

SEASONAL DIFFERENCES IN SPACE USE BY CLARK'S NUTCRACKERS IN THE CASCADE RANGE

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Abstract. Clark's Nutcrackers (*Nucifraga columbiana*) are important seed dispersers for at least ten species of conifer in western North America and are obligate mutualists for the whitebark pine (*Pinus albicaulis*), a subalpine tree. Despite the important role they play in forest regeneration, space use by nutcrackers has not been formally studied. Several hypotheses exist to explain their year-round patterns of space use. We tested the hypothesis that one population in the Cascade Range, Washington, migrates altitudinally between summer and autumn. In 2006 and 2007, we compared seasonal differences in summer and autumn space use by 26 radio-tagged nutcrackers. Five nutcrackers remained as year-round residents on their home ranges; 21 emigrated from the study area in summer. Among residents we found summer and autumn ranges overlapped and summer ranges were contained within autumn ranges. Residents increased their use of low-elevation habitats as autumn progressed, but rather than migrating from summer ranges, they used low-elevation forests only for seed harvesting. High-elevation portions of the summer range were used for all other activities including seed storage even though this required residents to transport seeds from source trees up to 29 km in distance and 1007 m in elevation. We were unable to test hypotheses regarding space use by emigrants. However, our results suggest that emigrants in this study did not migrate altitudinally because they showed no seasonal trend in movements either upslope or downslope.

Key words: altitudinal migration, Clark's Nutcracker, emigrant, home range, *Nucifraga columbiana*, seed dispersal, space use, whitebark pine.

Diferencias Estacionales en el Uso del Espacio por *Nucifraga columbiana* en las Montañas Cascade

Resumen. *Nucifraga columbiana* es un dispersor de semillas importante para por lo menos diez especies de coníferas en el oeste de Norte América, y es un mutualista obligado para *Pinus albicaulis*, un árbol subalpino. A pesar del papel importante que estas aves juegan en la regeneración del bosque, su uso del espacio no ha sido estudiado formalmente. Existen varias hipótesis para explicar los patrones de uso del espacio a lo largo del año. Pusemos a prueba la hipótesis de que una población de las montañas Cascade, Washington, migra altitudinalmente entre el verano y el otoño. En 2006 y 2007, comparamos las diferencias estacionales en el uso del espacio durante el verano y el otoño por parte de 26 individuos marcados con transmisores de radio. Cinco individuos permanecieron como residentes durante todo el año en su ámbito hogareño, mientras que 21 emigraron del área de estudio en el verano. Entre los residentes, encontramos que las distribuciones del verano y del otoño se superponían, y que las distribuciones del verano estaban contenidas dentro de las distribuciones del otoño. Los residentes incrementaron el uso de ambientes de elevaciones bajas conforme avanzó el otoño, pero en lugar de migrar desde sus distribuciones de verano, usaron los bosques de menores elevaciones sólo para recolectar semillas. Las porciones de tierras altas de las distribuciones del verano fueron usadas para todas las demás actividades, incluyendo el almacenamiento de semillas, aunque esto requirió que las aves residentes transportaran las semillas desde los árboles fuente a distancias de hasta 29 km y cubriendo un rango de elevación de hasta 1007 m. No pudimos poner a prueba hipótesis acerca del uso del espacio por parte de los emigrantes. Sin embargo, nuestros resultados sugieren que los emigrantes en este estudio no migraron altitudinalmente, pues no mostraron una tendencia estacional en sus movimientos cuesta arriba ni cuesta abajo.

INTRODUCTION

Clark's Nutcrackers (*Nucifraga columbiana*) are a critical component of montane ecosystems in the western United States. They act as seed dispersers for many conifers and therefore enable forest regeneration in many communities. Nutcrackers are effective dispersers for some common and

widespread species of pine including the whitebark (*Pinus albicaulis*), limber (*P. flexilis*), ponderosa (*P. ponderosa*), Colorado pinyon (*P. edulis*), and singleleaf pinyon (*P. monophylla*) (Vander Wall and Balda 1977, Lanner and Vander Wall 1980, Hutchins and Lanner 1982, Vander Wall 1988, Baud 1993). They also disperse seeds for Douglas-fir (*Pseudotsuga menziesii*) although the effectiveness of this dispersal for

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establishing seedlings has not been tested (Vander Wall et al. 1981, Lanner 1988). In autumn, nutcrackers forage on seeds produced by these conifers. Seeds are typically produced in such abundance that the majority cannot be consumed immediately. Nutcrackers store excess seeds in several thousand individual seed caches to be retrieved later in the year (Vander Wall and Balda 1977, Tomback 1982, Hutchins and Lanner 1982). Stored seeds are important food for the nutcrackers' winter survival and spring breeding (Mewaldt 1956, Giuntoli and Mewaldt 1978). Seeds placed in locations favorable for seed germination and not retrieved by nutcrackers are then able to germinate.

Among the large-seeded pines, the whitebark pine is unique because it coevolved with Clark's Nutcracker (Lanner 1982, Tomback 1983) and nutcrackers provide the only known mechanism of its seeds' dispersal (Hutchins and Lanner 1982). The whitebark pine is therefore an obligate mutualist of Clark's Nutcracker, and the nutcracker's cache-site selection determines the pine's patterns of regeneration on the landscape. The whitebark pine occurs in the subalpine zone across the northwestern United States and southwestern Canada. It functions as both an early successional species and as a climax species at treeline and contributes more to ecosystem function than would be expected from its relatively low biomass (Tomback et al. 2001). It is currently declining because the combined effects of the mountain pine beetle (*Dendroctonus ponderosae*), white pine blister rust (*Cronartium ribicola*), and advanced succession attributed to fire suppression. Mortality rates in stands throughout its range are as high as 90% (Kendall and Keane 2001).

Despite the importance of Clark's Nutcracker as a seed disperser and the decline of one of its primary food sources there has been no systematic study of the nutcracker's use of space anywhere in its range. Information on space use in autumn is particularly important because during autumn it stores seeds used for winter survival and spring breeding (Giuntoli and Mewaldt 1978).

Although there have been no systematic studies of the nutcracker's space use in autumn, multiple studies have noted variability in the ranging behavior of nutcrackers when harvesting and caching seeds in autumn. Within the same stand of trees some individuals cache seeds a few meters from harvest trees, whereas others transport seeds up to 5 km away (Vander Wall 1988). Others have noted nutcrackers cache seeds on a landscape scale and transport seeds farther than sympatric species (Vander Wall and Balda 1977, 1981, Tomback 1978). For example, the maximum seed-transport distance observed for the Pinyon Jay (*Gymnorhinus cyanocephalus*) is approximately 10 km (Vander Wall and Balda 1981), whereas Clark's Nutcrackers have been observed transporting seeds as far as 22 km between harvest stands and cache sites (Vander Wall and Balda 1977). Despite these extraordinary seed-transport distances, past studies have reported that

nutcrackers cache most seeds within a few kilometers of the harvest trees (Vander Wall 1988, Tomback 1998). While there is no explanation for variability in nutcrackers' seed-transport distances, the overall wide-ranging seed-harvest behavior is a response by nutcrackers to variation in cone productivity on a landscape scale. The production of conifer seed on a local scale varies from year to year because different species of conifer synchronize seed production within populations. A year of high seed production of one species within a local area is usually followed by one to three years of low or moderate seed production. Thus on a local scale there may be low seed production for two to three years in a row, but on a landscape scale there is nearly always one species of conifer producing seeds. For nutcrackers to maximize fitness across years, individuals opportunistically harvest seeds from different stands each year, requiring traveling on a landscape or even regional scale in autumn.

