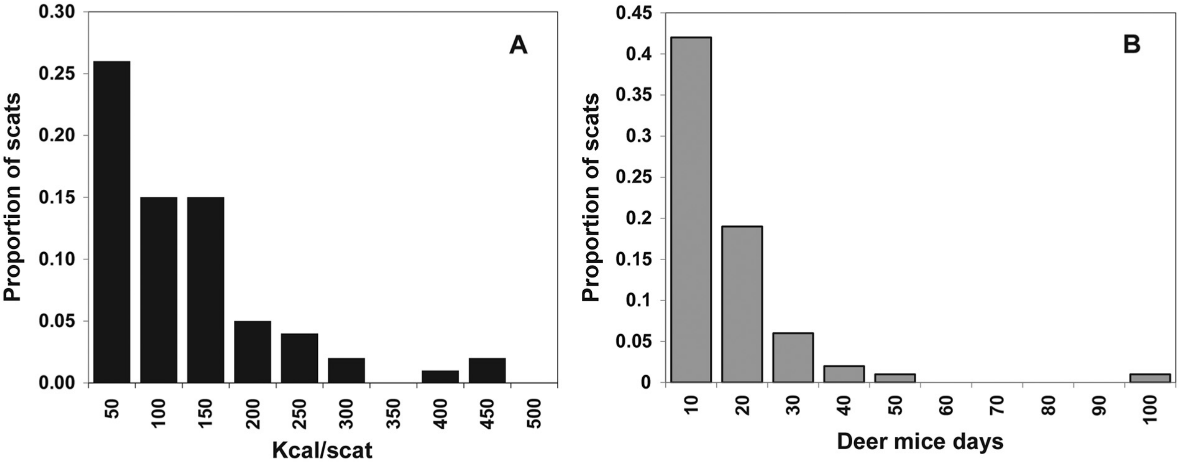

Fig. 4. Frequency distributions describing (A) variation in seed-based digestible energy (DE) content of bear scats, and (B) variation in energetic subsidy seed-filled bear scats provide to deer mice (i.e., deer-mice days = the number of days a deer mouse could meet its complete energetics needs). Deer-mice day calculations are based on seed-based DE content (Table 2) and deer mice daily energy requirements (10.9 kcal/d; Morris and Kendeigh 1981).

Table 3. Summary of the number of visits to seed-filled bear scats by small mammals, by habitat type, during July–October 2014 in near Haines, Alaska, USA.

	Conifer		Cottonwood	
Species	Number	Proportion	Number	Proportion
Deer mouse	1103	0.52	3192	0.90
Red-backed vole	832	0.39	267	0.08
Birds	132	0.06	58	0.02
Other vole	27	0.01	21	0.01
Shrew	12	0.01	2	<0.01
Hare	4	<0.01	4	<0.01

43% ($n = 832$) were northern red-backed voles, and the remaining 10% ($n = 175$) of the visits were shrews, long-tailed voles, snowshoe hares and birds (primarily varied thrush, *Ixoreus naevius*; Table 3). On the cottonwood forest grid, species visiting bear scats were 89% ($n = 3192$) northwestern deer mice, 8% ($n = 267$) northern red-backed voles, and 3% ($n = 85$) birds, shrews, snowshoe hares and long-tailed voles (Table 3; Videos S1–S3). Deer mice and red-backed voles were also recorded engaging in aggressive inter- and intraspecific interactions at seed-filled bear scats. We recorded 26 such interactions between deer mice and between deer mice and voles (Videos S4–S6).

