AN ABSTRACT OF THE THESIS OF

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In salmon-rich, northern coastal environments brown bears can occur at high densities and exert wide-ranging effects on ecosystem processes. Bear consumption of seasonally available fruit may provide important seed dispersal services to plants, and by extension, influence the ecology of seed consumers such as small mammals. In this study, we investigate relationships between bears, fruit, and small mammals in a coastal Alaskan ecosystem in order to understand the extent to which diplochory, two-phase seed dispersal, may influence the community ecology of this system. We collected field data to characterize patterns of bear frugivory and the extent that small mammals consumed and dispersed seeds deposited by bears. Our findings indicate that bears are an important initial dispersal agent for 12 species of fruit. Bear-deposited seed piles were intensively utilized and dispersed by several different small mammal species, primarily northwestern deer mice (*Peromyscus keeni*) and red backed voles (*Myodes rutilus*). In addition to serving as secondary seed dispersers, small mammals likely incurred significant nutritional benefits from bear deposited seeds. Our results illustrate the important direct role that bears play in seed dispersal and indirectly on the community ecology of small mammals. We further highlight the

prevalence of a two-phase mammalian seed dispersal mechanism by quantifying visitation rates and the energetic subsidies described in north coastal temperate rainforest ecosystems. Due to the presence of salmon, high density coastal bear populations play an important role in structuring the community ecology of temperate rainforest ecosystem.

Extensive Resource Subsidies from Salmon-Supported Bears to Granivores

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Yasaman N. Shakeri

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

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CHAPTER 1
GENERAL INTRODUCTION

Yasaman N. Shakeri

Prey Pulses and Predators

Many carnivores utilize pulses of temporally abundant prey which can result in profound population-level effects. In the Pacific northwest, eulachon (*Thaleichthys pacificus*) arrive by the hundreds of thousands to spawn in rivers, a resource pulse that provides a rich food source for seabirds, raptors (Scott 1973, Marston et al. 2002), whales dolphins, stellar sea lions (Hamilton and Bunnell 1987, Robards et al. 1999, Hay and McCarter 2000, Hay 2002, Sigler et al. 2004, Gustafson et al. 2010) and terrestrial mammals such as bears and wolves (Szepanski et al. 1999, Marston et al. 2002). In terrestrial ecosystems, the pulse of neonate ungulates born in the spring represents an easily accessible protein source for bears and wolves (Kunkel and Mech 1994, Linnell et al. 1995, Wilckens 2014).

Among the most widespread and iconic of resource pulses is the annual arrival of Pacific salmon returning to spawn in rivers throughout the Pacific Rim. The millions of salmon that spawn in rivers during summer and fall provide a dependable food source to a wide variety of large mammalian predators, perhaps most notably brown and black bears (*Ursus arctos* and *Ursus americanus*). This spectacular resource pulse provides bears with hyperabundant food and results in extremely high bear densities in coastal regions (Miller et al. 1997, Hilderbrand et al. 1999b, Peacock et al. 2007). Prey densities can be so high that relatively unique behaviors are exhibited, such that the aggregation of brown bears at salmon spawning grounds can result in aggressive behavior by socially dominant bears (Gende and Quinn 2004) and associated risk of infanticide for females with cubs (Ben-David et al. 2004). The abundance of salmon also allows for sex- and size-specific predation by brown bears that shape the evolutionary dynamics of salmon (Quinn and Kinnison 1999, Ruggerone et al. 2000, Gende et al. 2004). Salmon, by

increasing bear densities, may have widespread indirect effects that affect other species of wildlife.

Indirect and Direct Effects of Carnivores

Indirect effects occur when the abundance of one species can indirectly affect the abundance of another species by altering the abundance or behavior of an intermediary species that interacts with both (Wootton 1994). For example, the re-introduction of wolves in Yellowstone National Park resulted in reduced elk densities, increased elk vigilance and avoidance of risky areas, which together allowed for the regeneration of plants that were heavily browsed (Ripple and Beschta 2004). The indirect effects resulting from top predators have been extensively studied, but little is known about omnivores and their potentially wide-ranging effects on community structure of ecosystems. Bears are an example of a large omnivore that acts both as a top carnivore and herbivore on the landscape. When one food source is no longer available to a bear, it can change its foraging behavior to meet its dietary needs. An example of this would be increased predation on elk (*Cervus elaphus*) calves by grizzly bears in the Yellowstone ecosystem due to the loss of spawning cut-throat trout (*Oncorhynchus clarkii*) (Middleton et al. 2013). This dietary change can indirectly impact other predators that feed on elk and the plant species that are consumed by elk.

In coastal regions where brown bears are present, the availability of rich food sources such as salmon has an impact on body size, population density and reproductive success (Miller et al. 1997, Hilderbrand et al. 1999b). Brown bears can also directly affect nitrogen availability in terrestrial ecosystems by moving salmon carcasses away from streams and into forested areas, resulting in potentially significant subsidies of marine derived nitrogen into terrestrial ecosystem food webs (Hilderbrand et al. 1999a, Helfield and Naiman 2006, Holtgrieve et al. 2009). Energy

maximization theory suggests that bears should choose to consume strictly salmon due to the relatively high fat and protein content of this food resource, yet their feeding behavior suggests otherwise (Rode et al. 2006b, Fortin et al. 2007). Brown bears require a mixed diet that contains proteins, lipids and carbohydrates (Rode and Robbins 2000, Erlenbach et al. 2014) in order to maximize weight gain prior to hibernation. Such nutritional requirements result in the extensive consumption of fruit even when salmon are available.

Brown bears have been broadly described to have two different ecotypes, coastal and interior, based on regional variation in ecology. In coastal areas, brown bears have ready access to abundant meat resources such as salmon and can attain very high densities (>190 bears/1000km$^{2)}$; (Miller et al. 1997, Hilderbrand et al. 1999b). In less productive interior regions, meat resources are less available and population productivity and densities are much lower (<50 bears/1000km$^{2;}$ Miller et al. 1997, Hilderbrand et al. 1999b). The dense brown bear populations due to the utilization of Pacific salmon and the addition of black bears may result in ecologically significant indirect effects on plant species via seed dispersal, an outcome that can affect multiple plant species when brown bears consume fruit in mixed diets. Although fruit is often not the most important food item in brown bear diets (Rode and Robbins 2000), high densities of brown bears consuming fruit can result in extensive seed dispersal with subsequent ecosystem effects through defecation. The large seed-filled bear scats on the landscape may become important foraging resources for granivores.

Scatter-hoarding Rodents and Seed Dispersal

Scatter hoarding is a behavior exhibited by many small mammal species involving the distribution of food caches to many different locations, with most of those caches only containing a small number of items (Enders and Vander Wall 2012). Most previous studies of

scatter hoarding have focused on birds, yet small mammals have also been widely documented to exhibit the behavior (Brodin 2010). Unlike larder hoarding, where a cache is defended, scatter hoarding caches are not defended, but concealed to prevent theft in small caches (Vander Wall 2008, Brodin 2010). A species that hoards food can typically be categorized as a larder hoarder or scatter hoarder. One exception is the Eastern chipmunk, which as a sub-adult is a scatter hoarder and as a dominant adult is a larder hoarder (Clarke and Kramer 1994). Scatter hoarding behavior in rodents has been studied extensively in various habitat types around the world (Daly et al. 1992, Jansen et al. 2004, Vander Wall 2010, Beck and Vander Wall 2010, Xiao and Zhang 2016). The scatter hoarding of seeds is an important form of seed dispersal, particularly when scatter hoarding reduces negative density dependence by distributing seeds to a variety of microsites (Van der Pijl 1969, Vander Wall 2010). This occurs because caches are inevitably abandoned (due to animal mortality, for instance), which protects seeds below the surface and promotes successful germination. This can be a mutualistic, positive feedback mechanism if the germinating seed survives to produce fruit.

Diplochory

Diplochory involves two or more phases of seed dispersal and has been studied in various species such as birds, ants, dung beetles and black bears (D'hondt et al. 2008, Christianini and Oliveira 2010, Enders and Vander Wall 2012, Kurek and Holeksa 2015). The first phase of seed dispersal involves a seed escaping density-dependent mortality by being moved away from other seeds and seedlings. Phase two of dispersal involves a seed being moved to a predictable and discrete microsite where the probability of survival is high (Vander Wall and Longland 2004).

Rodents have been observed harvesting seeds from the feces of mammals, but it was previously assumed that this removal was strictly seed predation (Howe 1989, Bermejo et al.

1998, LoGiudice and Ostfeld 2002). However, extensive scatter hoarding of seeds in feces has now been demonstrated in multiple systems. For example, a Panamanian study involving agoutis revealed that 56-66% of cached seeds were taken from simulated feces, whereas in Costa Rica agoutis scatter hoarded 27-46% of seeds found in feces (Wenny 1999). In northern ecosystems, deer mice (*Peromyscus* spp.) are also considered scatter-hoarding rodents and can remove up to 25% of seeds from black bear scats, an outcome that results in a higher survival of seedlings due to displacement from the seed shadow (Howe 1989) and burial at optimal depths for germination (Enders and Vander Wall 2012).

In Pacific Northwest coastal habitats, brown bears may be primary seed dispersers for many fleshy-fruited understory plants while mice secondarily disperse seeds from bear scats. In this context, large omnivores benefit from the carbohydrates and lipids they acquire from fruit while providing a seed dispersal service for plants. And, small mammals benefit from seed-filled brown bear scats distributed across the landscape and act as secondary dispersers, provided that they exhibit scatter hoarding behavior that provides an improved probability of germination when they cache seeds.

Seed Dispersal and Brown Bears

Many large- and meso-carnivores are partially frugivorous and serve as potential seed dispersers (Cypher and Cypher 1999, Schaumann and Heinken 2002), and their long gut-retention times allow for seeds to be carried considerable distances prior to defecation (Willson 1993). In general, frugivory by carnivores has been understudied, and the associated ecological impacts underappreciated. Given their extraordinarily high densities in coastal ecosystems, the role of frugivorous brown bears as seed dispersers may be significant, yet there has only been one study conducted on coastal brown bears on this topic (Willson and Gende 2004). Recent

research conducted on seed dispersal by black bears has revealed extensive secondary seed dispersal by small mammals (Enders and Vander Wall 2012), yet the extent that brown bears play a comparable ecological role has not been previously examined. High brown bear densities and their heavy consumption of fruit in the summer and fall suggest they may be excellent seed dispersers (Willson and Gende 2004), indirectly involving small mammals via secondary seed dispersal and food provisioning. Previous research has documented how brown bears affect ecosystems via salmon-mediated nutrient transfer from marine to terrestrial food webs, yet the role of brown bears in facilitating ecosystem process may be more widespread and involve seed dispersal and small mammal food provisioning services. These effects may be especially pronounced in coastal systems where brown bear densities are extremely high. This study is intended to advance our understanding of ecological interactions involving salmon, brown bears, fruit and small mammals in highly productive coastal ecosystems.

CHAPTER 2

EXTENSIVE RESOURCE SUBSIDIES FROM SALMON-SUPPORTED BEARS TO

GRANIVORES

Yasaman N. Shakeri

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). Marine subsidies coupled with the ability of bears to hibernate when resources are scarce allow for brown bear densities two orders of magnitude higher than in systems without anadromous fish (Hilderbrand et al. 1999b).

Previous research has focused on the role of bears in distributing marine-derived nutrients from salmon to terrestrial plants, insects, and vertebrate scavengers (*Oncorhynchus* spp.) (Willson and Halupka 1995, Hilderbrand et al. 1999a) 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. 1999b, Gende et al. 2002). In particular, the abundant bears in salmon-bearing 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). The seeds contained within fruit successfully germinate after gut passage (Willson 1993, Traveset and Willson 1997, Alves-Costa and Eterovick 2007), and seeds remaining in bear scats have improved germination and seedling growth rates (Traveset and Willson 1997). In addition,

bear-dispersed seeds can be moved long distances due to long gut-retention times coupled with the large home ranges and movement rates of bears (Nagy and Haroldson 1990, Fedriani and Delibes 2009).