Two hypotheses have been suggested to explain how individual nutcrackers respond to such a variable and ephemeral autumn food supply. Vander Wall et al. (1981) observed latitudinal migrations of nutcrackers over three consecutive years in the Great Basin, and the term emigrant has been applied to describe these long-distance migrants (Vander Wall et al. 1981, Tomback 1998). During these same years, Vander Wall et al. (1981) reported that other flocks did not migrate but remained as residents in the Great Basin. They hypothesized that nutcrackers have adopted one of two life-history strategies: emigration and residency. In years of moderate or low seed production, emigrants range regionally in autumn and forage opportunistically where food is available. Residents remain within stable home ranges year round except in times of exceptional food shortage (Vander Wall et al. 1981). In years of high seed production emigrants also remain in the area. Tomback (1978, 1998) alternatively hypothesized that latitudinal migration is rare, although altitudinal migration is common. In California, Tomback (1978) observed that in summer nutcrackers concentrated at high elevations, where they foraged on communal caching grounds. These flocks remained at high elevations through early autumn, when they harvested whitebark pine seeds. Beginning in October large flocks appeared in low-elevation Jeffrey pine (*Pinus jeffreyi*) forests. The timing of this altitudinal shift coincided with the ripening of different types of pine seed in autumn; whitebark pine seeds ripened at high elevations in August whereas Jeffrey pine seeds ripened at low elevations in September. Tomback (1978) concluded that the population had migrated altitudinally because these flocks were observed at low elevations throughout the winter and early spring.

These studies did not track the daily movements of individual nutcrackers so did not allow testing of hypotheses of space use. We tested the hypothesis that one population of Clark's Nutcrackers in Washington state migrates altitudinally in autumn. The elevational distribution of whitebark

and ponderosa pines in south-central Washington's Cascade Range is similar to the elevational distribution of whitebark and Jeffrey pines described by Tomback (1978) in the Sierra Nevada of California. In both locations there is little or no overlap in productive stands of high-elevation whitebark pine and low-elevation ponderosa pine (Washington) and Jeffrey pine (California). In south-central Washington whitebark pine typically occurs between 1640 and 1890 m, and ponderosa pine dominates between 700 and 1440 m (Burns and Honkala 1990). At Tomback's (1978) study sites in the Sierra Nevada, whitebark pine occurred between 2670 and 3150 m and Jeffrey pine was common between 2100 and 2300 m. Moreover, in both locales Clark's Nutcracker typically harvests whitebark pine seeds in late summer or early autumn, prior to harvesting lower-elevation Jeffrey/ponderosa pine seeds (Tomback 1978, Dimmick 1993; Lorenz, pers. obs.).

If nutcrackers migrate altitudinally between summer and autumn, we predict that there will be no overlap in summer and autumn ranges. Nutcrackers will reside at high elevations in summer and early autumn and depart after the harvest of whitebark pine seeds in September. We predict that all of their daily activities after this point will occur at low elevations where they will overwinter and breed.

We tested this against the alternative hypothesis that nutcrackers do not migrate altitudinally. The summer range represents the year-round center of activity, and the presence of nutcrackers outside of this range in autumn can be attributed to forays in search of seeds. Under this hypothesis we predict summer and autumn home ranges will overlap and in autumn home ranges will expand. We also predict nutcrackers will continue to use high elevations after the whitebark pine cones have been harvested. In anticipation of needs for energy in winter and spring, nutcrackers will cache seeds within their summer home range, whereas they will harvest seeds both within and outside of the summer home range and at a range of elevations.

METHODS

STUDY AREA

We studied nutcrackers' space use in 2006 and 2007 in the Cascade Range 40 km west of Yakima, Washington (approximately 120° 58' W, 46° 45' N), within an area bordered by U.S. Hwy. 12 to the south, Interstates 82 and 90 to the east and north, and the Cascade crest to the west (Fig. 1). The majority of the land was administered by the Okanogan–Wenatchee

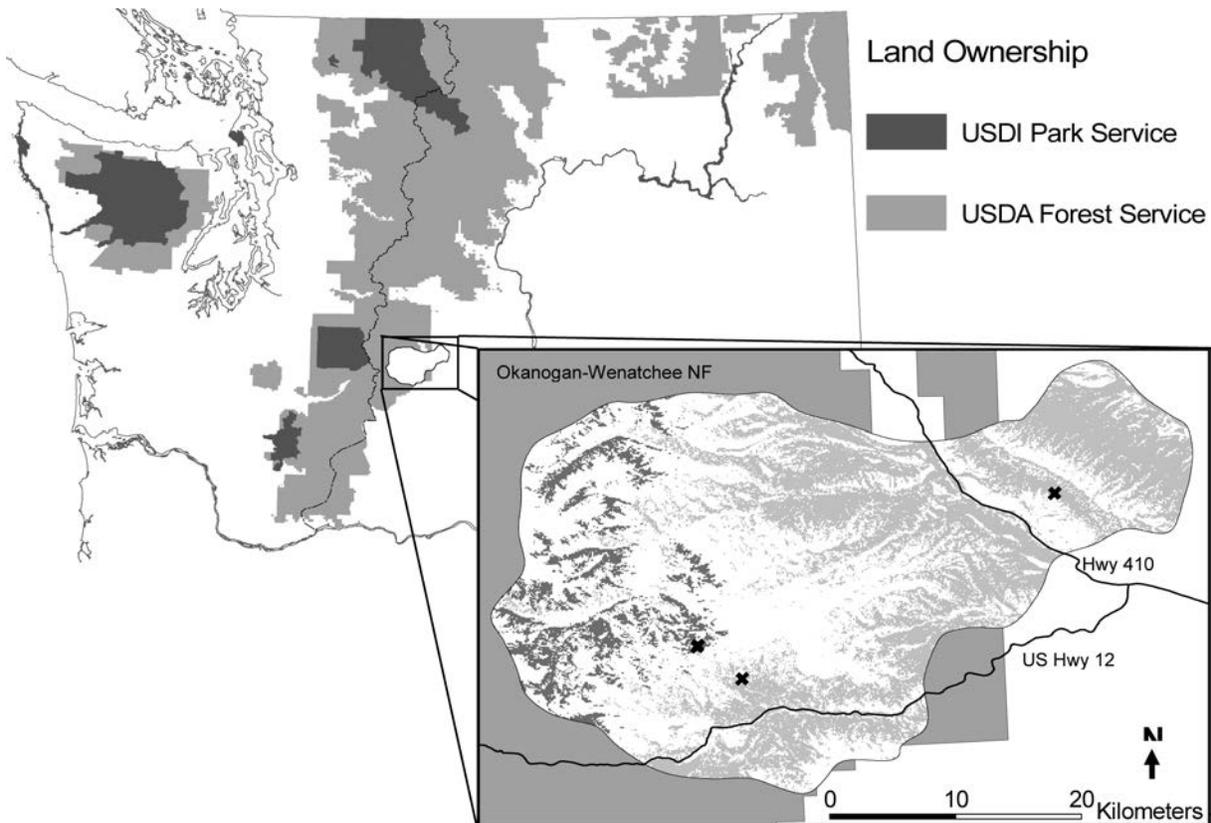


FIGURE 1. Study area in central Cascade Range of Washington state. In inset map, shading shows extent of whitebark pine (darker gray) and ponderosa pine (lighter gray) within study area. Markers (x) show the locations of the three sites where we captured and radio-tagged Clark's Nutcrackers.

National Forest and the Washington Department of Fish and Wildlife. Approximately one quarter of the land was designated as wilderness, and most of the remainder of the study area was closed to motorized use.

The study area was 730 km², and its boundaries were delineated by major ridges and river valleys to encompass the movements of all resident Clark's Nutcrackers under study. Elevation ranged from 525 m in some valleys to 2358 m on mountain peaks. The vegetation varied from nonforested shrub-steppe in the eastern and lowland areas to wet mountain hemlock on western ridges. Between 700 and 1100 m the predominant cover types were ponderosa pine and Douglas-fir. Between 1100 and 1500 m ponderosa pine and Douglas-fir gradually were replaced by grand fir (*Abies grandis*). Above 1500 m the dominant cover types were mountain hemlock (*Tsuga mertensiana*) and whitebark pine. Subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), and lodgepole pine (*Pinus contorta*) were common but usually not dominant within the study area. Both prescribed and wild fires were common in the study area. Within the last five years the understory of ~5300 ha of mixed stands of ponderosa pine and Douglas-fir had been burned in prescribed fires, and wildfire had burned 1500 ha of mixed ponderosa pine forests and 750 ha of mixed whitebark pine forests (J.W. Bailey, pers. comm.).