Visitation rates of northwestern deer mice and northern red-backed voles to bear scats generally tracked their densities at the conifer forest grid (Fig. 3). Visitation rates and density were both low early in the season but increased in the fall (Fig. 3). On the cottonwood forest, northwestern deer mouse visitations were constant from the time the bear scat was placed until the camera was removed, while northern red-backed vole visitations were low except for a peak in mid-August (Fig. 3). Overall, when accounting for variation in small mammal density we determined that deer mice utilized bear scats more than red-backed voles in the cottonwood forest (deer mouse, visits/mouse per day = 0.08–0.12; red-backed vole, visits/vole per day = 0.01–0.03); interspecific variation was less evident in the conifer site (deer mouse, visits/mouse per day = 0.00–0.08; red-backed vole, visits/vole per day = 0.00–0.12).

Seed preference by northwestern deer mice and northern red-backed voles

We conducted feeding experiments involving live capture of 10 northwestern deer mice and seven northern red-backed voles to verify small mammals were feeding on seeds, rather than fecal material, in bear scats. The results of our experiment indicated both deer mice and red-backed voles consumed all seed species available. In general, small mammals consumed 65%

or more of the seeds offered, irrespective of seed species, with the exception of the reduced consumption of bunchberry seeds by northern red-backed voles (35% of seeds were consumed, on average; Appendix S4: Fig. S1).

DISCUSSION

Our results indicate that brown bears disperse large quantities of seeds from at least 12 fruit-bearing shrub species in our study area. Due to their mobility and relatively long median gut retention time (fruit = 5.5 h; Elfström et al. 2013), brown bears can play a key role in dispersing seeds between disjunct and distant habitats, as evidenced by the appearance of scats comprised of alpine crowberry in our low-elevation study area (~3–5 km distant and 1000 m lower). The seeds in these aggregations may then be secondarily dispersed by scatter-hoarding small mammals, and the energy in seeds present in bear scats may then permeate through food webs by supplying small mammals with efficient foraging resources.

All previous data on seed dispersal by brown bears in salmon-rich systems come from a single study on Chichagof Island (170 km south of our study area; Willson and Gende 2004). Devil's club and blueberry, the most common seeds found in bear scats in our study, were found at a significant higher quantity (on a per scat basis) than described for Chichagof Island (Willson and Gende 2004). For example, the mean number of devil's club seeds found in bear scats in our study area was ~5000 per scat, while the Chichagof study had a mean of ~200 seeds per bear scat. With respect to blueberry, we observed ~10,000 seeds/scat while the Chichagof study documented ~4400/scat. While our results suggest the role of bears as seed dispersers (and nutrient providers for small mammals) may be more significant than previously recognized, some considerations apply. For instance, bear densities on Chichagof Island are likely significantly higher than our mainland coastal site. Thus, a lower concentration of seeds in Chichagof Island bears scats may be compensated by a higher number of bears resulting in a comparable quantity of seed dispersal across each landscape. Salmon and berry foraging dynamics may also differ between sites with bears on Chichagof Island relying more heavily on salmon than berries. Geographic variation in seed dispersal may also be due to subtle differences in plant community composition and abundance. While comparative data are not available to quantify differences in understory plant community composition between areas, anecdotal information suggests that our mainland study site is characterized by higher densities of devil's club than Chichagof Island. Overall, despite evidence of geographic variation in seed dispersal patterns, our study confirms previous findings that indicate that bears are important dispersers of virtually every species of fleshy-fruit-bearing plant in coastal ecosystems.

Small mammal utilization of seed-filled bear scats

Our field observations of small mammal visitations to seed-filled bear scats combined with feeding experiments clearly indicate that small mammals consume and presumably cache significant quantities of seeds to persist through the winter. Several species of the genus *Peromyscus* scatter hoard seeds (Borchert 2004, Pearson and Theimer 2004, Beck and Vander Wall 2010, Enders and Vander Wall 2012) and this wide spread behavior is likely present in *Peromyscus keeni* due its close phylogenetic relationship with *Peromyscus maniculatus*. The thousands of seeds that are available in bear scats result in minimal foraging time, which makes this an attractive food source to small mammals. We presume that larder-hoarding by *Myodes rufocanus* (Zhang et al. 2013) a closely related species to *Myodes rutilus* is strictly a seed predator. In contrast, the scatter-hoarding behavior of *Peromyscus* species may result in important benefits to plants by improving seedling recruitment at a greater number of microsites. *Peromyscus maniculatus* can produce over a hundred caches from artificial seed piles (Beck and Vander Wall 2010), which are very similar to seed-filled bear scats.

