

# The primacy of bears as seed dispersers in salmon-bearing ecosystems

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**Abstract.** Salmon–bear ecosystems that historically existed throughout most of the northern temperate and boreal regions of planet earth now persist only in the North Pacific. Extensive research on salmon–bear interactions has focused on the role that bears (*Ursus arctos* and *U. americanus*) play in provisioning terrestrial systems with marine-derived nutrients, but little attention has been paid to how the much higher bear population densities in salmon-bearing ecosystems then affect ecological communities. Salmon-supported brown bears secondarily consume large quantities of fruit and may thus serve as important seed dispersers, but the relative seed dispersal services provided by bears and birds are unknown. We sought to (1) quantify the number of seeds dispersed by bears relative to birds, and (2) by brown bears relative to black bears, and to (3) assess whether the two sympatric bears temporally partition berry resources as a result of competitively dominant brown bears switching to feed on salmon, thus opening niche space for black bears. We used a combination of motion-triggered camera traps and environmental DNA (eDNA) from residual saliva to quantify the roles of birds, black bears, and brown bears as seed dispersers of devil’s club (*Oplopanax horridus*), the dominant understory shrub at our field site in northern southeast Alaska. Brown bears were the numerically dominant seed dispersers, particularly before salmon became widely available, after which black bears became common seed dispersers, likely due to alleviation of interference competition. Birds accounted for only a small fraction of seed dispersal. This is the first demonstration of a temperate plant being primarily dispersed by mammalian gut passage. Our results suggest that bears are uniquely important seed dispersers, which may influence plant community composition in salmon-bearing ecosystems.

**Key words:** Alaska; devil’s club; interference competition; mutualism; seed dispersal.

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## 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 can subsist at population densities two orders of magnitude higher than bears in otherwise suitable habitat without salmon (Hilderbrand et al. 1999a). Brown bears are

sympatric with black bears (*Ursus americanus*) in most mainland salmon-bearing systems in northwestern North America, contributing additional bear biomass. Thus, marine subsidies create an unusual inversion of the trophic pyramid (Trebilco et al. 2013), 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. 1999b). 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, and 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 (>30% of pulp dry wt in *Vaccinium* spp., *Rubus* spp., *Streptopus* spp.) or 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 are then dispersed at finer spatial scales by scatter-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).

In temperate ecosystems, birds are widely assumed to be the primary seed dispersers of plants with fleshy fruits (Jordano 2000, Garcia et al. 2010), but mammals are also important dispersers of several fleshy-fruited plants, potentially contributing to seed dispersal of 40–50% of fleshy fruit bearing plant species in temperate ecosystems (Debussche and Isenmann 1989, Herrera 1989, Willson 1993). Should bears, rather than birds, be the primary seed disperser in salmon ecosystems, then bears could plausibly influence plant community structure to favor fleshy-fruited understory plants over their wind-dispersed counterparts. The widespread reduction of bear populations could thus reduce the relative fitness of fleshy-fruited shrubs to favor wind-dispersed plants.

Where brown and black bears are sympatric in salmon-rich systems, competitively dominant brown bears exclude black bears from accessing salmon (Belant et al. 2006, Levi et al. 2015), leaving black bears to primarily consume berries and green vegetation (Belant et al. 2006, 2010, Adams et al. 2017). However, extensive berry consumption by competitively dominant brown bears, which has been demonstrated in a system without black bears (Willson and Gende 2004), would cast doubt on resource partitioning as the mechanism of Ursid coexistence. An alternative hypothesis for the coexistence of these sympatric Ursids is that resources are spatially or temporally partitioned. For example, brown bears could dominate berry consumption prior to the arrival of salmon and subsequently open the berry niche to black bears when salmon become available. Similarly, black bears might consume salmon at higher elevations to avoid interference competition with brown bears that are drawn to lower elevations by salmon. In addition to explaining the coexistence of these sympatric Ursids, such partitioning could enhance seed dispersal services by increasing the probability that fruits are consumed across a gradient of space and time.

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, and (3) whether these bears temporally partition berry resources. 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 (Fig. 1), because its bright-red berries, each containing 1–2 seeds, are located in a highly visible terminal raceme at the top of the plant (Hall 1995, Fig. 2A), which facilitates monitoring of feeding activities, and because devil's club is consumed by both birds and bears with no negative effect on germination (Traveset and Willson 1997). 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 (Hilderbrand