CONE COUNTS

We counted cones on 40 whitebark pine trees in July 2006 and 2007. Ten mature whitebark pine trees were arbitrarily selected at three sites in the Cascade Range and one site in the Olympic Mountains. Trees were marked, and their location was recorded on a portable Global Positioning System (GPS). Using 8 × 42 binoculars, observers counted cones visible on the north- and south-facing side of each tree. We counted cones to compare the relative abundance of whitebark pine seed from year to year rather than to estimate the actual number of cones produced within this population.

TELEMETRY

We used radio telemetry to collect space-use data on nutcrackers. We captured nutcrackers at three trap sites, one in a high-elevation (1800 m) whitebark pine stand, one in a mid-elevation (1262 m) ponderosa pine stand, and one in a mid-elevation (1340 m) previously burned ponderosa pine stand. We captured nutcrackers in mist nets and noose-carpet traps at feeding stations baited with raw beef suet. We found that nutcrackers were most readily attracted to feeding stations in late winter and early spring and therefore trapped primarily from March through June and under wintry conditions. All nutcrackers were banded, weighed, and aged as either juvenile or adult by plumage and the color of the mouth lining (Mewaldt 1958). We also measured wing chord, tarsus, and tail length. Males are larger than females in all measurements, although

the sexes overlap in measurements of wing chord, tail, and weight (Mewaldt 1948). In our study we did not distinguish between the sexes because wing chord, tail, and weight measurements were affected by substantial feather wear and feeding prior to trapping. With the exception of two juveniles captured in 2006, all nutcrackers were fitted with a 3.9-g (3% of body weight) transmitter (Advanced Telemetry Systems, Isanti, MN) that was secured to the back with a harness. The transmitter's battery lasted approximately 415 days.

RADIO TRACKING

We radio-tracked nutcrackers from June through October 2006 and from April through October 2007. We categorized locations of radio-tagged nutcrackers as either summer or autumn. Nutcrackers undergo a shift in behavior between these seasons. In summer nutcrackers generally forage only for their daily energy needs, while in autumn they devote the majority of daylight hours to the harvest and storage of seeds for future consumption (Vander Wall and Balda 1977, Tomback 1978). In 2006, we defined summer as 13 June–9 August, autumn as 10 August–29 October. In 2007 we defined summer as 1 May–7 August, autumn as 8 August–1 November. We chose 10 August and 8 August as the dates dividing summer from autumn in 2006 and 2007, respectively, because they were the first dates in each year in which we observed radio-tagged nutcrackers placing seeds in their sublingual pouch for future storage.

We conducted focal observations during which we tracked nutcrackers as continuously as possible for 1–2 hr per week in summer and 1–6 hr per week in autumn. We classified all behavior observed during these sessions into one of three categories: seed caching, seed harvesting (placing seeds in sublingual pouch), and other (includes daily foraging, preening, bathing, roosting, vocalizing, and social interactions). For all foraging observations we also noted the type of food that was being consumed, when known, and we recorded the species of tree for all observations involving foraging, seed harvesting, and seed caching. We obtained additional telemetry locations on each nutcracker by relocating each individual at least twice weekly outside of focal observations. We arbitrarily selected times for focal observations and for recording additional relocation points that were separated by at least 24 hr. Overall, each individual was relocated on at least three different days during each week throughout both summer and autumn.

Tracking periods were spread over a range of daylight hours and weather conditions. We recorded 64% of points during the morning, 36% during the afternoon or evening. On average we obtained 9 points ($SD \pm 5$ points) per week on each bird in summer, 34 points ($SD \pm 13$ points) in autumn. We allocated more effort to the autumn season because nutcrackers ranged more widely in autumn than in summer. Additionally, we commonly observed long-distance seed transport in

autumn. It was not logistically possible to track nutcrackers continuously from individual harvest trees, along their flight path, and to cache sites of individual seeds. By stationing observers in the harvest stand and along the flight path, however, we are confident that we located the final cache sites for seeds that nutcrackers transported long distances.

We obtained point locations on telemetered nutcrackers mostly by homing (94% of points), although we used triangulations when nutcrackers were using inaccessible cliffs within their home range (6% of points). We recorded point locations obtained from homing in the field by using a hand-held GPS. Error associated with GPS fixes ranged from 3 to 8 m. We considered triangulations successful if we obtained two or three azimuths on a nutcracker within 5 min. If it was apparent from a change in directionality or strength of the signal that the nutcracker had moved within that 5-min period, we discarded the triangulation attempt. We used the program LOCATE II (Pacer Ltd., Truro, Nova Scotia) to estimate the locations of points obtained by triangulation.

The first year (2006) was a pilot year for this study, and we obtained on average only 8 points (± 2 points) per week per bird compared to 26 points (± 4 points) per week per bird in the second year of study (2007). Although we obtained more points in the second year, within each year we allocated fairly equal effort among the radio-tagged nutcrackers each week. While we attempted observations in all habitat types, the nutcrackers ranged over terrain that was steep and rugged and included vertical cliffs. Therefore observing nutcrackers at all times was not logistically possible. As noted above, we obtained triangulations on birds when they were using inaccessible parts of their home range, but it is possible that we underestimated the number of times nutcrackers harvested and cached seeds on cliffs and rock faces.

RESIDENCY STATUS

We captured and radio-tagged resident nutcrackers in 2006 and both resident and emigrant nutcrackers in 2007. In 2007 we classified nutcrackers as resident or emigrant only after monitoring their movements during summer. Resident nutcrackers remained on home ranges within the study area year round. We considered a nutcracker to be an emigrant if (1) we lost its radio signal in the study area by early July or (2) it died before 1 July but had moved continuously and directionally away from the trap site while alive. In July 2007 we surveyed our study area via aircraft to confirm the number of resident nutcrackers. Additionally, during August of 2007 we conducted 44 hr of aerial telemetry surveys over the eastern portion of the Washington Cascade Range to search for emigrant nutcrackers. The area surveyed was approximated bordered by the U.S.–Canadian border (49° N) to the north, 120° W to the east, 46° N to the south, and the Cascade crest to the west.

The radio tags used in this study were not equipped with mortality sensors. However, we homed to all nutcrackers at

least once weekly throughout the study. We recovered the radio tags of all nutcrackers that died during the study within 7 to 12 days of their death.

EMIGRANTS AND RESIDENTS: SPACE-USE AND HOME-RANGE ESTIMATION

Emigrant nutcrackers left the study area within days or weeks of capture, and we obtained little space-use data on them in comparison to resident nutcrackers. While emigrants resided in the study area, we used minimum convex polygons (MCPs) to describe their range of space use for individuals with more than 10 telemetry locations. We did not consider these MCPs to describe a spring or summer home range accurately, however, because we were unable to obtain a sufficient sample size of telemetry locations before they emigrated.

For residents we obtained 51–227 summer and 81–394 autumn telemetry locations per individual. We calculated 50, 95, and 99% fixed-kernel ranges and 95 and 100% MCPs for residents. We estimated fixed kernels by using least-squares cross validation (LSCV) (Worton 1987, 1989, Seaman and Powell 1996, Seaman et al. 1999). The autumn home range of one resident was multimodal, and we multiplied the cross-validated value of the smoothing parameter by 0.2 to calculate its kernel estimate (Worton 1995, Neatherlin and Marzluff 2004). We used the Animal Movement extension of ArcView (Hooge and Eichenlaub 1997) to estimate kernels, and grid size was selected automatically.