Of the most common seed species found in bear scats, only one (highbush cranberry) was over 25 mg, which Vander Wall et al. (2005) suggested was a mass threshold above which rodents remove seeds from bird feces. Our foraging experiments clearly demonstrated that deer mice and voles readily consume seeds smaller than 25 mg (Table 2; Appendix S4: Fig. S1 and Video S7). We suspect that this minimum seed size threshold does not apply to our system because bear scats present a much higher concentration of seeds and there is limited access to seeds over 25 mg on the landscape. Under such conditions, even foraging on the smallest seeds, such as blueberry (0.0002 mg; Video S7), may be energy efficient given an average of over 10,000 blueberry seeds per bear scat, with some scats exceeding 150,000 seeds. However, we were unable to discern whether small mammals are caching or dispersing such small seeds. While it seems plausible that seed size would influence foraging preference among seeds in bear scats, the high concentration of seeds likely makes foraging on small seeds energetically profitable.

In addition to provisioning small mammals with seeds, bears can extend the period of seed availability to small mammals. As bears track the spatial variation in fruiting phenology to consume fruit with the highest sugar content (Davis et al. 2006, Armstrong et al. 2016), they deposit seed-filled bear scats on the forest floor. These seeds would otherwise primarily be made available to granivores following senescence of the infructescence, or in the smaller seed aggregations after primary dispersal by birds. However, recent evidence (Harrer and Levi 2018) suggests that bears disperse substantially more seeds than do birds and that this seed dispersal is non-redundant given that the majority of seeds went undispersed. Thus, bears mobilize the availability of large quantities of profitable seed piles on the forest floor and make them available beginning with the onset of ripe fruit availability (Harrer and Levi 2018).

The energy available in bear scats can meet a substantial portion of the energy budget for small mammals. For example, in our study area, a single bear scat contained 73,230 devil's club seeds. This concentrated food resource was capable of providing 988 kcal of DE to small mammals such as deer mice and red-backed voles (excluding any partially undigested fruit that would further increase the energy available to small mammals). Given that deer mice require 10.9 kcal/d in the summer (Morris and Kendeigh 1981), a single bear scat can theoretically meet the daily energetic requirements of 91 deer mice. When extrapolating from a single bear scat to all scats produced by a bear population, the nutritional subsidy can be quite substantial depending on the density of bears. Although we subtracted the gross energy from dietary fiber from our nutritional analysis, our estimates of DE per bear scat would be overestimates if seed husks contain digestible macronutrients beyond fiber. However, our estimates on the energy available in bear scats are also underestimated because we assume perfect digestion of fruit by bears. The sugars and lipids in partially digested fruit may provide an additional resource subsidy to small mammals. Despite the uncertainty around precisely how much energy is available to small mammals within bear scats, our estimates provide an ecological context for our findings (i.e., the approximate number of deer-mice days in systems with different bear densities and salmon). Our analysis is a heuristic modeling exercise intended to highlight the potential implications of the novel ecological relationships occurring when (1) salmon support very high bears densities, (2) those bears also consume large quantities of fruit, and (3) the resulting scats provide tens to hundreds of thousands of seeds in piles distributed throughout the landscape. As such, our deer-mice days simulations are intended to be viewed as a tool for conceptualizing plausible ecological scenarios rather than a quantitative biological reality.

