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CACHE-SITE SELECTION IN CLARK'S NUTCRACKER (*NUCIFRAGA COLUMBIANA*)

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Abstract.—Clark's Nutcracker (*Nucifraga columbiana*) is one of the most specialized scatter-hoarding birds, considered a seed disperser for four species of pines (*Pinus* spp.), as well as an obligate coevolved mutualist of Whitebark Pine (*P. albicaulis*). Cache-site selection has not been formally studied in Clark's Nutcrackers, which are considered effective seed dispersers for pines because past studies have found that they harvest and store large quantities of seeds. Although many seeds are placed in sites suitable for germination and establishment, information is lacking on the proportions of seeds placed in suitable versus unsuitable sites. We used radiotelemetry to investigate cache-site selection and evaluate the suitability of selected cache sites for establishment of Whitebark and Ponderosa (*P. ponderosa*) pines. On a landscape scale, Clark's Nutcrackers cached seeds centrally within home ranges, even though this required them to transport seeds up to 32.6 km. They selected low-elevation forests for caching, presumably because these sites accumulated little snow. When caching at high elevations, the birds placed most seeds in aboveground microsites. Only 15% of Whitebark Pine seed caches ($n = 155$ caches) were placed below ground and in habitats where seeds could germinate and seedlings grow. For comparative purposes, 42% of Ponderosa Pine seed caches were placed in suitable habitats and below ground. Although Whitebark Pine is an obligate mutualist of Clark's Nutcracker, our study suggests that Clark's Nutcrackers in some populations may be more effective seed dispersers for Ponderosa Pine than for Whitebark Pine. *Received 20 April 2010, accepted 29 January 2011.*

Key words: avian seed dispersal, home-range fidelity, *Pinus albicaulis*, *P. ponderosa*, resource selection.

Selección de Sitios de Acumulación de Alimento en *Nucifraga columbiana*

Resumen.—*Nucifraga columbiana* es una de las especies de aves con el mayor grado de especialización con relación al comportamiento de almacenar alimento en sitios dispersos. Además, la especie es considerada dispersora de semillas de cuatro especies de pinos (*Pinus* spp.) y un mutualista obligatorio del pino *P. albicaulis*. La selección de los sitios de acumulación de semillas no ha sido estudiada formalmente en *N. columbiana*, a pesar de que esta ave se considera un dispersor de semillas efectivo para los pinos porque estudios anteriores han encontrado que recolecta y almancena grandes cantidades de semillas. Aunque muchas semillas son guardadas en lugares que son adecuados para su germinación y establecimiento, no se tiene información sobre la proporción de semillas ubicada en lugares adecuados vs. no adecuados. Utilizamos radio-telemetría para investigar la selección de sitios de acumulación por parte de individuos de *N. columbiana* y para evaluar la calidad de los sitios seleccionados para el establecimiento de los pinos *P. albicaulis* y *P. ponderosa*. A una escala de paisaje, las aves acumularon las semillas en el centro de sus ámbitos hogareños, a pesar de que eso requería en algunos casos que las aves transportaran las semillas hasta 32.6 km. Las aves seleccionaron bosques de baja elevación para los sitios de acumulación, probablemente porque esos sitios acumulan poca nieve. Cuando los sitios de acumulación estaban a altitudes mayores, las aves colocaron la mayoría de las semillas en micrositios bajo el nivel de la superficie del suelo. Sólo el 15% de los sitios de acumulación de semillas de *P. albicaulis* ($n = 155$ sitios) se ubicaron bajo tierra y en hábitats en los que las semillas podían germinar y las plántulas podían crecer. En comparación, 42% de los sitios de acumulación de semillas de *P. ponderosa* estaban localizados en sitios adecuados y bajo tierra. A pesar de que *P. albicaulis* es un mutualista obligatorio de *N. columbiana*, nuestro estudio sugiere que, en algunas poblaciones, *N. columbiana* seria un dispersor más eficiente para *P. ponderosa* que para *P. albicaulis*.

Scatter-hoarding mammals and birds are important seed dispersers for at least 25 species of pines (*Pinus* spp.) in western North America. Because of differences in natural-history traits, these animals differ in seed-dispersal effectiveness (*sensu* Schupp 1993). In general, birds are capable of dispersing seeds long distances, but small mammals such as chipmunks (*Tamias* spp.) and

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mice (*Peromyscus* spp.) are thought to select more favorable microsites for plant establishment than birds such as Steller's Jay (*Cyanocitta stelleri*), Pinyon Jay (*Gymnorhinus cyanocephalus*), and Clark's Nutcracker (*Nucifraga columbiana*) (Vander Wall 1997, Thayer and Vander Wall 2005). These findings are based on many detailed studies of rodent seed dispersal. There have been comparatively few studies of seed dispersal in birds, whose longer dispersal distances can be more difficult to track. This is especially true for avian seed dispersers like Pinyon Jays and Clark's Nutcrackers, which may transport seeds up to 10–22 km between harvest trees and storage sites (typically called "caches"; Vander Wall and Balda 1977, 1981; Tomback 1978).

Clark's Nutcracker (hereafter "nutcracker") is one of the most specialized scatter-hoarding birds, considered an effective seed disperser for at least four species of large-seeded, bird-dispersed pines as well as an obligate, coevolved mutualist with Whitebark Pine (Tomback and Linhart 1990; scientific names of plant species are given in Table 1). Previous studies have noted habitat features at cache sites (Tomback 1978, 1982; Dimmick 1993), but habitat selection, as defined by comparing habitats used with availability, has not been studied in seed-caching nutcrackers. Studies of habitat selection in animals are important for assessing features within the landscape that are used disproportionately to their availability (Johnson 1980, Manly et al. 2002). Studies of habitat selection by seed-caching nutcrackers can also provide valuable information on the quality of nutcracker seed dispersal—that is, whether nutcrackers disperse seeds to sites suitable for seed germination, seedling establishment, and plant maturation. This is particularly important because Whitebark Pine is undergoing range-wide population declines from the combined effects of an invasive disease, parasite epidemics, and advanced succession due to fire suppression (Tomback et al. 2001b). Resource managers need information on what proportions of seeds are placed in suitable sites by nutcrackers to assess whether diseased stands can be reliably restored by seed-caching nutcrackers, or whether humans should take a more active role through direct sowing of seeds or planting of seedlings. Detailed studies on the dispersal effectiveness of avian seed dispersers are also appropriate in light of recent research that has revealed that most seed-fate pathways are complex and may involve multiple phases of dispersal before seed germination (Vander Wall et al. 2005).

The objective of our study was to investigate cache-site selection in nutcrackers and to evaluate the quality of their seed dispersal. We conducted the study in the Cascade Range, where nutcrackers harvest and store seeds of Ponderosa Pine, Whitebark Pine, Douglas-Fir, and Western White Pine. We used radiotelemetry to track individuals and to eliminate bias associated with variation in detectability of nutcrackers caching in open versus forested habitat types. We studied cache-site selection by resident nutcrackers on three spatial scales corresponding to Johnson's second-, third-, and fourth-order selection (Johnson 1980); we investigated the selection of caching areas within the landscape, the selection of habitats within caching areas, and the selection of microsites within habitats. We evaluated the quality of nutcracker seed dispersal for Whitebark and Ponderosa pines by relating our findings on nutcracker cache-site selection to what is known about seed germination and seedling establishment requirements in these pines.