We calculated area-observation curves for summer and autumn kernel ranges of resident nutcrackers at increments of 5 and up to 65 points (5 points, 10 points, etc.) (Odum and Kuenzler 1955). Except during focal observations our data were discontinuous, so we selected points for area-observation curves randomly (Harris et al. 1990). To determine whether the number of point locations used per season affected the estimate of home-range size, we regressed home-range size against the number of point relocations obtained for each resident nutcracker. Home-range size was not correlated with the number of point relocations for the estimates of the summer kernel ($n = 5$, $r^2 = 0.01$, $P = 0.88$) or autumn kernel ($n = 5$, $r^2 = 0.01$, $P = 0.85$).

To minimize bias associated with autocorrelation we did not use all relocation points from focal observations when estimating residents' home ranges (Kernohan et al. 2001). To determine which points to use in our home-range estimates we plotted the 100% MCP of each individual on a Geographic Information System (GIS) and measured the length of each home range. We used a GIS to determine the distance between consecutive relocation points obtained during 1–3-hr focal observations during which the bird was tracked without interruption (M.G. Raphael, A.V. Bakian, pers. comm.). We determined that nutcrackers on average traversed a distance approximately equal to the length of their 100% summer MCP

once per hour in summer and once every 38 min in autumn. For home-range estimation we used only focal-session points that were separated by at least 60 min in summer and 38 min in autumn.

We assessed differences in the range of summer and autumn movements by residents and emigrants, although we did not obtain enough points on emigrants to estimate home ranges and conduct statistical tests. We also compared differences between residents and emigrants in foraging and seed-harvesting behavior. We conducted statistical tests only on seasonal differences in space use for residents, and we used 95% fixed kernels for all hypothesis testing. We report 50 and 99% fixed-kernel ranges and 95 and 100% MCPs for comparisons with other studies.

RESIDENTS: STATISTICAL ANALYSES FOR ALTITUDINAL MIGRATION BETWEEN SUMMER AND AUTUMN

We used one-tailed paired *t*-tests to test the hypothesis of an increase in home-range size from summer to autumn ($P < 0.05$). We assessed whether summer and autumn home ranges came from a common distribution by using multiresponse permutation procedures (MRPP) (Mielke and Berry 1982). The MRPP is a nonparametric test that compares intragroup average distances with average distances that would be obtained under the null hypothesis that two utilization distributions (UD) come from a common distribution. We computed MRPP by using ordinary Euclidean distances in BLOSSOM statistical software (Slauson et al. 1988). We used ordinary Euclidean distances because they have greater power over a wider range of distributions than squared Euclidean distances (Zimmerman et al. 1985).

We assessed the static interaction of summer and autumn ranges by computing both the area and volume of overlap. We determined the area of overlap by calculating the area-of-overlap index (AO) (Seidel 1992). To determine what portion of summer ranges are contained within autumn ranges we calculated the proportion of overlap of the summer and the autumn range ($S_{\text{summer, autumn}}$) (White and Garrott 1990). We calculated the volume of overlap of summer and autumn ranges by using the volume of intersection statistic (VI) (Seidel 1992, Millspaugh et al. 2004), which quantifies the volumetric proportion of overlap between home-range UDs. The VI ranges from 0 for no overlap to 1 for complete overlap. We plotted the locations of summer-range centroids (Garrott et al. 1987) in the ANIMAL MOVEMENTS extension of ArcView (Hooge and Eichenlaub 1997) and determined if summer range centroids were within the boundaries of the autumn range. We compared the elevations of summer- and autumn-range centroids and used one-tailed paired *t*-tests to test for significant differences.

We considered residents altitudinal migrants between autumn and summer if (1) there was no overlap in the area or

volume of summer and autumn ranges, (2) the summer-range centroid was not contained within the autumn range, and (3) there was a significant difference in the elevation of the autumn and summer centroids.

RESIDENTS: STATISTICAL ANALYSES FOR ALTITUDINAL MIGRATION WITHIN AUTUMN

Tomback (1978) observed that nutcrackers foraged on conifer seeds at high elevations in July and August and switched to low-elevation sources in September and October. Rather than migrating between distinct summer and autumn ranges, nutcrackers may therefore migrate altitudinally within the autumn season of seed harvest. To determine whether nutcrackers migrate altitudinally within autumn we determined the mean elevation used by individuals within each week of the seed-harvest season and regressed week on mean elevation for the 12 weeks from 6 August to 1 November. With data from focal observations we used one-tailed paired *t*-tests to assess whether there was a difference in the mean elevations used for harvesting and caching seeds and "other" activities during the seed-harvest seasons in high-elevation whitebark pine and low-elevation ponderosa pine/Douglas-fir. We compared these mean elevations to the elevation of the summer home-range centroid.

From focal observations we determined the number of times in autumn that nutcrackers cached and harvested seeds inside and outside of the summer range. We also measured the distance between the summer-range centroid and each site of autumn seed harvesting and caching. We compared means of these distances (centroid to caches and centroid to harvest trees) to the distance between the centroid and all summer movements. We used this to assess whether nutcrackers traveled within the range of summer movements when caching and harvesting seeds in autumn. We determined distances from the summer-range centroid to harvest trees and cache sites separately for whitebark and ponderosa pine. We used Mann-Whitney *U*-tests to test for differences in these travel distances.

We considered resident nutcrackers altitudinal migrants within autumn if (1) there was a significant decrease in mean elevation of point relocations through the autumn, (2) there was a significant difference in the mean elevations used for seed harvest, seed caching, and "other" activities between the harvests of whitebark and ponderosa pine seeds, and (3) while harvesting whitebark pine seeds nutcrackers harvested and cached seeds within the summer range, but while harvesting ponderosa pine seeds they harvested and cached seeds outside of this range.

For all analyses we treated individuals as independent data points. Statistical analyses were performed with SAS 9.1 software (SAS Institute 2003). We report means \pm standard deviation.

RESULTS

We captured 31 nutcrackers at three locations in 2006 and 2007, radio-tagging 27 adults and two juveniles. We classified five adult nutcrackers as residents and 19 adults and two juveniles as emigrants. We could not determine the migratory status of three adults because they behaved as both emigrants and residents before being killed or before their signal was lost. The five resident nutcrackers were trapped at the whitebark pine study site ($n = 3$) and the burned ponderosa pine site ($n = 2$). No residents were trapped at the unburned ponderosa pine site. Five nutcrackers died during the study and within the study area. One adult resident was depredated, one juvenile and two adult emigrants were depredated, and one resident was found dead from a shotgun wound. One additional emigrant shed its tag within 5 weeks after capture.

We counted an average of 43 (± 38) cones on whitebark pine trees in 2006 ($n = 40$) and 22 (± 27) cones in 2007 ($n = 40$). We did not count cones on ponderosa pine and Douglas-fir trees. In both 2006 and 2007, however, ponderosa pine cones were available in patches in the study area. Douglas-fir produced very few cones in 2006 and a large crop in 2007 (M.S. Poor, pers. comm.).

SUMMER BEHAVIOR OF EMIGRANTS

Large flocks of nutcrackers were conspicuous in the study area in September and October of 2006 presumably because of the large whitebark and moderate ponderosa pine crop. They ranged throughout the transitional and subalpine zones and between approximately 800 and 1800 m in elevation from autumn 2006 through early summer 2007. We captured and radio-tagged 21 emigrants in the spring following this large whitebark pine cone crop and monitored their movements from April through July 2007. During this time emigrants ranged over areas up to 7540 ha (100% MCP) and in elevation between 785 and 2118 m (Table 1). Emigrant nutcrackers moved over a wide range of elevations over the course of a single day. Moreover, individuals moved both upslope and downslope on summer days, and there was no general trend in movements indicating an altitudinal migration (Table 2).

