AN ABSTRACT OF THE THESIS OF

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Plants often encase seeds in a nutritional reward to incentivize seed dispersal by birds and mammals, but these seeds may also be removed and destroyed by seed predators. Although birds are typically thought to be the primary seed dispersers of berries in temperate systems, in southeast Alaska and other salmon-bearing ecosystems, where partially frugivorous bears (*Ursus arctos* and *U. americanus*) are especially abundant, mammalian seed dispersal pathways may be uniquely important. Salmon-bear ecosystems that have historically existed through most of the temperate and boreal regions of planet earth have shrunk to only exist in the North Pacific. Research on salmon-bear interactions has focused on the direct flow of marine-derived nutrients, but little attention has been paid to the indirect effects that salmon have on ecosystems by supporting high densities of bears. Brown and black bears are known seed dispersers of fleshy-fruited shrubs in southeast Alaska, where brown bears are supported in remarkably high densities by anadromous salmon. Salmon, through brown bears, could impact the understory plant community of this ecosystem if bears provide key seed dispersal services that are not redundant with those provided by birds. We used a combination of motion-triggered camera traps and eDNA to quantify the relative roles of thrushes, brown bears, and black bears as seed dispersers of devil's club (*Oplopanax horridus*) berries during the summers of 2014 and 2015. We found that overall, brown bears are the dominant seed dispersers of devil's club, followed by black bears, and that avian seed dispersers accounted for only a small fraction of the total berries harvested. This is the first record of a temperate plant being primarily dispersed by mammalian endozoochory. Additionally, we identified that red squirrels (*Tamiasciurus hudsonicus*) are the dominant, previously unidentified, seed predators of devil's club. This research demonstrates that bears serve disproportionately important roles as seed dispersers, and suggests that plant community structure may be influenced by the abundance of salmon-supported bears.

THE PRIMACY OF MAMMALS AS SEED DISPERSERS AND PREDATORS IN SALMON-BEARING ECOSYSTEMS

BY

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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.

Laurie E. F. Harrer, Author

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CHAPTER 1: GENERAL INTRODUCTION

SEED DISPERSAL MECHANISMS

Plants disperse their seeds to avoid filicide, colonize new landscapes, and to place seeds in optimal habitat (Howe and Smallwood 1982). This can be accomplished through a variety of mechanisms including self-dispersal, in which plants put out creeping diaspores (Frey and Kurschner 1991) or possess exploding fruit (Russel and Musil 1961). Plants also develop fruits with traits to be dispersed by water (Cappers 1993) and by wind (Katul et al. 2005). In addition, plants use animals to disperse their seeds in a number of ways. Clinging structures on fruit and seed coverings can stick to animal fur (Russel and Musil 1961). Using mimesis, plants can trick animals into ingesting fruits and seeds (Galetti 2002). Some plants provide large nutritious seeds that incentivize scatter-hoarding behavior in animals, which inevitably leaves some forgotten seeds buried at an optimal depth (Vander Wall 2010). And finally, plants provide a fleshy nutritional reward for animals to ingest and then defecate out seeds (Willson and Gende 2004); my research will focus on this final method of "endozoochorous" seed dispersal.

Foraging theory suggests that plants must provide a high net energetic or nutritional benefit compared to the energy costs of finding, eating, and carrying the seeds either internally or externally to entice animals to disperse their seeds via edible fruits (Pyke 1984). Plants appeal to frugivores that are possible dispersal agents by optimizing coloration, presentation or provisioning of their fruits (Murray 2012). There are strong links between plant recruitment success and frugivore fruit selection, meaning that the evolution of fleshy fruits can be driven by interactions with vertebrates (Bolmgren and Eriksson 2010).

The prevalence, or lack thereof, of seed dispersers can affect plant recruitment and, eventually, the continued persistence or eventual extinction of plant species in an area (Terborgh et al. 2008, Wright et al. 2007). In Alaska, many of the fruits from berry-producing plants differ from their counterparts in the contiguous United States by producing mostly red fruits, higher seed masses, and greater total reward of sugars and lipids, which may be due to a combination of differences in climate and the species composition of frugivores (Traveset et al. 2004). Southeast Alaska's ecosystem is unique in that 86% of its woody shrubs provide fleshy fruit rewards to incentivize the dispersal of their seeds, and the dominant understory plants are all dispersed by vertebrate endozoochory (Willson 1991). This could indicate that Alaska's flora has been greatly influenced by an abundance of fruit-consuming fauna, which provide dispersal services that increase the probability that fleshy-fruited plants colonize available microsites after disturbance or during primary succession following deglaciation.

BIRDS AS SEED DISPERSERS

Avian intestines can have a positive, negative or neutral effect on the germination of seeds worldwide (Traveset 1998). A greater abundance and richness of avian frugivores has been found to enhance the quantity and quality of seed dispersal (Saavedra et al. 2014). Birds that consume fruits from multiple plant species can lead to reciprocal indirect effects that change competitive relationships to mutualistic ones between plant species (Martinez et al. 2014). Birds typically ingest the seeds inside of fruits if they are relatively small compared to the birds' size, but if seeds are too large, birds often consume just the flesh around the seed or regurgitate the seeds before flying away, thus negating any dispersal effect they may have had (Howe and Smallwood 1982). Plants with large seeds could be selecting against avian dispersal in favor of dispersal by larger-bodied frugivores (Howe and Smallwood 1982, Debussche and Isenmann 1989).

MAMMALS AS SEED DISPERSERS

A wide variety of mammals are known frugivorous seed dispersers. Bats in tropical regions are important players in seed dispersal networks (Sarmento et al. 2014). Primates, whether they consume and defecate seeds or spit out seeds while they consume fruits, disperse large amounts of seeds (McConkey et al. 2014). Even carnivores like red foxes, martens, coyotes, raccoons, and badgers disperse seeds of a wide variety of plants (Lopez-Bao et al. 2015, Willson 1993). In the salmon-rich ecosystems of southeast Alaska, brown bears reach uniquely high population densities and can disperse large quantities of seeds (Willson and Gende 2004).

Brown and black bears (*Ursus arctos* and *Ursus americanus*, hereafter referred to collectively as "bears") in southeast Alaska consume as many as 200,000 fruits per day for their high contents of sugars and/or lipids (Willson 1993). The consumption of these seeds has little to no effect on seed viability (Traveset and Willson 1997), meaning that bears have the ability to disperse tens of thousands of viable seeds within individual scats (Willson and Gende 2004). The fecal material can improve the growth rates of the seeds and seedlings that remain within the bear scat (Traveset et al. 2001). Seeds in bear scats are secondarily dispersed by small mammals, which reduces the density-dependent competitive effect of so many seeds in the same scat (Bermejo et al. 1998), and seed burial may additionally improve seed germination and survival (Vander Wall 2010).

SEED PREDATORS

Seed predators are animals that eat and destroy seeds (Janzen 1971). A seed predator can also serve as a seed disperser if it is imperfect in seed extraction, consumption or recovery (Janzen 1971), or if it does not completely destroy all seeds it consumes (Heleno et al. 2011). Seed predators can consume seeds pre-dispersal directly from the parent plant, or post-dispersal if they remove and cache seeds from the parent plant or from already dispersed seeds (Janzen 1971, Vander Wall et al. 2005). Mammals, birds and insects are all common seed predators (Janzen 1971, Steele et al. 2005, Vander Wall et al. 2005, Heleno et al. 2011). In southeast Alaska, common mammalian seed predators include red squirrels (*Tamiasciurus hudsonicus*), voles (*Myodes gapperi* and *Microtus pennsylvanicus*) and northwestern deer mice (*Peromyscus keeni*) (Bermejo et al. 1998). Avian seed predators in southeast Alaska, such as the Red Crossbill (*Loxia curvirostra*), White-Winged Crossbill (*Loxia* *leucoptera*), and Purple Finch (*Haemorhous purpureus*), are relatively rare (Heinl 2016).

Although not as well studied as the berry-consuming habits of birds, red squirrels have also been noted to harvest berries in southeast Alaska (Murie 1927). Red squirrels primarily consume seeds from coniferous plants, but additionally supplement their diets with fungi, nestling birds, insects and berries when coniferous seeds are not plentiful (Moller 1983). Ferron et al. (1986) found that coniferous seeds become a less important food source to red squirrels during the months of July and August when red squirrels feed on berries that are only available during this time.

NEW TECHNIQUES FOR MONITORING BERRY CONSUMPTION

Previous studies designed to quantify berry consumption have relied upon direct observation and analysis of stomach and fecal contents (Debussche and Isenmann 1989, Willson and Gende 2004). Direct observation requires extensive survey effort, which makes it difficult to gather a large sample size. Analysis of stomach contents requires the capture of animals and either the forced regurgitation or death of those individuals, with the caveat that consumed products can be misidentified or unobserved (Norris 2016). Scat analysis, like stomach analysis, can misidentify or lack consumed materials (Klare et al. 2011), and feces of some species, such as birds or small mammals, can be difficult to find and identify.