Methods

Study area.—We studied nutcracker cache-site selection from June 2006 through August 2009 on the eastern slopes of the Cascade Range, ~40 km west of Yakima, Washington, (~120°58′W, 46°45′N). The land is administered by the U.S. Department of Agriculture, Forest Service, the Washington State Department of Natural Resources, and the Washington State Department of Fish and Wildlife, and elevations ranged from 500 to 2,500 m. Vegetation varied along an east–west and elevational gradient. Locations close to the Cascade Crest were dominated by closed-canopy hemlock–fir (*Tsuga* spp.–*Abies* spp.) forests and received, on average, >1,500 cm of snowfall annually. Locations 40 km eastward and near the shrub-steppe zone of the Columbia Basin were dominated by open-canopy Ponderosa Pine forests and received <400 cm of snowfall annually (Lillybridge et al. 1995).

We classified six forest and two nonforest habitat types within the study area using a Plant Association Group model developed by the Wenatchee National Forest, in combination with a canopy closure and 1-m digital elevation models (Table 1 and Fig. 1). Forest cover types included Ponderosa Pine, Parkland Ponderosa Pine, Douglas–Grand fir, Mountain Hemlock–Subalpine Fir, Whitebark Pine, and Parkland Whitebark Pine. Nonforest cover types included Cliffs–Talus and Burns. To estimate the relative abundance of Whitebark Pine seed among years, we counted Whitebark Pine cones at three sites in the Cascade Range from 2006 through 2009. Ten mature trees were arbitrarily selected for cone counts at each site. Across all sites and years, 10 cone-count trees were killed by Mountain Pine Beetle (*Dendroctonus ponderosae*) and one was uprooted and killed. These trees were replaced with different trees of comparable size. Observers counted all cones visible from the north and south aspects of each tree using 8 × 42 binoculars. Cone counts were conducted between 15 July and 16 August each year.

Telemetry.—Nutcrackers (n = 56) were captured at feeding stations from March through June of 2006, 2007, and 2008. We captured nutcrackers at six feeders in Whitebark Pine habitat, two feeders in Ponderosa Pine habitat, and one feeder in a burn. All after-hatch-year nutcrackers (n = 51) were fitted with a 3.9-g (~3% of body weight) radiotransmitter (Advanced Telemetry Systems, Isanti, Minnesota) that was secured to the back with a harness. The transmitter battery life was ~450 days.

Point locations (n = 5,906) on 18 resident adults were obtained by homing, and we recorded locations using portable global positioning system (GPS) units (location error range: 1–6 m). From mid-February through early April, we visited radiotagged nutcrackers at least once weekly and conducted 2–5 h observation sessions to record breeding behavior. From June through August, we tracked nutcrackers 1 to 3 days per week for 1 to 5 h. For home-range estimation, we included only one telemetry point per hour from continuous tracking sessions to eliminate bias caused by autocorrelation of sequential relocations.

Home ranges.—We captured nutcrackers in late winter each year, and all resident nutcrackers established home ranges in the vicinity of their capture site in spring and summer. In autumn, most residents did not have cones available within the boundaries of the spring–summer home range. These residents went on excursions from the spring–summer home range in autumn and early winter to harvest pine seeds from productive stands. Although birds were

Table 1. Definitions of habitat types classified within the study area in Washington State.

Habitat type	Description	Elevation range (m)	Proportion of study area that contained the habitat
Parkland Ponderosa Pine	Forest dominated by Ponderosa Pine (*Pinus ponderosa*) with canopy cover <10%	500–1,500	0.06
Ponderosa Pine	Forest dominated by Ponderosa Pine with canopy cover >10%	500–1,500	0.15
Douglas–Grand fir	Forest dominated by Grand Fir (*Abies grandis*) or Douglas-Fir (*Pseudotsuga menziesii*) and containing Ponderosa Pine, Western Larch (*Larix occidentalis*), and Western Hemlock (*Tsuga heterophylla*) as components in the overstory	500–2,000	0.46
Mountain Hemlock–Subalpine Fir	Forest dominated by Mountain Hemlock (*T. mertensiana*), Subalpine Fir (*A. lasiocarpa*), and Subalpine Larch (*Larix lyallii*) and containing Whitebark Pine (*P. albicaulis*), Engelmann Spruce (*Picea engelmannii*), Western White Pine (*Pinus monticola*), and Grand Fir as components in the overstory	1,000–2,000	0.15
Whitebark Pine	Forest dominated by Whitebark Pine with canopy cover >10%	1,500–2,000	0.09
Parkland Whitebark Pine	Forest dominated by Whitebark Pine with canopy cover <10%	1,500–2,300	0.01
Cliffs–Talus	Slopes with >40% incline and <2% canopy cover	800–2,300	0.06
Burns	Forest burned in mixed or high-severity wildfires between 2000 and 2008	600–2,000	0.01

captured at different locations and had spring–summer ranges that were separated by up to 50 km, birds from different parts of our study area would often use the same harvest stands during the seed-harvest season, occasionally harvesting seeds side-by-side. During this time, they made multiple trips to the spring–summer home range daily to cache seeds. As autumn progressed into winter, four individuals would spend several days in harvest stands foraging seeds without caching. However, following the autumn–winter seed harvest season, all residents returned to the spring–summer home ranges and from midwinter onward, birds were always detected in the spring–summer home range. In other words, nutcrackers appeared to show strong fidelity for a relatively small core area near their capture site for all daily activities except autumn–winter seed harvest. But in autumn and early winter they ranged widely while searching for

Fig. 1. Examples of seed-harvest stands used by Clark's Nutcrackers for Ponderosa Pine seed harvest (left) and Whitebark Pine seed harvest (right) from 2006 through 2009 in the present study.

cone-producing stands of pine. Moreover, within and among years, nutcrackers did not show fidelity to seed-harvest stands and used such stands only as long as seeds were present within cones. We therefore defined "home range" to refer to the core area (or the extent of the area) where a resident would occur with 95% probability from February to mid-August (spring–summer; Kernohan et al. 2001). We used the term "range of autumn movement" to define the area over which a nutcracker moved while harvesting and caching seeds from mid-August through January.

We delineated home ranges using the 95% contour interval of the fixed kernel distribution and least-squares cross validation (Worton 1989). We used the Animal Movement extension (Hooge and Eichenlaub 1997) in ARCVIEW, version 3.3 (ESRI, Redlands, California) to estimate kernels, and grid size was selected automatically. We used 90% kernels for four nutcrackers that had multimodal home ranges because they eliminated unused buffered areas around infrequently used locations.

Autumn seed harvest.—During the seed-harvest season, resident nutcrackers were tracked during behavior-watching sessions that lasted 1–7 h. Birds were located using aerial telemetry when they could not be located from the ground. We delineated 100% minimum convex polygons (MCP) for residents to estimate the range of space use during the seed-harvest season. We recorded all behavior observed during sessions as seed harvest (consuming seeds or placing seeds within the sublingual pouch), seed caching, seed transport flight, or other (all behavior not directly associated with seed harvest and storage, including roosting, preening, vocalizing, and social interactions). For observations of seed harvest, we noted the tree species visited. For observations of seed caching, we recorded whether the cache was made above ground or below ground.