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 microsites (Vander Wall 2008). In coastal temperate rainforest ecosystems, the northwestern deer mouse (*Peromyscus keeni*) is a scatter-hoarding rodent that has been documented to consume and disperse seeds found in bear scats (Enders and Vander Wall 2012). Secondary seed dispersal can also occur by larder hoarding small mammals, such as Northern red-backed voles (*Myodes rutilus*), yet the expected seed dispersal benefits are less pronounced due to increased seedling competition relative to scatter hoarding (Enders and Vander Wall 2012). Moreover, red backed voles store seeds underground which makes seedling survival less likely (Bailey 1926). Since most food sources during the summer and fall are ephemeral, storing food sources such as seeds is essential to small mammal overwinter survival.

In this study, we (1) identify fruit and seeds that brown bears consume and disperse across temperate rainforest landscapes in North Pacific coastal ecosystems, (2) quantify visitation of vertebrate consumers to bear scats, and (3) quantify the nutritional benefits of seed-filled bear scats to deer mice, which function as a basal resource in food webs (Fig. 1).

Materials and Methods

Study Approach

Our goal was to characterize ecological interactions involving salmon, bears, fruit, and small mammals (Fig. 1). 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 and mechanically sorted in the lab to determine the species and abundance of fruits consumed by bears and the number of seeds 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 seed-filled bear scats nutritionally subsidize small mammal populations.

Study Area

We studied ecological relationships between bears, fruit and small mammal the Upper Chilkat Valley, located 30 miles north of Haines (N59.52779, W136.08700), Alaska during June-October 2014-2015. We established an intensive study area located at the confluence of the Chilkat and Kelsall Rivers to collect fine scale data on small mammals (Fig. 2). At this site we established two 1.56 ha grids. 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.

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 in a variety of different habitat and landscape types 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 1). Scats were washed of fecal material, dried at 50C 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 per gram of scat biomass in order to derive estimates for the number of seeds within each scat (Willson and Gende 2004, Di Domenico et al. 2012). Seeds found in bear scats were identified and analyzed to determine nutritional characteristics, such as gross energy, total dietary fiber, crude fat and digestible dry matter (Wildlife Habitat and Nutrition Lab, Washington State University, Pullman, WA).

Small Mammal Density-Estimation

Small mammal trapping was conducted on two different 1.56 ha grids to estimate small mammal densities. One grid was established in mature second growth conifer forest and the other in a younger cottonwood stand in a riparian zone. We placed Sherman live traps (n = 156) at 10-m intervals in each 120 by 130 m grid. We conducted three trapping sessions (3-5 days) during July – October 2014 and one session during June and July 2015. Number of trapping days ranged from 3 to 5 days due to inclement weather and other logistic constraints. Traps were baited with oats, sunflower seeds and freeze-dried meal worms and were supplied with polyester

bedding for insulation. During trapping sessions, traps were opened at sunset and checked the following morning.

All small mammals captured were identified, sexed and received a passive integrated transponder (PIT) tag under the skin to quickly identify recaptures with a radio-frequency identification (RFID) reader. 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 densities of northwestern deer mice and northern red backed voles using Pollock's robust design, which enabled us to combine data from all trapping sessions to parameterize detection probabilities even though we were only interested in estimating density for the two focal July/August and August/September periods (Appendix 2)(Cormack 1964, Jolly 1965, Seber 1965, Kendall et al. 1995, 1997).

Small Mammal Utilization of Seed-Filled Bear Scats

In July 2014, we evenly distributed 10 seed-filled bear scats (dry weight, range = 800-2000 g) per grid. We placed a motion detection camera (Bushnell Trophy Cam; Bushnell Corp., Overland Park, KS, USA) ~1m from each scat to monitor small mammal and bird visitation rates. Bear scats were collected from the surrounding environment and taken to experimental grids. Cameras were set to record 20-second videos to help identify each species that visited a bear scat as well as date and time of day. The video mode on camera traps also allowed for observation of interspecific and intraspecific interactions at bear scats. Cameras were checked every two weeks to download videos and to refresh batteries when needed. Camera data were later analyzed to quantify the number of daily scat visits by each species.

Small Mammal Feeding Experiments

In order to determine seed preference by small mammals, and to verify that small mammals were indeed eating seeds found in bear scats as opposed to bear fecal material, Sherman live traps were baited with a set quantity (n = 100) of high bush cranberry, devil's club, bunchberry, and elderberry seeds. Elderberry was not present in seed-filled bear scats in the study area, 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, which made it challenging to not lose any seeds in the trap, but we separately video-monitored petri dishes containing blueberry seeds to qualitatively determine whether they were consumed by small mammals. Traps were set inside Ziploc bags to prevent seeds from being lost during the recovery of traps. Traps were set at sunset and checked the following morning. All small mammals captured were identified prior to release and all seeds and shells were removed from the trap and counted to determine how many seeds of each species were consumed by the small mammal that was captured.

Results

Berry Consumption by Bears

In order to characterize fruit and seed composition and abundance in bear diets we collected 71 bear scats during July-September 2014-2015. Of the 71 scats collected, genetic analyses indicated 43 were identified as brown bears and 6 were identified as black bears; 22 could not be identified to bear species and were classified as "unknown bears". We could not identify interspecific differences in berry consumption. For the following analyses, we pooled all bear scat samples and assumed that our data predominantly represented brown bears (i.e. 43/49 known samples, or 87%).

Our results indicate that bears consumed 12 different species of fruit. The most common seed found in bear scats was devil's club (*Oplopanax horridus*), which was present in over 80% of bear scats collected (mean = 5839±1256; Fig. 3, Table 1). Blueberry and highbush cranberry (*Viburnum trilobum*) were also very prevalent in bear scats and found in 47% and 40% of scats, respectively (blueberry, mean ± SE = 10719±3127; highbush cranberry, mean ± SE = 282±92; Fig. 3, Table 1). Other berries that were frequently found in brown bear scats were bunchberry (*Cornus canadensis*), watermelon berry (*Streptopus amplexifolius*) and redosier dogwood (*Cornus sericea*)(Fig. 3, Table 1). Illustrative of the potentially long-distance seed dispersal provided by bears, there were 2 instances where crowberry (*Empetrum nigrum*), a common 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 to 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 to 3,933 high-bush cranberry seeds (Fig. 4). We also found temporal variation in berry consumption by bears. For example, bears consumed blueberries consistently from early-July through early-September, while devil's club was consumed during a more limited time period during late-July through early-September (Fig. 5).

Fruit and Seed Nutrition

Gross energy and crude protein were higher in seeds than in fruits for all species analyzed. Blueberry seeds had the highest crude protein (18.58%), while redosier dogwood seeds had the lowest crude protein (7.81%). However, crude fat was highest in redosier dogwood fruit (27.36%), and lowest in *Vaccinium* fruit (4.42%). Digestible dry matter of fruit varied by

species with the whole blueberry having the highest digestible dry matter at over 70.2% and red-osier dogwood having the lowest at 51.4%.

Digestible energy between fruit and seeds varied slightly with whole blueberries having 2.6 kcal/g of digestible energy and the seed having 1.96 kcals/g digestible energy. The biggest contrast was seen in Redosier dogwood, with the whole fruit containing 2.8 kcal/g digestible energy and the seed containing 1.36 kcal/g. Whole fruit were very close in the amount of digestible energy available per gram, with devil's club being the highest at 2.77 kcal/g and bunchberry being the lowest at 2.12 kcal/gram. Seeds had a slightly wider range in digestible energy, which ranged from 2.1 kcal/g in high-bush cranberry to 1.36 kcal/g in redosier dogwood (Table 2).

Small Mammal Density and Utilization of Seed-filled Bear Scats

We trapped small mammals over 31 days resulting in 4,836 trap nights of effort. Overall, we captured 109 individual northwestern deer mice and 48 northern red-backed voles; we also caught shrews (*Sorex* spp.), red squirrels (*Tamiasciurus hudsonicus*), meadow jumping mice (*Zapus hudsonius*), long tailed voles (*Microtus longicaudus*) and northern flying squirrels (*Glaucomys sabrinus*). Our mark-recapture analyses revealed that small mammal densities varied between species, trapping session and habitat type. In the conifer forest grid, northwestern deer mice were absent during our August trapping session, but in September we estimated 13.43 northwestern deer mice on the 1.56 ha grid. We estimated 3.63 northern red-backed voles on the conifer grid during August and 13.48 northern red-backed voles in September. Both species increased in densities on the conifer forest grid from August through September. On the cottonwood forest grid we had an estimate of 31.4 northwestern deer mice in August and 43.81 in September. Northern red-backed vole densities on the cottonwood grid started out at 16.53 in

August and dropped to 5.75 by September. Overall, northwestern deer mice were more abundant in the cottonwood than the conifer forest. Northwestern deer mouse and northern red-backed vole densities were similar in conifer forest (Table 3).

Of the 10 cameras we deployed on each grid, we were only able to recover concurrent data from 1-8 cameras per day. We conducted a simulation analyses to determine the minimum number of cameras per day needed to derive reliable estimates (CV = 0.20-0.30). Consequently, we only calculated estimates for days when we had data from a minimum of 5 cameras. The most common small mammals to visit seed-filled bear scats were northwestern deer mice and northern red-backed voles (Fig. 6, Table 4). At the conifer forest site, 47% of visits were northwestern deer mice, 43% were northern red-backed voles, and the remaining 10% of the visits were shrews, long-tailed voles, snowshoe hares and birds (primarily varied thrush). On the cottonwood forest grid northwestern deer mice made up 89% of visits to bear scats, northern red-backed voles made up 8% of visits, and the remaining 3% were birds, shrews, snowshoe hares and long-tailed voles (Fig. 6, Table 4). Deer mice and red-backed voles were also recorded fighting at seed filled bear scats. We recorded 26 fights between deer mice and between deer mice and voles.

The visitation rates of northwestern deer mice and northern red-backed voles to bear scats generally tracked their densities at the conifer forest grid. Visitation rates and density were both low early in the season but increased in the fall. 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. 7 and Appendix 2).

Seed Preference by Northwestern Deer Mice and Northern Red-backed voles

We conducted feeding experiments involving live capture of 10 northwestern deer mice and 7 northern red-backed voles. The results of our experiment indicated limited differences in the proportion of equally available seeds consumed by deer mice and red-backed voles. In general, small mammals consumed 65% or more of the seeds offered, irrespective of seed species, with the exception being reduced consumption of bunchberry seeds by northern red-backed voles (35% of seeds were consumed on average)(Fig. 8).

Discussion

Our results indicate that brown bears disperse large quantities of seeds from twelve fruit bearing shrub species in our study area. Due to their mobility and long gut retention time, brown bears can play a key role in dispersing seeds between disjunct and distant habitats, as evidenced by the appearance of scats full of alpine crowberry in our low-elevation study area. Brown bears are enticed by readily available, calorie rich fruit resources (Appendix 3), and through a mutualistic interaction also provide an important service to plant species through dispersal of their seeds.

Due to the large body size of brown bears, seeds are defecated in large aggregations. The seeds in these aggregations may then be secondarily dispersed by scatter-hoarding small mammals. 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 about 5000 per scat, while the Chichagof study had a mean of 200 seeds per bear scat. Our mean for blueberry seeds was about 10,000 while the Chichagof study had a mean of 4,400. 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

Small mammals such as northwestern deer mice and northern red-backed voles utilize seed-filled bear scats as a food source and also play a role as secondary seed dispersers. 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. The ecological implications of this behavior is

notable as dense concentrations of seeds in bear scats can be a poor environment for successful establishment, and the scatter hoarding behavior of northwestern deer mice may result in important benefits to plants by improving seedling recruitment at a greater number of microsites.

Since northwestern deer mice are scatter hoarders, we assume that a portion of the seeds that northwestern deer mice collected from bear scats were cached for later consumption. Northwestern deer mice typically cache 1–3 seeds that are buried 5–10 mm deep; optimal growing conditions for seedlings (Enders and Vander Wall 2012). Northern red-backed voles have not been previously documented to feed on seed-filled bear scats, but in our study they were the second most common species utilizing seeds in bear scats. The northern red-backed vole is considered to be a seed predator due to their larder hoarding behavior (Bailey 1926) though further research is needed to determine the degree to which they contribute to seed dispersal.