In riparian habitats, such as habitats where we sampled small mammals, bear densities can be extremely high during the salmon spawning season; a period that temporally overlaps to a significant degree with the berry fruiting season (Deacy et al. 2017). For example, in riparian habitats on Chichagof Island, brown bear populations attained densities of 4.0–6.3 bears/km^2 (Flynn et al. 2007). If we assume the baseline deer mouse population densities and seed composition of bear scats that we documented in our study are comparable to other sites, the nutritional subsidy to small mammals can be significant. For example, seed-filled bear scats deposited on Chichagof Island riparian areas could nutritionally sustain up to 45–65% of the deer mouse population in the summer through early-winter. While it is unclear whether bear density estimates from Chichagof Island are comparable to our mainland site, Wheat et al. (2016) reported that a <1 km stretch of Herman Creek, a local stream in our study area, harbored 20–25 individual brown bears, suggesting that local densities, and associated ecosystem-level effects, can be comparably high in our study area. Overall, our research suggests that bears can indirectly provide an extensive nutritional subsidy to small mammal populations via deposition of seed-filled bear scats across the landscape (Fig. 4; Appendix S5: Table S1, Appendix S6: Table S1, Appendix S7: Table S1).

Ecological and conservation implications of bear frugivory

Salmon may exert widespread indirect effects on ecosystems through their role in increasing brown bear densities. A companion study conducted in our study area (Harrer and Levi 2018) used cameras traps to find that bears were by far the dominant seed dispersers of devil's club, the most common understory shrub. The seed composition that we found in bear scats is broadly consistent with patterns of shrub cover (Harrer and Levi 2018).

The elevated brown bear densities in salmon-bearing ecosystems supply extensive seed dispersal services for fleshy-fruited plants, and substantial resource subsidies to small mammals via seed aggregation and elongation of the phenology of seed availability. Small mammals are themselves a basal resource in terrestrial food webs, suggesting that the indirect effects of salmon could permeate into higher trophic levels. Such effects were once far more widespread as brown bear salmon systems once covered much of north-temperate regions worldwide, but this keystone interaction has declined throughout most of its former range. The decline or extirpation of brown bears and salmon may have consequences for plant community composition if wind-dispersed plants, rather than fleshy-fruited shrubs, colonize available microsites after disturbance. While black bears can fill the ecological niche where brown bears are absent, it is unknown to what extent black bears can mitigate their loss on the landscape. High densities of black bears have been observed in the absence of brown bears and the presence of salmon, but additional research is needed to understand the extent that black bears can fill the ecological role of extirpated brown bears. Overall, this research in a relatively pristine salmon-bear system can help us understand how extensively modified Pacific Northwest forests functioned ecologically prior to the extirpation of brown bears and the decline of salmon, and how seed dispersal, plant communities, and small mammal populations may have been impacted.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2297/full