Nutcrackers ranged widely when harvesting seeds, and we worked in teams of up to four people to watch individuals as continuously as possible during the behavior-watching sessions. When harvesting seeds from distant seed sources, it was not logistically possible to continuously track nutcrackers from individual harvest trees, along their flight path, and to cache sites of individual seeds. However, because we stationed observers in the harvest stand, along the flight path between harvest stands and home ranges, and in the home range, we are confident that nutcrackers did not cache seeds along their flight paths. We observed radiotagged nutcrackers filling their sublingual pouches in harvest stands, and then flying off in the direction of the home range once their pouches were full. Within 5 to 25 min, these same individuals were observed flying with full pouches into the home range, where we observed them caching seeds.

We observed 7 nutcrackers making 199 Whitebark Pine caches and 11 nutcrackers making 450 Ponderosa Pine caches. Six caches were of an undetermined seed type. We revisited all belowground cache sites that were not on cliffs or in similarly inaccessible areas ($n = 171$) in 2009, when we measured microsite characteristics at cache sites and at paired random sites that were located 30 m from cache sites in a random direction. We chose 30 m as an appropriate distance for establishing random sites because it ensured that they occurred within the same habitat as caches, while representing a distinct set of microsite conditions. We measured slope and aspect at each cache and each random site, using a clinometer and compass, respectively. Within a circle with a 1-m radius centered on each cache, we visually estimated the percentage of ground covered by litter, soil, vegetation, or rock. We measured overstory and understory cover at five locations with a moosehorn densiometer (centered on the cache site and 1 m out in the four cardinal directions). We estimated the distance to potential cover by measuring the distance from the cache or random site to the stem of the nearest tree with a minimum diameter at breast height of 15 cm and a minimum height of 3 m. We broadly classified all caches and random sites into one of five possible patch types based on a visual estimate of canopy cover within and outside of a 75-m-diameter circle centered on the site: small forest patch (<75 m diameter), small open patch (<75 m diameter), large forest patch (>75 m diameter), large open patch (>75 m diameter), and edge. We classified the patch as "forested" when canopy cover was ≥10% and as "open" when canopy cover was <10%. We chose 75 m to differentiate between large and small patches because this is the approximate scale at which Keane and Parsons (2010) hypothesized that nutcrackers select patches when caching.

Data analysis.—For second-order selection (landscape-scale selection), we used HAWTH'S TOOLS (Beyer 2004) in ARCGIS, version 3.2 (ESRI) to calculate minimum, maximum, and median distances between cache sites and harvest trees. We also determined proportions of seeds placed in harvest stands versus home ranges. For third-order selection (habitat-scale selection), we overlaid our habitat map on nutcracker home ranges. Because our data were categorical, we used compositional analysis (Aebischer et al. 1993) and SAS statistical software (BYCOMP.SAS; Ott and Hovey 1997) to investigate selection for habitats within the home range. Compositional analysis uses the individual animal as the sample unit. If study animals are not detected in one or more habitats, a small, nonzero number is substituted so that the log ratio can be calculated for use of the habitat. The substitution of very small values can increase the probability of Type I error (Bingham and Brennan 2004). Bingham and Brennan (2004) suggested that a substitution value between 0.3% and 0.7% be used to minimize Type I error rates. Six radiotagged nutcrackers had zero use of at least one habitat type. We completed four iterations of our analysis using substitution values of 0.1%, 0.3%, 0.5%, and 0.7% and found no difference in the overall significance of the test. We therefore substituted 0.1% for all zero-habitat-use values.

For fourth-order selection (microsite-scale selection), we used logistic regression to identify features at the microsite scale that influenced cache-site selection for belowground caches only. Prior to building our models, we assessed the correlation of all pairwise combinations of covariates. Multicollinearity was evaluated using Pearson product-moment correlations and a correlation coefficient >0.5 was regarded as strong. Covariates that induced multicollinearity were eliminated from further model consideration. Evidence of quadratic and cubic covariate effects was investigated in pairwise correlation plots. In our study, litter was correlated with understory cover, and therefore the explanatory variables used in our model were percent overstory, understory, and ground cover (percentage of the ground covered by grasses and forbs, rock and gravel, and bare ground), as well as aspect, slope, and distance to cover.

Prior information from similar studies was not available to help formulate a set of testable hypotheses. Consequently, we developed a set of 37 *a priori* models, including 34 fixed-effects models, two mixed-effects models, and a null model with which to explore microsite selection. The 34 fixed-effects models included a maximal model containing the above-listed single factors as well as all two-way interactions, 32 simplified models of decreasing complexity

from the maximal model, and a null model with only an intercept. Unbalanced sampling of nutcracker cache sites occurred across individuals and patch types, introducing additional sources of variability to our logistic regression models. To compensate for such heterogeneous sampling and for repeated sampling per nutcracker, we separately added two random intercepts, δ_i^{bird} and δ_i^{patch}, to our best-fitting fixed-effects logistic regression model to assess whether the addition of random effects improved the model's fit.

We used a hierarchical information-theoretic approach for model selection in which the best-fitting fixed-effect model was chosen. First, we reduced the number of candidate fixed-effects models from 34 to 5, calculated the Akaike weights and ΔAIC_c of these five candidate models (Hosmer and Lemshow 2000, Burnham and Anderson 2002), and selected the model with the lowest AIC_c as the most parsimonious fixed-effects model. We did not find evidence of overdispersion ($\hat{c} = 1.04$), and therefore we did not use a quasi-likelihood adjustment ($QAIC_c$). Model fit of the top fixed-effects model was confirmed through the Hosmer-Lemshow goodness-of-fit test statistic. Two new mixed-effects models were then formulated by adding bird and patch intercept random effects to the top fixed-effects model, and their model fit was evaluated using AIC_c.

We used SAS, version 9.2, statistical software (SAS Institute, Cary, North Carolina) and R (R Development Core Team 2009) for all statistical analyses. We report values as means ± SD unless otherwise noted, and we considered statistical results significant at $\alpha = 0.05$.

Results

Telemetry.—Median home-range size of 18 resident adult nutcrackers was 413.2 ha (range: 138.61–5,207.44 ha). Home-range size was not correlated with the number of point relocations ($r^2 = 0.13$, $P = 0.127$, $n = 18$). Six resident nutcrackers occupied home ranges that contained Ponderosa Pine but lacked Whitebark Pine (hereafter "Ponderosa Pine residents") and 12 occupied home ranges that contained both Whitebark Pine and Ponderosa Pine ("Whitebark Pine residents"). Two residents shed their radiotransmitters, and one died in summer before the harvest season, so no caching data were collected for these individuals.

Whitebark Pine cone production was higher in 2006 (55.6 ± 38.07 cones tree^{-1}) than in 2007 (17.3 ± 21.13 cones tree^{-1}) and 2009 (14.4 ± 14.49 cones tree^{-1}). No Whitebark Pine cones were produced in the study area in 2008, and resident nutcrackers focused their seed-harvest efforts on Ponderosa Pine in 2008. Three Whitebark Pine residents abandoned their home ranges in autumn 2008, presumably because of a lack of Whitebark Pine cones. Two of these birds were never detected again, and one (nutcracker 091) established a new "home range" ~8 km from the Ponderosa Pine stand used for seed harvest (the original home range had been ~40 km from the Ponderosa Pine stand used for seed harvest). From this point onward, nutcracker 091 treated the newly established home range as other residents treated their summer home range; all seed caching occurred in this range, and the range was used for roosting and foraging throughout autumn and winter until the bird shed its radio tag in February 2009. Among the 12 remaining residents, seed caches were observed for 11 birds. Thus, all told, we observed seed caching by 12 of the original 18 residents.