Seed-filled bear scats produce multiple benefits for small granivores. First, they provide a concentrated food source for efficient foraging. Second, this resource can be cached to provide food during the energetically limiting winter period. Third, the deposition of seed-filled bear scats throughout summer extends the phenology of seed availability to small granivores that would otherwise only access seeds after senescence.

The energy available in bear scats can meet a substantial portion of the energy budget for small mammals. For example, a single bear scat from our study contained 73,230 devil's club seeds, which provides 1,139 kcals to a northwestern deer mouse (excluding any partially undigested fruit that would further increase the energy available to small mammals). Deer mice require 10.4 kcal per day in the summer (Morris and Kendeigh 1981), which by extension means that this single bear scat meets the daily energetic needs of 109 deer mice. When extrapolating

from a single bear scats to all scats produced by a bear population, the nutritional subsidy can be quite substantial depending on the density of bears.

Bear densities vary widely throughout the Pacific Rim and interior regions largely due to the availability of salmon, but also due to land and wildlife management practices. Consequently, the indirect effects of bears as seed provisioners for small mammal populations is likewise expected to exhibit substantial geographic variation. For example, in interior regions characterized by low bear densities, small mammal energetic provisioning by seed-filled bear scats is expected to be relatively modest, as compared to coastal areas with extremely high bear densities (Table 6). In the most extreme case, the density of 55 bears/100 km^2 in the protected Katmai National Park (Hilderbrand et al. 1999b) area could result in the deposition of 8,085 bear scats per months in a 70 km^2 area (i.e., the size of our study area), meeting the energy demands of 3,420 northern deer mice; interior areas are capable of energetically provisioning 124 deer mice per month. In our study area it would be 640 deer mice per month, which accounts for 2.1% of the deer mice in conifer habitat and 0.4% in cottonwood habitat.

Small mammal and habitat relationships

The relatively high density of northern red-backed voles that we found in coniferous forest could be linked to the maturity of the forest and associated prevalence of fungus (Boonstra and Krebs† 2006). Northern red-backed voles are highly mycophagous and are not typically considered to be highly granivorous (Ure and Maser 1982, Kasimos 2007, Krebs et al. 2010, Dokuchaev 2013), yet there is strong evidence from our observational and experimental data that they commonly visit seed-filled bear scats and consume seeds. However, with a higher density of voles and a less optimal environment for understory fruiting plants, older forest stands are likely to have lower seedling recruitment from seed-filled bear scats. Consequently, the bear and small

mammal primary and secondary seed dispersal mechanisms that we documented may be more beneficial after a disturbance (fire, logging, windstorm, etc.) in these forest types.

In riparian cottonwood habitats the density of northwestern deer mice was significantly higher than northern red-backed voles, and deer mice were also the dominant visitors to seed-filled bear scats . The high density of northwestern deer mice in cottonwood forests could be an indication that younger forests provide more optimal habitat for this species, resulting in a higher rate of seed dispersal when seed-filled bear scats are present. It is plausible that these seed-filled bear scats are deposited in cottonwood forests as brown bears transition between feeding on berries in upland habitat to feeding on salmon in riparian habitats, thus promoting recruitment of fleshy-fruited plants in these early successional habitats.

Ecological and Conservation Implications of Bear Frugivory

Our results indicate that salmon may exert widespread indirect effects on ecosystems through their role in increasing brown bears densities. The elevated brown bear densities in salmon-bearing ecosystems are responsible for extensive seed dispersal services for fleshy-fruited plant species, 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.

Brown bear-salmon systems once covered much of north-temperate regions of planet earth, but this keystone interaction has declined throughout most of its former range. The decline or extirpation of brown bears may have consequences for plant community composition if wind-dispersed plants, rather than fleshy-fruited shrubs, colonize available microsites after disturbance. 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.