Camera traps have been used to quantify species diversity, determine species density, and observe animal behavior (O'Connell et al. 2010). For this study, we pioneer the use of camera traps to quantify berry consumption by vertebrates. Many camera traps can be placed across a study area to observe the berries of one or more plant species for 24 hours per day, greatly increasing the sample size over what was previously attainable with human observers. Cameras can record a video of predetermined length when triggered by movement, allowing them to record when an individual visits a plant and the berries it may consume. This allows us to see every species that visits and consumes the berries off of a plant and does not limit our analysis of animal consumption to only those species that generate recoverable scats. Finally, the use of camera traps does not require the handling or death of any animals, making it a safer, cost-effective, and more humane form of monitoring berry consumption.

In addition to camera traps, and to better understand brown and black bear partitioning of resources, we also pioneered using saliva left from a browsing bear on the stalks of berry-producing plants as a platform for noninvasively collecting bear DNA. Previous research has demonstrated that the identity of plant browsers can be obtained from residual DNA on ungulate or primate browse (Inoue et al. 2006, Nichols et al. 2012, Smiley et al. 2010), and bears can be genotyped using residual DNA on salmon carcasses (Wheat et al. 2016), but the use of environmental DNA to assess the identity of seed dispersers has never been attempted. Environmental DNA on browsed berry stalks could be an efficient tool to identify the relative seed dispersal services provided by black and brown bears.

ENDOZOOCHOROUS FRUIT-BEARING SHRUBS CONSIDERED IN THIS STUDY

We focused on monitoring the consumption of devil's club (*Oplopanax horridus*) fruit because it is the dominant fleshy-fruited understory plant at our study site in northern southeast Alaska (Chapter 2 – Fig. 1), and because its bright-red berries, each containing 1 – 2 seeds, are located in a highly visible terminal panicle at the top of the plant (Hall 1995), which makes them ideal for monitoring feeding activities. Devil's club is consumed by both birds and bears with no negative effect on germination (Traveset and Willson 1997). Additionally, devil's club is one of the few berry-producing plants that occurs throughout all habitat types and elevation gradients below the subalpine zone in our study area. Devil's club is distributed from south-central Alaska down to southern Oregon and over to Idaho and western Montana (Howard 1993). Devil's club prefers moist to wet soils (Howard 1993) and grows along seepages and streams (Hall 1995). Devil's club is widely used by native peoples for its symbolic and healing properties (Hall 1995).

In addition to devil's club, we also monitored berry consumption of soapberry (*Shepherdia canadensis*), blueberry (*Vaccinium alaskaense* and *V. ovalifolium* among others), high-bush cranberry (*Viburnum edule*) and pacific red elderberry (*Sambucus racemosa*). Each of these berry species occurs throughout southeast Alaska and other parts of North America and each species is known to have avian and mammalian consumers (Fryer 2008, Matthews 1992a, 1992b, Tirmentein 1990, Walkup 1991).

Soapberry, also called buffaloberry, is a nitrogen fixer and is generally found in nutrient-poor sandy, rocky soils (Walkup 1991). This shrub, which can grow up to two meters tall, has silvery bark with tiny reddish brown scales and oppositely arranged leaves that are ovate and slightly hairy on their tops (Hall 1995). Its yellowish or brownish small flowers grow in short lateral spikes, and the fruit is bright red when mature (Hall 1995).

Of the four species of blueberry in Alaska, the primary two species being considered here, Alaska blueberry and oval-leaf blueberry, are very similar and often hybridize (Hall 1995). Alaska blueberry is thought to have originated as a hybrid derived from oval-leaf blueberry and red huckleberry (*Vaccinium parvifolium*) (Matthews 1992a). Both of these shrubs can grow to be about two meters tall, have slender stems that become grey with age, oval, rounded leaves and pink flowers (Hall 1995). The fruits of both of these plants are blue to blueish-black to purple and contain many tiny black seeds.

High-bush cranberry can occur as a dominant or co-dominant understory shrub in open or closed coniferous forests (Matthews 1992b). This deciduous shrub can grow 0.5-3.5 meters tall and has smooth gray bark with palmate, oppositely arranged leaves that have sharply toothed lobes (Hall 1995). The whitish flowers grow in terminal clusters and fruit can be red or orange and contains one flat pit (Hall 1995).

Pacific red elderberry often occurs as a single plant or in scattered patches, but it does have the ability to form thickets (Fryer 2008). Red elderberry is typically between two and six meters tall, has soft bark, and opposite, large compound leaves (Fryer 2008). The flowers grow in a large panicled cyme, and its fruits are red, berrylike drupes (Fryer 2008).

STUDY GOALS

The goals of this research are to determine (1) whether birds or bears disperse more seeds, (2) the relative contribution of brown bears and black bears to seed dispersal, while (3) simultaneously quantifying the role of any avian or mammalian seed predators in salmon-bearing ecosystems.

CHAPTER 2: THE PRIMACY OF BEARS AS SEED DISPERSERS IN SALMON-BEARING ECOSYSTEMS

INTRODUCTION

In temperate coastal ecosystems throughout much of the world, anadromous fish historically supported large omnivorous bear populations. Brown bears (*Ursus arctos*) that consume more salmon have larger litters, approximately twice the body mass, and subsist at population densities two orders of magnitude higher than bears in otherwise suitable habitat without salmon (Hilderbrand et al. 1999b). For example, average brown bear densities are typically ~5 bears per 1000 km^2 in interior systems where salmon are rare or absent but reach over 500 bears per 1000 km^2 in regions where salmon are abundant (Hilderbrand et al. 1999b). These elevated population densities coupled with large body size lead to landscapes with ~150kg of brown bear per km^2 (0.5 bears per km^2 x 300kg/bear), often with additional biomass contributions from sympatric black bears (*Ursus americanus*). Thus, marine subsidies create an unusual inversion of the trophic pyramid, and the community-level consequences of such high levels of bear biomass have been largely unstudied.

Research on the salmon-bear interaction has focused on the role of bears in mediating the flow of salmon nutrients from the ocean to terrestrial ecosystems (Hilderbrand et al. 1999a). The nutrients in the remains of salmon carcasses can provide up to a quarter of the nitrogen budget to riparian communities and influence all trophic levels from primary producers to large carnivores in both terrestrial and aquatic ecosystems (Helfield and Naiman 2006, Hocking and Reynolds 2011). However, the ecology of omnivorous bears is far more complex than their role in fertilizing riparian forests and depositing carcass remains for scavengers. Bears are also top predators of ungulates, primary consumers of vegetation, myrmecovores that raid ant nests, and in particular bears may play a key role in seed dispersal (Boertje et al. 1988, Willson and Gende 2004).

Brown and black bears disperse the seeds of a diverse assemblage of endozoochorous fruit, which they consume for their high sugar content (>30% of pulp dry wt in *Vaccinium* spp., *Rubus* spp., *Streptopus* spp.) and high lipid contents (>25% of pulp dry wt in *Oplopanax horridum, Sambucus racemosa, Cornus stolonifera*) (Willson 1993). Single brown bear scats can contain tens of thousands of seeds (Willson and Gende 2004) that remain viable and readily germinate (Traveset and Willson 1997). These seeds might then be dispersed at finer spatial scales by hoarding rodents, potentially increasing seedling recruitment success by reducing negative density dependence and by colonizing a greater number of microsites where successful establishment is possible (Bermejo et al. 1998, Enders and Vander Wall 2012). The seeds remaining in bear scats are fertilized with bear manure, which may increase germination and seedling growth rates (Traveset et al. 2001).

The seeds in berries are also dispersed by avian frugivores, but the relative quantity of seeds dispersed by bears and birds has never been studied. Should bears, rather than birds, be the primary seed disperser in salmon ecosystems, then salmon, by supporting bears, could indirectly influence plant community structure to favor fleshy-fruited understory plants.

Where brown and black bears occur sympatrically in salmon-rich systems, black bears are thought to primarily consume berries and green vegetation while the larger-bodied brown bears are thought to primarily consume salmon due to resource competition, whereby brown bears suppress black bears from accessing salmon, the highest-quality resource at the time (Belant et al. 2006, Belant et al. 2010). However, seed dispersal by brown bears has only been quantified once using scats (Traveset and Willson 1997) and never where black bears are sympatric. It is plausible that brown bears, which are typically supported by salmon to a greater extent than are black bears, are responsible for an unusually large portion of seed dispersal services in salmon-rich systems. It is also possible that brown bears exclude black bears from the highest quality resources at any given time, which include berries readily available in large quantities before peak salmon spawning times.