One Whitebark Pine resident (nutcracker 893) was tracked over two autumns (2007 and 2008). Two Whitebark residents and one Ponderosa resident (nutcrackers 312, 332, and 193) were tracked over one complete harvest season (2008) and the beginning of a second (2009) before their transmitter batteries failed in August 2009. Home-range data for these individuals were combined for both years of tracking, but seed-harvest ranges and seed transport were considered separately for the two seasons. One other Ponderosa Pine resident (nutcracker 505) died of a shotgun wound during the Ponderosa Pine seed-harvest season in October 2006. We tracked nutcracker 505 for the entire 2006 Whitebark Pine seed-harvest season and ~1 month of the Ponderosa Pine seed-harvest season.

Although we did not measure flock size when radiotagged nutcrackers were caching, we observed nutcrackers caching by themselves and in the presence of large numbers of conspecifics. On several occasions, we estimated flocks of harvesting and caching nutcrackers to number at least 100 birds. However, the vast majority of caching was done alone or in small groups of ≤10 individuals.

Cache-site selection.—Forty-three percent of all seed-harvest events occurred outside of the boundaries of the home range, and 97% of caches were placed within the boundaries of the home range. The remaining 3% of caches were placed in harvest stands outside of the home range by three individuals. Caching in the harvest stand occurred under two different circumstances. Nutcracker 312 cached Ponderosa Pine seeds and nutcracker 893 cached Whitebark Pine seeds in the harvest stand late in the harvest season, when harvesting efficiency appeared to be low because of diminishing availability (after 8 October for nutcracker 312 and after 21 September for nutcracker 893). Nutcracker 193 cached seeds in the harvest stand in the first 5 days of the harvest season and when harvest efficiency appeared to be low because of unripe cones. Harvest stands were ≥12 km distant from home ranges in these three circumstances (32 km distant for nutcracker 312, 12 km distant for nutcracker 893, and 26 km distant for nutcracker 193).

The median distance between cache sites and harvest trees was greater for Ponderosa Pine seeds (median = 5.2 km) than for Whitebark Pine (median = 2.1 km) (Table 2). However, there was considerable variation among individuals in seed transport, depending on the location of the seed source in relation to the home range. One individual did not transport seeds farther than 2.4 km, whereas another did not transport seeds a distance <20.8 km. Maximum distances were nearly equal for both species of pine; Whitebark Pine seeds were transported ≤32.6 km and Ponderosa Pine seeds ≤32.5 km (Table 2). Our measurements of seed transport account only for direct, straight-line distances between harvest trees and cache sites. They do not account for nutcrackers deviating from a direct flight path, and they do not account for changes in elevation and mountain ranges that Joccurred between seed-harvest stands and cache sites (Fig. 2). For example, nutcracker number 312 transported seeds 32 km flying over two ridges of 1,850 m elevation between seed-harvest stands and the home range. Thus, seed-transport flights reported here represent minimum energetic costs.

Once within the home range, Ponderosa Pine residents selected Ponderosa Pine stands for caching both Whitebark and

TABLE 2. Home-range kernel size, range of autumn movement (harvest MCP), and distances between seed-harvest trees and cache sites for 12 radiotagged resident adult Clark's Nutcrackers tracked from 2006 through 2009 in the Cascade Range, Washington.

Bird ID (year tracked)	Home-range kernel (ha) (number of telemetry relocations)	Harvest MCP (km^2)	Species of pine harvested	Number of caches	Distance between harvest trees and cache sites (km)			
					Median	Range	First quartile	Third quartile
505 (2006)[a]	138.61 (255)	280.98	Whitebark	13	29.49	26.54–32.55	29.05	30.78
			Ponderosa	8	20.41	12.95–26.07	16.35	23.21
746 (2008)	138.75 (324)	143.79	Ponderosa	96	18.82	6.15–20.78	15.71	19.78
091 (2008)	161.40 (302)	14.71	Ponderosa	33	5.96	0.00–8.74	1.90	6.76
043 (2008)	183.48 (663)	51.70	Whitebark	64	0.63	0.00–2.39	0.34	0.89
632 (2008)	188.74 (368)	6.63	Ponderosa	84	3.90	3.11–5.63	3.76	4.21
719 (2006)	249.55 (161)	17.16	Whitebark	15	3.37	0.05–7.49	0.94	6.69
			Ponderosa	13	0.30	0.00–3.03	0.18	0.42
211 (2007)	290.25 (533)	17.56	Ponderosa	80	0.70	0.01–8.26	0.42	6.97
893 (2007)	355.76 (526)	54.50	Whitebark	64	0.85	0.00–12.77	0.48	1.20
			Ponderosa	13	3.74	0.03–6.24	3.58	4.40
893 (2008)	355.76 (302)	145.72	Ponderosa	17	12.77	2.76–18.38	8.58	15.24
312 (2008)	366.34 (292)	114.34	Ponderosa	25	29.22	0.01–32.53	28.73	29.22
312 (2009)[a]	366.34 (210)	1.42	Whitebark	20	0.00	0.00–2.03	1.57	1.94
781 (2008)	460.04 (373)	67.70	Ponderosa	39	4.35	3.56–5.24	4.10	4.70
332 (2008)	776.00 (202)	83.68	Ponderosa	7	23.18	20.80–25.58	22.16	24.17
332 (2009)[a]	776.00 (150)	1.34	Whitebark	10	1.70	0.00–2.31	1.56	2.31
193 (2008)	2,074.73 (326)	9.35	Ponderosa	34	0.50	0.00–4.38	0.13	1.03
193 (2009)[a]	2,074.73 (185)	130.34	Whitebark	14	0.02	0.00–25.72	0.01	0.05
Median	269.95	53.10			3.74			

[a]Birds 505, 332, 312, and 193 were not tracked for the entire seed-harvest season: nutcracker 505 died from a shotgun wound during the Ponderosa Pine seed-harvest season (6 October 2006), and nutcrackers 312, 332, and 193 had radiotransmitter batteries fail during the Whitebark Pine seed-harvest season (last dates of tracking prior to transmitter failure were 16, 12, and 20 August 2009, respectively).

Ponderosa pine seeds, and avoided burns and higher-elevation Douglas–Grand fir forests (Wilks's $\lambda = 0.020$, $F = 32.19$, df = 3 and 2, $P = 0.030$). Whitebark Pine residents did not show significant overall selection for one habitat type when caching Whitebark and Ponderosa pine seeds (Wilks's $\lambda = 0.232$, $F = 2.20$, df = 3 and 2, $P = 0.328$). However, Douglas–Grand fir forests were more commonly used than higher-elevation Mountain Hemlock–Subalpine Fir and Whitebark Pine forests.