Figures

Figure 1- A) Diplochory cycle involving salmon, brown bears and northwestern deer mice. The northern red-backed vole is a larder hoarder, which does not aid in seed dispersal of fruiting plants. B) A northwestern deer mouse (top), a northern red-backed vole (bottom) feeding at bear scats.
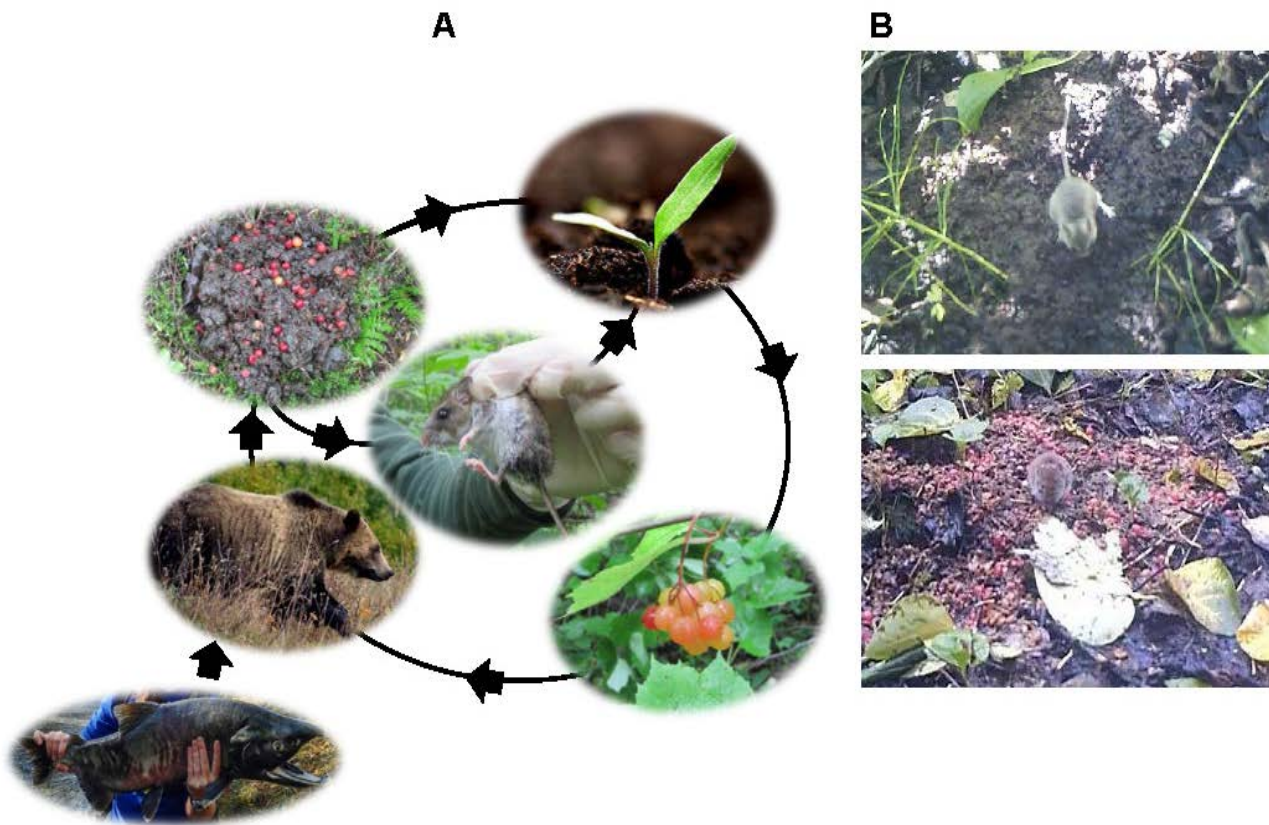
Figure 2: Map of the study area where we studied ecological relationships between bears, berries and small mammals during June-October 2015-2015, near Haines, Alaska. Bear scats collection locations are marked with a X. The orange (cottonwood forest) and yellow (conifer forest) dots depict locations where small mammal data were collected.
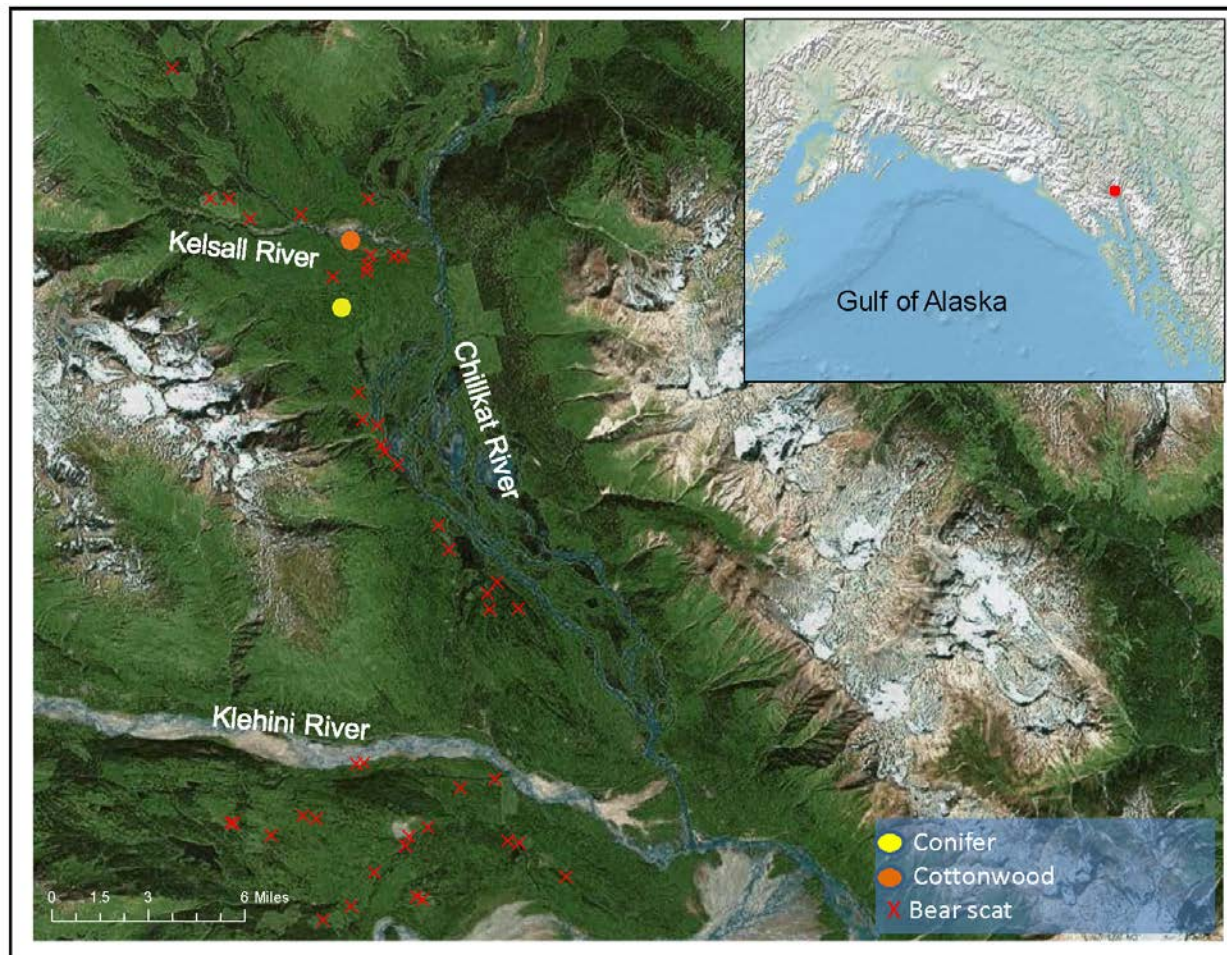
Figure 3: Summary describing the number of seeds, by species, found in individual brown bear scats during June-October 2014-2015, near Haines, Alaska.
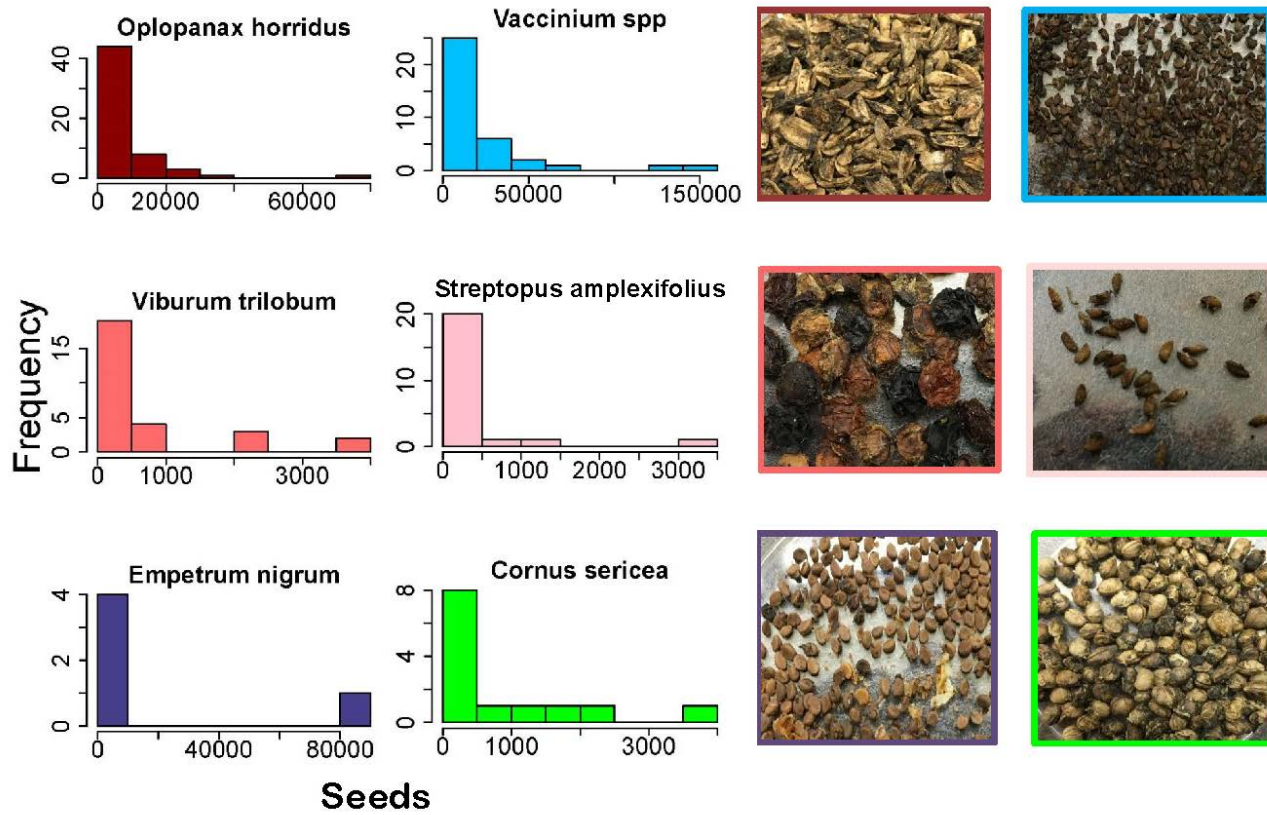
Figure 4: A) The frequency of occurrence of seeds found in bear scats. Bars for each species indicates the frequency it was found in all the bear scats that were sorted (N=71). B) Mean number of seeds found in all bear scats during. Bars indicate the mean number of seeds found in all bear scats that were sorted (N=71). June-October 2014-2015, near Haines, Alaska.
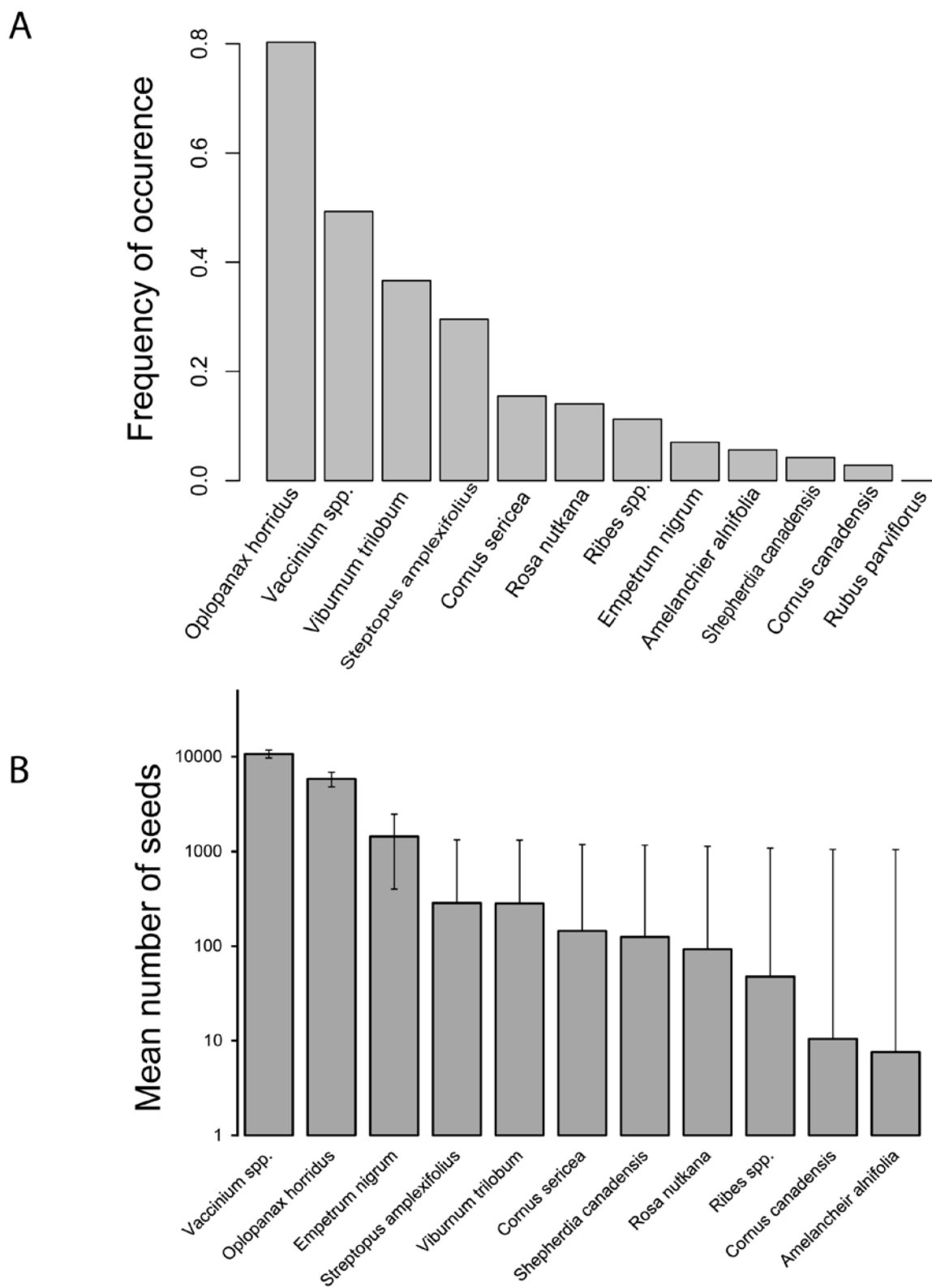
Figure 5: The numbers of seeds in bear scats during different periods from early July to early September for *Vaccinium* and *Oplopanax horridus* in 2014-2015 in Haines, Alaska.
