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Linking Space Use and Behavior in Clark's Nutcracker: An Explanation for Seasonal Variation in Space Use

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LINKING SPACE USE AND BEHAVIOR IN CLARK'S NUTCRACKER:

AN EXPLANATION FOR SEASONAL VARIATION IN SPACE USE

by

Teresa J. Lorenz

A thesis submitted in partial fulfillment
of the requirements for the degree

of

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ABSTRACT

Linking Space Use and Behavior in Clark's Nutcracker:

An Explanation for Seasonal Variation in Space Use

by

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Utah State University, 2009

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Clark's Nutcrackers (*Nucifraga columbiana*) are important seed dispersers for at least 10 species of conifer in western North America and are obligate mutualists for the subalpine tree, whitebark pine (*Pinus albicaulis*). 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 space use patterns. I tested one hypothesis that Clark's Nutcrackers migrate altitudinally between summer and autumn in one population in the Cascade Range, Washington. In 2006 and 2007, I 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 and 21 emigrated from the study area in summer. Among residents I 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 harvest trees up to 29 km in distance and 1007 m in elevation. I was unable to test hypotheses regarding space use by emigrants. However, my results suggest that emigrants in this study did not migrate altitudinally because they did not show a seasonal trend in movements either upslope or downslope.

(51 pages)

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Teresa Lorenz

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CHAPTER 1

INTRODUCTION

Clark's Nutcracker (*Nucifraga columbiana*) is a songbird in the family Corvidae that inhabits montane forests in western North America. Nutcrackers have received considerable attention in the literature because of their association with large seeded pines. They exhibit keystone functions in some ecosystems by effectively dispersing the seeds of several pine species (Tomback and Linhart 1990). 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 as many as ten thousands individual seed caches to be retrieved later in the year (Vander Wall and Balda 1977, Hutchins and Lanner 1982, Tomback 1982). Stored seeds are important food for winter survival and spring breeding (Mewaldt 1956, Giuntoli and Mewaldt 1978). For many reasons, an individual nutcracker may not retrieve some of its seed caches and seeds placed in locations favorable for seedling emergence are then able to germinate. Nutcrackers disperse seeds for many common and widespread pine species including whitebark (*Pinus albicaulis*), limber (*P. flexilis*), ponderosa (*P. ponderosa*), Colorado pinyon (*P. edulis*), and singleleaf pinyon (*P. monophylla*) pines (Vander Wall and Balda 1977, Lanner and Vander Wall 1980, Hutchins and Lanner 1982, Vander Wall 1988, Baud 1993).

Whitebark pine (*Pinus albicaulis*) is unique among these pines because it has coevolved with Clark's Nutcracker (Tomback 1983) and nutcrackers provide the sole

mechanism of phase I seed dispersal for whitebark pine (Hutchins and Lanner 1982).

Whitebark pine is a five-needle pine that is restricted to upland and subalpine habitats in

western North America (Arno and Hoff 1989). It plays a critical role throughout its range

as a pioneer species and in stabilizing soils and providing forage and cover for wildlife

(Tomback et al. 2001). Whitebark pine communities are typically remote and have not

been considered as threatened by human-induced changes as lowland forests. Within the

last century, however, whitebark pine has been undergoing population declines. These

declines stem from the combined effects of mountain pine beetle, white pine blister rust,

and fire suppression and all of these mortality agents can indirectly be attributed to

human activities (Keane 2001, Tomback et al. 2001). This decline has ramifications for

many taxa, most notably Clark's Nutcracker (Lanner 1982, Tomback 1978, 1982).

Declines in whitebark pine may affect the nutcracker-pine mutualism by upsetting a

critical balance between populations, resulting in reduced seed dispersal and pine

regeneration (Tomback and Kendall 2001).

Whitebark pine seeds are large and consequently they are highly valued as food

by many avian and mammalian granivores (Hutchins and Lanner 1982). To prevent

widespread predation of seeds by granivores, many species of pine, including whitebark

pine, have evolved a strategy called masting in which populations synchronize their

reproductive activity. Masting results in variation in the proportion of seeds effectively

dispersed (Kelly 1994). In years of high seed production, granivores store more seed

than they are able to consume in the following year, enabling some seeds to escape

predation and germinate. In years of low seed production, most seeds may be preyed

upon but future populations of granivores are culled. This has important implications for

the number of seeds dispersed within populations and therefore the adaptive evolution

of whitebark pine (Siepielski and Benkman 2007). Overall, the number of seeds

effectively dispersed varies among years year owing to many factors such as the number

of seeds produced within any given conifer population, the size of granivore populations,

and the availability of alternate foods for these granivores.