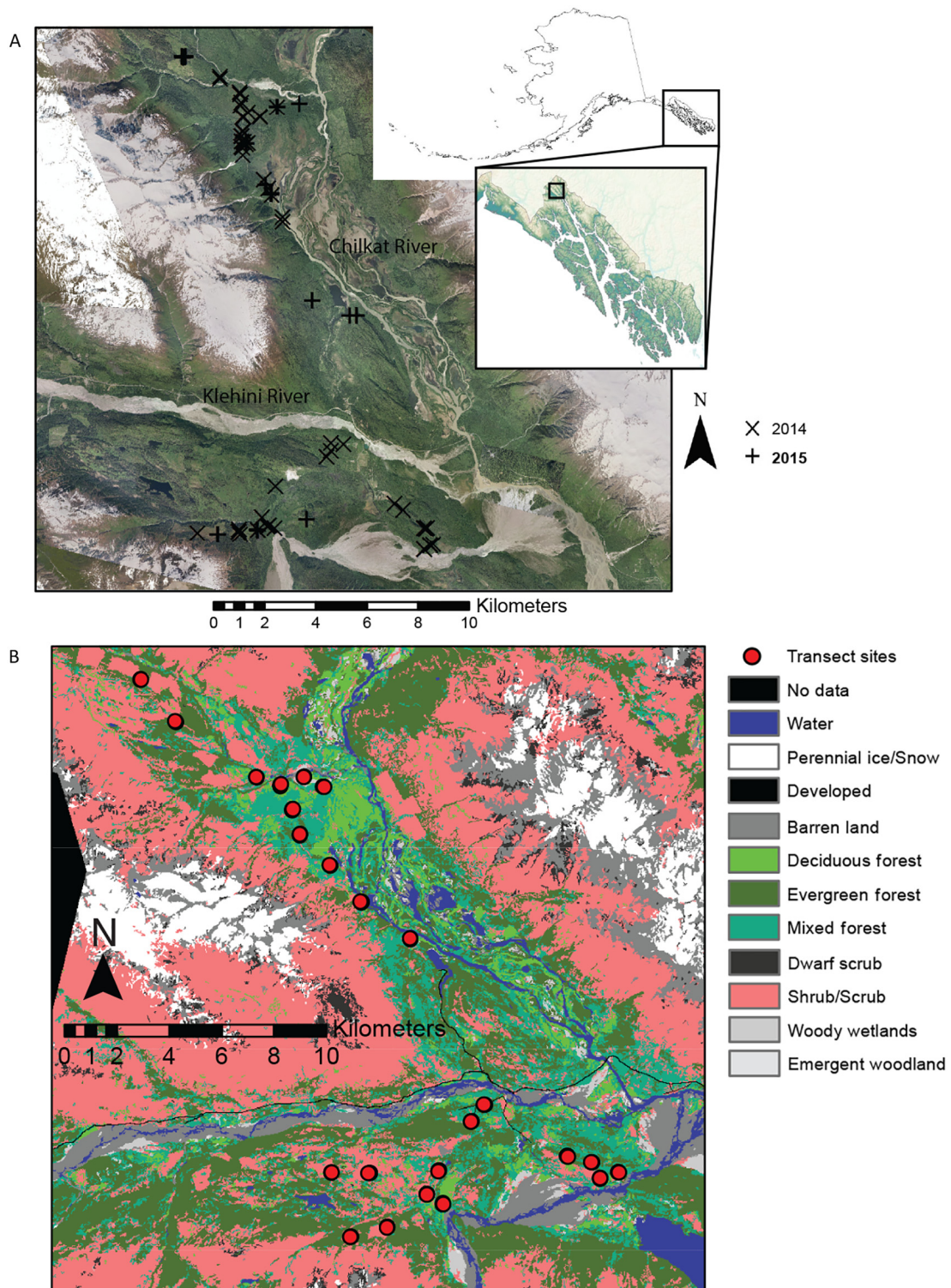
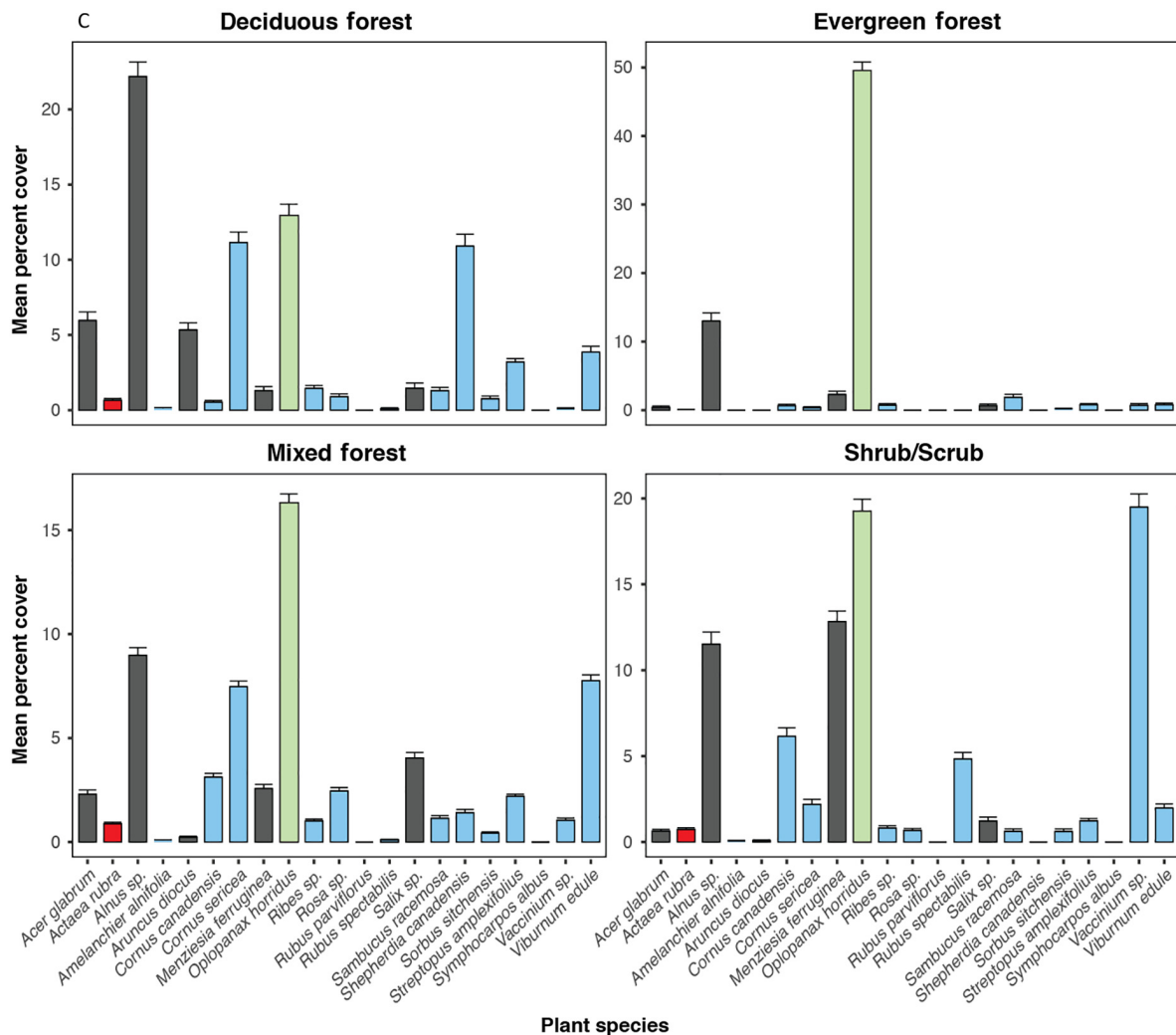