We observed foraging by emigrants 181 times totaling 755 min (Table 3). Resident nutcrackers were most commonly observed foraging on insects and other invertebrates (81% of observations). In contrast, emigrants were most commonly observed foraging on germinating whitebark pine seedlings

TABLE 1. Range size (ha; 100% minimum convex polygon) and range of elevations (m) used by 21 emigrant nutcrackers from the date that they were released with a radio tag until either the last day they were detected in the study area or the day that their tag was retrieved, for deaths and shed tags. Ranges were calculated only for emigrants with >10 relocation points.

Emigrant nutcracker	Age ^a	Number of fixes	Period of tracking	100% minimum convex polygon (ha)	Range of elevations used within study area (m)
043 ^b	ad.	13	12 May–5 June	122.27	1441–1829
107	ad.	25	12 May–20 June	1701.21	1038–2036
220 [1] ^c	ad.	5	3 May–1 June	—	1144–1698
220 [2] ^c	juv.	3	9 June–3 July	—	1759–1775
240	ad.	20	3 May–1 June	108.85	1749–1920
322	ad.	6	28 April–31 May	—	1118–1539
382	ad.	11	28 April–5 June	427.27	1426–1836
422	ad.	129	12 May–3 July	7539.95	1319–2118
483	ad.	12	28 April–23 May	95.97	1161–1781
505	ad.	25	19 April–27 June	1946.04	1350–1889
521	ad.	6	24 April–1 June	—	851–1538
529	ad.	15	28 April–7 June	233.70	1290–1800
546	ad.	0	12 May–25 May	—	—
557	ad.	6	22 November–21 March	—	785–1633
591	ad.	85	24 April–27 June	4995.74	1348–2081
607	ad.	8	3 May–31 May	—	1063–1772
621 [1] ^b	ad.	4	3 May–30 May	—	1136–1783
621 [2] ^c	juv.	2	9 June–19 June	—	1753–1762
733	ad.	12	3 May–30 May	3882.03	1174–1909
884	ad.	4	24 April–28 May	—	1226–1407
983	ad.	4	24 April–25 May	—	1657–1778

^aNutcrackers were aged as either juvenile (hatch year) or adult (after hatch year) according to Mewaldt (1958).

^bDepredated (043[1] and 621[1]); tag later fitted to a second nutcracker in the same year (resident 043 [2] and emigrant 621 [2]).

^cTag shed (220[1]) and later fitted to a second nutcracker within the same year (220 [2]).

TABLE 2. Daily elevational movements by emigrant nutcrackers during summer 2007. Whitebark pine typically occurred in stands between 1640 and 1890 m, ponderosa pine between 700 and 1440 m.

Emigrant nutcracker	Date	Daily change in elevation (m)	Daily maximum elevation (m)	Daily minimum elevation (m)
043 [1] ^a	15 May	236	1763	1527
	23 May	-385	1827	1441
	1 June	290	1740	1450
107	1 June	582	1620	1038
	12 June	435	2036	1601
	14 June	-70	2001	1931
240	23 May	170	1920	1749
	29 May	79	1872	1793
382	15 May	-66	1783	1717
	5 June	-196	1622	1426
422	31 May	-231	1656	1425
	1 June	-18	1639	1620
	14 June	69	2004	1935
	18 June	36	2060	2025
	23 June	-153	2118	1965
	26 June	-134	1497	1362
	2 July	106	2037	1931
483	23 May	-40	1316	1277
505	28 May	-504	1854	1350
	12 June	-191	1835	1645
	13 June	-52	1757	1704
	21 June	-203	1694	1491
529	23 May	239	1529	1290
	1 June	-22	1800	1779
	7 June	25	1696	1671
591	15 May	301	1853	1552
	22 May	-44	1781	1737
	14 June	-151	2058	1907
	18 June	97	2033	1936
733	15 May	36	1798	1763
	23 May	235	1640	1405
	28 May	-447	1626	1179

^aFirst individual carrying this tag.

on communal caching grounds (71% of observations). Emigrants foraging on germinating seedlings scrutinized the ground surface, focusing particularly on areas where snow had recently melted or at the bases of logs and vegetation. Whitebark pine seeds were located and consumed as seedlings emerged and became visible above the ground surface. This behavior has previously been reported in nutcrackers and called prolonged searching by Vander Wall and Hutchins (1983). We did not observe emigrants retrieving caches from memory. Emigrants also foraged in other parts of the study area on insects and ponderosa pine seeds retained in cones from the previous autumn's cone crop. When engaged in prolonged searches and foraging on ponderosa pine seeds they were typically in conspicuous and vocal flocks of 10–150 individuals. Overall emigrants appeared to track concentrations of food by traveling with flocks of conspecifics rather than by migrating altitudinally.

Emigrants vacated the study area singly over 6 weeks in late spring and early summer. The first emigrant left the study area on 24 May and the last departed on 3 July.

SUMMER BEHAVIOR OF RESIDENTS

Compared to emigrants, residents ranged over smaller areas and within a more restricted range of elevations in spring and summer. From May through July residents ranged over areas between 157 and 737 ha (100% MCP) (Table 4) and elevations between 957 and 1841 m. We observed residents foraging 140 times totaling 432 min and they foraged predominately on insects in their summer home range (Table 3). We observed only nine instances of cache retrieval by residents, and seven of those retrieved caches were fed to nestlings or fledglings. All caches were retrieved from sites within the summer home range. We did not observe residents visiting or engaging in prolonged searches on communal caching grounds. Residents foraged only singly

TABLE 3. Number (proportion) of independent foraging events and total time (proportion) spent foraging for various food items by resident and emigrant Clark’s Nutcrackers from May through July.

Description of food item	Residents		Emigrants	
	Number (proportion) of independent foraging events	Total time (proportion) spent foraging for food item (min)	Number (proportion) of independent foraging events	Total time (proportion) spent foraging for food item (min)
Insects and other invertebrates	114 (0.81)	309 (0.72)	36 (0.20)	231 (0.31)
Germinating whitebark pine seed	0	0	129 (0.71)	364 (0.48)
Ponderosa pine seed within cones	5 (0.04)	45 (0.10)	11 (0.06)	138 (0.18)
Whitebark pine seed within cones	7 (0.05)	47 (0.11)	0	0
Seed retrieved from own cache	9 (0.06)	15 (0.03)	0	0
Unknown	5 (0.04)	16 (0.04)	5 (0.03)	22 (0.03)
Total	140	432	181	755

or in small groups of two to ten individuals, behavior contrasting markedly with the characteristically large and vocal flocks of emigrants. Composition of residents’ summer home ranges varied. All home ranges contained sources of ponderosa pine and Douglas-fir seeds, and three of five home ranges also contained whitebark pine. Two home ranges were located within a mixed-severity burn four years old in an open ponderosa pine stand facing southwest. Three home ranges were on a ridge-line that contained mixed whitebark pine and mountain hemlock on north-facing aspects and ponderosa pine, Douglas-fir, and grand fir on south-facing aspects. All five residents’ home ranges contained steep south-facing slopes or cliffs.

AUTUMN BEHAVIOR OF EMIGRANTS

In autumn 2007, none of the 21 emigrants radio-tagged the previous spring returned to the study area. We relocated two

emigrants north of the study area during aerial telemetry surveys. One emigrant, number 591, was relocated 173 km north of the study area along Sawtooth Ridge, east of Lake Chelan, Washington (approximately 120° 15’ W, 48° 6’ N). We tracked 591 only during the whitebark pine seed-harvest season. It ranged over 274 km² in August and crossed Lake Chelan to Domke Lake (approximately 120° 36’ W, 48° 10’ N) before we lost its radio signal on 5 September. We assumed it continued wandering and left the Washington Cascades because we did not relocate it during two flights and 9 hr of aerial tracking in mid-September. Because of logistical constraints, between 22 August and 5 September we obtained relocation data on only five days and seed-harvest and caching data on two days. We observed only seven seed caches created by this nutcracker, but all seeds were placed within the harvest stand. Within ten days of placing these caches nutcracker 591 had ranged over

TABLE 4. Estimates of summer and autumn home ranges (ha) of resident Clark’s Nutcrackers. The 95% kernel estimate depicted space use by all nutcrackers most accurately and was used for all analyses.