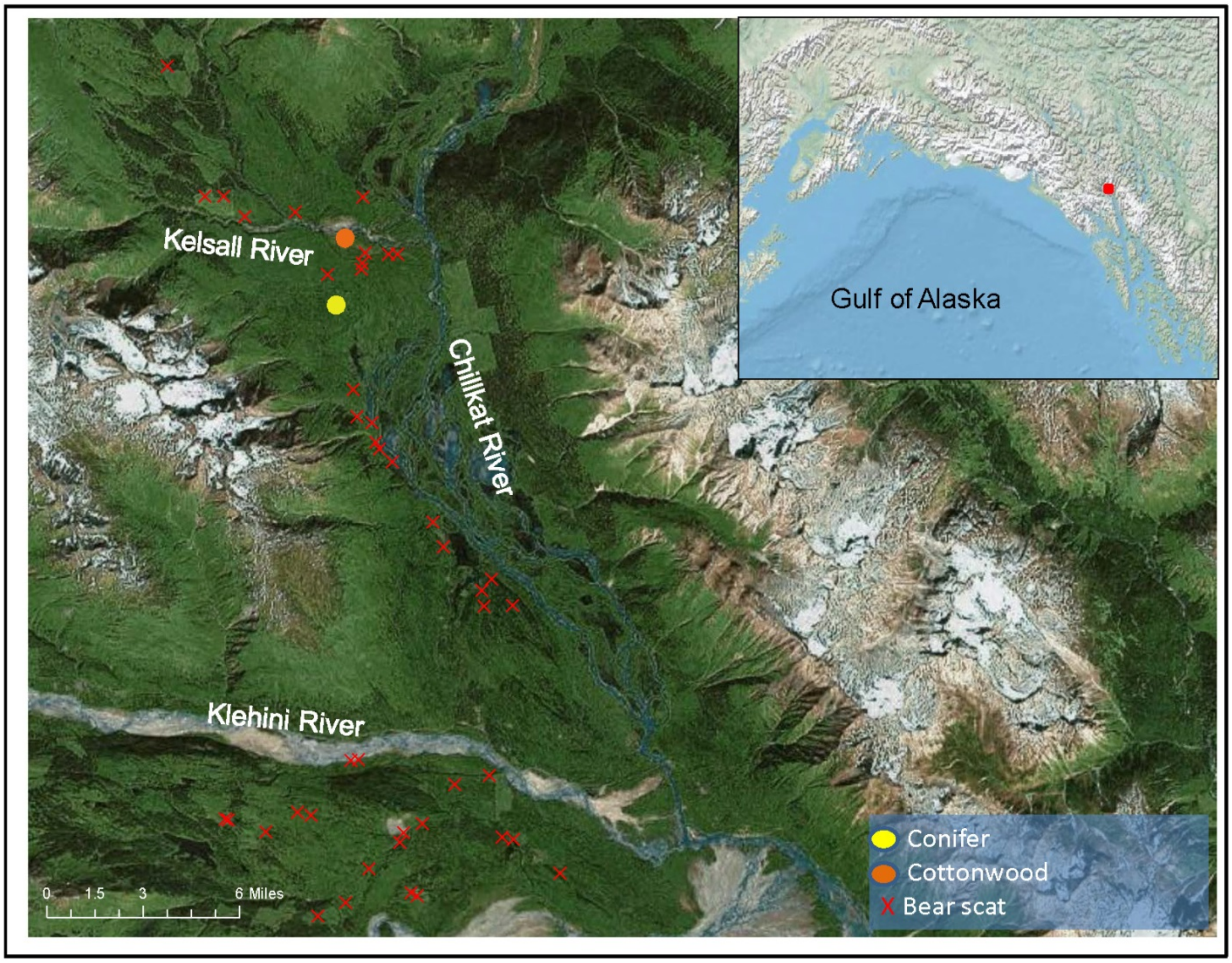
Ecosphere

Salmon-supported bears, seed dispersal, and extensive resource subsidies to granivores

Yasaman Shakeri, Kevin S. White, Taal Levi

Appendix S1

Figure S1. Map of the study area where we studied ecological relationships between bears, fruit, and small mammals during June-October 2014-2015, near Haines, Alaska. Bear scats collection locations are marked with a red X. The orange (cottonwood forest) and yellow (conifer forest) circles depict locations where small mammals were intensively studied.



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Appendix S2

Methods for DNA extraction and amplification.

DNA extraction and amplification was conducted at Oregon State University. DNA was isolated using the Aquagenomics solution from MultiTarget Pharmaceuticals using the protocols indicated by the manufacturer for swab samples. DNA was amplified

using 200nm of primers L1085 and H1259 (Nowak et al. 2014) to determine species ID