Of all of the species involved with whitebark pine seed fate, Clark's Nutcracker is

the only species known to be required for seed dispersal. Because of this relationship,

whitebark pine has evolved several unique features that facilitate seed harvest by

nutcrackers and encumber other granivores. Whitebark pine seeds are wingless and they

are retained in indehiscent cones (Price et al. 1998). When harvesting seeds of pines with

seed-wings, nutcrackers must remove seed wings before using the seeds and this uses

valuable time. The wingless seeds of whitebark pine enable nutcrackers to harvest seeds

more rapidly. The indehiscent cones slow seed harvest by species of granivore that lack

long, powerful bills. Additionally, the cones of whitebark pine are borne conspicuously

at the ends of upswept branches, making it relatively easy for birds to locate cones when

flying overhead and difficult for mammals to assess cone availability from the ground

(Lanner 1982).

Like whitebark pine, Clark's Nutcrackers also have evolved several distinctive

morphological adaptations for this mutualism. Their bill is long and sharply pointed,

which enables them to chisel into cones and extract seeds from narrow cracks in cone

scales (Vander Wall and Balda 1981). Nutcrackers are also fast and strong fliers

compared to sympatric species, which likely aids them when searching for cone-bearing

trees and when transporting seeds (Vander Wall and Balda 1981). They are capable of

transporting as many as 150 whitebark pine seeds at a time because of a unique, expandable sublingual pouch (Bock et al. 1973, Tomback 1978, Vander Wall and Balda 1981). Nutcrackers also have specialized brains that they use to remember the precise locations of their individual seed caches. The hippocampus is larger than those of non-caching birds of similar size (Basil et al. 1996). This enlarged hippocampus enables nutcrackers to remember the locations of tens of thousands of individually buried seeds for nearly a year (Balda and Kamil 1992). They remember the locations of caches by memorizing the positions of objects surrounding their caches (Vander Wall 1982, Kamil and Cheng 2001).

Despite their close evolutionary relationship, Clark's Nutcracker is not an obligate mutualist of whitebark pine and nutcrackers do not require whitebark pine for survival. Insects appear to be a critical component of their diet range-wide in late spring and summer (Giuntoli and Mewaldt 1978). Seeds from other large-seeded pines including limber pine and the pinyon pines replace those of whitebark pine as important food in the southern parts of the nutcracker's range (Vander Wall and Balda 1977, Vander Wall 1988, Samano and Tomback 2003). In northern parts of the nutcracker range, ponderosa pine and Douglas-fir (*Pseudotsuga menziesii*) are important foods (Giuntoli and Mewaldt 1978, Vander Wall et al. 1981). In fact, even where the ranges of nutcrackers and whitebark pine overlap, whitebark pine may not be the primary food source for a population. In western Montana, Giuntoli and Mewaldt (1978) found that whitebark pine seed on average accounted for less than 20 percent of the annual diet of nutcrackers. Ponderosa pine seed accounted for more than half of the annual diet over 3 years,

compared to 19 percent whitebark pine seed, 13 percent insects and spiders, and 11 percent Douglas-fir seed.

Since all conifers produce mast crops of cones at irregular and unpredictable intervals, nutcrackers must be highly mobile and move on a landscape scale in autumn to exploit seeds of many different species. For example, Tomback (1978) and Vander Wall (1988) observed an altitudinal shift in seed harvest behavior by nutcrackers in different parts of their range. The timing of this altitudinal shift coincided with the ripening of different types of pine seed in autumn. Whitebark and limber pine seeds ripened at high elevations in August followed by Jeffery and pinyon pine seeds which ripened at low elevations in September. Vander Wall et al. (1981) observed latitudinal migrations of nutcrackers and hypothesized that the landscape-scale distribution of these conifers determined the migratory status of individuals. Under this model a portion of the population of nutcrackers are residents who remain on stable, year-round home ranges. Resident nutcrackers occupy home ranges that contain multiple species of conifer so that in nearly all years residents have at least one species of conifer available to them for harvesting seed. The remainder of the population occupies less suitable habitat where only one species of cone producing conifer may be available. Since cone production is not consistent between years, in most years these individuals must vacate their home ranges and search either on a landscape scale or on a regional scale for additional seed sources. Vander Wall et al. (1981) hypothesized that these emigrants will search for productive concentrations of cones throughout autumn and will settle for the winter only under favorable circumstances. This settling response may be affected by factors that are difficult to measure, such as size of cone crops on a regional scale, the number of

dominant resident nutcrackers, and the rate at which seeds can be extracted from cones in different stands (Vander Wall et al. 1981). Therefore, an apparent abundance of cones in one area may not be enough to induce a settling response by emigrant nutcrackers. In years in which emigrants cannot find suitable food sources, population irruptions occur and nutcrackers may be found far outside of their traditional range (Davis and Williams 1957, Fisher and Myres 1979). Extralimital sightings during these population irruptions include reports of nutcrackers in eastern North America, in the desert southwest, and in costal areas (Mitchell 1894, Bryant 1895, Presnall 1936, Fisher 1943, Davis and Williams 1957, 1964, Westcott 1964, Fisher and Myres 1979).