Resident nutcracker	Season	<i>n</i>	50% Kernel estimate	95% Kernel estimate	99% Kernel estimate	95% Minimum convex polygon	100% Minimum convex polygon
Residents of whitebark pine							
043 [2] ^a	summer	36	12.3	157.0	245.6	139.2	157.4
043 [2] ^a	autumn	122	109.5	732.9	1838.8	1747.7	4478.1
893	summer	34	48.9	547.0	940.7	664.0	737.0
893	autumn	127	245.6	1356.9	3150.1	3652.9	5411.7
719	summer	30	25.6	197.7	267.2	117.8	154.6
719	autumn	82	32.9	317.9	712.1	400.4	835.9
Residents of burned ponderosa pine							
211	summer	31	31.1	473.7	628.4	353.5	357.0
211	autumn	67	145.0	962.2	2390.0	1140.2	1631.5
505	summer	29	15.9	216.2	385.3	207.3	306.7
505	autumn	34	88.4	1028.7	2113.8	9468.3	11 464.5

^aSecond individual carrying this tag.

250 km² and between mid-elevation transitional forest types at 1354 m and high-elevation whitebark pine stands at 2123 m. We did not observe it retrieve its caches before emigrating, and to our knowledge nutcracker 591 did not have fidelity to the area where it cached.

The second emigrant nutcracker, number 505, was relocated approximately 92 km north of the study area on Mount Stuart, Washington (approximately 120° 53' W, 47° 29' N) and ranged over 175 km² (100% MCP) during the whitebark pine seed-harvest season (16 August–14 September). During this time it moved between ponderosa pine stands at 721 m and whitebark pine stands at 1974 m. It was not logistically possible to watch seed harvesting and caching by 505 at all times because it was harvesting and pouching seeds on nearly vertical cliffs. Using triangulations we estimated that nutcracker 505 was traveling from 600 to 1700 m between harvest trees and caching grounds. After 14 September nutcracker 505 stopped wandering and settled on a stable winter range near Teanaway Ridge (approximately 120° 49' W, 47° 23' N), where it remained until its radio battery failed in June 2008. During this time, nutcracker 505 harvested whitebark pine, ponderosa pine, and Douglas-fir seeds up to 8.2 km from the winter range on Teanaway Ridge, and all seeds were transported to the winter range for caching. It harvested whitebark pine seeds at 2075 m elevation, Douglas-fir and ponderosa seeds at 804 m elevation. The winter range of 505 on Teanaway Ridge contained mostly mid-elevation forests between 972 and 1288 m.

AUTUMN BEHAVIOR OF RESIDENTS

All resident nutcrackers remained in the study area through the autumn. The sizes of areas over which residents ranged when harvesting seeds differed considerably. One individual was never observed traveling more than 4 km from its home range's center, whereas another individual traveled >29 km and ranged over 115 km² for seed harvesting (Table 4). All five residents harvested ponderosa pine seeds, but only four also harvested whitebark pine seeds, and three additionally harvested Douglas-fir seed. We observed four resident nutcrackers harvesting whitebark pine seeds 215 times, five nutcrackers harvesting ponderosa pine seeds 225 times, and three nutcrackers harvesting Douglas-fir seeds 16 times. We observed four resident nutcrackers place a total of 205 caches; 108 of whitebark pine seeds by two nutcrackers and 97 of ponderosa pine/Douglas-fir seeds by four nutcrackers. Residents harvested whitebark pine seeds at high elevations both individually and in loose flocks of up to 100 individuals. When harvesting ponderosa pine seeds at low elevations they were usually in flocks of 25 to 150 individuals. They traveled alone or in small groups of two to four when transporting seeds between harvest trees and cache sites.

Throughout this study, all residents showed strong fidelity to their summer range when caching seeds. We also observed that resident nutcrackers harvested, transported, and cached seeds purposefully and often rather hastily. Periods of

seed harvest, transport, and caching were fairly predictable, and residents adhered to an established daily routine. At dawn radio-tagged residents congregated with flocks of conspecifics in stands of pines where they filled their sublingual pouches for up to 80 min. Once pouches were full or nearly full the birds departed from the harvest stand and flew off in the direction of the summer range. Within 5 to 25 min, these same individuals were observed flying with full sublingual pouches into the summer range, where we observed them caching seeds. After caching seeds for 20 to 40 min, residents left their summer range and returned to the harvest stand. Residents made between three and ten seed-transport flights each day and continued harvesting seeds until dusk. The number of trips made each day was associated with the distance between the harvest stand and summer range, the length of the day, weather, and the efficiency with which the nutcrackers could fill their pouches in the harvest stand.

RESIDENTS: COMPARISONS OF SUMMER AND AUTUMN SPACE USE

We obtained 503 summer and 1582 autumn point locations from residents, and we used 190 and 432 point relocations for estimating summer and autumn home ranges, respectively. Area-observation curves reached an asymptote with 25 points for summer and 45 points for autumn. Summer home-range estimates for resident nutcrackers contained 32 ± 2 point relocations, and 95% kernels were 318 ± 178 ha. Autumn home-range estimates contained 86 ± 39 point relocations and were 880 ± 385 ha (Table 4). The size of the home range of all residents increased in autumn ($t_4 = 4.4$, $P_{\text{one-tailed}} = 0.006$), and the UD of summer and autumn ranges did not come from a common distribution (MRPP $P < 0.04$ for all individuals). The proportion of area of overlap for autumn and summer home ranges was 0.24 ± 0.05 , although summer home ranges were nearly completely contained within the boundaries of the autumn ranges ($S_{\text{summer, autumn}} = 0.75 \pm 0.17$) (Table 5). The volume of overlap of summer on autumn ranges was 0.70 ± 0.22 , of autumn on summer ranges 0.21 ± 0.08 . For all nutcrackers, the summer-range centroid was within the boundaries of the autumn home range and there was no difference in the elevation of summer-range centroids (1568 \pm 274 m) and autumn-range centroids (1426 ± 383 m) ($t_4 = 1.3$, $P_{\text{one-tailed}} = 0.14$).

RESIDENTS: SPACE-USE CHANGES WITHIN AUTUMN

Nutcrackers shifted their seed-harvesting efforts from high-elevation (1640–1890 m) whitebark pine to low-elevation (700–1440 m) ponderosa pine and Douglas-fir on 14 September in 2006 and on 21 September in 2007. Over the course of the seed-harvest season, the mean weekly elevation of relocation points declined by 23 m per week ($n = 5$, $P = 0.04$, $r^2 = 0.35$), indicating that nutcrackers shifted their use of space to encompass lower elevations as autumn progressed.

TABLE 5. Area and volume of summer and autumn range overlap and proportion of summer range overlapped by autumn range for resident Clark’s Nutcracker home ranges.

Resident nutcracker	Area of overlap of summer and autumn ranges (AO) ^a	Proportion of summer range overlapped by autumn range ($S_{\text{summer, autumn}}$) ^b	Volume of intersection of summer on autumn ranges ($VI_{\text{summer, autumn}}$) ^c	Volume of intersection of autumn on summer ranges ($VI_{\text{autumn, summer}}$)
043 [2] ^d	0.21	0.99	0.99	0.14
893	0.29	0.79	0.88	0.27
719	0.27	0.56	0.56	0.32
211	0.25	0.61	0.50	0.19
505	0.16	0.81	0.58	0.15

^aAO = $\frac{\text{summer} \cap \text{autumn}}{\text{summer} \cup \text{autumn}}$ (Siedel 1992).

^b $S_{\text{summer, autumn}} = \frac{\text{summer} \cap \text{autumn}}{\text{summer}}$ (White and Garrott 1990).

^cVI = $\int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \min(\hat{f}_{\text{summer}}(x, y), \hat{f}_{\text{autumn}}(x, y)) dx dy$ (Siedel 1992, Millsbaugh et al. 2004).