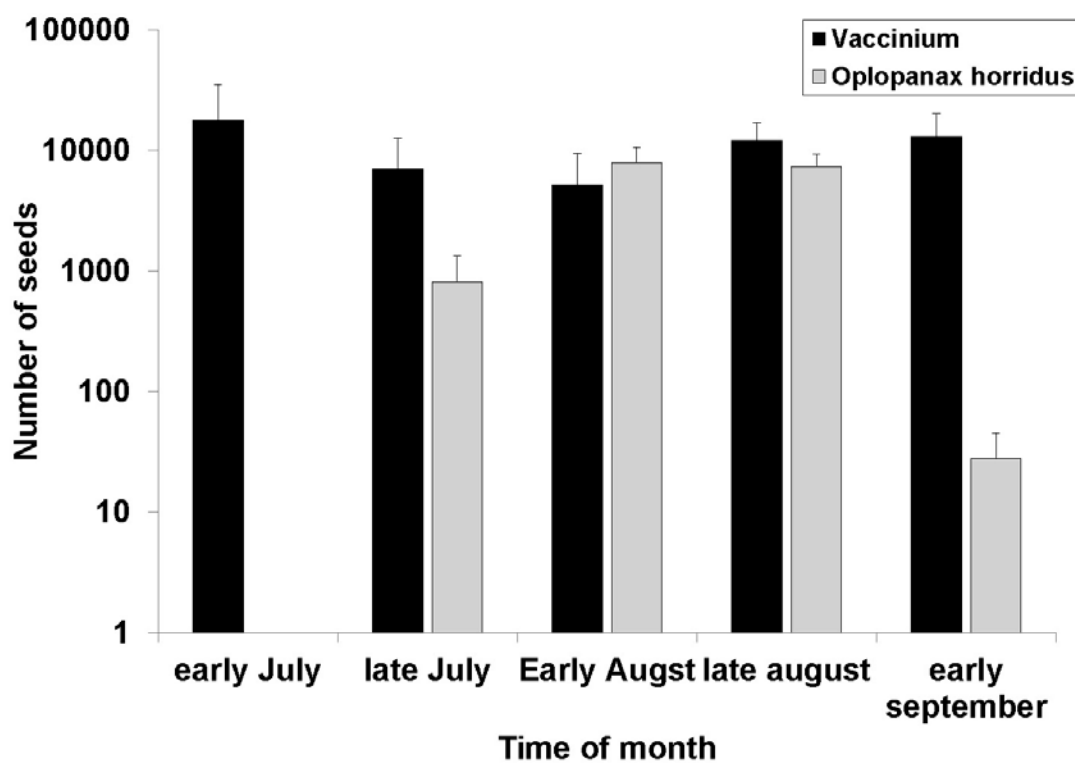
Figure 6: The number of observed visits by small mammals and birds using continuous 24-hour monitoring at seed-filled bear scats in two different habitat types during June-October 2014, near Haines, Alaska.
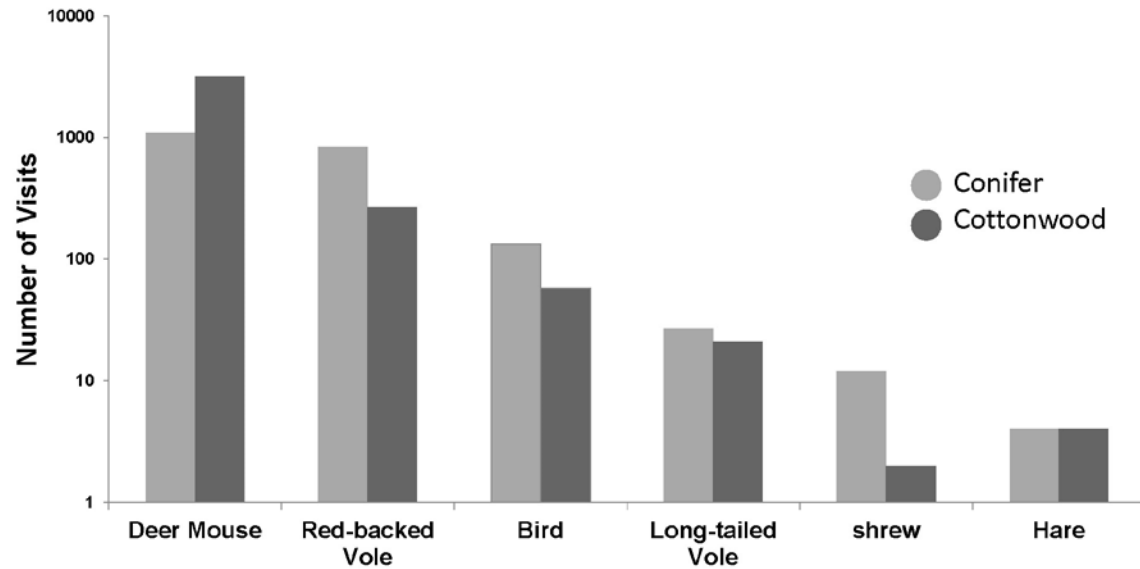
Figure 7: Daily encounters by northwestern deer mice and northern red-back voles per bear scat monitored by trail cameras during June-October 2014 and the estimated densities (ha) of each species near Haines, Alaska.
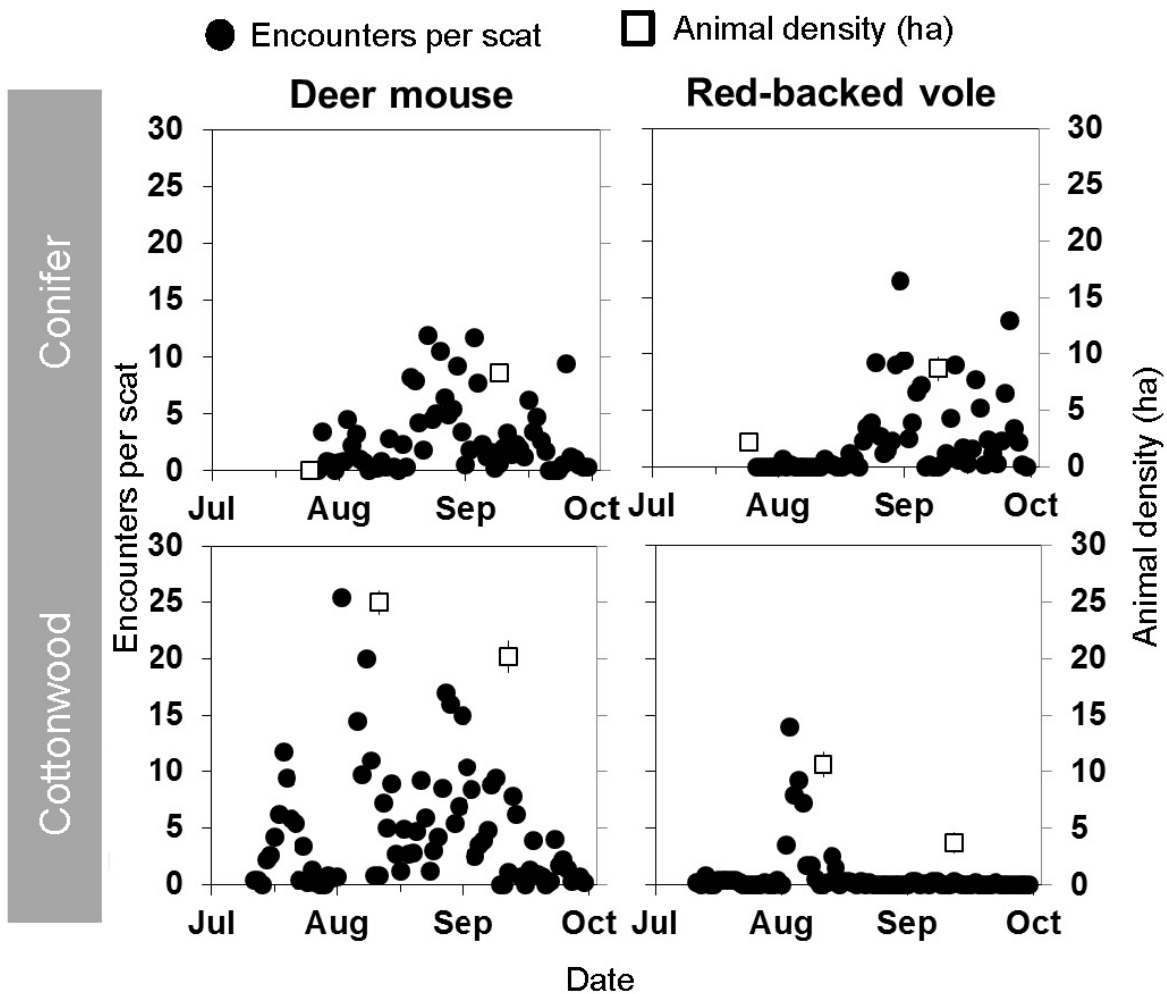
Figure 8: Proportion of seeds consumed by northwestern deer mice and northern red-backed voles during seed feeding experiments conducted during 2015-2014, near Haines, Alaska.
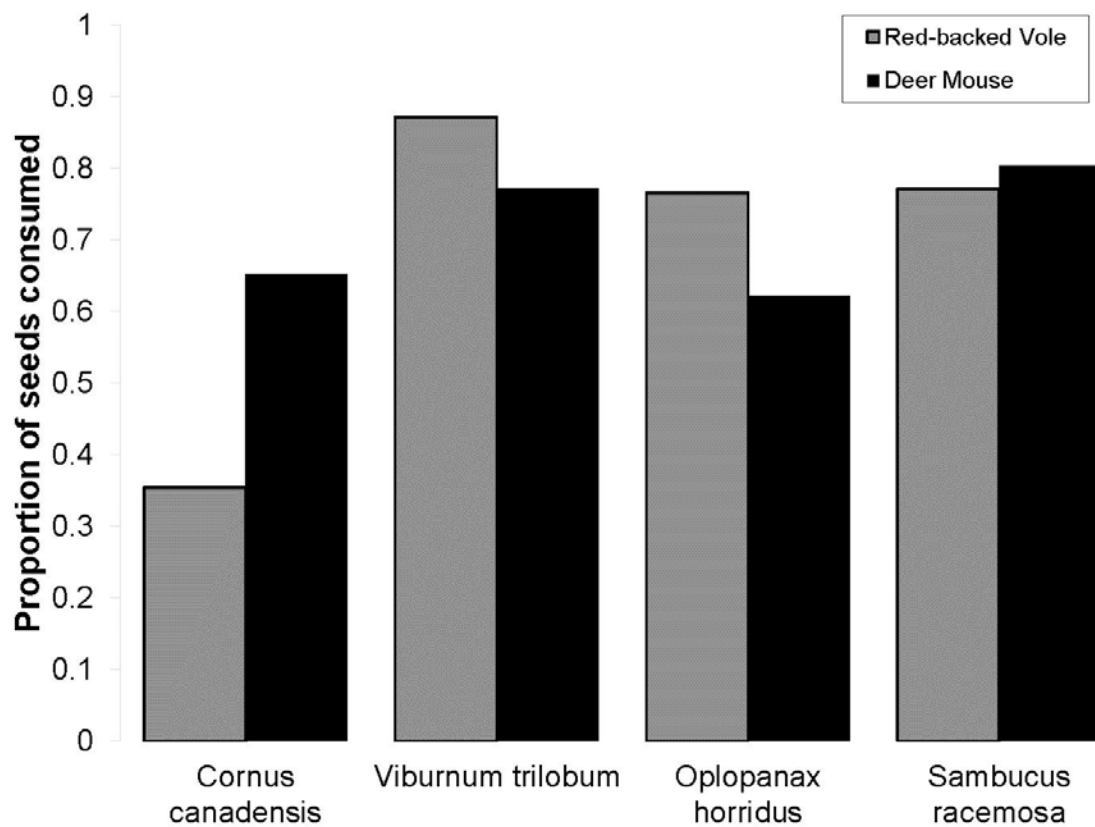
Figure 9: A) The distribution of kcals of digestible energy among seeds in scats B) The distribution of the number of days a deer mouse could meet its complete energetics needs (deer mice days) entirely from one bear scat. C) The distribution of digestible energy among fruit in scats. D) The distribution of the number of days a deer mouse could meet its complete energetic needs (deer mice days).
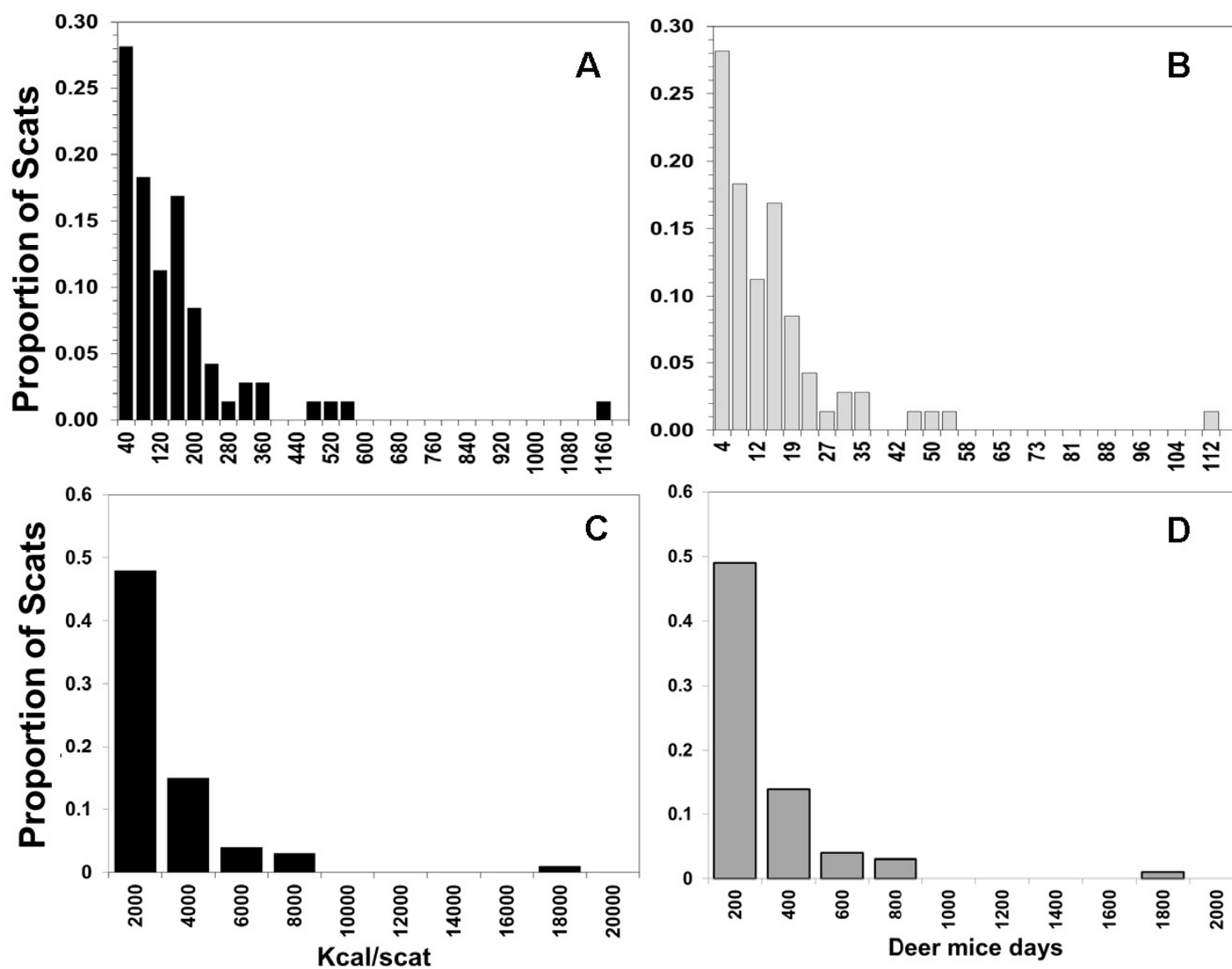
Figure 10: Brown bear densities and the number of small mammals that can survive on seed-filled bear scats in a 70 km^2 area; if bears are producing 7 scats a day with an average of 132 kcals per scat.
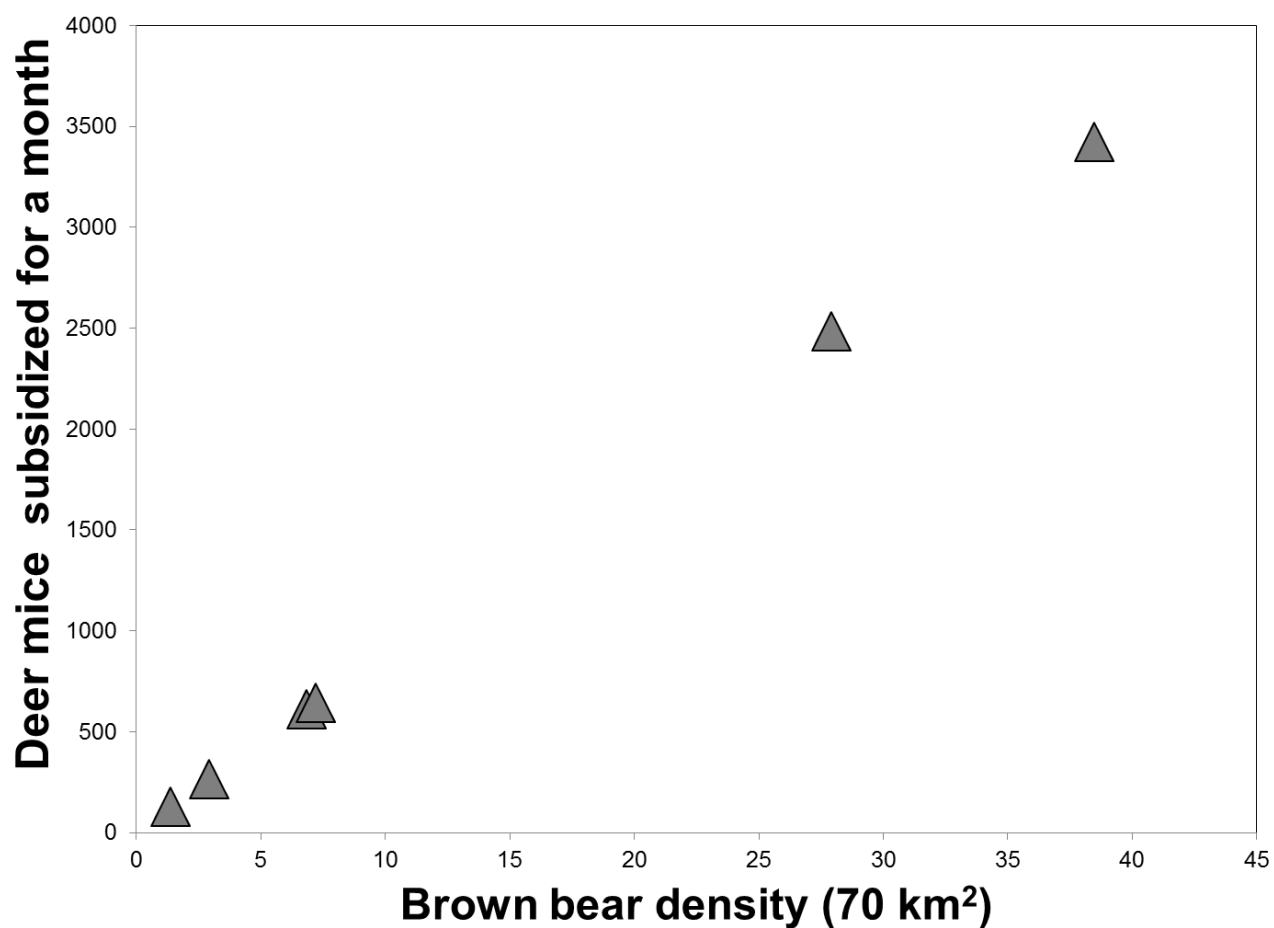
Table 1. Mean number of seeds of 12 fruit species found in seed-filled bear scats (N=71) in

