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Seed Dispersal by Brown Bears, *Ursus arctos*, in Southeastern Alaska

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Mammals often consume fleshy fruits and disperse significant quantities of the enclosed seeds. In southeastern Alaska, Brown Bears (*Ursus arctos*) are among the most important dispersers of seeds for the numerous plant species producing fleshy fruits, because these bears are abundant, often eat large quantities of fruit, and commonly excrete seeds in germinable condition. Scat analyses showed that Brown Bears on Chichagof Island ate increasing quantities of fruit through summer and fall. Scats commonly contained several thousand seeds, often of two or more species. Four kinds of seeds of fleshy-fruited plants that normally grow in forest understory germinated at similar levels when experimentally deposited (in bear scats) in the two most common habitats (forest and muskeg), suggesting that habitat distribution of these plants is not determined simply by germination patterns. Although seed passage through bear digestive tracts and the composition of scats are known to affect germination rates to some degree, the most important role of bears in seed dispersal is probably transport.

Key Words: Brown Bears, *Ursus arctos*, Southeastern Alaska, seed dispersal, fleshy fruits, *Rubus*, *Ribes*, *Oplopanax*, *Vaccinium*, *Streptopus*.

Coastal rainforest ecosystems in southeastern Alaska include many shrubs and herbs with fleshy fruits, commonly consumed by vertebrates that disperse the enclosed seeds (Willson 1991; Traveset et al. 2004). Potential dispersal agents include corvids, thrushes, warblers, waxwings, Pine Marten (Hickey et al. 1999) and bears (Willson 1993, 1994). Bears are important dispersers of seeds, because they can consume large quantities of fruit (Welch et al. 1997; Farley and Robbins 1995) and often range over considerable distances (Patten 1993), distributing seeds far from the source. Furthermore, bears are numerous in southeastern Alaska, with density reaching several hundred bears per 1000 km — perhaps as many as 700 or even more in some areas (Miller et al. 1997; J. Whitman, personal communication). The abundance of Brown Bears (*Ursus arctos*) in southeastern Alaska provides an opportunity to examine the consequences of bear frugivory for seed dispersal.

The purpose of this paper is to describe the phenology of Brown Bear frugivory, patterns of scat deposition on a small spatial scale, seed abundance and composition in bear scats, and field tests of seed germination from bear scats. We then integrate this information with previous reports, in order to describe what is known about this ecologically important interaction in southeastern Alaska.

Study Area and Methods

Field work was conducted on northern Chichagof Island in the Alexander Archipelago, at the southern end of Port Frederick (approximately 58°N, 135°30'W). The only bears on this island are Brown Bears. The rainforest is composed chiefly of Sitka Spruce (*Picea sitchensis*) and hemlock (*Tsuga* spp.), with occasional muskegs (bogs) of *Sphagnum* moss, scattered Lodgepole Pines (*Pinus contorta*), and low shrubs. Brown Bear scats were collected from abandoned logging roads, at less than 300 m elevation, in the Neka River valley and near Salt Lake Bay on opposite sides of Port Frederick. During each road survey, all scats were cleared from the road, so that the subsequent survey recorded only scats deposited in the between-survey interval. The roads passed through forests of differing ages, clearcuts, and muskegs.

Seed composition of scats

The frequency of occurrence of seeds, and the principal kinds of seeds present, were recorded in June-September 1990-1993 in 4378 scats. A subset of 570 seed-containing scats was collected in August and September 1990 and 1991, for quantitative estimates of seed abundance. Each of these scats was mixed to distribute the seeds throughout, and a subsample averaging 24% ± 2% (S. E.) of the total scat mass was taken. In the weighed subsample, the seeds were identified to genus and counted; the number of seeds in the entire scat was then estimated by extrapolation. The frequency of seeds in scats through the summer and early fall was examined, using 1 June as Day 1. June scat collections represent the previous spring months; collections in July, August, and September represent only the preceding 30 days, approximately.