The goals of this chapter are to determine (1) whether birds or bears disperse more seeds and (2) the relative contribution of brown bears and black bears to seed dispersal. In this chapter, we focused on monitoring the consumption of devil's club fruit (Image 1) using a combination of motion-triggered camera traps and a novel application of environmental DNA.

We hypothesized that brown and black bears collectively consume a greater amount of devil's club berries than do birds. Additionally, we hypothesized that brown bears, despite their more carnivorous diet, are responsible for consuming a larger portion of the berry crop than are black bears because of their unique abundance in salmon ecosystems, their larger nutritional requirements, and their competitive dominance over black bears (Belant et al. 2010, Hilderbrand et al. 1999b). Based on previous research at our study site demonstrating that brown bears exclude black bears from salmon runs (Levi et al. 2015), we hypothesized that brown and black bears would partition fruit consumption by time, with brown bears disproportionately consuming devil's club berries before salmon are widely available and black bears disproportionately consuming devil's club berries once brown bears transition into consuming a salmon-based diet.

MATERIALS AND METHODS

Study Area and Vegetation

This research was conducted in northern southeast Alaska approximately 30 miles north of the town of Haines (Fig. 1A) where an extensive road system and navigable rivers allow access to sites along an elevation gradient and to watersheds with different levels of salmon availability (USGS 1997). Overstory vegetation below the subalpine zone is dominated by Western hemlock (*Tsuga heterophylla*) and Sitka spruce (*Picea sitchensis*), with black cottonwood (*Populus balsamifera*) forests present in lowland riparian areas (Gallant et al. 1995). Common berry-producing shrubs within this ecosystem include devil's club, soapberry, high-bush cranberry, and blueberry (Figs. 1B - 1C). Endozoochorous seed dispersers common to the area include brown bears, black bears, and several species of thrushes (Family Turdidae).

We conducted vegetation surveys using a total of 96 belt transects that were 55 meters long and 2 meters wide grouped into sites of 4 parallel transects. At each meter, we noted approximate percent cover of each plant species as one of five categorical variables (0 = 0%, 1 = 1-25%, 2 = 26-50%, 3 = 51-75%, 4 = 76-100%). To estimate the average percent cover of each species across the 55 cover estimates per transect, we averaged the median values from the range of percent cover in each group (i.e. 0 = 0, 1 = 12.5, 2 = 37.5, 3 = 62.5, 4 = 87.5).

We stratified transects by forest types: evergreen forest, deciduous forest, mixed forest, or shrub/scrub using the 2011 National Land Cover Database's land cover raster layer for Alaska (Homer et al. 2015). This stratification was performed under the constraints that the slope was less than 10 degrees, there were no apparent changes in overstory forest type within the transect and that there were no rivers, streams or roads running through the transect.

Motion-Triggered Video Camera Traps

We placed motion-triggered camera traps throughout the study area to record which vertebrate species visited the devil's club berry clusters. During the fruiting season of 2014, we set Bushnell Trophycam Black LED cameras to record 15-second videos with a 5 second delay between videos when the cameras sensed motion in their fields of view. During the fruiting season of 2015, in addition to the Bushnell cameras, we used Browning Dark Ops cameras. We set the cameras to record 20-second videos with a 5 second delay between videos when the cameras sensed motion in their fields of view. We preferentially monitored berry clusters that contained mostly intact and ripe or nearly ripe berries that were near trees that could support our cameras. Clusters were located throughout the study area in all habitat types and across the entire elevation gradient.

We placed cameras on trees within ~2 meters of berry clusters. In cases where several berry clusters could be visible from one camera's field of view, we placed the camera to best view one or two target clusters and possibly more background clusters to capture any additional feeding events. We considered all feeding activity caught on the target or background clusters for analysis. Where there were many clusters and several conveniently located trees to view those clusters, we used multiple cameras in the same area.

We checked the cameras and the status of the berry clusters approximately once per week. If the berries were completely gone – the entire stalk had been removed or all the berries had been removed from the stalk – we moved the camera to a new location. If there were still some berries on the cluster – no obvious observed change in the number of berries or some berries were gone but not all – we retained the camera in place to continue to monitor the same cluster(s).

We recorded the time and date of all animal activity caught by the camera. We estimated the number of berries consumed by birds by counting the number of pecks made and adjusting this value based on results from a calibration experiment (see below). We estimated the number of berries consumed by bears by counting the number of berries remaining on each cluster and subtracting that from the average number of berries per devil's club berry cluster, which we determined by counting the number of berries on 30 berry clusters in each of 2014 and 2015.

Because cameras may imperfectly detect bird activity, we used a bird feeder as a substitute berry cluster and calibrated results from video monitoring to results from direct observational surveys. We placed cameras at 1 and 2 meters away from the bird feeder to simulate the average distances of the cameras from their respective focal berry clusters in the field. To be consistent with our field methods, we again set the cameras to take 20 second videos with a 5 second delay between videos. We compared one hour of data collected from the videos to that collected from direct observation to determine the capture rate of the cameras. Our calibration should be conservative in favor of an over-representation of berry consumption by birds because the activity of birds at feeders is consistent, causing us to miss observations of birds during the five second delay period, whereas berry consumption by birds in the wild is often more sporadic.

Additionally, we used our videos to record the phenology of fruit ripening on devil's club berry clusters over the fruiting season. Following the guidelines from the USA National Phenology Network (NPN), we assigned a ripeness index for clusters each day they were monitored (1 = less than 5% of all fruits ripe, 2 = 5-24% of all fruits ripe, 3 = 25-49% of all fruits ripe, 4 = 50-74% of all fruits ripe, 5 = 75-94% of all fruits ripe, 6 = >95% of all fruits ripe) (USA-NPN 2012). We averaged the ripeness index per day for all clusters with recorded phenology data across both years to determine the average ripeness index each day of the fruiting season.

DNA Swabs

To increase our sample size in order to distinguish between devil's club consumption by black and brown bears, we collected residual bear DNA from berry clusters showing evidence of bear browse (berries absent from most of the top of clusters with stalk intact) (Image 2). During the fruiting season of 2014, we checked all clusters weekly and swabbed newly bear-browsed clusters. We used one sterile cotton swab that had been moistened with DI water per browsed cluster. We stored all swabs in 100% ethanol at -20°C to be later analyzed at the Levi lab at Oregon State University.

We isolated the DNA using the Aquagenomics solution from MultiTarget Pharmaceuticals according to the manufacturers protocol for swab samples. Species ID was determined by amplifying a portion of the mitochondrial control region (D-loop) using unlabeled HSF21 and 5' 6-FAM-labeled LTPROBB13 primers (Wasser et al. 1997), and sex ID was determined using a PET-labeled SRY (a y-chromosome locus) primer pair (Taberlet et al. 1997). In this portion of the D-loop, brown bears have a 14 base pair (bp) deletion, which allows us to differentiate between black and brown bear species. Polymerase Chain Reaction (PCR) was performed in a total reaction volume of 20 μl 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 1 μl of DNA template was used. PCR cycling conditions included an initial denaturation step at 95°C for 15 minutes, followed by 39 cycles of denaturation at 94°C for 30 seconds, annealing at 57°C for 90 seconds, and extension at 72°C for 60 seconds. A final elongation step at 60°C for 30 minutes 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 deduced based on fragment sizes with black bears showing peaks of 205bp, and brown bears at 191bp. Males of both species amplify an 80bp fragment with the SRY primers while females show no peak. We used this more complex approach to identify multiple bear species and sexes that may have fed on the same cluster.

Bear Resource Partitioning

We used the peak of entry into Chilkat Lake, located less than 10km south of our study area, as an index of salmon phenology. We assumed that salmon arrived on spawning grounds in our study area where bears can access them by the time of the peak of the run. We determined the average date of the peak sockeye salmon run for 2014 and 2015 by averaging the timing of the peak salmon counts collected from the Chilkat Lake weir in the summers of 2014 (August 31 through September 6) and 2015 (August 2 through August 8). We tested the hypothesis that before the peak salmon run, a greater number of brown bears than black bears consumed devil's club berries, and after the peak salmon run, a greater number of black bears consume devil's club berries than brown bears using a binomial generalized linear model with the timing of bear consumption of devil's club fruit before or after August 19 (the peak of the salmon run) as a binary predictor variable and the bear species that consumed monitored devil's club as our response variable.