Fig. 1. (A) Map of study area and sites where camera traps monitored devil's club berry clusters in 2014 (+) and 2015 (X). (B) Map of the study area color-coded by National Land Cover Database cover types. Sites of vegetation belt transects indicated by red dots.



(Fig. 1. Continued)

(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 is highlighted in green to distinguish it from other understory shrubs. All other endozoochorous fruiting shrubs known to be dispersed by bears are highlighted in blue. *Actaea rubra*, an endozoochorous fruiting shrub known to only be dispersed by birds, is highlighted in red.

et al. 1999a, Belant et al. 2010). 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 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. We additionally hypothesized that devil's club consumption would be partitioned spatially,

with black bears feeding more at higher elevations while brown bears concentrate at lower elevations where salmon are available.

Such fine-resolution determination of seed dispersal services is now possible using new technologies. We monitored the consumption of devil's club fruit using a combination of motion-triggered camera traps and a novel application of environmental DNA. Based on previous research that successfully identified vertebrate species using DNA from ungulate and primate browse (Inoue et al. 2006, Smiley et al. 2010, Nichols



Fig. 2. (A) A devil's club berry cluster. (B) A devil's club berry cluster that has been browsed by a bear. (C) A brown bear consumes devil's club berries by first stripping the berries off of the main stalk and then biting the remaining berries around the bottom of the stalk. (D) A black bear consumes devil's club berries by biting the berries off the sides of the main stalk.

et al. 2012), as well as recent research demonstrating the efficacy of identifying individual bears using residual saliva on salmon carcasses (Wheat et al. 2016), we used residual saliva left from browsing bears on the stalks of berry-producing plants to noninvasively detect the species and sex of bears that consumed devil's club fruit.

## METHODS

### *Study area and vegetation*

This research was conducted in northern south-east 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 (*Shepherdia canadensis*), high-bush cranberry (*Viburnum edule*), and blueberry (*Vaccinium alaskaense*

and *Vaccinium ovalifolium* among others; Fig. 1B–C). Endozoochorous seed dispersers common to the area include brown bears, black bears, and several species of thrushes (family Turdidae), for which fruit composes a large part of the summer diet, and to a lesser extent marten and coyote, which are primarily carnivorous (Buskirk and MacDonald 1984, Willson 1993, Lukasik and Alexander 2011).