a portion of the mitochondrial control region (D-loop) was amplified using unlabeled HSF21 and 5’6-FAM- labeled LTPROBB13 primers (Wasser et al. 1997). In brown bears the D-loop has 14 base pairs (bp), which is how they are differentiated from black bears. Polymerase Chain Reaction (PCR) was performed in a total reaction volume of 20 ul using the Qiagen Mutliplex PCR kit which utilizes HotStartTaq DNA polymerase. Primers LTPROBB13/HSF21 and SRY were added at a concentration of 200nM and 100nM, respectively and 1ul of DNA template was used. PCR cycling conditions included an initial denaturation step at 95C for 15 min, followed by 39 cycles of denaturation at 94C for 30 s, annealing at 57C for 90 s, and extension at 72C for 60 s. A final elongation step at 60C for 30 min completes the reaction. PCR products were run on an agarose gel and visualized under UV light. Dilutions were made based on band intensity and ran on an Applied Biosystems 3730 capillary DNA sequencer for analysis of fluorescently labeled DNA fragments. Fragments were analyzed using Genemapper v4.1 (Applied

Biosystems). Species ID was concluded using fragment sizes with brown bears showing of 191bp and black bears peaking at 205b**.**

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Appendix S3

Table S1. Density of small mammals (per hectare) during each trapping session in each forest type near Haines, AK 2014 and 2015

			Deer mouse				Red-backed Vole			
Session	Date	Habitat	Density (ha)	LCI	UCI	SE	Density (ha)	LCI	UCI	SE
1	6/27/2014	Conifer	0	0	0	0	4.1	3.9	8.5	0.7
2	8/7/2014	Conifer	0	0	0	0	2.2	1.9	6.7	0.7
3	9/21/2014	Conifer	8.6	8.4	12.8	0.7	8.6	7.9	13.2	1.1
4	6/29/2015	Conifer	2.6	2.6	2.6	0	1.3	1.3	1.3	0
1	7/10/2014	Cottonwood	11.9	11.6	0.7	0.7	6.9	6.5	11.3	0.9
2	8/24/2014	Cottonwood	24.9	24	1.1	1.1	10.6	9.8	15.3	1.1
3	9/24/2014	Cottonwood	20.1	24.9	1.4	1.4	3.7	3.3	8.2	0.9
4	7/6/2015	Cottonwood	28	27.6	31.4	0.7	0.64	0.64	0.64	0

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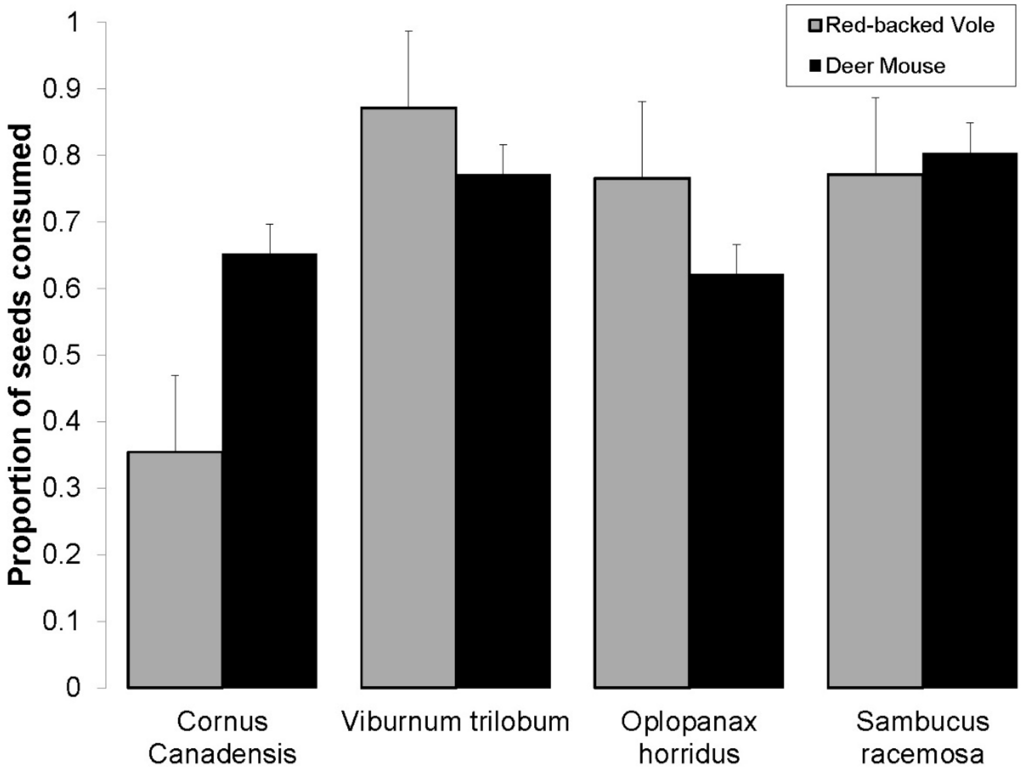
Appendix S4