Estimation of Seed Dispersal Services

To illustrate the capacity of bears to disperse devil's club, we calculated the average number of berries consumed by brown and black bears per second. We divided the total number of devil's club berry clusters consumed by each bear species in each video by the length of that video to get the number of clusters consumed per second. We averaged this cluster consumption rate across all videos and multiplied it by the average number berries consumed by each bear species per cluster. We calculated the number of berries consumed per hour, assuming all foraging time was spent consuming only devil's club. The number of berries per hour for each forest type was calculated assuming bears only feed on devil's club berries when they randomly encounter them at the rate of the percent understory cover of devil's club in each forest type. We calculated the number of berries consumed per square kilometer using brown and black bear densities from studies conducted in similar areas in southeast Alaska.

RESULTS

Vegetation Data

Devil's club, on average, covered the largest area of all berry-producing shrubs in deciduous (12.95%, SE = 0.75), evergreen (49.55%, SE = 1.24) and mixed (16.32%, SE = 0.42) forest types (Fig. 1C). In the shrub/scrub forest type, blueberry species had the largest average understory cover (19.49%, SE = 0.77) but the average cover of devil's club in this forest type was only slightly smaller (19.26%, SE = 0.70) (Fig. 1C).

Visits to Devil's Club

Our sample size of devil's club berry clusters monitored by camera traps was 142 clusters in 2014 and 271 clusters in 2015, for a total of 413 monitored clusters. Out of these clusters, 71 in 2014 and 166 in 2015 were located behind temporary electric fences designed to keep bears out. We included these clusters in our analyses because these fences had no effect on bird visitation and were readily breached by bears. If the fences had any effect on our results, it would underbias the consumption of devil's club by bears.

We found that on average, there were 395 berries per cluster of devil's club berries (SE = 21). The cameras captured between 80% and 100% of bird movements on and off of the substitute berry cluster; however the cameras only captured roughly between 20% and 65% of the total time birds were on the substitute berry cluster, largely due to the 5 second lag that we set between videos. We determined that our cameras were able to accurately depict the frequency of bird visits to berry clusters but we conservatively assumed that only 20% of berries consumed by birds were actually captured. The amounts and proportions of berries consumed by birds have been adjusted for this rate.

Brown bears were viewed consuming devil's club earlier in the fruiting season, mostly through the first half of the month of August and decreasing during the second half of August, with no visits in September (Fig. 2). Black bears were viewed consuming devil's club berries later in the season during the second half of August, but their activity also stops in September (Fig. 2). The species of birds that consumed devil's club berries were birds of the family Turdidae: American Robin (*Turdus migratorius*), Swainson's Thrush (*Catharus ustulatus*), Hermit Thrush (*Catharus guttatus*), and Varied Thrush (*Ixoreus naevius*). Birds consumed devil's club at low levels throughout the entire fruiting season and increased only towards the end of August and early September (Fig. 2).

Feeding Effort

On average, brown bears consumed 321 (SE = 12) berries, or 80.22% (SE = 3.11) of an average devil's club berry cluster (Fig. 3A). Black bears, on average, consumed 360 (SE = 8) berries, or 90.12% (SE = 1.97) of an average devil's club berry cluster (Fig. 3A). Birds collectively consumed on average 71 (SE = 23) berries, or 17.77% (SE = 5.77) of an average devil's club berry cluster (Fig. 3A).

In 2014, brown bears were observed consuming an estimated total of 9,947 berries and 963 berries in 2015, for a combined estimated total of 10,910 berries. This equates to brown bears consuming 17.76% of the monitored berries in 2014 and 0.89% of the berries in 2015. Over the two fruiting seasons considered in this study, brown bears overall consumed 6.67% of the devil's club berries that were monitored by camera traps (Fig. 3B).

Black bears were observed consuming an estimated 5,047 berries in 2014 and 721 berries in 2015, for a combined estimated total of 5,768 berries over the two fruiting seasons. Out of all of the berries monitored by camera traps, black bears ate 9.01% of the berries monitored in 2014 and 0.67% of the berries monitored in 2015. Over the two field seasons included within this study, black bears ate 3.53% of all of the berries that were monitored by camera traps (Fig. 3B).

Collectively, we observed bears consuming 16,678 devil's club berries across the two fruiting seasons included in this study, which is 10.20% of all devil's club berries that we monitored with camera traps (Fig. 3B).

We observed birds consume 235 of the berries monitored by camera traps in 2014 and 490 of the berries monitored by camera traps in 2015, these values were increased in order to correct for a camera trap capture rate of 20% of bird feeding activity to be 1,175 berries and 2,450 berries, respectively. In total, birds were observed consuming 725, corrected to be 3,625, of the berries monitored by camera traps in both fruiting seasons. Out of the berries monitored in 2014, birds consumed 0.42% (corrected to be 2.10%). Out of the berries monitored in 2015, birds consumed 0.46% (corrected to be 2.28%). Out of all of the berries monitored by camera traps in both the 2014 and 2016 fruiting seasons, birds consumed 0.44% (corrected to be 2.22%) (Fig. 3B).

DNA Swabs

We swabbed 136 berry clusters that showed signs of having been browsed by bears, 82 of which had been monitored by camera traps. Of the 136 swabs, 105, or 77.21% of them, had enough viable DNA to determine bear species and sex. We found that the largest number of berry clusters that were swabbed for bear DNA were consumed by female brown bears, followed by female black bears, then male brown bears, and lastly male black bears (Fig. 3C). Of the 105 swabs with viable DNA, two swabs clearly had the DNA of two different bears on them: one swab had both a male and female black bear's DNA and one swab had a female brown bear's and a female black bear's DNA.

Out of the 107 identified bears, 68 (63.55%) of them were brown bears and 39 (35.45%) of them were black bears (Fig. 3C). 76 (71.03%) of all identified bears were female and 31 (28.97%) of them were male. Both brown and black bears had more females than males within the same species, with females comprising of 72.06% (49) of the brown bears and 69.23% (27) of the black bears (Fig. 3C).

Bear Resource Partitioning

The data from the camera traps and the DNA swabs were combined to gain a stronger understanding of these bears' use of devil's club berries relative to timing and elevation. Brown bears consumed devil's club berries across the entire range of elevations included in this study while black bears were only detected in the lowest and highest of elevations (Fig. 4).

Brown bears started consuming devil's club berries during the last week of July exclusively at elevations below 100m (Fig. 4). During the first week of August, brown bears continued consuming berries at elevations below 100m and began consuming berries at higher elevations (~250m). Through the middle and end of August, brown bears continued to feed from berry clusters at elevations <100m, but with less regularity than they did at the end of July and beginning of August. Brown bears also fed at higher elevations (>150m) during the middle and end of August, but this was with much less regularity than when they fed at lower elevations earlier in the season (Fig. 4).

Black bears were not observed feeding on devil's club berry clusters until the middle of August, at which point they fed on berry clusters that were located at elevations just under 100m and between 150m and 200m (Fig. 4). Towards the end of August, black bears were observed consuming devil's club berries at an elevation of just below 450m as well as at elevations between 150m and 200m, but no longer at elevations <100m.

Prior to the arrival of salmon (as indexed by the peak entry of salmon through the Chilkat Lake weir), brown bears consumed nearly all the devil's club fruit that we monitored. After the arrival of salmon, black bears became the primary consumers of devil's club fruit. Black bears were significantly less likely to consume devil's club than brown bears before the peak salmon run ($\beta = -1.005$, p-value < 0.0001) and significantly more likely to consume devil's club than brown bears after the peak salmon run ($\beta = 0.811$, p-value $= 0.0002$).

Before the final week of July, on average fewer than 25% of the berries on devil's club berry clusters are ripe (Fig. 4). From the final week of July through the first week of August, an average of between 25% and 75% of the berries on devil's club berry clusters are ripe (Fig. 4). Through the final three weeks of August, the average percent of devil's club berries that are ripe on each cluster becomes greater than 95% (Fig. 4). By the end of August, we noted that the ripe berries remaining in clusters fell off the stalks when jostled.

Estimation of Seed Dispersal Services

On average, brown bears consumed 0.092 clusters per second (SE = 0.008) and black bears consumed 0.089 clusters per second (SE = 0.014) while foraging on devil's club (Table 1). When multiplied by the average number of berries consumed by each bear species per cluster, we can estimate that a single brown bear consumes approximately 29 devil's club berries per second and a black bear consumes approximately 32 devil's club berries per second. We extrapolated these values further to calculate that a brown bear can consume over 105,000 devil's club berries in a single hour of foraging on devil's club, and a single black bear could consume over 115,000 devil's club berries in an hour (Table 1).

If we assume that bears do not select for devil's club and only feed on it as they randomly encounter it within each of the four main forest types of our study area, brown bears could consume over 13,000 devil's club berries in one hour spent in deciduous forests (the forest type with the least amount of devil's club understory cover) and over 52,000 devil's club berries in one hour spent in evergreen forests (the forest type with the greatest amount of devil's club understory cover) (Table 1). A single black bear, using these same assumptions, could consume over 15,000 devil's club berries in one hour spent in deciduous forests and over 57,000 devil's club berries in evergreen forests (Table 1).