We conducted vegetation surveys using a total of 96 belt transects that were 55 m long and 2 m wide grouped into sites of four 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 mid 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 <10 degrees, that 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 devil's club berry clusters. During the fruiting season of 2014, we set Bushnell Trophycam Black LED cameras to record 15-s videos with a 5-s delay to maintain battery and storage while using video mode to monitor vegetation where false triggers are common. During the fruiting season of 2015, in addition to the Bushnell cameras, we used Browning Dark Ops cameras. In this second season, we set both camera brands to record 20-s videos with a 5-s delay between videos when the cameras sensed motion in their fields of view. We increased the length of videos between seasons based on the successful maintenance of battery and storage during 2014. 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 m 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. We considered all feeding activity caught on the target clusters or on additional clusters <3 m away from the camera for analysis. We used multiple cameras in large contiguous stands where there were many clusters and several trees well located to view those clusters (see Supporting Information for example videos).

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). At the end of the fruiting season, if no animals had visited an entirely ripe cluster for a full two weeks and fruits were dehiscing, we determined that the fruits were likely to fall beneath the parent plant and go undispersed.

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 (using motion-triggered video camera traps). 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. We found that on average, there were 395 berries per cluster of devil's club berries (SE = 21).

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 m 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-s videos with a 5-s delay between videos. We compared one hour of data of birds consuming suet pellets (manufactured pellets approximately the same size and shape as devil's club berries) from the bird feeder collected from the videos to data collected from direct observation during that same hour to determine the capture rate of the cameras.

The cameras at distances 1 and 2 m captured 100% and 80% of bird movements on and off of the bird feeder, respectively; however, the 1 and 2 m distance cameras only captured roughly 65% and 20%, respectively, of the total time birds were on the substitute berry cluster. We conservatively assumed that only 20% of berries consumed by birds were actually captured by our cameras in the field. This correction is 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. The amounts and proportions of berries consumed by birds have been adjusted for this rate.

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 = <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 observed during both years of monitoring to determine the average ripeness index throughout the fruiting season.

We monitored 142 devil's club berry clusters in 2014 and 271 clusters in 2015 ( $n = 413$ ). 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 did not significantly influence bird visitation ( $\beta = -1.533$ ,  $P = 0.117$ ) and were readily breached by bears. Any effect of fences on our results would under-bias the consumption of devil's club by bears.

### DNA swabs

To increase our sample size in order to distinguish between devil's club consumption by male and female 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; Fig. 2B). 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 distilled (DI) water per browsed cluster. We stored all swabs in 100% ethanol at  $-20^{\circ}\text{C}$  to be later analyzed at the Levi Lab at Oregon State University.

We isolated the DNA using the AquaGenomic solution from MultiTarget Pharmaceuticals according to the manufacturer's 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  $\mu\text{L}$  using the Qiagen Multiplex PCR kit, which utilizes Hot Start Taq DNA polymerase. Primers LTPROBB13/HSF21 and SRY were added at a concentration of 200 and 100 nmol/L, respectively, and 1  $\mu\text{L}$  of DNA template was used. Polymerase chain reaction cycling conditions included an initial denaturation step at  $95^{\circ}\text{C}$  for 15 min, followed by 39 cycles of denaturation at  $94^{\circ}\text{C}$  for 30 s, annealing at  $57^{\circ}\text{C}$  for 90 s, and extension at  $72^{\circ}\text{C}$  for 60 s. A final elongation step at  $60^{\circ}\text{C}$  for 30 min completes the reaction. Polymerase chain reaction 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, Foster City, California, USA). Species ID was deduced based on fragment sizes with black bears showing peaks of 205 bp, and brown bears at 191 bp. Males of both species amplify an 80-bp fragment with the

SRY primers, while females show no peak (Woods et al. 1999). This method allowed us to identify berry clusters that may have been consumed by both black and brown bears and/or both males and females.

### *Bear resource partitioning*

We used the peak of entry into Chilkat Lake, located at the southern end 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 estimated the peak date, 19 August, by selecting the mid-date of the peak salmon counts from the weekly data collected from the Chilkat Lake weir in the summers of 2014 (31 August–6 September) and 2015 (2–8 August). We tested the hypothesis that the dominant species of bear consuming devil's club switched from brown bears before salmon became available to black bears after salmon were available using a binomial generalized linear model with the timing of bear consumption of devil's club fruit before or after 19 August as a binary predictor variable and the bear species that consumed monitored devil's club as our response variable. We determined the date that berries were consumed either using camera trap data, when available, or using the midpoint between the date when the infructescence was observed to be consumed and the previous check date.