Nutcrackers placed 59% of caches (385 caches) above ground (Table 3). Aboveground caches were placed mostly in living trees (86%, or 330 caches). We did not measure height of caches within trees, but most caches were placed in the midstory or upper canopy of a tree. Aboveground caches were placed in clumps of needle foliage at the tips of branches, in clumps of lichen within foliage, or wedged under slips of bark along branches. Nutcrackers often covered aboveground caches; after placing a seed in an aboveground cache, they would strip bits of lichen or moss from nearby twigs and stuff it into the cache. Post hoc contingency-table analyses of habitats used for above- and belowground caches revealed significant differences in the proportion of Whitebark Pine seeds ($P < 0.0001$) and Ponderosa Pine seeds ($P < 0.0001$) cached below and above ground as a function of habitat type. Individuals in high-elevation Whitebark Pine and Mountain Hemlock–Subalpine Fir forest types placed 90% of caches in aboveground sites. In low-elevation forest types (Douglas–Grand fir and Ponderosa Pine forest types), they placed 56% of caches above ground in trees (Table 3).

Of 649 caches where the seed type was known, 41% (264 caches) were placed below ground, where germination was possible. Fifteen percent of Whitebark Pine caches (30 caches) were placed in belowground sites and in cliffs or talus slopes, Whitebark Pine, or Mountain Hemlock–Subalpine Fir habitat types where seedling germination and establishment would be possible (Table 3). A higher proportion of Ponderosa Pine seeds were placed in habitats suitable for establishment; 42% of Ponderosa Pine caches (190 caches) were placed below ground in cliffs or talus slopes, burns, Ponderosa Pine, or Douglas–Grand fir habitat types where establishment was possible (Table 3).

We measured microsite characteristics at 171 belowground caches and paired random sites. Cache sites were closer to cover ($\bar{x}_{cover} = 4$ m) and had more overstory ($\bar{x}_{overstory} = 20\%$) and understory cover ($\bar{x}_{understory} = 16\%$) than random sites ($\bar{x}_{cover} = 9$ m, $\bar{x}_{overstory} = 8\%$, $\bar{x}_{understory} = 3\%$). The most parsimonious model describing cache-site selection included only understory and distance to cover ($AIC_c = 420.86$, $w_i = 0.3706$, $k = 2$; Table 4). The goodness-of-fit test indicated that the variables in the best model adequately fit the data ($\chi^2 = 4.62$, df = 8, $P = 0.79$). However, the addition of "patch type" as a random intercept slightly improved the final model's overall fit, indicating that selection varied as a function of patch type. Odds of a nutcracker selecting a site for a cache decreased 13% for every 1-m increase in distance from a tree offering cover, and increased 2% for every 1% increase in understory cover. There were no pine germinants present at any of the 171 cache sites that we visited.

DISCUSSION

We examined caching behavior of Clark's Nutcrackers at three spatial scales and found evidence of selection at each. On a landscape scale, nutcrackers placed most of their caches within their

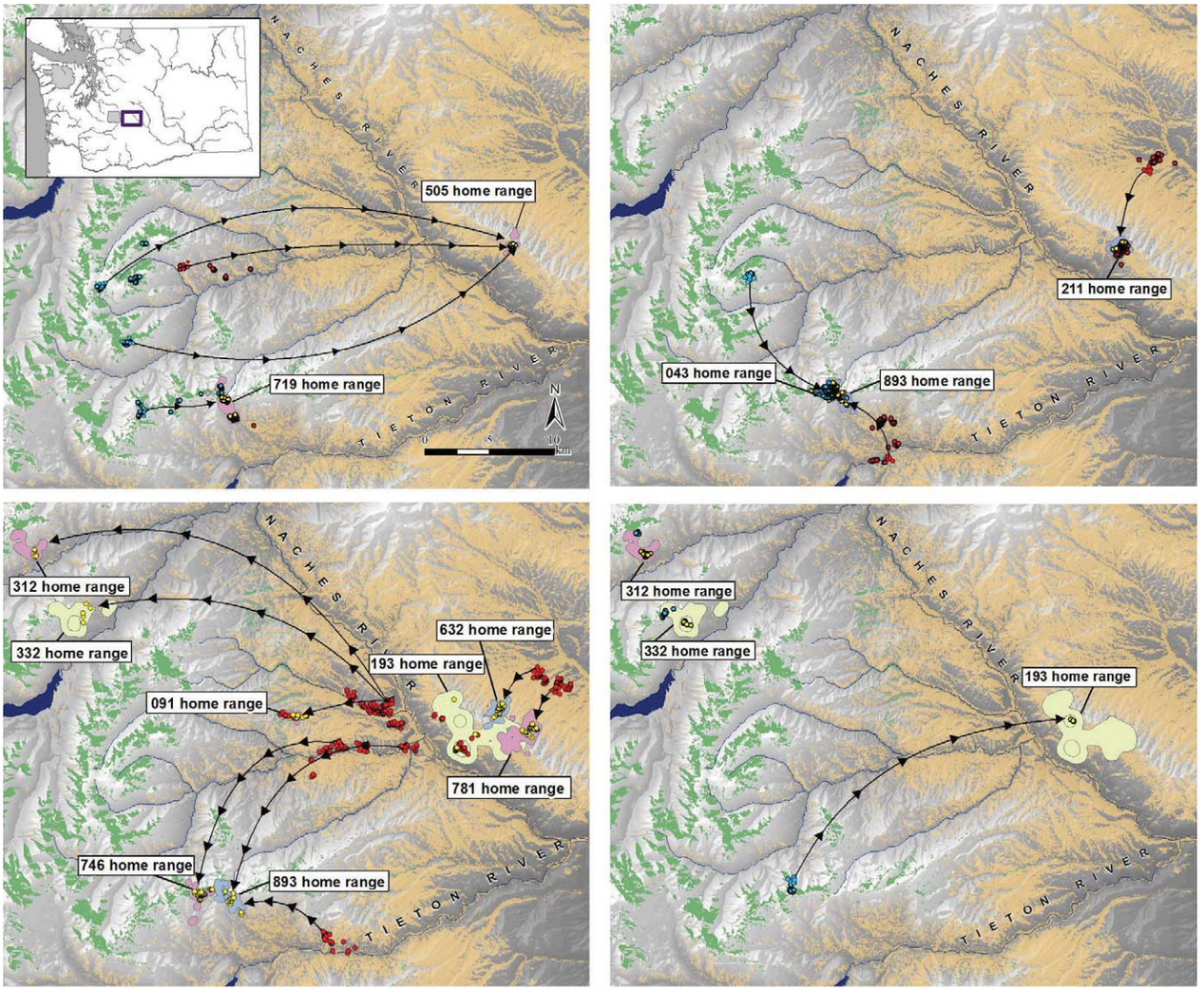

Fig. 2. Home-range kernels (February–August) and landscape-scale seed harvest and caching by 12 adult, resident Clark's Nutcrackers during August–November 2006 (upper left), August–November 2007 (upper right), August–November 2008 (lower left), and August 2009 (lower right) in the central Cascade Range of Washington State. Orange circles represent Ponderosa Pine seed-harvest events (August–November), blue circles represent Whitebark Pine seed-harvest events (August–October), and yellow circles represent seed-caching events (August–November). Arrows indicate generalized long-distance seed-transport flights (>3 km) from harvest stands to cache sites by nutcrackers. Green shading represents Whitebark Pine habitat and orange shading represents Ponderosa Pine habitat.

home range even when seeds were harvested outside of the home-range boundary. Once within the home range, they placed seeds in belowground cache sites in low-elevation Ponderosa Pine forests or aboveground cache sites in high-elevation hemlock–fir forests. At belowground sites, they selected areas for seed storage with high amounts of tree cover compared with random sites.