Figure S1. Proportion of seeds consumed by northwestern deer mice and northern red-backed voles during seed feeding experiments conducted during 2014-2015, near Haines, Alaska.



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Appendix S5

Table S1. Mean and maximum number of seeds found in bear scats of 4 fruiting plant species, kcals available and number of northwestern deer mice sustained (based on energy requirements) in Haines.

Seed Species	Mean	Max	kcals (mean)	kcals (max)	Deer mice sustained a day
Vaccinium spp.	10719 ± 3,136.9	157,178	12.7	187.1	1 - 17.1
Oplopanax horridus	5839 ± 1256.4	73,230	78.7	988	7 – 90.6
Viburum trilobum	281 ± 91.6	3,933	11.4	159	1 – 14.6
Cornus sericea	144 ± 67.5	3,849	5	104	0.5 – 9

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Appendix S6

Table S1. Number of kcals of digestible energy in each bear scat and by each species of seed available to small mammals.

Species	Oplopanax horridus	Vibrurnum trilobum	Vaccinium spp.	Cornus Sericea	Cornus canadensis	Rosa nutkana	Streptopus amplexifolius	Ribes spp.	Shepherdia canadensis	Empetrum nigrum	Total kcals
Brown	0	0	87	0	0	0	0	0	0	0	87
NA	0	0	0	0	0	0	0	0	0	0	0
Brown	0	0	0	0	0	0	0	0	3	0	3
Brown	0	0	0	0	0	0	0	0	73	0	73
Brown	0	0	0	0	0	0	0	0	0	0	0
Brown	2	10	0	0	0	0	1	1	0	0	15
Brown	6	0	0	0	0	0	0	0	102	0	108
NA	64	0	15	0	0	0	0	0	0	0	78
Black	0	0	0	0	0	0	0	0	0	0	0
NA	0	0	62	0	0	0	0	0	0	0	63
Brown	0	0	0	0	0	0	0	0	0	0	0
NA	27	0	0	0	0	0	2	0	0	0	29
Brown	0	7	0	0	0	0	0	4	0	0	11
Brown	26	13	0	0	0	0	0	0	0	0	39
Brown	46	0	1	0	0	0	0	1	0	0	48

Brown	34	6	0	0	0	0	0	0	0	0	40
Brown	56	0	9	0	0	0	1	0	0	0	67
NA	37	1	0	0	0	0	8	0	0	0	46
NA	5	96	0	3	0	0	0	0	0	0	104
Black	56	0	63	0	0	0	1	0	0	0	121
NA	388	0	2	0	0	0	0	0	0	0	390
NA	66	0	0	0	0	0	0	0	0	0	66
NA	54	0	192	0	0	0	0	0	0	0	246
NA	35	87	0	1	0	0	0	0	0	0	123
NA	988	0	1	0	0	0	0	0	0	0	989
NA	161	0	0	0	0	0	0	0	0	0	161
NA	33	10	23	0	0	0	1	0	0	8	75
Brown	54	0	7	0	0	0	0	0	0	0	61
Brown	0	0	6	0	0	0	0	0	0	0	6
Brown	0	0	30	0	0	0	0	0	0	0	31
Brown	0	0	48	0	0	0	0	0	0	0	48
Black	79	0	0	0	0	0	0	0	0	0	79
NA	115	2	40	0	0	0	0	0	0	0	157
Brown	10	0	43	0	0	0	0	0	0	7	60
Brown	0	31	0	41	0	0	0	0	0	0	72
NA	1	11	0	0	0	0	0	0	0	0	12
Brown	1	0	0	5	3	1	0	0	0	0	11
Brown	0	12	0	0	0	5	0	0	0	0	17
Brown	0	0	0	0	0	28	0	0	0	0	29
Brown	15	36	0	0	0	3	0	0	0	0	54
Brown	1	151	0	1	0	0	0	0	0	0	153
Brown	0	0	11	0	0	0	0	0	0	0	11
Brown	0	0	42	0	0	0	0	0	0	88	130
NA	1	0	10	0	0	0	0	0	0	0	11
Brown	42	0	0	0	0	0	1	1	0	0	44
Brown	414	0	0	3	0	0	0	0	0	0	417