### *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. For each bear species, we first divided the number of devil's club berry clusters consumed in each video by the length of that video. We then multiplied the cluster consumption rate by the average number of berries consumed per cluster (Fig. 4A), and then averaged the berry consumption rate across all videos. We extrapolated berry consumption rates per km<sup>2</sup> using bear density estimates from Flynn et al. (2012) in nearby Berners Bay, Alaska. The number of seeds dispersed is approximately twice the number of berries consumed. We use the observed standard error of the mean seed consumption rate to bracket our uncertainty about the rate of seed dispersal by foraging bears.

## RESULTS

### *Vegetation data*

Fleshy-fruited endozoochorous plants dominated the understory across all vegetation types. 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 (19.49%, SE = 0.77) and devil's club (19.26%, SE = 0.70) had covered approximately equivalent area (Fig. 1C).

### *Visits to devil's club*

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. 3). Black bears were viewed consuming devil's club berries later in the season

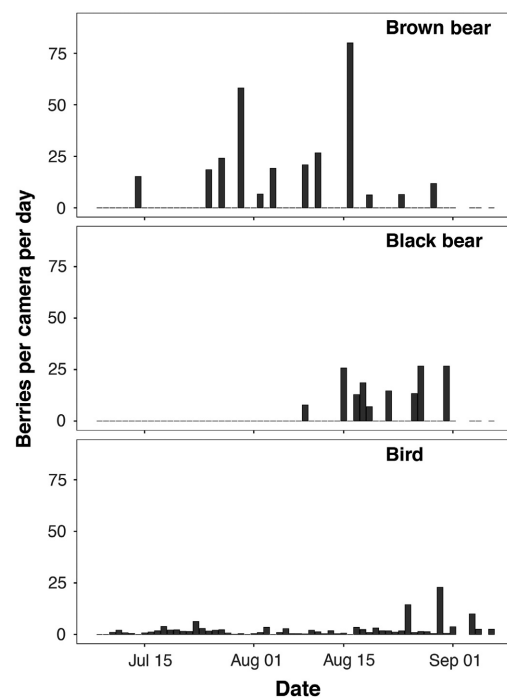


Fig. 3. The number of berries consumed by brown bears, black bears, and birds over time corrected for sampling effort (number of camera traps out). Data from 2014 and 2015 have been combined. Bird berry consumption has been increased to account for a camera trap capture rate of 20% of bird feeding activity.



during the second half of August, but their activity also stops in September (Fig. 3). No mammalian seed dispersers other than bears were observed consuming devil's club berries, potentially because the large height of devil's club fruit makes fruit consumption challenging for coyote and marten, or because these species are less abundant and less frugivorous than bears. 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 toward the end of August and early September (Fig. 3).

#### Feeding effort

On average, brown bears were estimated to consume 316 (SE = 12) berries, or  $79.97 \pm 3.15\%$

of each visited devil's club berry cluster (Figs. 2C, 4A). Black bears, on average, were estimated to consume 355 (SE = 8) berries, or  $89.99 \pm 2.00\%$  of each visited devil's club berry cluster (Figs. 2D, 4A). Birds collectively were estimated to consume, on average, 76 (SE = 25) berries, or  $19.12 \pm 6.28\%$  of each devil's club berry cluster (Fig. 4A).

Collectively, we estimated that bears consumed 16,427 (SE = 421.56) of the estimated 161,555 monitored devil's club berries across the two fruiting seasons included in this study, which is approximately  $10.17 \pm 0.26\%$  of all devil's club berries monitored with camera traps. Brown bears were estimated to consume 10,739 (SE = 373.08) devil's club berries, while black bears were estimated to consume 5688 (SE = 149.90), which is  $6.65 \pm 0.23\%$  and  $3.52 \pm 0.09\%$  of the monitored devil's club berries, respectively. Birds were observed consuming an estimate of