Nutcrackers were likely affected by different factors at each scale of selection. Landscape-scale caching decisions may have been driven by home-range fidelity and central-place foraging decisions, and 97% of all seeds were cached within the home range. Even seeds harvested in stands >30 km from home ranges were transported back to the home range for storage. It is important to consider that we may have underestimated the proportion of seeds cached within harvest stands (and therefore overestimated the proportions placed within home ranges) because while they were in the harvest stands, birds sometimes moved too rapidly between trees or patches for observers on foot to maintain visual contact. Also, when birds first began to use harvest stands that were distant from their home range and in wilderness areas, there was a lag in time between when a bird was first located using aerial telemetry and when an observer on foot homed to the bird to begin behavior observations. However, assuming that nutcrackers transport ~75 seeds per pouch load (Tomback 1978) and given that we observed many pouch loads of seeds transported to home ranges, birds in

Table 3. Number of seeds of Whitebark and Ponderosa pine placed in above- and belowground cache sites and in different habitats by 12 resident adult Clark's Nutcrackers from 2006 through 2009 in the Cascade Range, Washington. Proportions are calculated separately for each pine species as the number of caches within each habitat type and microsite, divided by the total number of caches.

		Whitebark Pine seed caches		Ponderosa Pine seed caches	
Habitat type	Number placed in habitat type	Number (proportion) of aboveground caches	Number (proportion) of belowground caches	Number (proportion) of aboveground caches	Number (proportion) of belowground caches
Cliffs–Talus	83	13 (0.07)	23 (0.12)	11 (0.02)	36 (0.08)
Mountain Hemlock–Subalpine Fir	75	64 (0.32)	5 (0.03)	4 (0.01)	2 (0.00)
Douglas–Grand fir	183	36 (0.18)	32 (0.16)	73 (0.16)	42 (0.09)
Parkland Whitebark Pine Forest	3	2 (0.01)	0	0	1 (0.00)
Parkland Ponderosa Pine Forest	134	5 (0.03)	4 (0.02)	58 (0.13)	67 (0.15)
Whitebark Pine Forest	57	7 (0.04)	2 (0.01)	47 (0.10)	1 (0.00)
Ponderosa Pine Forest	108	2 (0.01)	4 (0.02)	62 (0.14)	40 (0.09)
Burns	6	0	0	1 (0.00)	5 (0.01)
Total		129	70	256	194

Table 4. Akaike's information criterion corrected for small sample sizes (ΔAIC_c), Akaike weights (w_i) for top-ranked logistic-regression candidate models assessing microsite-scale cache-site selection by Clark's Nutcrackers in Washington State during 2006–2009. Explanatory variables were percent ground cover by grass and forbs, rock, and bare ground; percent understory cover; percent overstory cover; aspect; slope; and distance to cover. Akaike's information criterion is based on $-2 \times$ log likelihood ($-2(L)$) and the number of parameters (k) in the model. Models are ranked by AIC_c, and the best model has the lowest AIC_c.

Model	$-2(L)$	k	AIC_c	ΔAIC_c	w_i
understory+distance+δ_i^{patch}	412.00	3	420.0	0.9	NA
understory+distance	414.86	2	420.9	0.0	0.3706
understory+overstory+grassforb+distance	411.60	4	421.8	0.9	0.24255
understory+overstory+distance	413.97	3	422.1	1.2	0.20728
understory+overstory+grassforb+rock+distance	411.06	5	423.3	2.4	0.11252
understory+overstory+grassforb+rock+baregrnd+distance	410.82	6	425.2	4.3	0.04478
understory+overstory+grassforb+rock+baregrnd+aspect+distance	410.72	7	427.2	6.3	0.01643
understory+overstory+grassforb+rock+baregrnd+aspect+slope+distance	410.68	8	429.2	8.3	0.00584

our study carried at least several thousand seeds back to their home ranges for caching. Because of such home-range fidelity, we found that distances between harvest trees and cache sites were greater than reported in the literature. Prior to telemetry studies with Clark's Nutcrackers, the maximum distance reported between harvest trees and caches sites for Whitebark Pine was 12.5 km (Tomback 1978) and the maximum distance ever reported was 22 km (Vander Wall and Balda 1977). Among 12 resident nutcrackers in the present study, five transported seeds farther than 12.5 km and three transported seeds farther than 22 km. These results suggest that nutcrackers have the potential to influence genetic diversity in Whitebark and Ponderosa pines more than previously thought and more than other seed-dispersal mechanisms. For example, Vander Wall (2003) estimated that the combined effects of wind and rodent dispersal for Ponderosa Pine result in maximum seed-dispersal distances of 82 m, although seeds may be dispersed up to 1 km by exceptionally strong winds. Despite our small sample size of 12 resident nutcrackers, Ponderosa Pines growing in the center of our study area had seeds transported over an area totaling 523 km^2 and seeds were cached up to 26 km east, 33 km northwest, 26 km west, and 21 km south of seed-harvest trees.

Once they were within their home ranges, nutcrackers cached more seeds in low-elevation habitats than at high elevations, possibly to facilitate access to cache sites in winter, when snow would cover the ground. All nutcrackers consistently placed most caches in the lowest-elevation habitats available within home ranges, but because home ranges varied in the types of habitats available, they differed in the forest types selected for caching. Ponderosa Pine residents selected Ponderosa Pine stands and avoided Douglas–Grand fir forests at higher elevations. Whitebark Pine residents more commonly cached seeds in Douglas–Grand fir forests than in higher-elevation Mountain Hemlock–Subalpine Fir and Whitebark Pine stands. This meant that in an effort to use the lowest-elevation habitat type within home ranges, residents of Whitebark Pine habitat most commonly cached seeds in the habitat type that was avoided by residents of Ponderosa habitat. Considering the habitat-scale behavioral plasticity within this one population, we think that it is important to study habitat selection of caching nutcrackers in other regions before conclusions of habitat preferences are made. For example, had we investigated cache-site selection by residents of Whitebark Pine habitat only, we would have erroneously concluded that Douglas–Grand fir forests were favored for caching.

Our habitat-scale results are of management interest for two reasons. First, they suggest that resident nutcrackers may forgo caching in preferred habitat types that are outside the home range

in order to cache seeds in less preferred habitats that are inside the home range. For instance, when transporting seeds between harvest stands and the home ranges, Whitebark Pine residents transported seeds over preferred Ponderosa Pine stands en route to less preferable caching habitat such as Douglas–Grand fir forests within their home range. Thus, management techniques designed to alter potential caching habitat to encourage seed caching by nutcrackers (e.g., thinning and prescribed burning; Keane and Arno 2001) may not affect the caching behavior of residents. Second, because of their propensity for selecting forest types at low elevations, nutcrackers in our study were more effective seed dispersers for Ponderosa Pine than for Whitebark Pine. This is surprising because before the present study, the role of nutcrackers as seed dispersers for Ponderosa Pine had received comparatively little attention.