DISCUSSION

Although endozoochorous seed dispersal by mammals is common in both temperate and tropical systems, no known temperate plant species is primarily mammal-dispersed (Willson 1991), which contrasts with the many tropical plants relying on mammalian seed dispersal (Peres et al. 2016). Our results suggest that devil's club, the dominant understory shrub in northern southeast Alaska, is primarily dispersed by bears rather than birds (Figs. 2 - 3). Furthermore, both species of bear alone consumed more berries than did birds collectively, and brown bears, which are more subsidized by salmon at our field site (Levi et al. 2015), consumed more fruit than did black bears (Figs. 2 - 3).

Devil’s club is an important berry resource for both brown and black bears (Belant et al. 2006, Hamilton and Bunnell 1987). Devil’s club berries ripen before salmon runs peak in this ecosystem, making this resource a vital source for bears to accumulate lean body mass in the spring (Belant et al. 2006). Brown bears do not start feeding on devil’s club berries until, on average, 25-75% of the fruits are ripe. All species stop regularly consuming devil’s club berries when the berries start falling off the plant. The senescence of these fruit clusters indicates that devil’s club berries not consumed by the beginning of September are doomed to fall beneath the parent plant. Birds or small mammals might disperse these fallen berries; however those that are not dispersed are doomed to remain within the reach of the parent plant. The long-distance dispersal of bears and birds before berries drop may be especially important to a stand-producing colonial plant like devil’s club (Howard 1993).

Brown bears exclude black bears from limited resources (Belant et al. 2010) and our data suggests that brown bears exclude black bears from accessing devil’s club berries in the spring and relieve this exclusionary pressure once salmon numbers peak. Brown bears were viewed almost exclusively consuming devil’s club berries at low altitudes before salmon runs started. As the summer progressed and salmon runs began in the middle of August, brown bear pressure on devil’s club decreased, which is when black bears started consuming this resource, however black bears still avoided feeding at the lowest elevations where encounters with brown bears were more likely. The availability of spatially concentrated and abundant salmon may thus reduce the effect of brown bear dominance on black bears.

Large clusters of densely-packed berries, like devil's club, increase bear bite size and bite rate, thus allowing bears to reach their maximum capacity for daily gain (Welch et al. 1997). Our study suggests that a single brown bear can consume between 13,000 and 105,000 devil's club berries per hour, depending on whether or not they are preferentially feeding from devil's club and their habitat. Given that the salmon-rich ecosystems of southeast Alaska can support between 191 and 551 brown bears per 1000km^2 (Miller et al. 1997), at their lowest density using our most conservative feeding rate estimate, brown bears could be dispersing over 5,000 devil's club seeds per square kilometer per hour. This potential amount of seed dispersal through them is exceptional.

Each devil's club berry offers 3.5mg of dry weight crude protein and 19.72mg of dry weight dietary fiber (Welch et al. 1997), and given that brown bears consume approximately 320 berries per cluster, a brown bear gains 1.12g of dry weight crude protein and 6.31g of dry weight dietary fiber with each cluster consumed. Bears have been known to abandon salmon-rich streams when berry crops are especially abundant (McCann 2014), and given their potential to consume massive amounts of berries with high efficiency, devil's club berries are a resource that bears could prefer over salmon if it was present in high enough densities.

Although we recorded fewer brown and black bears consuming devil's club in 2015 than in 2014, seed counts from bear scats suggest that bears were consuming even more devil's club in 2015 than 2014 (Shakeri and Levi, unpublished data). This could be due in part to differential berry productions between the two summers of this study.

The summer of 2014 had unusually high precipitation (16.31in. total in June through August), while the summer of 2015 had more typical rainfall (11.48in. total in June through August) (average rainfall from 2000 to 2016 for Haines, AK is 7.1in. total in June through August) (NWSCIW 2016), noticeably reducing berry availability in 2014. Increased berry production during the sunnier summer of 2015 may have reduced the contact rate between our cameras and bears.

Anadromous fish supporting abundant bears was once a common species interaction throughout the Northern Hemisphere, but brown bears, Pacific salmon, and particularly Atlantic salmon, have declined or been extirpated from large parts of their range. The ecosystem-level consequences of the loss of the salmon-bear interaction from much of their former range have been largely unexplored. Given the widespread elimination of bear-salmon interactions, our results suggest that this may have resulted in a previously underappreciated loss of the most quantitatively important seed-dispersal pathway for fleshy-fruited shrubs. Further, it is plausible that abundant frugivorous bears are themselves responsible for structuring plant communities by providing efficient seed dispersal services that allow bear-dispersed fruit to preferentially colonize microsites during succession or after disturbance. Secondary seed dispersal by rodents further increases the number of microsites colonized by seeds and reduces negative density dependence associated with the large number of seeds per bear scat.

CHAPTER 2 TABLES

	Cluster/ sec	Berries/ sec	Berries/ hr	Berries/hr Deciduous	Berries/hr Evergreen	Berries/hr Shrub/Scrub	Berries/hr Mixed
Brown Bear	0.092	29	105,984	13,778	52,992	20,137	16,957
Brown Bear/km^2*	0.042	13	48,011	6,241	24,005	9,122	7,682
Brown Bear/km^2**	0.018	6	20,243	2,632	10,121	3,846	3,239
Brown Bear/km^2***	0.051	16	58,397	7,592	29,199	11,095	9,344
Black Bear	0.089	32	115,855	15,061	57,927	22,012	18,537
Black Bear/km^2*	0.052	19	67,543	8,781	33,772	12,833	10,807

Table 1. Consumption rates of brown and black bears on devil's club berries. All feeding rates rounded to the nearest berry. Berries/hr for each forest type calculated assuming random encounter rather than selection for devil's club stands at the rate of the % cover of devil's club in each forest type: deciduous = 13%, evergreen = 50%, shrub/scrub = 19%, and mixed = 16%. *Density determined using 0.453 brown bears/km^2 and 0.583 black bears/km^2 from Flynn et al. (2012). **Density determined using lowest brown bear density in SE Alaska, 0.191 brown bears/km^2, from Miller et al. (1997). ***Density determined using highest brown bear density in SE Alaska, 0.551 brown bears/km^2, from Miller et al. (1997)

CHAPTER 2 FIGURES

Image 1. A devil's club berry cluster.

Image 2. A devil’s club berry cluster that has been browsed by a bear.