Haines Alaska, 2014-2015

Species	Mean	Standard deviation	SE
Vaccinium spp.	10719.35	26431.7	3136.9
Oplopanax horridus	5839.00	10586.3	1256.4
Empetrum nigrum	1438.38	10249.2	1216.4
Shepherdia canadensis	285.34	1671.4	198.4
Viburnum trilobum	281.72	771.7	91.6
Cornus sericea	144.45	569.0	67.5
Streptopus amplexifolius	125.14	423.3	50.2
Rosa nutkana	92.83	442.5	52.5
Ribes lacustre	47.59	218.0	25.9
Cornus canadensis	10.45	60.8	7.2
Amelancheir alnifolia	7.58	46.3	5.5
Rubus parviflorus	0.14	1.2	0.1

Table 2. The nutritional content of fruits and their seeds found in seed-filled bear scats, near

Haines, AK. Digestible dry matter (%) was estimated.

Species	Average Weight (g)	Gross Energy kcal/gm	Crude Fat (%)	Crude Protein (%)	Total Dietary Fiber (%)	DDM (%)	Digestible Energy kcal/gm
Vaccinium spp							
whole fruit	0.2900	3.9	4.42	6.24	23.9	70.2	2.7
Seed	0.0002	5.6	23.29	18.58	68.1	35.9	2.0
Cornus canadensis							
whole fruit	0.2800	4.1	8.37	7.33	47.6	51.8	2.12
Seed	0.0072	5.3	11.85	8.36	78.0	28.1	1.5
Oplopanax horridus							
whole fruit	0.1700	5.0	26.94	8.49	42.9	55.4	2.77
Seed	0.0079	5.6	23.35	12.33	69.1	35.1	1.96
Viburum trilobum							
whole fruit	0.5300	4.4	7.75	4.83	38.5	58.9	2.6
Seed	0.0233	5.7	20.03	10.75	69.2	35.1	2.1
Cornus sericea							
whole fruit	0.3200	5.4	27.36	6.97	48.1	51.4	2.8
Seed	0.0254	5.2	11.50	7.81	80.6	26.1	1.36

Table 3. Density (animals/ha) of northwestern deer mouse and northern red-backed vole in relation to habitat type and season during 2014, near Haines, Alaska.

Date	Deer mouse					Red backed vole			
	Density	LCI	UCI	SE		Density	LCI	UCI	SE
Conifer									
August	0.0	0.0	0.0	0.0		2.2	1.9	6.7	0.7
Sept	8.6	8.4	12.8	0.7		8.6	7.9	13.2	1.1
Cottonwood									
August	24.9	24.0	29.1	1.1		10.6	9.8	15.3	1.1
Sept	20.1	18.6	24.9	1.4		3.7	3.3	8.2	0.9

Table 4. The number of visits by each species to seed-filled bear scats and on each habitat type in Haines, Alaska 2014-2015.

Species	Conifer	Proportion	Cottonwood	Proportion
Birds	132	0.06	58	0.02
Deer Mouse	1103	0.52	3192	0.90
Other Vole	27	0.01	21	0.01
Red-backed Vole	832	0.39	267	0.08
Shrew	12	0.01	2	0
Hare	4	0	4	0

Table 5. 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, AK.

Seed Species	Mean	Max	kcals (mean)	kcals (max)	Deer mice sustained a day
Vaccinium spp.	10719 ± 3,136.9	157,178	14.7	220.7	1 - 21.1
Oplopanax horridus	5839 ± 1256.4	73,230	72.5	1,162	7 - 109
Viburum trilobum	281 ± 91.6	3,933	11.8	165	1 - 15.8
Cornus sericea	144 ± 67.5	3,849	5	104	0.5 – 10.1

Table 6. The estimated number of deer mice subsidized by seed-filled bear scats with a mean of 132 kcals per scat available to deer mice, based on different brown bear density estimates documented in Alaska.

Location	Bears/100 km^2	Bears/70 km^2[a]	Deer mice days	Reference
Interior	2.0	1.4	124	Miller et al. 1997
Kenai Peninsula	4.2	2.9	261	Mowat et al. 2013
Yakutat	9.8	6.9	609	Crupi et al. 2017
Berners Bay	10.3	7.2	640	Flynn et al. 2012
ABC islands	39.9	27.9	2,481	Miller et al. 1997
Katmai	55	38.5	3,420	Hilderbrand et al. 1999b

CHAPTER 3

GENERAL CONCLUSION AND FUTURE RESEARCH

Yasaman N. Shakeri

Brown bears exert a significant influence on seed dispersal of virtually all species of fleshy fruited plants in coastal Alaska. The seed dispersal pathways initiated by bears are enhanced when small mammals disperse seeds collected from seed-filled bear scats, a largely mutualistic interaction that also nutritionally benefits small mammals. The high density of brown bears in coastal ecosystems, made possible due to the seasonal pulsed availability of pacific salmon (Hilderbrand et al. 1999), likely results in significant landscape level effects. This occurs because of the predilection of brown bears to have a mixed omnivorous diet resulting in significant consumption of fruit, even in the presence of highly available salmon food resources (Erlenbach et al. 2014), and potentially because dominant bears exclude other bears, particularly females with cubs, from salmon streams (Schoen and Beier 1990).

In our study area, 12 different fruit species were consumed and dispersed by bears on the landscape. Devils club was the most heavily consumed fruit followed by blueberry, but the quantity and composition of fruit consumed by brown bears appears to vary geographically. On Chichagof Island blueberries and currants, followed by devils club, were the most common fruit consumed by brown bears (Wilson and Gende 2004), which suggest that other ecological factors such as bear density and plant community composition play a role in modulating ecological interactions between bears, fruit and small mammals. For example, a study on Admiralty Island indicated that devils club was the most frequently consumed fruit in brown bear diets, but frequencies of occurrence were 50% less than we documented in our study area near Haines, Alaska (Gende and Willson 2004).

With small mammals simultaneously benefiting from and dispersing seeds in seed-filled bear scats, we conclude that the indirect effects of salmon, through brown bear populations, has a far greater impact on terrestrial ecosystems than previously believed. Our research demonstrates

that northwestern deer mice and northern red-backed voles frequently consumed seeds from seed-filled bear scats and that the density of the species played a role on the frequency of visitations by small mammals. We also determined that small mammals consume a variety of different seeds from bear scats, which allowed us to make estimates regarding the number northwestern deer mice that can be sustained by seed-filled bear scats on the landscape.

In coastal areas where brown bear densities are high, we expect higher fruit consumption across the landscape, yet the contributions of the northwestern deer mouse as the secondary disperser are essential to seedling recruitment. Bear densities differ among coastal brown bears, likely due to hunting pressure in unprotected areas and local variation in salmon availability. Variation in bear density is expected to regulate effects on seed dispersal and the number of small mammals that can be sustained by seed-filled bear scats.

To better understand the importance of coastal brown bears as seed dispersers it would be important to conduct research in areas where coastal brown bears have been extirpated to understand how the landscape has changed due to the loss of an important seed disperser. Most such landscapes have also been modified by anthropogenic disturbance, confounding efforts to disentangle the effects of brown bear extirpation. Understanding if black bears provide similar ecosystem services, when densities are high, could also be important to understand in areas that are absent of brown bears. This would allow us to monitor the type of changes to expect over time in areas where brown bears are absent. Additional research on how bears alter their ecosystems is crucial to better understanding the many interactions that occur amongst the many wildlife and plant species in this unique but globally significant ecosystem.

References

Alves-Costa, C. P. and P. C. Eterovick. 2007. Seed dispersal services by coatis (*Nasua nasua, Procyonidae*) and their redundancy with other frugivores in southeastern Brazil. Acta Oecologica 32:77–92.

Bailey, V. 1926. A biological survey of North Dakota: I. Physiography and life zones. II. The mammals. Federal Government Series, U.S. Fish and Wildlife Service.

Beck, M. J. and S. B. Vander Wall. 2010. Seed dispersal by scatter-hoarding rodents in arid environments. Journal of Ecology 98:1300–1309.

Ben-David, M., K. Titus and L. R. Beier. 2004. Consumption of salmon by Alaskan brown bears: a trade-off between nutritional requirements and the risk of infanticide? Oecologia 138:465–474.

Bermejo, T., A. Traveset and M. F. Willson. 1998. Post–dispersal seed predation in the temperate rainforest of southeast Alaska. ResearchGate 112.

Boonstra, R. and C. J. Krebs†. 2006. Population limitation of the northern red-backed vole in the boreal forests of northern Canada. Journal of Animal Ecology 75:1269–1284.

Brodin, A. 2010. The history of scatter hoarding studies. Philosophical Transactions of the Royal Society B: Biological Sciences 365:869–881.

Chavez-Ramirez, F. and R. D. Slack. 1993. Carnivore Fruit-Use and Seed Dispersal of Two Selected Plant Species of the Edwards Plateau, Texas. The Southwestern Naturalist 38:141–145.

Christianini, A. V. and P. S. Oliveira. 2010. Birds and ants provide complementary seed dispersal in a neotropical savanna. Journal of Ecology 98:573–582.