On a microsite scale, we found that nutcrackers commonly cached seeds above ground in the forest canopy, and more caches were placed above ground than below ground in our study. Aboveground caching has been reported in the nutcracker but is generally considered a rarity, compared with belowground caching (Vander Wall and Balda 1977, Dimmick 1993). It is possible that high frequencies of aboveground caching are unique to this population of nutcrackers. Aboveground caching may also be more common in populations that reside in wetter, colder climates and at higher latitudes. Previous studies of nutcracker caching have occurred in lower latitudes or drier forest types, for example in Arizona (Vander Wall and Balda 1977), Wyoming (Hutchins and Lanner 1982), and California (Tomback 1978, Dimmick 1993). However, we consider it unlikely that aboveground caching is limited to wet and cold environments. This is because in our study, residents of both high-elevation Whitebark Pine and low-elevation Ponderosa Pine forests placed most of their caches above ground. It is more likely that nutcrackers caching seeds above ground are less conspicuous and may easily be missed in observational studies that do not employ radiotelemetry.

Although seeds placed in the forest canopy may be vulnerable to pilfering by arboreal songbirds and rodents, from the bird's perspective there are multiple benefits of caching in trees: the bird is concealed from predators; it is elevated and, thus, can take flight more quickly if pursued; the seeds are incapable of "escaping" through germination; the seeds are protected from pilfering chipmunks; and, most importantly, the seeds are above the level of winter snow pack. From the plant's perspective, however, there are no benefits to aboveground caching, and all aboveground caches are a reproductive loss to the parent tree. In our study, aboveground caching was more detrimental for Whitebark Pine than for Ponderosa Pine. This is because nutcrackers were more likely to select aboveground cache sites at high-elevation habitats (e.g., Mountain Hemlock–Subalpine Fir forests and Whitebark Pine stands) than when caching at low-elevation habitats (e.g., Douglas–Grand fir forests and Ponderosa Pine stands). All told, among 199 Whitebark Pine seed caches in our study, only 15% were cached below ground in Whitebark Pine habitat, but among 450 Ponderosa seed caches, 42% were cached below ground in Ponderosa Pine habitat. Yet it is important to consider that despite evidence for significant selection of habitats and microsite features, nutcrackers placed some seed caches in all habitat types and utilized a range of microsite features. This suggests that despite apparent preferences for certain features, nutcrackers may employ hyperdispersion as a strategy for protecting some seed caches, like other seed-caching songbirds (Male and Smulders 2007).

For the sample of belowground caches that we revisited, we found no germinating seedlings for either Whitebark or Ponderosa pine. However, this should not be interpreted as a direct measure of germination success from caches. Whitebark Pine has delayed germination (Tomback et al. 2001a), and it is possible that seeds germinated in the years after we visited cache sites. It is also possible that no seedlings were present at cache sites because nutcrackers moved the seed caches to different sites after we observed their initial placement (Hutchins and Lanner 1982). Yet regardless of the observed germination rates, sites selected for belowground caches in this study did not appear to be entirely favorable for seedling establishment. Both Whitebark and Ponderosa pine seedlings have highest survivorship when sown in sites with partial shade and mineral soil (McCaughey and Weaver 1990, Keyes et al. 2009). Because of the propensity of nutcrackers to cache seeds close to or underneath trees in our study, many cache sites were shaded that would increase survivorship of germinants. However, this also meant that cache sites had high amounts of litter. Although seedlings can survive under many conditions, not all of the seeds cached by nutcrackers in belowground sites and in suitable habitats were placed in microsites favorable for seed germination, seedling survival, and plant maturation. Thus, the actual effectiveness of nutcracker seed dispersal in our study is undoubtedly lower than suggested by our analyses.

Nutcrackers may have chosen sites near trees for belowground caches because these sites often accumulate less snow and melt off more quickly than sites in forest openings (Balda and Bateman 1971, 1972). Alternatively, they may have selected shaded locations to reduce risk of predation by aerial predators; nutcrackers caching in these sites were either partially concealed or close to a tree that could be used for cover if a predator should appear. However, caches placed close to cover may also be more vulnerable to pilferage by rodents, because rodents appear more prone to stay close to cover to reduce their own predation risk (Thayer and Vander Wall 2005). Thus, a nutcracker's choice of a cache site may represent a tradeoff between the risk of being killed by a predator and the risk of losing the cache to rodents. The results of our study are consistent with predictions of foraging theory, in that animals perceive predation risk as a greater threat than starvation risk (Brodin and Clark 2007). However, they differ from past studies that have reported that nutcrackers commonly cache in open areas such as meadows and talus slopes, sometimes forming large flocks on "communal caching grounds" (Vander Wall and Balda 1977, Tomback 1978). Although we occasionally found telemetered nutcrackers caching in large openings, far from cover, and in large groups, these circumstances were observed infrequently compared with solitary caching in more forested areas. Reasons for disparities between our study and past studies may be due to several factors, such as differences in research methodologies or study populations. However, given that we observed telemetered nutcrackers caching in a range of flock sizes, we suggest that communal caching represents only one extreme in the spectrum across which nutcrackers cache seeds, and without telemetry it is the most easily observable condition; nutcrackers in any population likely cache seeds alone, in small groups, or in very large

groups, depending on circumstances, and more study is needed on factors that contribute to these differences.

Overall, the quality of nutcracker dispersal for its mutualistic partner, Whitebark Pine, was poor compared with the quality of dispersal reported for other animal seed dispersers in western North America. Rodent dispersers such as chipmunks and mice do not transport seeds out of harvest stands (therefore, 100% of seeds are cached in suitable habitats), and between 31–83% of seeds are scatter-hoarded in the soil (Vander Wall 2003, Hollander and Vander Wall 2004). This is a higher proportion of seeds dispersed to suitable sites than we report here for nutcracker dispersal of Whitebark Pine seeds. Furthermore, Vander Wall and Joyner (1998) reported germination rates of 14% for pine seeds dispersed by rodents. We found that only 15% of Whitebark Pine seeds were even placed in sites where germination could have occurred. Nevertheless, it is important to consider that dispersal effectiveness is a product of both the quality of the sites in which seeds are placed and the quantity of seeds dispersed (Schupp 1993). Nutcrackers may enable effective seed dispersal simply by the sheer number of seeds that they disperse. An individual nutcracker may store between 32,000 and 98,000 Whitebark pine seeds in one year (Hutchins and Lanner 1982, Tomback 1982). Even if only 15% of seeds are cached below ground in suitable habitats, that equates to an impressive minimum of 4,800 seeds dispersed per bird each year. Additionally, nutcracker dispersal effectiveness may vary spatially and temporally. In our study, Ponderosa Pine was more abundant than Whitebark Pine, which makes it likely that the majority of nutcracker home ranges occurred in Ponderosa Pine stands. Because we found that resident nutcrackers stored most seeds within their home ranges, most Whitebark Pine seeds would then be placed in Ponderosa forests, where seedling establishment is not possible. In locations where Whitebark Pine is the most abundant seed source, however, nutcrackers may have home ranges that contain more Whitebark Pine, possibly leading to more effective Whitebark Pine dispersal. Temporally, Whitebark Pine is a species that produces large cone crops in synchrony, and effective dispersal more likely occurs episodically and during mast years than in intervening years (Vander Wall 2002). Given this variability, additional studies are needed to investigate nutcracker caching behavior in other regions and during mast years to better assess the effectiveness of nutcracker dispersal.