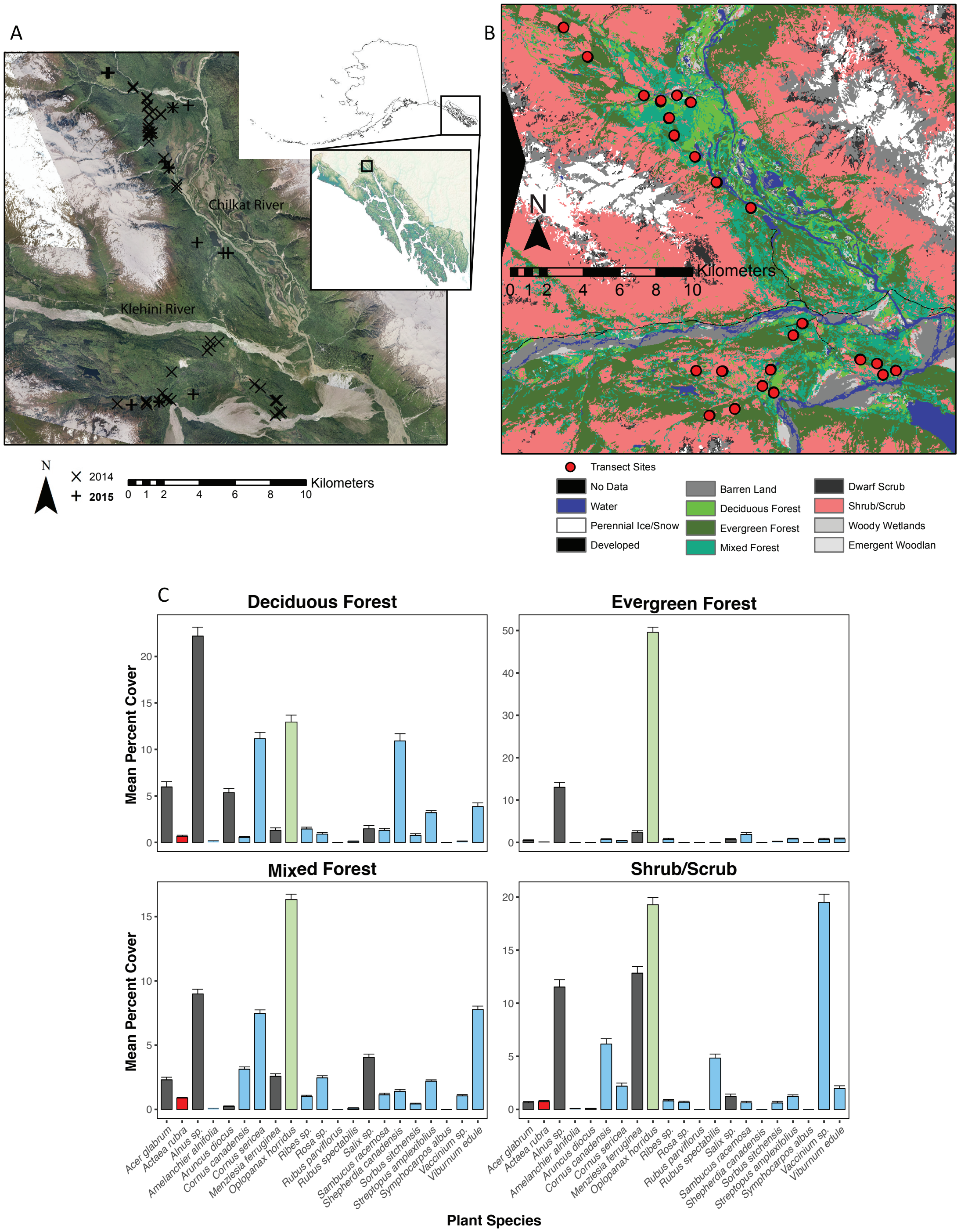

Figure 1. A - Map of study area and sites where camera traps monitored devil's club berry clusters in 2014 (+) and 2015 (X). B - Map of the study area color coded by National Land Cover Database cover types. Sites of vegetation belt transects indicated

by red dots. C - The average percent cover of each shrub species with standard error bars for the four major forest types found in this study area. Devil's club has been highlighted in green to distinguish it from other understory shrubs. All other endozoochorous fruiting shrubs know to be dispersed by bears have been highlighted in blue. *Actaea rubra*, an endozoochorous fruiting shrub known to only be dispersed by birds, is highlighted in red.

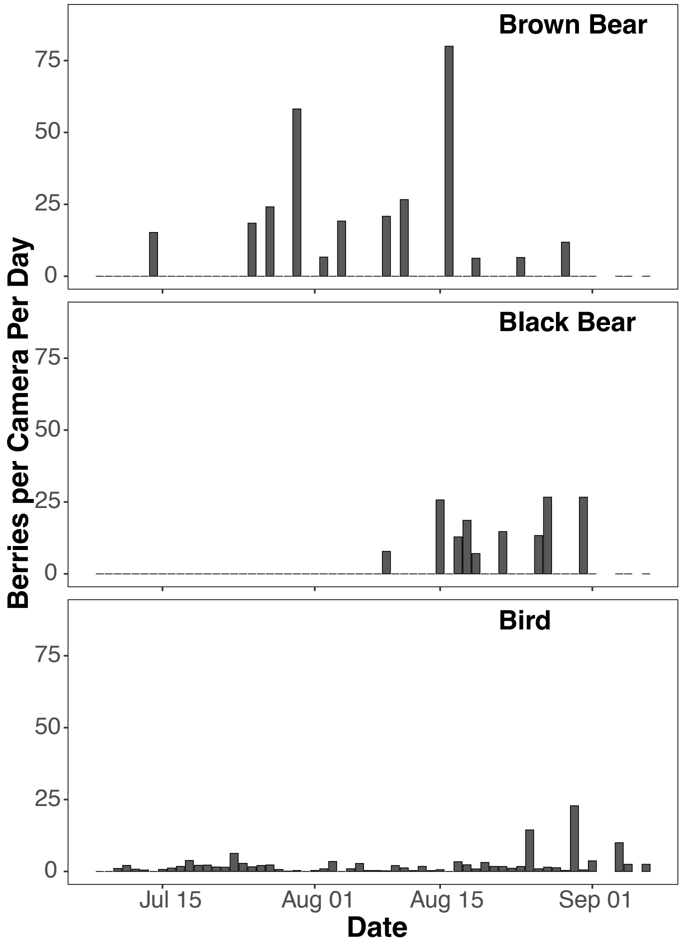

Figure 2. The number of berries consumed by brown bears, black bears and birds over time corrected for sampling effort (number of camera traps out). Data from 2014 and 2015 have been combined. Bird berry consumption has been increased to account for a camera trap capture rate of 20% of bird feeding activity.

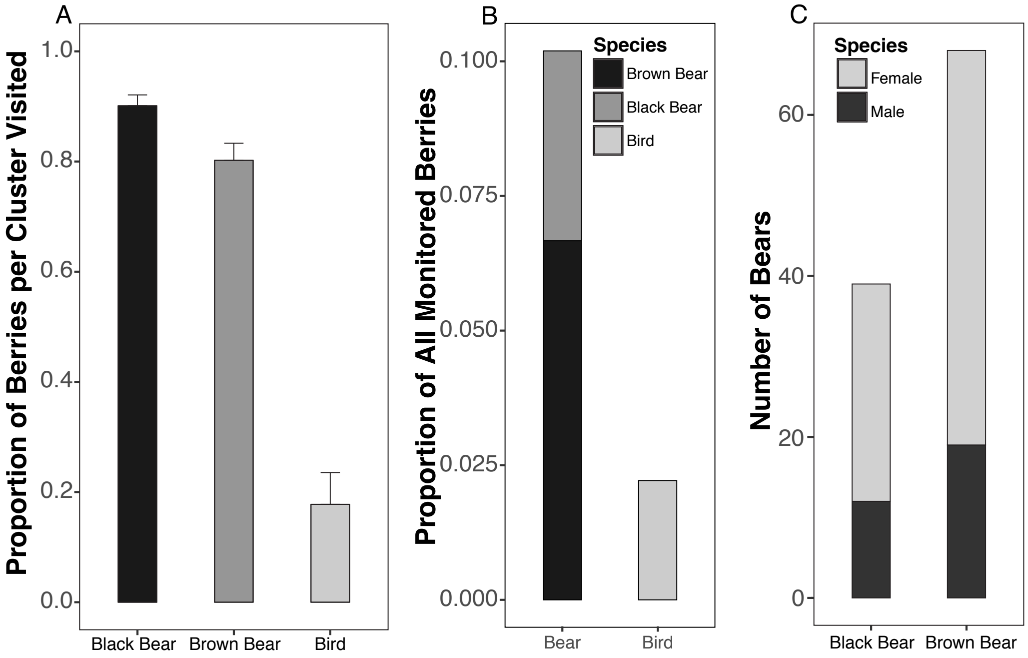

Figure 3. A - The average number of berries consumed per cluster by black bears, brown bears and birds, conditional on visitation by each respective species, over the course of the entire fruiting season. Bird berry consumption has been increased to account for a camera trap capture rate of 20% of bird feeding activity. B - The proportion of berries consumed by each seed disperser out of all berries monitored by camera traps over the fruiting seasons of 2014 and 2015. Bird berry consumption has been increased to account for a camera trap capture rate of 20% of bird feeding activity. C – The amount of DNA swabs that returned bear DNA that identified male and female brown and black bears.