Seed germination

In order to compare seed germination in two principal habitats, over 150 of the scats for which total seed content was estimated were placed in two common habitats (muskeg or forest). Scats were "planted" in

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transects in each habitat, in whatever microhabitats were available at about 2 m intervals. Muskeg and forest transects near Salt Lake Bay were established in late summer, 1990, and in the Neka Valley in 1991. Seedlings were counted in the planted scats annually (in August) for three (Neka) or four (Salt Lake Bay) years. For seedling censuses, each planted scat was covered with a grid, and seedlings were counted in a random selection of the grid squares. The proportion of grid squares sampled usually ranged from 20% to about 50% of the total scat. Emerging seedlings were counted individually when possible, but so many seeds germinated in some squares that it was impossible to count them without destructive sampling, in which case the abundance of seedlings was estimated visually. The total number of emerging seedlings per scat was extrapolated from this subsample. Curious bears and heavy fall rains disturbed some of the planted scats and thus reduced the usable sample size slightly. Because it was impossible to mark individual seedlings in the very dense clusters, the data are simply estimates of annual germination, not of survivorship of seedlings. Mortality of seedlings was very high and only a few survived more than one year. We did not observe rodent and bird predation on seeds in the experimental transects, although seed predation was sometimes evident in scats on the road system.

The estimated percent of seeds germinating each year was compared between habitats using a repeated-measures ANOVA on arc-sine transformed data (PROC GLM, SAS Systems Inc., Cary, North Carolina). Because the power of this test was low (two sites, two habitats), our results were re-examined, to see if the outcome was merely a result of the few degrees of freedom in the ANOVA. For this we used a t-test (in which the planted scats were the replicates, so there were more degrees of freedom in the test) to test for differences in seedling germination between habitats for the first and the last years at each site (no seedlings in the censused grid squares survived for the entire length of the experiment).

Results

Phenology of fruit consumption

Scats collected in early summer contained mostly vegetable fiber and occasional deer remains (hair, bone, hoof) with few seeds, as expected, because few fruits are available at that time of year (some overwintered *Viburnum* and *Maianthemum*; some early *Rubus spectabilis*). The frequency of seed-containing scats increased through the summer, from less than 1% in mid-June to over 90% in late August and early September ($R_s = 0.79$, $p < 0.001$, $n = 12$; Figure 1).

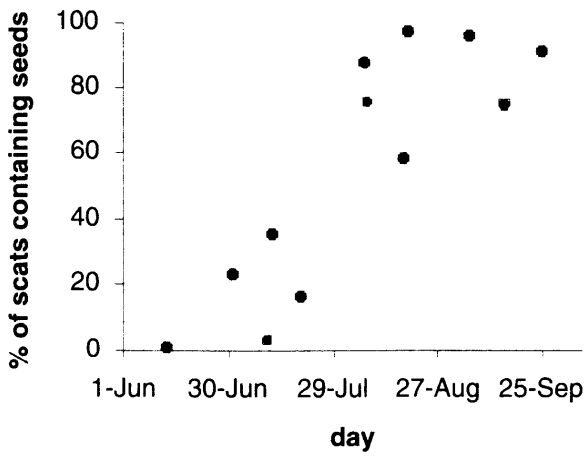

FIGURE 1. Seasonal changes, for four years, in the percent of bear scats containing seeds, Chichagof Island, southeastern Alaska. $R_s = 0.79$, $p < 0.001$.

Scat distribution at a small spatial scale

In addition to widespread deposition of scats on the landscape (Patten 1993), defecations by a moving bear can spread multiple deposits of a single defecation over several meters, which could be ecologically important. A survey of 1163 "scat trails" revealed that 42% were multiple deposits, with 3% of them comprised of over 20 separate droppings spread over as much as 84 m.

Seed composition in scats

Seeds were identified at least to genus; in some cases, the genus was represented by only one species in this area (*Sambucus racemosa*, *Rubus spectabilis*, *Oplopanax horridum*). In the case of *Ribes*, the species was most likely *bracteosum*, which grew commonly in this area. Likewise, *Streptopus amplexifolius* was far more common in this area than two congeners. Both *Vaccinium ovalifolium* and *V. alaskense* were present and were not distinguishable in the scats. The most commonly occurring seeds were *Oplopanax*, *Vaccinium*, *Ribes*, *Rubus*, and *Streptopus* (Table 1).

Seeds had a high probability of being deposited not only with numerous conspecifics but also with at

TABLE 1. Summary of frequency of occurrence of common kinds of seeds in scats on northern Chichagof Island. Data are the number of months that the frequency of occurrence equaled or exceeded the stated value.