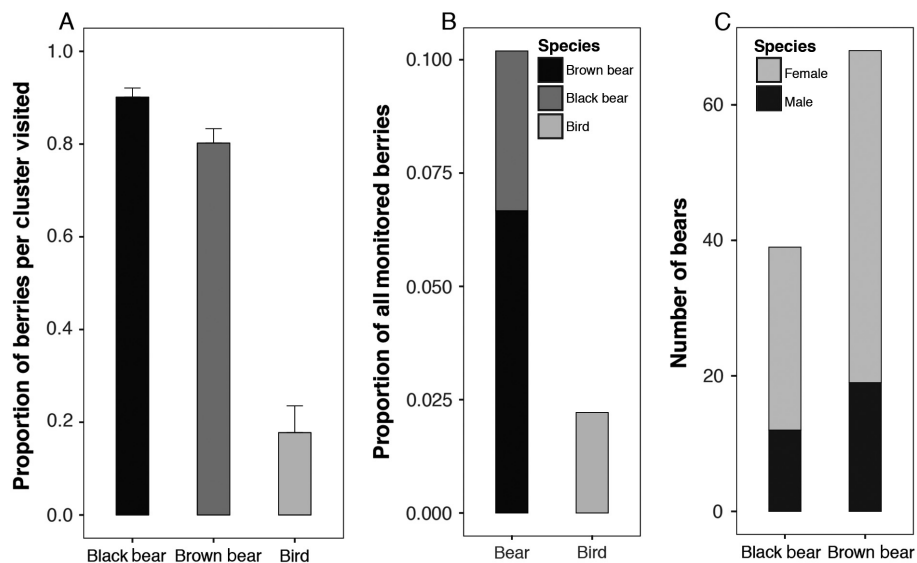


Fig. 4. (A) The average and standard error of the number of berries consumed per cluster by black bears, brown bears, and birds, conditional on visitation by each respective species, over the course of the entire fruiting season. Bird berry consumption has been increased to account for a camera trap 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 fivefold to account for a camera trap capture rate of 20% of bird feeding activity.  $10.17 \pm 0.26\%$  of berries were dispersed by bears,  $6.65 \pm 0.23\%$  and  $3.52 \pm 0.09\%$  by brown bears and black bears, respectively, and a corrected estimate of  $2.15 \pm 0.71\%$  by birds. The low value of the y-axis suggests nonredundancy in fruit removal because most seeds went undispersed or were predated, primarily by red squirrels in 2015 after a regional spruce mast in 2014. (C) DNA swabs of consumed devil's club resulted in  $49 \pm 5.2$  female brown bears,  $19 \pm 3.9$  male brown bears,  $27 \pm 4.5$  female black bears, and  $12 \pm 3.3$  male black bears with standard errors determined from 10,000 bootstrap samples.

695 (SE = 228.06) berries (corrected to be 3475 [SE = 1140.30]), which is  $0.43 \pm 0.14\%$  (corrected to be  $2.15 \pm 0.71\%$ ) of all monitored berries (Fig. 4B). American Robins were estimated to consume  $0.05 \pm 0.01\%$  (corrected to be  $0.26 \pm 0.04\%$ ) of observed berries, Varied Thrushes were estimated to consume  $0.08 \pm 0.02\%$  (corrected to be  $0.38 \pm 0.09\%$ ), and Swainson's Thrush and Hermit Thrush combined were estimated to consume  $0.25 \pm 0.10\%$  (corrected to be  $1.24 \pm 0.52\%$ ) of monitored berries (precise identity was sometimes difficult to attribute between these two species). We estimated that an additional  $0.05 \pm 0.02\%$  (corrected to be  $0.27 \pm 0.12\%$ ) of berries were consumed by avian seed dispersers not identified to species. The remaining berries were either harvested by seed predators ( $35.64 \pm 0.48\%$ ; primarily *Tamiasciurus hudsonicus*) or went undispersed (remained on the berry stalk and fell off to land below the plant; 52.04%).

#### 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 (77.21%) had enough viable DNA to determine bear species and sex. Out of the 107 identified bears, 68 (63.55%) were brown bears and 39 (35.45%) were black bears (Fig. 4C). Female brown and black bears consumed more devil's club than did males, with females comprising of 72.06% (49) of the brown bears and 69.23% (27) of the black bears (Fig. 4C). One swab amplified DNA from both a male and female black bear (perhaps a female and cub), and one swab amplified DNA from a female brown bear and a female black bear. To account for uncertainty in our observations, we generated 10,000 bootstrap samples with replacement, which generated estimates of  $49 \pm 5.2$  female brown bears,  $19 \pm 3.9$  male brown bears,  $27 \pm 4.5$  female black bears, and  $12 \pm 3.3$  male black bears.

#### 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 started consuming devil's club berries during the last week of July exclusively at low elevations (Fig. 5) and fed at progressively higher elevations

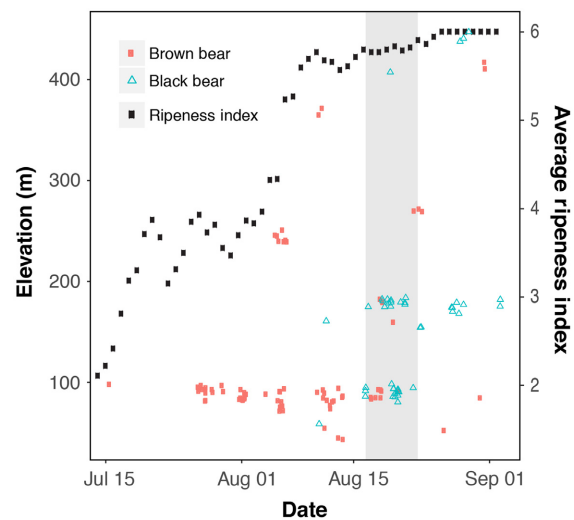


Fig. 5. The spread of brown and black bear consumption of devil's club berries by date and elevation and average ripeness index of devil's club berry clusters over time. Icons for bear species have been jittered to view multiple berry clusters at the same date and elevation. Ripeness index from USA-NPN (2012) ripe fruits phenophases: 1 = <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 gray bar.

throughout the fruiting season, but with much less regularity after the peak salmon run. 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 generally located at elevations higher than where brown bears fed.