^dSecond individual carrying this tag.

The regression of elevation on week had a poor fit, however, because as autumn progressed nutcrackers shifted only their seed-harvesting efforts to low elevations. They continued to use high elevations for all other activities (Figs. 2, 3). We observed only two nutcrackers creating caches of both whitebark and ponderosa pine/Douglas-fir seeds. They harvested ponderosa pine/Douglas-fir seeds at lower elevations (945 ± 108 m) than whitebark pine seeds (1789 ± 41 m) ($t_1 = -18.1$, $P_{\text{one-tailed}} = 0.02$), but they carried all of these seeds up into high-elevation portions of their summer range, and there was no difference in the elevations that they used for caching whitebark (1750 ± 10 m) and ponderosa pine/Douglas-fir seeds (1773 ± 13 m) ($t_1 = 1.6$, $P_{\text{one-tailed}} = 0.19$).

Observations for all resident nutcrackers pooled, the mean elevation of observations of seed harvesting was 1814 ± 55 m for

the whitebark pine season ($n = 3$ residents) and 1025 ± 528 m for the ponderosa pine/Douglas-fir season ($n = 5$ residents). The mean elevation of observations of seed caching was 1750 ± 7 m for the whitebark pine season ($n = 2$ residents) and 1607 ± 182 m for the ponderosa pine/Douglas-fir season ($n = 4$ residents). For all nutcrackers the mean elevation observed for “other” activities, including roosting, preening, and social interactions, was the same for both the whitebark pine (1502 ± 258 m) and ponderosa pine/Douglas-fir (1346 ± 271 m) seed-harvest seasons ($t_4 = 1.6$, $P_{\text{one-tailed}} = 0.09$). Whitebark pine seeds were harvested 205 ± 338 m above the summer-range centroid, whereas ponderosa pine/Douglas-fir seeds were obtained 507 ± 301 m below it. There was much less variability in the elevations nutcrackers used for caching seeds, and they

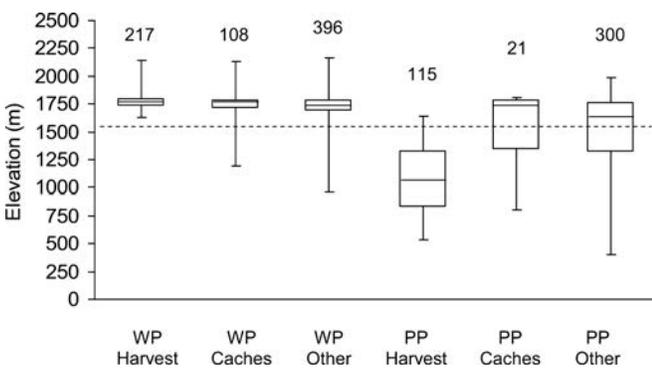


FIGURE 2. Elevations (m) used for seed harvesting, seed caching, and other activities during the seed-bearing season of the whitebark (WP) and ponderosa (PP) pines by three adult Clark’s Nutcrackers with a summer home range in a stand of whitebark pines. Observations of activities of all nutcrackers are pooled. The rectangle represents the interquartile range, the center line inside represents the median, and the whiskers represent minimum and maximum values. Numbers above individual box plots indicate sample sizes, and the dashed line indicates the mean elevation of the summer home-range centroid.

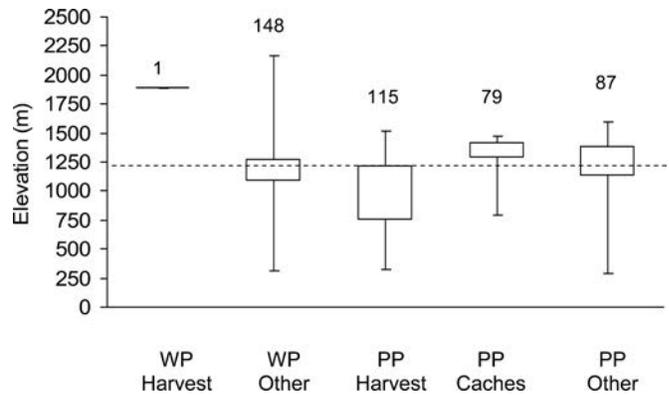


FIGURE 3. Elevations (m) used for seed harvesting, seed caching, and other activities during the seed-bearing season of the whitebark (WP) and ponderosa (PP) pines by two adult Clark’s Nutcrackers with a summer home range in a stand of burned ponderosa pines. Observations of activities of both nutcrackers are pooled. The rectangle represents the interquartile range, the center line inside represents the median, and the whiskers represent minimum and maximum values. Numbers above individual box plots indicate sample sizes, and the dashed line indicates the mean elevation of the summer home-range centroid.

cached all seeds at nearly the same elevation as their summer-range centroid. On average whitebark pine seeds were cached 17 ± 9 m below the center of the centroid, ponderosa pine/Douglas-fir seeds 31 ± 41 m above it.

While harvesting both whitebark and ponderosa pine seeds, nutcrackers cached seeds within or very close to the summer range. Resident nutcrackers placed 88% of ponderosa pine/Douglas-fir and 77% of whitebark pine seed caches within their summer home range. Yet only 24% of ponderosa pine/Douglas-fir and 61% of whitebark pine seeds were harvested within the summer range. Some caches were placed outside of the boundaries formed by the 95% contour interval of the UD but were still close to the summer-range centroid and within the range of summer movements. For example, we observed that in summer nutcrackers were detected on average 0.6 ± 1.4 km from the summer-range centroid. This distance was not different from the average distance traveled between that centroid and autumn caching relocations ($n = 5$, $U = 1.0$, $P = 0.27$), although it was significantly less than the average distance between the summer-range centroid and autumn harvest relocations ($n = 5$, $U = 2.5$, $P = 0.01$) (Fig. 4).

Overall, caches were located closer to the birds' summer-range centroid (1.1 ± 0.5 km) than to the trees used for seed harvesting (5.4 ± 6.8 km) ($n = 5$, $U = 2.1$, $P = 0.04$). Nutcrackers harvested whitebark pine seeds up to 29.3 km (10.6 ± 16.2 km) from their summer-range centroid, ponderosa pine and Douglas-fir seeds up to 25.5 km (6.3 ± 6.0 km) and 3.8 km (2.4 ± 1.3 km) from the centroid, respectively. Nutcrackers cached whitebark pine seeds on average 0.8 ± 0.6 km and ponderosa pine/Douglas-fir seeds 1.0 ± 0.5 km from their summer-range

centroid. Thus, irrespective of the distances and elevations required to transport seeds, resident nutcrackers in our study placed caches of seeds of all trees either within or very close to their summer home range.

DISCUSSION

The resident Clark's Nutcrackers we studied did not migrate altitudinally either between summer and autumn or during autumn. Summer and autumn ranges of residents overlapped, and throughout autumn they used the summer range for roosting, preening, and seed caching regardless of whether they were harvesting whitebark pine seeds in early autumn at high elevations (1640–1890 m) or ponderosa pine/Douglas-fir seeds in late autumn at low elevations (700–1440 m). Since nutcrackers forage on cached seeds during winter and spring (Mewaldt 1956, Giuntoli and Mewaldt 1978) this suggests that the summer range is also the winter and spring range and that residents in this population do not migrate altitudinally at any time during the year. Overall, our inferences are limited because of small sample sizes. This study is the first, however, to demonstrate that nutcrackers in one population in the Cascade Range are nonmigratory and that summer ranges of residents may represent the core of their year-round space use.