Clarke, M. F. and D. L. Kramer. 1994. Scatter-hoarding by a larder-hoarding rodent: intraspecific variation in the hoarding behaviour of the eastern chipmunk, *Tamias striatus*. Animal Behaviour 48:299–308.

Cooch, E. and G. White. 2001. Using MARK—a gentle introduction. Cornell University, Ithaca.

Cormack, R. M. 1964. Estimates of Survival from the Sighting of Marked Animals. Biometrika 51:429–438.

Crooks, K. R. and M. E. Soulé. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. Nature 400:563–566.

Crupi, A. P., J. N. Waite, R. W. Flynn and L. R. Beier. 2017. Brown Bear Population Estimation in Yakutat, Southeast Alaska. Alaska Dept of Fish and Game Research Report.

Cypher, B. L. and E. A. Cypher. 1999. Germination Rates of Tree Seeds Ingested by Coyotes and Raccoons. The American Midland Naturalist 142:71–76.

Daly, M., L. F. Jacobs, M. I. Wilson and P. R. Behrends. 1992. Scatter hoarding by kangaroo rats (*Dipodomys merriami*) and pilferage from their caches. Behavioral Ecology 3:102–111.

D'hondt, B., B. Bossuyt, M. Hoffmann and D. Bonte. 2008. Dung beetles as secondary seed dispersers in a temperate grassland. Basic and Applied Ecology 9:542–549.

Di Domenico, G., E. Tosoni, L. Boitani and P. Ciucci. 2012. Efficiency of scat-analysis lab procedures for bear dietary studies: The case of the Apennine brown bear. Mammalian Biology - Zeitschrift für Säugetierkunde 77:190–195.

Dokuchaev, N. 2013. Storing Larch Seeds by Northern Red-Backed Vole (*Clethrionomys Rutilus*). Zoologichesky Zhurnal 92:1293–1295.

Enders, M. S. and S. B. Vander Wall. 2012. Black bears *Ursus americanus* are effective seed dispersers, with a little help from their friends. Oikos 121:589–596.

Erlenbach, J. A., K. D. Rode, D. Raubenheimer and C. T. Robbins. 2014. Macronutrient optimization and energy maximization determine diets of brown bears. Journal of Mammalogy 95:160–168.

Estes, J. A., J. Terborgh, J. S. Brashares, M. E. Power, J. Berger, W. J. Bond, S. R. Carpenter, T. E. Essington, R. D. Holt, J. B. C. Jackson, R. J. Marquis, L. Oksanen, T. Oksanen, R. T. Paine, E. K. Pikitch, W. J. Ripple, S. A. Sandin, M. Scheffer, T. W. Schoener, J. B. Shurin, A. R. E. Sinclair, M. E. Soulé, R. Virtanen and D. A. Wardle. 2011. Trophic Downgrading of Planet Earth. Science 333:301–306.

Fedriani, J. M. and M. Delibes. 2009. Functional diversity in fruit-frugivore interactions: a field experiment with Mediterranean mammals. Ecography 32:983–992.

Flynn, R. W., S. B. Lewis, L. R. Beier, G. W. Pendleton, A. P. Crupi and D. P. Gregovich. 2012. Spatial use, habitat selection and population ecology of brown bears along the proposed Juneau Access Improvements Road Corridor, Southeast Alaska. Alaska Department of Fish and Game, Juneau.

Fortin, J. K., S. D. Farley, K. D. Rode and C. T. Robbins. 2007. Dietary and spatial overlap between sympatric ursids relative to salmon use. Ursus 18:19–29.

Gende, S. M., R. T. Edwards, M. F. Willson and M. S. Wipfli. 2002. Pacific Salmon in Aquatic and Terrestrial Ecosystems. BioScience 52:917–928.

Gende, S. M. and T. P. Quinn. 2004. The relative importance of prey density and social dominance in determining energy intake by bears feeding on Pacific salmon. Canadian Journal of Zoology 82:75–85.

Gende, S. M., T. P. Quinn, R. Hilborn, A. P. Hendry and B. Dickerson. 2004. Brown bears selectively kill salmon with higher energy content but only in habitats that facilitate choice. Oikos 104:518–528.

Gustafson, R. G., M. J. Ford, D. Teel and J. S. Drake. 2010. Status Review of Eulachon(Thaleichthys pacificus) in Washington, Oregon and California.

Hamilton, A. N. and F. L. Bunnell. 1987. Foraging Strategies of Coastal Grizzly Bears in the Kimsquit River Valley, British Columbia. Bears: Their Biology and Management 7:187–197.

Hay, D. 2002. The eulachon in northern British Columbia. Information supporting past and present ecosystem models of Northern British Columbia and the Newfoundland Shelf. Fisheries Centre Research Reports 10:98–107.

Hay, D. E. and P. B. McCarter. 2000. Status of the Eulachon Thaleichthys pacificus in Canada. Canadian Stock Assessment Secretariat Research Document. 2000/145. Fisheries and Oceans Canada. Ottawa, Ontario.

Helfield, J. M. and R. J. Naiman. 2006. Keystone Interactions: Salmon and Bear in Riparian Forests of Alaska. Ecosystems 9:167–180.

Hilderbrand, G. V., T. A. Hanley, C. T. Robbins and C. C. Schwartz. 1999a. Role of brown bears (*Ursus arctos*) in the flow of marine nitrogen into a terrestrial ecosystem. Oecologia 121:546–550.

Hilderbrand, G. V., C. C. Schwartz, C. T. Robbins, M. E. Jacoby, T. A. Hanley, S. M. Arthur and C. Servheen. 1999b. The importance of meat, particularly salmon, to body size, population productivity and conservation of North American brown bears. Canadian Journal of Zoology 77:132–138.

Hocking, M. D. and J. D. Reynolds. 2011. Impacts of Salmon on Riparian Plant Diversity. Science 331:1609–1612.

Holtgrieve, G. W., D. E. Schindler and P. K. Jewett. 2009. Large predators and biogeochemical hotspots: brown bear (*Ursus arctos*) predation on salmon alters nitrogen cycling in riparian soils. Ecological Research 24:1125–1135.

Howe, H.F. and J. Smallwood. 1982. Ecology of Seed Dispersal. review-article. http://www.annualreviews.org.ezproxy.proxy.library.oregonstate.edu/doi/10.1146/annure v.es.13.110182.001221.

Howe, H. F. 1989. Scatter-and clump-dispersal and seedling demography: hypothesis and implications. Oecologia 79:417–426.

Jansen, P. A., F. Bongers and L. Hemerik. 2004. Seed Mass and Mast Seeding Enhance Dispersal by a Neotropical Scatter-Hoarding Rodent. Ecological Monographs 74:569–589.

Jolly, G. M. 1965. Explicit Estimates from Capture-Recapture Data with Both Death and Immigration-Stochastic Model. Biometrika 52:225–247.

Kasimos, C. 2007. Impact of seed and seedling predators on recruitment of Newfoundland red maple.

Kendall, W. L., J. D. Nichols and J. E. Hines. 1997. Estimating Temporary Emigration Using Capture–Recapture Data with Pollock's Robust Design. Ecology 78:563–578.

Kendall, W. L., K. H. Pollock and C. Brownie. 1995. A Likelihood-Based Approach to Capture-Recapture Estimation of Demographic Parameters under the Robust Design. Biometrics 51:293–308.

Krebs, C. J., K. Cowcill, R. Boonstra and A. J. Kenney. 2010. Do changes in berry crops drive population fluctuations in small rodents in the southwestern Yukon? Journal of Mammalogy 91:500–509.

Kunkel, K. E. and L. D. Mech. 1994. Wolf and bear predation on white-tailed deer fawns in northeastern Minnesota. Canadian Journal of Zoology 72:1557–1565.

Kurek, P. and J. Holeksa. 2015. Grains in the Diets of Medium-Sized Carnivores — A Case of Diplochory? Polish Journal of Ecology 63:286–290.

Levi, T. and C. C. Wilmers. 2012. Wolves–coyotes–foxes: a cascade among carnivores. Ecology 93:921–929.

Linnell, J. D., R. Aanes and R. Andersen. 1995. Who killed Bambi? The role of predation in the neonatal mortality of temperate ungulates. Wildlife Biology 1:209–223.

LoGiudice, K. and R. Ostfeld. 2002. Interactions between mammals and trees: predation on mammal-dispersed seeds and the effect of ambient food. Oecologia 130:420–425.

Marston, B. H., M. F. Willson and S. M. Gende. 2002. Predator aggregations during eulachon Thaleichthys pacificus spawning runs. Marine Ecology Progress Series 231:229–236.

Middleton, A. D., T. A. Morrison, J. K. Fortin, C. T. Robbins, K. M. Proffitt, P. J. White, D. E. McWhirter, T. M. Koel, D. G. Brimeyer, W. S. Fairbanks and M. J. Kauffman. 2013. Grizzly bear predation links the loss of native trout to the demography of migratory elk in Yellowstone. Proceedings of the Royal Society of London B: Biological Sciences 280:20130870.

Miller, S. D., G. C. White, R. A. Sellers, H. V. Reynolds, J. W. Schoen, K. Titus, V. G. Barnes, R. B. Smith, R. R. Nelson, W. B. Ballard and C. C. Schwartz. 1997. Brown and Black

Bear Density Estimation in Alaska Using Radiotelemetry and Replicated Mark-Resight Techniques. Wildlife Monographs:3–55.

Morris, J. G. and S. C. Kendeigh. 1981. Energetics of the Prairie Deer Mouse *Peromyscus maniculatus bairdii*. The American Midland Naturalist 105:368–376.

Mowat, G., D. C. Heard and C. J. Schwarz. 2013. Predicting Grizzly Bear Density in Western North America. PLOS ONE 8:e82757.

Nagy, J. A. S. and M. A. Haroldson. 1990. Comparisons of Some Home Range and Population Parameters among Four Grizzly Bear Populations in Canada. Bears: Their Biology and Management 8:227–235.

Nowak, C., M. Büntjen, K. Steyer and C. Frosch. 2014. Testing mitochondrial markers for noninvasive genetic species identification in European mammals. Conservation Genetics Resources 6:41–44.

Peacock, E., M. M. Peacock and K. Titus. 2007. Black bears in Southeast Alaska: the fate of two ancient lineages in the face of contemporary movement. Journal of Zoology 271:445–454.

Pijl, D. L. van der. 1969. Introduction. Pages 1–5 Principles of Dispersal in Higher Plants. Springer Berlin Heidelberg.

Quinn, T. P. and M. T. Kinnison. 1999. Size-selective and sex-selective predation by brown bears on sockeye salmon. Oecologia 121:273–282.

Rausch, R. L. 1963. Geographic Variation in Size in North American Brown Bears, *Ursus Arctos L.*, as Indicated by Condylobasal Length. Canadian Journal of Zoology 41:33–45.

Ripple, W. J. and R. L. Beschta. 2004. Wolves and the Ecology of Fear: Can Predation Risk Structure Ecosystems? BioScience 54:755–766.

Ritchie, E. G. and C. N. Johnson. 2009. Predator interactions, mesopredator release and biodiversity conservation. Ecology Letters 12:982–998.

Robards, M. D., J. F. Piatt, A. B. Kettle and A. A. Abookire. 1999. Temporal and geographic variation in fish communities of lower Cook Inlet, Alaska. Fishery Bulletin 97:16.

Rode, K. D., S. D. Farley and C. T. Robbins. 2006a. Sexual Dimorphism, Reproductive Strategy and Human Activities Determine Resource Use by Brown Bears. Ecology 87:2636–2646.

Rode, K. D., S. D. Farley and C. T. Robbins. 2006b. Behavioral responses of brown bears mediate nutritional effects of experimentally introduced tourism. Biological Conservation 133:70–80.

Rode, K. D. and C. T. Robbins. 2000. Why bears consume mixed diets during fruit abundance. Canadian Journal of Zoology 78:1640–1645.

Ruggerone, G. T., R. Hanson and D. E. Rogers. 2000. Selective predation by brown bears (*Ursus arctos*) foraging on spawning sockeye salmon (*Oncorhynchus nerka*). Canadian Journal of Zoology 78:974–981.

Schaumann, F. and T. Heinken. 2002. Endozoochorous seed dispersal by martens (*Martes foina, M. martes*) in two woodland habitats. Flora - Morphology, Distribution, Functional Ecology of Plants 197:370–378.