The production of conifer seed in autumn has a far-reaching affect on the natural history and behavioral ecology of Clark's Nutcracker. Past studies have found that the winter survival, spring breeding, and migratory status of nutcrackers may depend entirely on an individual's ability to locate and store sufficient quantities of conifer seed in autumn. Despite these important findings, most studies of the life history strategies of Clark's Nutcrackers in the wild have relied only on visual observations of groups of nutcrackers; Tomback (1978), Vander Wall and Balda (1977), and Vander Wall et al. (1981) primarily collected data on nutcrackers gathering in conspicuous flocks to harvest seeds. Additionally, past studies have not collected behavior data on individuals or the response of individuals to variable seed production.

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 rarely occurs, although altitudinal migration is common. In California, Tomback (1978) observed nutcrackers concentrated at high elevations in summer where they foraged on communal caching grounds. These flocks remained at high elevations through early autumn when high elevation whitebark pine seeds were harvested. Beginning in October large flocks appeared in low elevation Jeffery 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 followed by Jeffery pine seeds which ripened at low elevations in September. Tomback (1978) concluded that an autumn altitudinal migration had occurred in this population because these flocks were observed at low elevations throughout the winter and early spring months.

I tested the hypothesis that Clark's Nutcrackers exhibit an autumn altitudinal migration in one population in Washington State. The elevational distribution of whitebark and ponderosa pines in Washington's Cascade Range is similar to the elevational distribution of whitebark and Jeffery pines described by Tomback (1978) in

the Sierra Nevada Range of California. In both locations there is little or no overlap in

productive stands of high elevation whitebark pine versus low elevation ponderosa pine

(Washington) and Jeffery pine (California). In Washington whitebark pine typically

occurs in stands between 1640–1890 m and ponderosa pine dominates stands between

700–1440 m (Burns and Honkala 1990). In the Sierra Nevada, whitebark pine occurred

on study sites between 2670–3150 m and Jeffery pine was common on sites between

2100–2300 (Tomback 1978). Moreover, in both locals Clark's Nutcracker typically

harvests whitebark pine seeds in late summer or early autumn and prior to harvesting

lower elevation Jeffery/ponderosa pine seeds (Tomback 1978, Dimmick 1993, Lorenz,

pers. obs.).

If nutcrackers migrate altitudinally between summer and autumn, I predict that

there will be no overlap in summer and autumn ranges. Nutcrackers will reside in high

elevations in summer and early autumn and vacate high elevations after the harvest of

whitebark pine seeds in September. I predict that all of their daily activities after this

point will occur at low elevations where they plan to overwinter and breed.

I 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 I predict summer and autumn home ranges will

overlap and home range size will increase in autumn. I also predict nutcrackers will

continue to use high elevations after the whitebark pine seed harvest season. In

anticipation of winter and spring energetic needs, nutcrackers will cache seeds within

their summer home range whereas seed harvesting will occur both within and outside of

the summer home range and at a range of elevations.