Although the residents we studied did not migrate altitudinally, they did use space differently in summer than they did in autumn. For example, autumn ranges were significantly larger than summer ranges. During autumn one individual increased its use of space by an astounding factor of 37. Autumn ranges were large because nutcrackers went on forays in search of harvestable seeds far outside their summer range. Yet rather than migrating and vacating their summer range when harvesting seeds from distant sources, nutcrackers returned to their summer range to cache seeds multiple times each day. We observed residents transporting seeds up to 29.2 km from sources to caches. Our observations of long-distance seed transport are comparable to and build upon previously published observations of seed transport by nutcrackers. Vander Wall and Balda (1977) reported seed-transport flights of up to 22 km in Arizona, and others have reported seed-transport flights of 3–12.5 km in California, Utah, and Wyoming (Tomback 1978, Vander Wall 1988, Hutchins and Lanner 1982, Dimmick 1993). Though such extraordinary long-distance seed-caching flights were first reported 30 years ago, the reasons for them have remained speculative (Vander Wall and Balda 1977, Vander Wall 1988). Our study is the first to show that nutcrackers transport seeds long distances in order to cache them within the summer home range.

Long-distance seed transport has previously been regarded as an exception to the general rule; past studies have concluded that the majority of seeds are cached within a few meters to a few kilometers of harvest trees (Vander Wall 1988, Tomback 1998). Conversely, we found long-distance seed

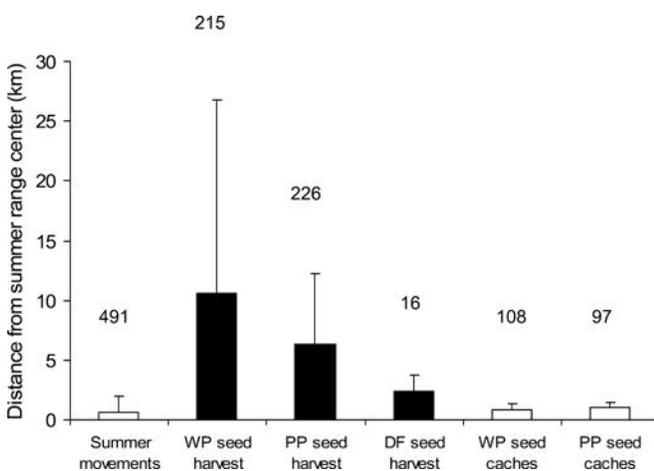


FIGURE 4. Mean distances traveled (km) by five resident Clark's Nutcrackers from the center of the summer home range to all summer movements and all sites of harvesting and caching whitebark pine (WP), ponderosa pine (PP), and Douglas-fir (DF) seeds in autumn. Data for all individuals are pooled. Bars represent means \pm SD; numbers above bars represent sample sizes.

transport to be common. For example, the average distance we observed whitebark pine seeds transported (10.6 km) is nearly as great as the maximum distance (12.5 km) previously reported for whitebark pine seeds (Tomback 1978). We believe that long-distance seed transport may have been underreported because past studies relied on visual observations and were unable to track individuals continuously over long distances. Long-distant seed transport during autumn would be an evolutionarily stable strategy for all nutcrackers if they cache seeds in locations where they plan to overwinter and breed. Even though nutcrackers might expend large amounts of energy during autumn for seed transport, they are typically not food limited during this season because fresh pine seed is abundant. Nutcrackers that store their caches centrally can conserve energy in winter when conditions are most severe and fresh food is scarce (Vander Wall and Balda 1977). Whenever possible, nutcrackers would enhance their fitness further if they cache seeds within their own, familiar, year-round home range, because they are cognizant of how best to find food and evade predators in their home range.

Although we did not test hypotheses regarding space use by emigrant nutcrackers, our results suggest that, like residents, emigrants do not migrate altitudinally. During both summer and autumn emigrants moved over larger areas than did residents and over a range of elevations encompassing both whitebark and ponderosa pine forest. In both seasons emigrants frequently moved between ponderosa and whitebark pine habitats in one day, and there was no trend in movements by emigrants either upslope in summer or downslope in autumn. Space use of the emigrant nutcrackers in this study was complex and poorly described by altitudinal migration.

Collectively our results show that the space use of residents and emigrants differ. They provide the first empirical support for the model of differential space use by resident and emigrant nutcrackers proposed by Vander Wall et al. (1981). As predicted by Vander Wall et al. (1981) all the residents we studied occupied home ranges in which several species of large-seeded conifer were available within the distance they could transport seeds. In autumn, they harvested seeds from many sources, although they demonstrated fidelity to the summer home range for all other activities, especially seed caching. We suggest that residency is a preferred strategy and residents occupy landscapes in which multiple species of large-seeded conifer are available within 30 km of the home range. Residents rarely need to emigrate since seeds of at least one species are available every autumn.

Regarding emigrant nutcrackers, Vander Wall et al. (1981) predicted that in autumn they track concentrations of cones on a regional scale and move throughout areas that they have never encountered. We suggest that these individuals originate from home ranges in landscapes that are less diverse, in which seed production is not consistent enough from year to year for a stable, resident lifestyle. Vander Wall et al. (1981) proposed that

emigrants tend to move in conspicuous flocks which may provide protection from predators; protection offered by the flock in unfamiliar areas may compensate for competition for resources. Emigrants do not show fidelity to one wintering area. Rather, they settle among conifers supplying ample food and cache seeds in preparation for winter. Those that winter successfully attempt to breed in spring and return to the area from which they emigrated in June and July of the following year. We do not know the locations of the natal ranges of emigrant nutcrackers we radio-tagged because we have no data on their movements prior to their capture in spring 2007. We therefore have no information on whether these emigrants originally occupied landscapes without multiple sources of seeds. However, we observed that radio-tagged emigrants ranged more widely in autumn than did residents. In late autumn, we observed that one emigrant settled in a location where three species of conifer were producing cones. Additionally, we observed that radio-tagged emigrants occupied the study area during one year of high cone production but did not show fidelity to this wintering area in the following year.

We observed seed harvesting and caching by two emigrants in autumn. Before settling they cached seeds in harvest stands, although they did not retrieve these seeds before they emigrated from the area. Despite the apparent waste of energy, emigrants have very little to lose but possibly much to gain by caching seeds near the source as they travel. Because seeds are not transported long distances the energy expended to cache them in the harvest stand is fairly minimal. Emigrants benefit from caching the seeds because they make these seeds unavailable to other seed predators. As predicted by Vander Wall et al. (1981), emigrants travel on a regional scale to locate the most productive stands of conifers. If an emigrant does not locate a highly productive stand, it could return to any of the previously visited stands and retrieve its caches during the winter. Yet if it locates a more productive stand, an emigrant could readily settle. Under these circumstances it establishes a winter home range and abandons seeds previously cached elsewhere.

The Clark's Nutcrackers we studied did not migrate altitudinally. A portion of the population remained as year-round residents on stable home ranges, whereas others migrated latitudinally. Resident and emigrant nutcrackers used space differently in summer and autumn. Residents occupied stable home ranges in summer. In autumn they harvested seeds outside of their summer range but cached seeds centrally within their summer home range. Emigrants moved over a regional scale and used habitats at a wide range of elevations in both seasons. Small sample sizes precluded hypothesis testing with emigrants, although space use by emigrants appeared to be complex and highly variable. Additional studies of space use, seed caching, and cache retrieval with larger samples sizes of nutcrackers are needed to investigate differences in space use by resident and emigrant nutcrackers further.

CONSERVATION IMPLICATIONS

Clark's Nutcrackers play an important role in the composition of subalpine and montane forests in western North America through their patterns of seed dispersal. Understanding the factors affecting nutcrackers' caching decisions is becoming increasingly important as the whitebark pine, an obligate mutualist of Clark's Nutcracker, declines and land managers seek to optimize the number of seeds effectively dispersed to suitable sites. Our results show that in some populations seed dispersal by nutcrackers is affected by multiple factors, such as migratory status and the position of the summer home range relative to autumn seed sources. Ultimately, nutcrackers' caching decisions affect community composition in many forests in western North America, whitebark pine ecosystems in particular. We suggest that it is important for land managers to consider the behavioral ecology of Clark's Nutcracker when managing and restoring forested lands in which nutcrackers act as dispersal agents.

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