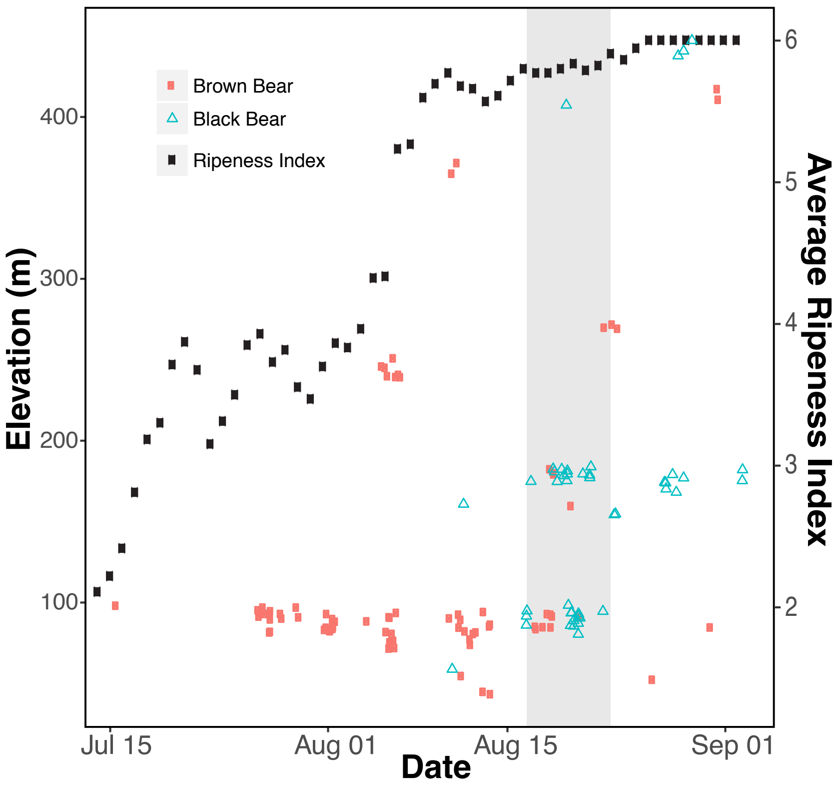

Figure 4. The spread of brown and black bear consumption of devil's club berries by date and elevation and average ripeness index of devil's club berry clusters over time. Icons for bear species have been jittered to view multiple berry clusters at the same date and elevation. Ripeness index from USA-NPN (2012) ripe fruits phenophases: 1 = less than 5% of all fruits ripe, 2 = 5-24% of all fruits ripe, 3 = 25-49% of all fruits ripe, 4 = 50-74% of all fruits ripe, 5 = 75-94% of all fruits ripe, 6 = >95% of all fruits ripe. Average peak sockeye salmon run time for 2014 and 2015 indicated by grey bar.

CHAPTER 3: ADDITIONAL NATURAL HISTORY OBSERVATIONS

SEED PREDATORS

We identified two previously unknown seed predators of devil's club, the red crossbill (*Loxia curvirostra*) and the red squirrel (*Tamiasciurus hudsonicus*). Red crossbills were only viewed feeding on 6 different berry clusters, consuming a total of 30 berries, during the fruiting season of 2015. Red squirrels were observed harvesting devil's club berries during both seasons, but became dominant harvesters of devil's club in 2015 after a spruce mast occurred in 2014.

Squirrels were the most active earlier in the season, during late July and early August, but in 2015 their activity continued throughout the season, albeit with less regularity. Squirrels harvested an average of 371.77 (SE = 4.93), or 92.87% (SE = 1.27) of an average devil's club berry cluster. Red squirrels were observed harvesting devil's club berries and seeds in two ways: by biting off sections of a berry cluster and carrying them away and by harvesting the seeds from individual berries.

In 2014, we estimate that squirrels harvested 2,602 of the devils' club berries that were monitored by camera traps. In 2015, we estimate that squirrels harvested 55,765 of the berries that had been monitored by camera traps. In total, we estimate that squirrels harvested 58,367 berries during the fruiting seasons of 2014 and 2015. Out of all of the berries monitored in 2014 and 2015, squirrels harvested 4.65% of the berries in 2014, 51.83% of the berries monitored in 2015, and 35.68% of all of the berries in both fruiting seasons.

Mammals are not only the dominant seed dispersers in this system, but are also by far the most important seed predators. In 2014 this was a rare occurrence, but a spruce mast in 2014 (Lisuzzo and Bowser 2014) led to a large increase in the red squirrel population in 2015 (Boutin et al. 2006), which was likely responsible for such extensive seed predation by red squirrels. Four small mammal trapping grids in our study area did not trap any red squirrels in 2014, but red squirrels in traps were common in 2015.

There are no prior publications that indicate that squirrels harvest devil's club berries. Other publications have noted red squirrels harvesting high-bush cranberries (Murie 1927), bunchberries (*Cornus canadensis*), raspberries (Schaumann and Heinken 2002) strawberries, (*Fragaria virginia*), and blackberries (*Rubus* sp.) (Ferron et al. 1986). In 2015, devil's club berries were a highly abundant resource that squirrels used to supplement their usual diet. Red squirrels kill almost all seeds they harvest (Steele et al. 2005), and cache seeds in middens that do not promote seed germination (Gurnell 1984), so they are not an effective dispersal pathway for seeds.

FEEDING BEHAVIOR ON DEVIL'S CLUB BERRIES

Brown Bears

When a brown bear approached devil's club berry clusters, it often used one paw to bring the cluster closer to its mouth. If the cluster was already at the height of the bear's head, sometimes the bear consumed the berries without using its paws at all (Image 3A). The bear removed berries off the stalk by placing its mouth over the cluster of berries and stripping the berries off of the stalk with its teeth, leaving the central stalk of the cluster bare but intact (Image 3B). When the bear's mouth was not large enough to fit the entire cluster within its mouth, the bottom quarter of the berries remained on the stalk after the first bite. Sometimes the bear took another one or two bites on the sides of the cluster to eat those remaining berries (Image 3C).

Black Bears

When a black bear approached the devil's club berry clusters, it used one or two paws to direct the berry clusters closer to its mouth. The black bear manipulated the cluster with its paws and bit berries off of the sides of the stalks, leaving the central stalk and many of the smaller side stalks empty but intact. Sometimes a black bear sat on its rump while it ate the berries off of the stalk.

Red Squirrels

Red squirrels frequently climbed up the main stem of the devil's club or leaped from an adjacent plant or tree to get to the berry clusters. A squirrel then bit the central stalk approximately halfway down from the top, separating the top half of the berry cluster from the bottom half (Image 5B), and carried away the top half of the stalk and berries. Squirrels usually visited the same berry cluster multiple times, removing more stalks of berries until few, if any, remained. When a squirrel harvested berries, it either carried them out of the view of the camera or sat on the plant to process the berries.

When a squirrel processed devil's club berries, it appeared to remove the seeds from inside of the fleshy berry. The squirrel then dropped the uneaten fleshy parts of the berry as it moved on to another berry (Image 5C). The squirrel worked through all of the berries on a single stalk before harvesting more stalks from the remaining cluster.

No videos showed what the squirrels did with the berries after they carried them away, however the squirrels that stayed on the plants to consume the devil's club seeds indicated that they may have consumed seeds in a similar manner in a different location. By chance, we found piles of the red fleshy parts of devil's club berries near patches of devil's club that had been visited by squirrels.

Birds

All thrush species had similar feeding behavior. A thrush of any given species perched on top of the berry cluster while feeding from it, but in some rare cases a thrush flew in and plucked a berry without landing on the berry cluster. Thrushes plucked one berry at a time with their beaks and swallowed that berry whole. The only exceptions to this were when a thrush dropped a plucked berry instead of swallowing it, and several cases where a Swainson's thrush was observed holding one berry in its mouth while plucking another one or two berries to hold up to 3 berries in its beak and then flew away without swallowing them.

One bird species that exhibited distinct behavior was the red crossbill. Red crossbill behaved similarly to the other birds by plucking individual berries while perched on the devil's club berry cluster. Instead of swallowing berries whole like the other bird species, a red crossbill worked the berry in its beak and removed seeds from the red berry flesh. The crossbill then shook its head and flicked the uneaten berry flesh from its beak before selecting another berry.

Discussion

Avian and mammalian seed dispersers all swallowed whole fruits without mastication. Avian and mammalian seed predators both stripped the fruit casing off of devil's club seeds before seed consumption, which increases digestibility of seeds (Norconk et al. 1998). Red squirrels invested a large amount of time to harvest devil's club seeds, indicating that this was an important resource. Each devil's club seed offers 2.2mg of dry weight crude protein and 11.55mg of dry weight dietary fiber (Welch et al. 1997). When an average squirrel harvests seeds from an average devil's club berry cluster, they are potentially gaining 1.63g of dry weight crude protein and 8.55g of dry weight dietary fiber (squirrels harvest on average 370 berries * 2 seeds per berry).

PRELIMINARY STUDY OF OTHER BERRY CONSUMPTION

In addition to devil's club fruits, we also monitored the fruits of soapberry (*Shepherdia canadensis*) in 2014 and blueberry (*Vaccinium alaskaense* and *V. ovalifolium* among others), high-bush cranberry (*Viburnum edule*) and pacific red elderberry (*Sambucus racemosa*) in 2015. These berry species were not the focus of this study because they were less prevalent throughout all forest types of the study area than devil's club (Chapter 2 - Fig. 1) and proved more difficult to quantify berry consumption due to high levels of variation in berry cluster size and orientation of berries along branches rather than in bunches. We include our results from this part of our study as preliminary data on which species may be seed dispersers or predators of these shrubs in this ecosystem. We monitored the berry consumption of the other four shrub species using the same methods as devil's club berry clusters. In the case of blueberry and soapberry shrubs, we used a single branch or section of the bush as the focal point of the camera.

Soapberry

We monitored 11 different sites for soapberry consumption. We observed only seed dispersers consuming soapberry fruit, including brown bears, black bears, American Robins, Swainson's Thrushes, and Red-breasted Sapsuckers (*Sphyrapicus ruber*). Birds were observed consuming soapberry fruit at 5 of the sites. The bird species often visited earlier in the season, behaving similarly to the bird seed dispersers of devil's club, and eating single berries at a time.