Schoen, J. W. and L. Beier. 1990. Brown bear habitat preferences and brown bear logging and mining relationships in southeast Alaska. Federal aid in wildlife restoration area. 4.17, Alaska Department of Fish and Game, Juneau.

Schoen, J. W., J. W. Lentfer and L. Beier. 1986. Differential Distribution of Brown Bears on Admiralty Island, Southeast Alaska: A Preliminary Assessment. Bears: Their Biology and Management 6:1–5.

Scott, J. M. 1973. Resource allocation in four syntopic species of marine diving birds.

Seber, G. A. F. 1965. A Note on the Multiple-Recapture Census. Biometrika 52:249–259.

Szepanski, M. M., M. Ben-David and V. V. Ballenberghe. 1999. Assessment of anadromous salmon resources in the diet of the Alexander Archipelago wolf using stable isotope analysis. Oecologia 120:327–335.

Traveset, A. and M. F. Willson. 1997. Effect of Birds and Bears on Seed Germination of Fleshy-Fruited Plants in Temperate Rainforests of Southeast Alaska. Oikos 80:89–95.

Ure, D. C. and C. Maser. 1982. Mycophagy of red-backed voles in Oregon and Washington. Canadian Journal of Zoology 60:3307–3315.

Vander Wall, S. B. 2008. On the Relative Contributions of Wind Vs. Animals to Seed Dispersal of Four Sierra Nevada Pines. Ecology 89:1837–1849.

Vander Wall, S. B. and W. S. Longland. 2004. Diplochory: are two seed dispersers better than one? Trends in Ecology & Evolution 19:155–161.

Vander Wall, S. B. V. 2010. How Plants Manipulate the Scatter-Hoarding Behaviour of Seed-Dispersing Animals. Philosophical Transactions: Biological Sciences 365:989–997.

Wasser, S. K., C. S. Houston, G. M. Koehler, G. G. Cadd and S. R. Fain. 1997. Techniques for application of faecal DNA methods to field studies of Ursids. Molecular Ecology 6:1091–1097.

White, G. C. and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46:S120–S139.

Willson, M. F. 1993. Mammals as Seed-Dispersal Mutualists in North America. Oikos 67:159–176.

Willson, M. F. and S. M. Gende. 2004. Seed Dispersal by Brown Bears, Ursus arctos , in Southeastern Alaska. The Canadian Field-Naturalist 118:499–503.

Zhou, Y.-B., C. Newman, C. D. Buesching, A. Zalewski, Y. Kaneko, D. W. Macdonald and Z.-Q. Xie. 2011. Diet of an opportunistically frugivorous carnivore, *Martes flavigula*, in subtropical forest. Journal of Mammalogy 92:611–619.

APPENDICES

Appendix 1: 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

Appendix 2: Density of small mammals (per hectare) during each trapping session in each forest type near Haines, AK 2014 and 2015

Session	Date	Habitat	Deer mouse				Red-backed Vole			
			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

Appendix 3: Number of kcals of digestible energy in each bear scat and by each species of fruit consumed.

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	1606	0	0	0	0	0	0	0	1606
NA	0	0	0	0	0	0	0	0	0	0	0
Brown	0	0	0	0	0	0	0	0	59	0	59
Brown	0	0	0	0	0	0	0	0	1497	0	1497
Brown	0	0	0	0	0	0	0	0	0	0	0
Brown	39	6	0	0	0	0	20	15	0	0	80
Brown	105	0	0	0	0	0	2	0	2090	0	2198
NA	1127	0	273	0	0	0	0	0	0	0	1401
Black	5	0	0	0	0	0	0	0	0	0	5
NA	0	0	1148	0	0	0	0	5	0	0	1152
Brown	0	0	0	0	0	0	0	0	0	0	0
NA	469	0	0	0	0	0	69	0	0	0	538
Brown	3	4	0	0	0	0	0	44	0	0	52
Brown	462	8	0	0	0	0	0	0	0	0	469
Brown	807	0	25	0	0	0	0	6	0	0	838
Brown	596	4	6	0	0	0	0	0	0	0	605
Brown	995	0	175	0	0	0	31	0	0	0	1200
NA	655	1	0	0	0	0	243	0	0	0	898
NA	86	58	8	45	0	0	0	0	0	0	198
Black	1000	0	1171	0	0	0	24	0	0	0	2195
NA	6866	0	39	0	0	0	0	0	0	0	6904
NA	1163	0	0	0	0	0	0	0	0	0	1163
NA	948	0	3537	0	0	0	7	0	0	0	4492
NA	619	53	0	23	0	0	9	0	0	0	705
NA	17487	0	10	0	0	0	5	0	0	0	17501
NA	2847	0	0	0	0	0	0	0	0	0	2847
NA	578	6	430	0	0	0	31	0	0	221	1266
Brown	953	0	137	0	0	0	0	0	0	0	1091
Brown	0	0	108	0	0	0	0	0	0	0	108
Brown	5	0	560	0	0	0	0	0	0	0	564
Brown	0	0	878	0	0	0	0	0	0	0	878
Black	1407	0	0	0	0	0	0	0	0	0	1407
NA	2041	1	730	0	0	0	2	0	0	0	2775
Brown	186	0	786	0	0	0	0	0	0	201	1173
Brown	4	19	0	729	0	0	0	0	0	0	751

NA	19	7	0	0	0	0	0	0	0	0	26
Brown	26	0	0	91	233	19	0	0	0	0	369
Brown	0	7	0	0	0	75	0	0	0	0	82
Brown	0	0	0	0	0	397	14	0	0	0	411
Brown	257	22	0	0	0	48	0	0	0	0	327
Brown	9	92	0	25	0	0	0	0	0	0	127
Brown	0	0	208	0	0	0	0	0	0	5	213
Brown	0	0	776	0	0	0	0	0	0	2423	3200
NA	17	0	185	0	0	0	0	0	0	9	211
Brown	745	0	3	0	0	0	18	10	0	0	777
Brown	7325	0	5	59	0	0	0	0	0	0	7389
NA	4902	0	0	0	0	0	1	0	0	0	4903
Brown	780	0	0	0	284	0	9	0	0	0	1073
Black	1982	0	0	0	0	0	23	0	0	0	2005
Brown	1677	1	0	0	0	10	0	4	0	0	1693
Brown	2173	0	280	0	0	0	3	0	0	0	2456
Black	5141	0	7	0	0	0	0	0	0	0	5148
NA	403	0	0	48	0	0	0	0	0	0	451
Brown	12	1	0	5	0	8	0	0	0	0	25
Brown	2214	0	4	0	0	0	31	0	0	0	2250
Brown	2493	0	1	0	0	0	0	0	0	0	2494
Brown	2482	0	243	0	0	0	0	0	0	0	2725
Brown	0	16	0	1002	0	871	0	0	0	0	1888
NA	4	6	0	5	0	235	21	0	0	0	270
Black	2064	0	9	0	0	0	114	79	0	0	2266
Brown	12	19	0	1745	0	0	0	0	0	0	1776
Brown	1537	2	0	0	0	0	2	0	0	0	1541
Brown	8	98	0	278	0	28	0	0	0	0	413
NA	5	62	0	595	0	23	0	3	0	0	688
Brown	3844	0	123	0	0	0	5	0	0	0	3972
Brown	2401	0	29	0	7	0	0	0	0	0	2437
Brown	2109	0	0	0	0	0	0	0	0	0	2109
NA	1017	4	93	0	0	0	0	0	0	0	1114
NA	4587	2	2723	0	0	0	0	0	0	0	7312
Brown	2958	1	810	0	0	0	0	0	0	0	3769
Brown	4341	0	0	0	0	0	0	0	0	0	4341

Appendix 4: 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	24	0	0	0	0	0	0	0	24
NA	0	0	0	0	0	0	0	0	0	0	0
Brown	7	0	0	0	0	0	0	0	148	0	155
NA	73	0	4	0	0	0	0	0	0	0	77
Brown	0	0	0	0	0	0	0	0	0	0	0
NA	31	0	0	0	0	0	3	0	0	0	34
NA	447	0	1	0	0	0	0	0	0	0	448
NA	76	0	0	0	0	0	0	0	0	0	76
NA	62	1	52	0	0	0	0	0	0	0	115
NA	40	106	0	2	0	0	0	0	0	0	149
NA	1139	0	0	0	0	0	0	0	0	0	1140
NA	185	0	0	0	0	0	0	0	0	0	185
NA	38	12	6	0	0	0	2	0	0	12	69
Brown	0	0	2	0	0	0	0	0	0	0	2
Brown	0	0	8	0	0	0	0	0	0	0	9
Brown	0	0	13	0	0	0	0	0	0	0	13
Black	92	0	0	0	0	0	0	0	0	0	92
NA	133	3	11	0	0	0	0	0	0	0	146
Brown	12	0	12	0	0	0	0	0	0	11	34
Brown	0	37	0	56	0	0	0	0	0	0	94
NA	1	13	0	0	0	0	0	0	0	0	14
Brown	2	0	0	7	4	10	0	0	0	0	22
Brown	0	14	0	0	0	39	0	0	0	0	53
Brown	0	1	0	0	0	204	1	0	0	0	205
Brown	17	44	0	0	0	25	0	0	0	0	86
Brown	1	184	0	2	0	0	0	0	0	0	186
Brown	0	0	3	0	0	0	0	0	0	0	3
Brown	0	0	12	0	0	0	0	0	0	127	139
NA	1	0	3	0	0	0	0	0	0	0	4
Brown	0	0	0	0	0	0	0	0	4	0	4
Brown	0	0	0	0	0	0	0	0	106	0	106
Brown	0	0	0	0	0	0	0	0	0	0	0
Brown	3	13	0	0	0	0	1	2	0	0	18
Black	0	0	0	0	0	0	0	0	0	0	0
NA	0	0	17	0	0	0	0	1	0	0	18

Brown	0	8	0	0	0	0	0	6	0	0	15
Brown	30	16	0	0	0	0	0	0	0	0	46
NA	6	117	0	3	0	0	0	0	0	0	126
Black	65	0	17	0	0	0	1	0	0	0	84
NA	43	1	0	0	0	0	12	0	0	0	56
Brown	53	0	0	0	0	0	0	1	0	0	54
Brown	39	8	0	0	0	0	0	0	0	0	47
Brown	65	0	3	0	0	0	1	0	0	0	69
Brown	62	0	2	0	0	0	0	0	0	0	64
Brown	49	0	0	0	0	0	1	2	0	0	51
Brown	477	0	0	5	0	0	0	0	0	0	482
Brown	51	0	0	0	4	0	0	0	0	0	56
Black	129	0	0	0	0	0	1	0	0	0	130
Brown	109	3	0	0	0	5	0	1	0	0	118
Brown	144	1	0	0	0	0	2	0	0	0	146
Brown	162	0	0	0	0	0	0	0	0	0	162
Brown	162	0	4	0	0	0	0	0	0	0	165
Brown	0	31	0	77	0	447	0	0	0	0	555
Black	134	0	0	0	0	0	6	11	0	0	152
Brown	100	3	0	0	0	0	0	0	0	0	103
Brown	250	0	2	0	0	0	0	0	0	0	252
Brown	142	0	4	0	0	0	0	0	0	0	146
Brown	156	0	0	0	0	0	0	0	0	0	157
Brown	137	0	0	0	0	0	0	0	0	0	137
NA	66	8	1	0	0	0	0	0	0	0	76
NA	299	5	40	0	0	0	0	0	0	0	344
Brown	193	2	12	0	0	0	0	0	0	0	207
NA	319	0	0	0	0	0	0	0	0	0	319
Brown	283	0	0	0	0	0	0	0	0	0	283
Black	335	0	0	0	0	0	0	0	0	0	335
NA	26	0	0	4	0	0	0	0	0	0	30
Brown	1	2	0	0	0	4	0	0	0	0	7
NA	0	11	0	0	0	120	1	0	0	0	133
Brown	1	38	0	134	0	0	0	0	0	0	173
Brown	1	197	0	21	0	14	0	0	0	0	233
NA	0	124	0	46	0	12	0	0	0	0	183