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Literature Cited

Aebischer, N. J., P. A. Robertson, and R. E. Kenward. 1993. Compositional analysis of habitat use from animal radio-tracking data. Ecology 74:1313–1325.

Balda, R. P., and G. C. Bateman. 1971. Flocking and annual cycle of the Pinyon Jay. Condor 75:287–302.

Balda, R. P., and G. C. Bateman. 1972. The breeding biology of the Pinyon Jay. Living Bird 11:5–42.

Beyer, H. L. 2004. Hawth's analysis tools for ArcGIS. [Online.] Available at www.spatialecology.com/htools.

Bingham, R. L., and L. A. Brennan. 2004. Comparison of Type I error rates for statistical analyses of resource selection. Journal of Wildlife Management 68:206–212.

Brodin, A., and C. W. Clark. 2007. Energy storage and expenditure. Pages 221–269 *in* Foraging: Behavior and Ecology (D. W. Stephens, J. S. Brown, and R. C. Ydenberg, Eds.). University of Chicago Press, Chicago, Illinois.

Burnham, K. P., and D. R. Anderson. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. Springer-Verlag, New York.

Dimmick, C. R. 1993. Life history and the development of cache-recovery behaviors in Clark's Nutcracker. Ph.D. dissertation, Northern Arizona University, Flagstaff.

Hollander, J. L., and S. B. Vander Wall. 2004. Effectiveness of six species of rodents as dispersers of singleleaf piñon pine (*Pinus monophylla*). Oecologia 138:57–65.

Hooge, P. N., and B. Eichenlaub. 1997. ANIMAL MOVEMENT extension to ARCVIEW, version 1.1. Alaska Science Center Biological Science Office, U.S. Geological Survey, Anchorage.

Hosmer, D. W., Jr., and S. Lemeshow. 2000. Applied Logistic Regression. Wiley, New York.

Hutchins, H. E., and R. M. Lanner. 1982. The central role of Clark's Nutcracker in the dispersal and establishment of whitebark pine. Oecologia 55:192–201.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

Keane, R. E., and S. F. Arno. 2001. Restoration concepts and techniques. Pages 367–400 *in* Whitebark Pine Communities: Ecology and Restoration (D. F. Tomback, S. F. Arno, and R. E. Keane, Eds.). Island Press, Washington, D.C.

Keane, R. E., and R. A. Parsons. 2010. Restoring whitebark pine forests of the northern Rocky Mountains, USA. Ecological Restoration 28:56–70.

Kernohan, B. J., R. A. Gitzen, and J. J. Millspaugh. 2001. Analysis of animal space use and movements. Pages 125–166 *in* Radio Tracking and Animal Populations (J. J. Millspaugh and J. M. Marzluff, Eds.). Academic Press, San Diego, California.

Keyes, C. R., D. A. Maguire, and J. C. Tappeiner. 2009. Recruitment of ponderosa pine seedlings in the Cascade Range. Forest Ecology and Management 257:495–501.

Lillybridge, T. R., B. L. Kovalchik, C. K. Williams, and B. G. Smith. 1995. Field guide for forested plant associations of the Wenatchee National Forest. U.S. Department of Agriculture, Forest Service General Technical Report PNW-GTR-359.

Male, L. H., and T. V. Smulders. 2007. Hyperdispersed cache distributions reduce pilferage: A field study. Animal Behaviour 73:717–726.

Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Resource Selection by Animals: Statistical Design and Analysis for Field Studies, 2nd ed. Kluwer Academic Publishers, Boston.

McCaughey, W. W., and T. Weaver. 1990. Biotic and microsite factors affecting whitebark pine establishment. Pages 140–150 *in* Proceedings-Symposium on Whitebark Pine Ecosystems: Ecology and Management of a High-Mountain Resource (W. C. Schmidt and K. J. McDonald, Eds.). U.S. Department of Agriculture, Forest Service General Technical Report INT-270.

Ott, P., and F. Hovey. 1997. BYCOMP.SAS and MACOMP.SAS, version 1.0. British Columbia Forest Service, Victoria.

R Development Core Team. 2009. R: A Language and Environment for Statistical Computing, version 2.10.1. R Foundation for Statistical Computing, Vienna, Austria. [Online.] Available at www.r-project.org/.

Schupp, E. W. 1993. Quantity, quality and the effectiveness of seed dispersal by animals. Plant Ecology 107–108:15–29.

Thayer, T. C., and S. B. Vander Wall. 2005. Interactions between Steller's Jays and yellow pine chipmunks over scatter-hoarded sugar pine seeds. Journal of Animal Ecology 74:365–374.

Tomback, D. F. 1978. Foraging strategies of Clark's Nutcracker. Living Bird 16:123–161.

Tomback, D. F. 1982. Dispersal of whitebark pine seeds by Clark's Nutcracker: A mutualism hypothesis. Journal of Animal Ecology 51:451–467.

Tomback, D. F., A. J. Anderies, K. S. Carsey, M. L. Powell, and S. Mellmann-Brown. 2001a. Delayed seed germination in whitebark pine and regeneration patterns following the Yellowstone fires. Ecology 82:2587–2600.

Tomback, D. F., S. F. Arno, and R. E. Keane. 2001b. Whitebark Pine Communities: Ecology and Restoration. Island Press, Washington, D.C.

Tomback, D. F., and Y. B. Linhart. 1990. The evolution of bird-dispersed pines. Evolutionary Ecology 4:185–219.

Vander Wall, S. B. 1997. Dispersal of singleleaf piñon pine (*Pinus monophylla*) by seed-caching rodents. Journal of Mammalogy 78:181–191.

Vander Wall, S. B. 2002. Masting in animal-dispersed pines facilitates seed dispersal. Ecology 83:3508–3516.

Vander Wall, S. B. 2003. Effects of seed size of wind-dispersed pines (*Pinus*) on secondary seed dispersal and the caching behavior of rodents. Oikos 100:25–34.

Vander Wall, S. B., and R. P. Balda. 1977. Co-adaptations of Clark's Nutcracker and piñon pine for efficient seed harvest and dispersal. Ecological Monographs 47:89–111.

Vander Wall, S. B., and R. P. Balda. 1981. Ecology and evolution of food storing behavior in conifer-seed-caching corvids. Zeitschrift für Tierpsychologie 56:217–242.

Vander Wall, S. B., P. M. Forget, J. E. Lambert, and P. E. Hulme. 2005. Seed fate pathways: Filling the gap between plant and offspring. Pages 1–8 *in* Seed Fate: Predation, Dispersal, and Seedling Establishment (P. M. Forget, J. E. Lambert, P. E. Hulme, and S. B. Vander Wall, Eds.). CABI Publishing, Cambridge, United Kingdom.

Vander Wall, S. B., and J. W. Joyner. 1998. Recaching of Jeffrey pine (*Pinus jeffreyi*) seeds by yellow pine chipmunks (*Tamias amoenus*): Potential effects on plant reproductive success. Canadian Journal of Zoology 76:154–162.

Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70:164–168.

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