NA	277	0	0	0	0	0	0	0	0	0	277
Brown	44	0	0	0	3	0	0	0	0	0	48
Black	112	0	0	0	0	0	1	0	0	0	113
Brown	95	2	0	0	0	1	0	0	0	0	98
Brown	123	0	15	0	0	0	0	0	0	0	138
Black	290	0	0	0	0	0	0	0	0	0	291
NA	23	0	0	3	0	0	0	0	0	0	25
Brown	1	1	0	0	0	1	0	0	0	0	3
Brown	125	1	0	0	0	0	1	0	0	0	127
Brown	141	0	0	0	0	0	0	0	0	0	141
Brown	140	0	13	0	0	0	0	0	0	0	153
Brown	0	25	0	57	0	62	0	0	0	0	145
NA	0	9	0	0	0	17	1	0	0	0	27
Black	117	0	0	0	0	0	4	8	0	0	129
Brown	1	31	0	99	0	0	0	0	0	0	130
Brown	87	3	0	0	0	0	0	0	0	0	90
Brown	0	161	0	16	0	2	0	0	0	0	179
NA	0	102	0	34	0	2	0	0	0	0	138
Brown	217	0	7	0	0	0	0	0	0	0	224
Brown	136	0	2	0	0	0	0	0	0	0	137
Brown	119	0	0	0	0	0	0	0	0	0	119
NA	57	7	5	0	0	0	0	0	0	0	69
NA	259	4	147	0	0	0	0	0	0	0	410
Brown	167	2	44	0	0	0	0	0	0	0	213
Brown	245	0	0	0	0	0	0	0	0	0	245

Ecosphere

Salmon-supported bears, seed dispersal, and extensive resource subsidies to granivores

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Appendix S7

Table S1. Summary of the estimated number of deer mice that can energetically sustained per day (i.e. deer mice days/km^2) due to seed-filled bear scats for a range of different bear densities in Alaska systems. Calculations are based on bear density (references below), bear defecation rates (7 scats/day; Roth 1980), seed-based digestible energy content (113 kcals/scat; this study) and deer mice daily energy requirements (10.9 kcals/day; Morris and Kendeigh 1981).

Study Sites	Number of bears	Study area (km^2)	Bear density (km^2)	Mice subsidized/day[1]	Mice subsidized/day (km^2)	Mouse energetic subsidy (% increase)[1]		Reference
						Conifer	Cottonwood	
Freshwater Creek, Chichagof Island[2]	87	13.9	6.3	6,313	454	53%	18%	Flynn et al. 2007
Spasski Creek, Chichagof Island[2]	77	19.3	4.0	5,588	290	34%	12%	Flynn et al. 2007

[1] Based on baseline deer mice densities estimated via from small mammal trapping from this study: conifer: 860/ km^2, cottonwood: 2,490/ km^2

[2] Study area size based on 95th percentile of GPS radio-location distribution surrounding 5 km stream sampling reaches (Flynn et al. 2007).

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