Brown bears were observed at 6 of the sites, often in pairs, and consumed every visible berry in view of the camera. Black bears were only observed consuming berries at one soapberry site. After a bear had browsed through a site, few to no birds were observed returning to that site to feed on berries.

Blueberry

We monitored 9 different blueberry sites for blueberry consumption. We only observed brown bears and red squirrels consuming blueberries; however humans also visited several of our sites, thus negating them from consideration in our study.

High-bush Cranberry

Out of 33 sites monitored by camera traps, we did not view any bear or bird feeding activity on high-bush cranberry. We observed red squirrels harvesting berries from 9 different sites. On average, squirrels harvested about 2 berries per site (average =

2.44, SE = 0.88). Additionally, we viewed a vole harvest one berry while it was climbing on a high-bush cranberry branch at night.

Pacific Red Elderberry

We observed only birds consuming pacific red elderberry fruits out of 50 monitored clusters. Bird species included Varied thrushes, Swainson's thrushes, Hermit thrushes, American robins, and Steller's jays (*Cyanocitta stelleri*). The thrush species all behaved similarly to the bird seed dispersers of devil's club and ate a single berry at a time; however Steller's jays were observed harvesting an entire section of a berry cluster at a time and carrying it away.

Discussion

Our method of using camera traps to record feeding activity and quantify berry consumption did not work as well on these shrubs as it did on devil's club. Blueberry and soapberry bushes produce berries along their branches, which made it difficult to quantify a focal group of berries. Additionally, unless a camera was placed within 1m of the bush, bear, bird and squirrel consumption was difficult to quantify. Elderberry clusters were easier to quantify, however over time the exact location of elderberry clusters was highly variable. If branches were weighed down by moisture or by a perching bird, elderberry clusters could hang below the view of our camera.

Our preliminary results from observing the consumption of other berry producing shrubs have indicated that primary seed dispersers are much more prevalent than primary seed predators in this ecosystem. All avian fruit consumers observed on all four shrubs were seed dispersers. Red squirrels were surprisingly prevalent seed predators, observed harvesting all berry types except for soapberry and elderberry.

We observed very little activity on blueberry and high-bush cranberry fruits. This could be due in part to the proximity of our cameras on these plants to areas of human activities. In the case of blueberry shrubs, humans regularly visited the area to harvest blueberries, which could have caused bears and other animals to avoid any signs of human influence (i.e. our camera traps). We know that bears were consuming large quantities of blueberries and high-bush cranberries from the prevalence of those berries in bear scats found throughout our study area. Camera traps may not be an appropriate method for observing bear feeding behavior when bears have a high chance of encountering humans while foraging.

We did not observe any mammals feeding on red pacific elderberries. This was surprising because bears are known to consume vast quantities of red pacific elderberries in other parts of southeast Alaska (McCann 2014). However, elderberry occur as individual plants or small stands in our study area, typically on roadsides, which may not be good foraging habitat for bears.

CHAPTER 3 FIGURES

Image 3. A – A brown bear selects a devil's club berry cluster to browse. B – The brown bear strips the berries off of the main stalk by placing its mouth over the whole stalk and stripping the berries off with its teeth. C – The brown bear bites off the remaining berries from the bottom of the stalk. D – The bear moves on to another berry cluster.

Image 4. A black bear consumes devil's club berries by biting the berries off the sides of the main stalk.

Image 5. A – A red squirrel selects a devil's club cluster to harvest. B – The squirrel harvests the top part of the cluster by biting the central stalk with its teeth and carries it away. B – The squirrel perches on the plant while it harvests the seeds out of the fleshy berry casings. The red box shows where a discarded piece of berry that is dropped by the squirrel can be seen.

CHAPTER 4: GENERAL CONCLUSIONS AND FUTURE RESEARCH

Devil’s club is the most widespread fruit-producing shrub in all of the most common forest types of this study area (Chapter 2 – Fig. 1). The success of this shrub may be related to its ability to grow in a variety of forest types and perhaps to its ability to effectively colonize habitat as a result of effective endozoochorous seed dispersal. Typically identified as having a marginal effect on seed distribution in temperate ecosystems, in the temperate rainforest of southeast Alaska, mammals have the greatest impact on the berry consumption and therefore seed distribution of the devil’s club plant. Birds also consumed devil’s club berries, but their quantitative impact was small compared to the visiting and feeding rates of mammals.

In temperate ecosystems, birds are widely assumed to be the primary seed dispersers of plants with fleshy fruits (Garcia et al. 2010, Herrera 1995, Jordano 2000); however there is evidence that suggests mammals are also important dispersers of several fleshy-fruited plants (Armesto et al. 1987, Corlett 1998, Debussche and Isenmann 1989, Herrera 1989, Willson 1993). While there are more bird species distributing a larger number of plant species in these ecosystems, mammals are dispersers of between 40% and 50% of the fleshy fruit bearing plant species (Debussche and Isenmann 1989, Herrera 1989, Willson 1993). The importance of birds as seed dispersers has been exaggerated due to the large number of different bird species that repeatedly visit different shrubs; however fewer mammals are able to disperse more seeds over larger distances than birds, making them more efficient seed dispersers (Willson 1991). In fact, plants that produce larger berries with large seeds seem to be selecting against ornithochory in preference for mammalochory (Howe and Smallwood 1982, Debussche and Isenmann 1989).

Bears are the dominant seed dispersers of devil's club. The regular success of these seeds relies heavily on bear consumption because birds consume and potentially disperse only a small fraction of devil's club berries and squirrels are only sporadically abundant and have the potential to destroy the majority of the seeds they harvest. Devil's club has most likely evolved to prioritize bear dispersal over any other dispersal mechanism, making it the first known temperate plant to be primarily dispersed by mammalian endozoochorous seed dispersal. In southeast Alaska where bears are still abundant in high densities, this has caused devil's club to be highly successful.

We have provided strong evidence that brown and black bears partition devil's club by time in relation to the peak salmon run in this area. Brown bears almost exclusively consumed devil's club berries before the peak sockeye salmon run. After the peak salmon run, black bears consumed significantly more devil's club berries than brown bears. Our study suggests that brown bears only relieve exclusionary pressure of black bears on devil's club when salmon are present in high enough densities to signify a change in their foraging habits.

We used motion-triggered video camera traps and eDNA to quantifying berry consumption by species. The camera traps worked well to monitor berry consumption of devil's club, but they did not work well on other shrubs that did not have such tightly clustered, relatively immobile berries. Future work could look for cameras with wider fields of view and higher detection rates so that cameras could be positioned farther away from berries to minimize the camera's effect on animal visitation. Future work could also look into image-based methods of quantifying berry abundance so that the number of berries in the field of view of the camera could be quantified after every visitation event. Our novel methods of using eDNA left from bear saliva on the browsed berry stalks worked exceptionally well. Over 75% of our swabs returned enough bear DNA to identify bear species and gender. Future work could include swabbing additional plant materials that have been browsed by bears, or attempting to identify individual bears from these swabs. If we can identify individual bears from this eDNA, browsed berry stalks could be used as an affordable and effective means to track bear movements and to estimate the population density of bears.

Our study only spanned two fruiting seasons, so we were unable to test whether the seasonal differences we experienced had a significant effect on berry crop availability or the rate of bear feeding activity on these berry crops. A long-term study in this area could monitor annual berry production as well as the amount of rainfall and sunny days, the temperature, and size and timing of salmon runs to see how these variables affect brown and black bear berry consumption.

Identifying red squirrels as the major seed predator of devil's club berries and as a seed predator of half of the other berry species monitored in this study calls for more research into this squirrel population. Future work could look into red squirrel caches and/or gut contents to determine which berry crops are of highest importance to squirrels. Future work could also determine whether red squirrels in this area use berries to supplement their diets only when coniferous seeds are scarce, or if berries are an integral part of their regular nutritional requirements.

The berry-producing shrubs of southeast Alaska provide this ecosystem with an abundant and nutritious food source that has direct and indirect effects on other species. Understanding the relative roles of the seed predators and dispersers of these plants can give us a glimpse of how the flora and fauna of Pacific coastal regions developed historically. The loss of salmon-bear interactions could have severed an important seed dispersal pathway for plants that may have relied primarily on bear dispersal, which could explain why southeast Alaska has a uniquely high proportion of berry-producing plants in North America (Willson 1991). Salmon, through bears, could be vital players in the network of understory plants in coastal ecosystems by both indirectly affecting nutrients available to the plant community (Hilderbrand et al. 1999a) and by supporting large bear populations that preferentially disperse shrubs with fleshy fruits.

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