Before the final week of July, an average of fewer than 25% of the berries on devil's club berry clusters are ripe (Fig. 5). 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, which is primarily when brown bears are feeding heavily on these berries (Fig. 5). Through the final three weeks of August, the average percent of devil's club berries that are ripe on each cluster becomes >95%, which is when black bears are feeding (Fig. 5). By the end of August, we noted that the ripe berries remaining in clusters fell off the stalks when jostled. This berry dehiscence coincided with a termination of frugivory.

Table 1. Consumption rates of devil's club berries by brown and black bears during continuous foraging bouts, and extrapolated berry consumption rates per km<sup>2</sup> using bear density estimates from Flynn et al. (2012) of 0.453 brown bears/km<sup>2</sup> and 0.583 black bears/km<sup>2</sup> in nearby Berners Bay, Alaska.

Unit of consumption	Brown bear	Black bear	Total bear
Clusters/s	0.092 ± 0.008	0.089 ± 0.014	0.181 ± 0.022
Berries/s	29 ± 2.5	32 ± 5.0	61 ± 7.5
Berries/h	104,659 ± 9000	114,246 ± 18,000	218,905 ± 27,000
Clusters·s <sup>-1</sup> ·km <sup>-2</sup>	0.042 ± 0.004	0.052 ± 0.008	0.094 ± 0.012
Berries·s <sup>-1</sup> ·km <sup>-2</sup>	13 ± 1.1	19 ± 2.9	32 ± 4.0
Berries·h <sup>-1</sup> ·km <sup>-2</sup>	47,411 ± 3960	66,605 ± 10,440	114,016 ± 14400

Note: The number of seeds dispersed is approximately twice the number of berries consumed.

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 ( $\beta = -1.005$ ,  $P < 0.0001$ ) and significantly more likely to consume devil's club than brown bears after the peak salmon run ( $\beta = 0.811$ ,  $P = 0.0002$ ).

#### Estimation of seed dispersal services

Brown and black bears consumed devil's club at approximately the same rate of an estimated 0.09 clusters per second (SE = 0.008 for brown bears and 0.014 for black bears), or approximately 30 berries per second (SE = 2.5 for brown bears and 5.0 for black bears) and 100,000 berries per hour (SE = 9000 for brown bears and 18,000 for black bears) of foraging (Table 1). Using black and brown bear densities estimated by Flynn et al. (2012) from an equivalent system in nearby Berners Bay, Alaska, we estimate that both species of bear can collectively consume over 100,000 berries·h<sup>-1</sup>·km<sup>-2</sup> (SE = 3960 for brown bears and 14,400 for black bears), leading to estimated dispersal of over 200,000 seeds·h<sup>-1</sup>·km<sup>-2</sup> of foraging.

## DISCUSSION

Although endozoochorous seed dispersal by mammals is common in both temperate and tropical systems, no known temperate plant species is primarily dispersed by mammalian gut passage (Willson 1991), which contrasts with the many tropical plants relying on mammalian

endozoochory (Peres et al. 2016). Our approach was to use novel technology, camera traps and residual DNA from bear saliva on devil's club infructescences, to monitor endozoochorous seed dispersal. Environmental DNA, in particular, allowed us to dramatically increase our sample size and resolve differences in seed dispersal by sex in addition to species. Our results support the hypothesis 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). Although we only monitored devil's club with cameras, bears disperse seeds from at least 12 species at our field site with devil's club having the highest frequency of occurrence (80%) followed by blueberry (47%), which follows the broad trends in their percent cover on the landscape (Fig. 1; Y. Shakeri, K. White, and T. Levi, *unpublished data*).

In search of the nutrition in devil's club fruit, we estimate that a single bear can consume over 100,000 devil's club berries per hour of continuous foraging, and brown and black bears can collectively disperse an incredible 200,000 seeds·h<sup>-1</sup>·km<sup>-2</sup> for foraging. These seeds are then secondarily dispersed by scatter-hoarding small mammals, which reduces negative density dependence, promotes colonization of a greater number of microsites, and promotes germination due to seed burial (Vander Wall 2010). Although the number of seeds dispersed by bears is much larger than the number dispersed by birds, it is possible that bird-dispersed seeds have substantially

higher survival and seedling recruitment rates because of the relatively scant seed rain produced by birds avoiding negative density dependence. Whether this is the case depends on the strength of the benefit of seed burial by scatter-hoarding small mammals relative to the costs imposed by seed predation and density dependence.