	Kind of seed				
	Vaccinium	*Ribes*	*Oplopanax*	*Rubus*	*Streptopus*
Number of months ≥ 20%	5	4	5	1	1
Number of months ≥ 50%	3	1	3	–	–

TABLE 2. Average (S.E.) number of seeds per scat on northern Chichagof Island. N = 570 scats.

Year	Month	Kind of seed											
		Vaccinium		*Ribes*		*Oplopanax*		*Rubus*		*Streptopus*		*Sambucus*	
1990	July	3581	(667)	914	(767)	52	(18)	383	(91)	–		–	
	August	4655	(461)	700	(165)	134	(22)	723	(182)	30	(8)	126	(42)
	September	2534	(468)	1918	(281)	360	(42)	830	(291)	41	(15)	88	(33)
1991	July	4375	(933)	2817	(–)	63	(25)	650	(137)	47	(26)	–	
	August	7193	(760)	364	(109)	228	(40)	583	(120)	81	(20)	–	
	September	4329	(795)	1302	(293)	374	(76)	54	(20)	56	(12)	683	(606)
		4445		1971		231		634		51		110	
$\bar{x}$ number of seeds/fruit*		47		12		2		42		22		3	
$\bar{x}$ number of fruits		95		89		116		15		2		37	

*from Traveset et al. 2004.

least one other kind of seed: in monthly samples, a median of 60% (range 16-87%) of scats contained at least two kinds of seeds, and sometimes as many as five kinds. *Vaccinium* and *Ribes* were consistently the most abundant seeds in scats collected (Table 2). In most months, *Rubus* was next most abundant, followed by *Oplopanax* and others. The maximum numbers per scat for each of the genera listed in Table 2 were approximately 37 000 *Vaccinium*, 14 500 *Ribes*, 7600 *Rubus*, 2000 *Oplopanax*, 1900 *Sambucus*, and 400 *Streptopus*. In addition to those represented in Table 2, other kinds of seeds appeared in the scats sporadically (from fleshy fruits, *Viburnum*, *Maianthemum*; non-fleshy fruits, *Kalmia*, *Heracleum*, *Carex*, grass).

Because the number of seeds per fruit differs greatly among genera (Traveset et al. 2004), the approximate number of consumed fruits of each type per scat differs markedly from the abundances of seeds (Table 2). The average scat represented only approximately 89 – 116 fruits of the most commonly consumed types.

Seed germination

Germination patterns were examined only for *Vaccinium*, *Ribes*, *Rubus*, and *Oplopanax*. A few *Vaccinium* seeds germinated in the year they were planted (<1% of all seeds estimated to be present); germination levels were generally low (<6%) over the next four years (Table 3). Annual germination of *Oplopanax* was also rather low (≤18%). In contrast, both *Ribes* and *Rubus* germinated relatively well (up to 31-34% per year), with the highest levels of germination often in the second year after planting. All these kinds of seeds were clearly capable of dormancy for at least four years.

There were no differences in germination percentages between habitats for any species (ANOVA; range of p-values: 0.17 – 0.82). The subsequent exploratory t-test also revealed no differences between habitats except for *Vaccinium* in one site – one statistically significant outcome in 16 tests, which might happen by chance alone. Variation among scats planted within a habitat was relatively large, but it probably reflected the biological reality of variation on a small spatial scale.

Discussion

Bears are well-known frugivores, consuming many species of fleshy fruits (Auger et al. 2002; Willson 1993). Fruits can be an important resource for preparing for winter dormancy and lactation (females give birth in winter dens), and berry-crop failures can lead to lower reproductive success (Rogers 1987). Bears can consume many kilograms of fruits in a day (Welch et al. 1997; Farley and Robbins 1995). Although a single bear scat in the present study often contained thousands of seeds, this represented relatively few fruits and therefore only a small proportion of possible daily consumption.

Composition of the fecal deposit can affect seed germination and seedling growth (Traveset et al. 2001), and the concentration of seeds in scats can lead to post-dispersal seed predation and secondary dispersal via scattering (Bermejo et al. 1998). Germination of seeds passed by captive bears was generally similar to or faster than that of seeds extracted from fruits by researchers, although germination of some species was quite low in all conditions and was sometimes dependent on the substrates on which the seeds happen to land (Traveset and Willson 1997, 1998). But rapid germination is not necessarily beneficial, if seed dormancy is indeed an adaptation for dispersal in time.