CHAPTER 2

METHODS

Study Area

I studied nutcracker space use in 2006 and 2007 in the Cascade Range 40 km west of Yakima, WA (approximately 120°58' W, 46°45' N). The study was conducted within an area bordered by US 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 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 km^2 and the boundaries were delineated along major ridges and river valleys to encompass the movements of all resident Clark's Nutcrackers under study. Elevation ranged between 525 m in some valleys to 2358 m on mountain peaks. The vegetation varied from non-forested 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
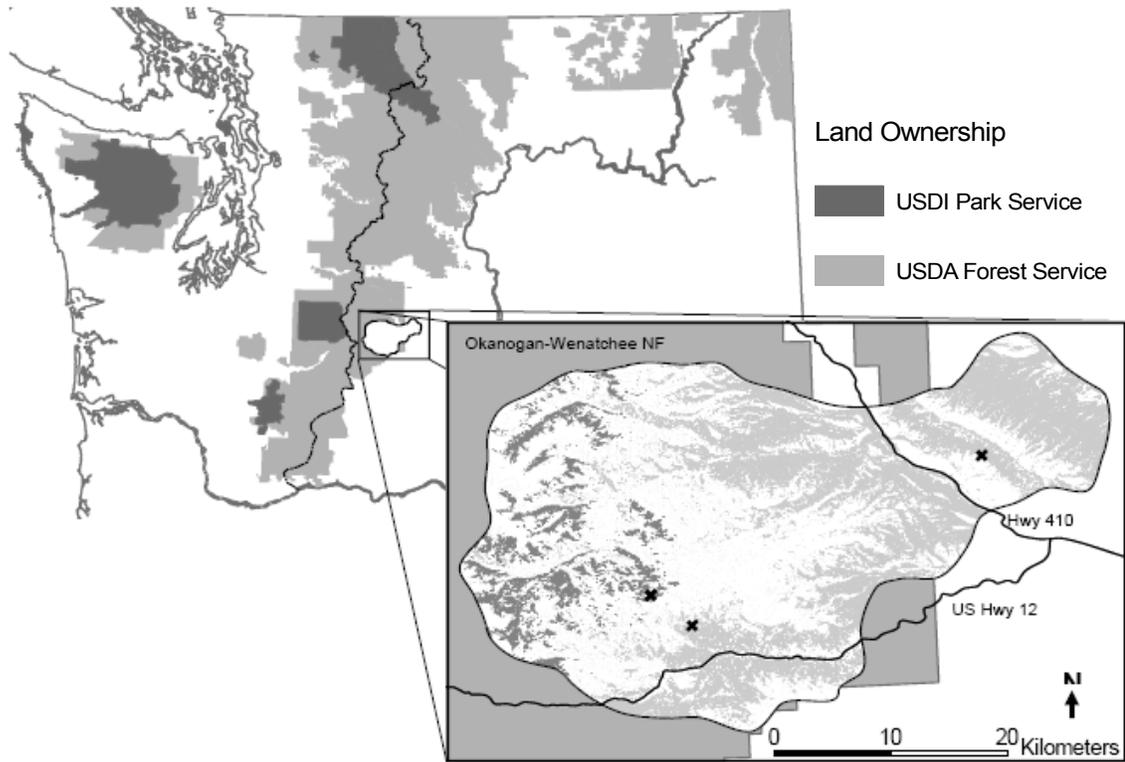
Figure 1. Map of study area in central Cascade Range of Washington State. Shaded areas in study area inset map show extent of whitebark pine (darker gray) and ponderosa pine (lighter gray) within study area. Markers (**x**) show locations of the three trap sites for capturing and radio tagging Clark's Nutcrackers.

dominant in forests within the study area. Both prescribed and wild fires were

common in the study area. Approximately 5300 ha of prescribed under-burns had

occurred in mixed ponderosa pine and Douglas-fir stands, 1500 ha of wildfire had

occurred in mixed ponderosa pine forests, and 750 ha of wildfire had occurred in mixed

whitebark pine forests within the last five years (J.W. Bailey, pers. comm.).

Cone Counts

I conducted cone counts on 40 whitebark pine trees in July of 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 portable a Global Positioning System (GPS). I counted cones visible on the

north and south facing side of each tree using 8 x 42 binoculars. I conducted cone counts

to compare the relative abundance of whitebark pine seed between years rather than to

estimate the actual number of cones produced within this population.

Telemetry

I used radio telemetry to collect space use data on nutcrackers. I captured

nutcrackers at three trap sites. One trap site was located 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. I captured nutcrackers

in mist nets and noose carpet traps at feeding stations baited with raw beef suet. I found

that nutcrackers were most readily attracted to feeding stations in late winter and early

spring and therefore most trapping occurred from March through June and under wintry

conditions. All nutcrackers were banded, weighed, and aged as either hatch-year (hereafter referred to as juvenile) or after hatch-year (adult) based on plumage characteristics and the color of the mouth lining (Mewaldt 1958). I also measured wing chord and tarsus and tail length. Males are larger than females in all measurements although there is overlap between measurements of wing chord, tail, and weight (Mewaldt 1948). I did not distinguish between sexes in my study because wing chord, tail, and weight measurements were affected by substantial feather wear and feeding activity 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 battery lasted approximately 415 days.