It is important to note that most fruit went undispersed, suggesting that fruit removal by bears appears to be nonredundant with fruit removal by other seed dispersers in this system. Most devil's club berries senesced, falling from the infructescence beginning in mid-September (52%), and a large portion of seeds were consumed by seed predators (36%). The vast majority of seed predation was due to red squirrels (*Tamiasciurus hudsonicus*) in 2015 after a spruce (*P. sitchensis*) mast from the previous year led to an increase in their abundance (Y. Shakeri and T. Levi, *unpublished data*). The nonredundancy of seed dispersal by bears suggests that they contribute additively to seed dispersal and are not competing with birds for a limited fruit resource. Thus, a decline in bear densities, or their extirpation, is likely to lead to a reduction in seed dispersal services with unknown consequences for plant communities. This may particularly be the case if a decline in brown bears causes black bears to switch to consume salmon. Similarly, a decline in salmon may lead to a short-term increase in seed dispersal services due to prey switching, likely followed by a long-term decline in seed dispersal services as brown bear populations decline to the much lower levels maintained in the absence of salmon.

Although brown bears are the dominant seed dispersers in this system, the seed dispersal potential of black bears may be restricted due to interference competition. Brown bears nearly completely exclude black bears from salmon in the Chilkat and Chilkoot watersheds of southeast Alaska (Levi et al. 2015). In support of our third hypothesis, our results suggest that brown bears also partially exclude black bears from devil's club until the arrival of salmon, after which black bears become the most common seed disperser (Fig. 5), although it is also possible that black bears select for devil's club during later phenological stages. The presence of these two sympatric Ursids may substantially enhance seed dispersal services by focusing brown bear foraging effort

on early fruit and forcing black bears to focus on berries while salmon are monopolized by brown bears. We did not find clear evidence of species partitioning resources across an elevation gradient, with brown bears feeding across a large elevation as observed by Naoe et al. (2016), although black bears consumed fruit at a higher elevation on average and rarely at low elevation (Fig. 5). Thus, the phenology of seed dispersal services is extended by having two large mammal dispersers with a strict dominance hierarchy, but both species likely contribute to seed dispersal across a range of elevations. Similarly, the overlapping phenology of two resource pulses, ripe berries and salmon (Deacy et al. 2017), may facilitate resource partitioning, and thus coexistence, of these two congeneric Ursids.

The extent of devil's club as a nutritional resource and the consequent seed dispersal services are previously underappreciated for both brown and black bears in this system (Hamilton and Bunnell 1987, Belant et al. 2006). Devil's club is the dominant understory shrub, reaching nearly 50% cover in the evergreen forest habitat, and produces abundant berries that ripen before salmon are available, thus extending the period of food availability to allow bears to accumulate body mass (Belant et al. 2006). Large clusters of densely packed berries, such as devil's club, increase bear bite size and bite rate, thus allowing bears to reach their maximum capacity for daily weight gain (Welch et al. 1997). Thus, the overall abundance of bears, and the seed dispersal services they provide, is likely due to the interplay of salmon and berries. Salmon support abundant brown bears that then disperse seeds in an apparent mutualism between salmon and berry-producing shrubs, and berries support black bears in a direct mutualism due to exclusion from salmon (Levi et al. 2015).

Seed dispersal mutualisms can unravel through the loss of vertebrate seed dispersers, leading to plant recruitment failure with consequences that cascade through ecological communities (Nuñez-Iturri and Howe 2007, Terborgh et al. 2008). The seed dispersal services provided by bears in salmon-bearing ecosystems were once provided to plant communities on much larger spatial scales. Anadromous fish once supported bears throughout the Northern Hemisphere, but brown bears, Pacific salmon, and particularly Atlantic salmon have

declined or been extirpated from large parts of their former range (National Research Council 1996, Mattson and Merrill 2002). The ecosystem-level consequences of the loss of bear–salmon interactions have been largely unexplored (Levi et al. 2012), but our results suggest that this may have resulted in a previously underappreciated loss of the most quantitatively important seed dispersal pathway for some fleshy-fruited shrubs. If understory shrubs are primarily, or partially, dispersal-limited rather than niche-limited (Moore and Elmendorf 2006), the prevalence, or lack thereof, of seed dispersers can affect plant recruitment and, eventually, the continued persistence of plant species (Terborgh et al. 2008, Levi and Peres 2013, Peres et al. 2016). We speculate that these seed dispersal services could contribute to the uniquely high proportion of berry-producing plants in southeast Alaska and British Columbia (Willson 1991). In summary, high densities of salmon-supported bears could be vital players in the network of understory plants both by affecting nutrients available to the plant community (Hilderbrand et al. 1999b) and by providing dispersal services to shrubs with fleshy fruits.

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