The most important consistent effects of frugivory by bears on seed dispersal may be transport, rather than shifts of germination behavior of seeds passed through the digestive tract. In a companion study, the probability of seed deposition by Brown Bears on Chichagof Island was greatest at 600-900m from a source (Patten 1993). The greatest distance estimated for seed transport by Brown Bears was over three km (Patten 1993), and even though few seeds are likely to be carried this far from their source, the extended tail of the seed distribution pattern can be disproportionately important for dispersal ecology (Portnoy and Willson 1992) and plant community ecology (Vellend et al. 2003). Little habitat preference was shown by the bears tracked on Chichagof, except for an avoidance of bare-rock areas, so the probability of seed deposi-

TABLE 3. Estimated average percent of seeds germinating per year in two common habitats at two sites on Chichagof Island, southeastern Alaska.

Site	Habitat	Year	Kind of seed							
			Vaccinium		*Ribes*		*Oplopanax*		*Rubus*	
Neka	Forest	1992	3.9	(0.9)	0.2	(0.2)	<0.1	–	22.5	(7.2)
	n = 30	1993	2.8	(0.5)	30.8	(15.7)	18.4	(10.1)	28.5	(9.8)
		1994	3.3	(0.9)	14.7	(9.0)	9.5	(4.9)	13.6	(4.8)
	Muskeg	1992	5.9	(2.2)	–		1.1	(1.0)	20.7	(7.7)
	n = 30	1993	2.9	(1.0)	–		10.2	(8.4)	19.7	(7.5)
		1994	1.2	(0.4)	–		11.0	(10.6)	5.6	(3.3)
Salt Lk Bay	Forest	1991	2.4	(0.9)	19.1	(11.5)	5.3	(2.1)	17.0	(9.3)
	n = 60	1992	3.6	(0.8)	30.8	(16.2)	1.6	(0.8)	34.2	(8.7)
		1993	1.8	(0.3)	2.5	(1.5)	1.1	(0.5)	19.7	(6.9)
		1994	1.3	(0.2)	1.0	(0.6)	3.0	(1.3)	9.8	(4.8)
	Muskeg	1991	1.1	(0.5)	0.5	(0.5)	4.6	(2.7)	7.1	(5.1)
	n = 49	1992	3.0	(1.0)	25.6	(10.4)	1.2	(0.7)	19.6	(6.9)
		1993	1.8	(0.7)	6.3	(5.2)	0.9	(0.7)	10.7	(4.5)
		1994	1.6	(0.8)	0.3	(0.2)	0.6	(0.4)	4.3	(3.0)

tion was proportional to habitat availability, including logged areas (Patten 1993). Because forest was the common habitat, this meant that the forest fruits, such as most of the species examined here, had a fairly high probability of deposition in the appropriate habitat (Patten 1993). On a smaller scale, defecation by moving bears could increase the probability that seeds from one defecation episode are deposited in more than one habitat or microhabitat, as well as decrease the intensity of seedling competition.

Germination of several forest and forest-edge species was similar in forest and muskeg, indicating that habitat distribution of these shrubs is not determined by germination requirements at the habitat scale. The large variances of the estimates of germination level not only decreased the probability of detecting habitat differences, but they also suggest that microhabitats of seed deposition may be more important in determining germination success than habitats. Mortality of seedlings was very high, in part an apparent result of desiccation during periods of warm, sunny weather. Especially at high densities, intra- and interspecific competition was undoubtedly intense and probably contributed to seedling mortality. However, occasionally small groups of seedlings persisted and were still alive when field work ended; similar "bear gardens" were also found in natural settings (Willson 1994).

Bears are good seed dispersers: they commonly transport germinable seeds up to hundreds of meters from a source, often in appropriate habitat, simultaneously with a load of fertilizer that may influence germination and growth. Although scats containing numerous seeds produce conditions of high seedling competition, several factors tend to reduce the impact of competition on the effectiveness of dispersal. Germination may be spread over several years. Relatively rapid passage through the gut and multiple defecations per day within a bear's home range spread scats over the landscape. Scat trails of moving bears spread out the seeds on a more local scale. Bears may be more reliable dispersal agents for many kinds of seeds than most frugivorous birds in this area, since the coastal region is not a major flyway for migratory forest birds.

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