I radio tracked nutcrackers from June through October 2006 and from April through October 2007. I placed locations of radio tagged nutcrackers into either the summer or autumn season. 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, I defined summer as the period between 13 June and 9 August, and autumn as the period between 10 August and 29 October. In 2007 I defined summer as the period between 1 May and 7 August, and autumn as the period between 8 August and 1 November. I chose 10 August and 8 August as the dates for differentiating between summer and autumn in 2006 and 2007 because they were the first dates in each year in which I observed radio tagged nutcrackers placing seeds in their sublingual pouch for storage purposes.

I conducted focal observation sessions during which nutcrackers were tracked as continuously as possible for 1–2 hours per week in summer and 1–6 hours per week in autumn. I 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 I also noted the type of food that was being consumed, when known, and I recorded the species of tree for all observations involving foraging, seed harvesting, and seed caching. I obtained additional telemetry locations on each nutcracker by relocating each individual at least twice weekly outside of focal observation sessions. I arbitrarily selected times for focal observations sessions and for collecting additional relocation points that were separated by at least 24 hours. Overall, each individual was relocated on at least three different days during each week throughout both the summer and autumn seasons.

Tracking periods were spread over a range of daylight hours and weather conditions. 64% of points were obtained during morning hours and 36% of points were obtained during the afternoon or evening. On average I obtained 9 points (± 5 points) per week on each bird in summer and 34 points (± 13 points) per week on each bird in autumn. I allocated more effort to the autumn season because nutcrackers ranged more widely in autumn compared to summer. Additionally, I commonly observed long distance seed transport in autumn. 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, by stationing observers in the harvest stand and along the

flight path I are confident that I located the final cache sites for seeds that nutcrackers transported long distances.

I obtained point locations on telemetered nutcrackers mostly by homing (94% of points) although I used triangulations when nutcrackers were using inaccessible cliffs within their home range (6% of points). I recorded point locations obtained from homing in the field using a handheld GPS. Error associated with GPS fixes ranged from 3–8 m. I considered triangulations successful if I obtained 2–3 azimuths on a nutcracker during a 5 minute period. If it was apparent from a change in directionality or strength of the signal that the nutcracker had moved within that 5 minute period, I discarded the triangulation attempt. I 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 I 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 I obtained more points in the second year, within each year I allocated fairly equal effort among individuals each week. While I attempted to obtain behavior observations in all habitat types, radio tagged nutcrackers ranged over terrain that was steep and rugged and included vertical cliffs. Therefore it was not logistically possible to obtain behavior observations on nutcrackers at all times. As noted above, I obtained triangulations on birds when they were using inaccessible parts of their home range but it is possible that I underestimated the number of seed harvesting and caching events that occurred on cliffs and rock faces.

Residency Status

I captured and radio tagged resident nutcrackers in 2006 and both resident and emigrant nutcrackers in 2007. In 2007 I 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. I considered a nutcracker to be an emigrant if 1) I lost its radio signal in the study area by early July, or 2) it died before July 1 but it showed continued directional movement away from the trap site while alive. In July 2007 I surveyed my study area via aircraft to confirm the number of resident nutcrackers. During August of 2007 I additionally conducted 44 hours 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 US-Canadian border (49th parallel) to the north, the 120th meridian to the east, the 46th parallel to the south, and the Cascade Crest to the west.

The radio tags used in this study were not equipped with mortality sensors. However, I homed to all nutcrackers at least once weekly throughout the study period. I recovered the radio tags of all nutcrackers that died during the study within seven to twelve 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 compared to resident nutcrackers I obtained little space use data on these individuals. While emigrants resided in the study area, I used minimum convex polygons (MCPs) to describe their range of space use for individuals with more than 10 telemetry locations. I

did not consider these MCPs to accurately describe a spring or summer home range, however, because I were unable to obtain a sufficient sample size of telemetry locations before they emigrated.

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

I performed 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). With the exception of focal observation sessions my data were discontinuous and therefore I randomly selected points for area-observation curves (Harris et al. 1990). To determine whether the number of point locations used per season affected the estimate of home range size, I 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 estimate of the summer kernel ($n = 5$, $r^2 = 0.01$, $P = 0.88$) or autumn kernel ($n = 5$, $r^2 = 0.01$, $P = 0.85$) estimates.

To minimize bias associated with autocorrelation I did not use all relocation points from focal observation sessions when estimating resident home ranges (Kernohan et al. 2001). To determine which points to use in my home range estimates I plotted the

100% MCP of each individual on a Geographic Information System (GIS) and

measured the length of each home range. I used a GIS to determine the distance between

consecutive relocation points obtained during 1–3 hour focal observation sessions during

which the bird was tracked without interruption (M.G. Raphael, A.V. Bakian, pers.

comm.). I determined that nutcrackers on average traversed a distance approximately

equal to the length of their 100% summer MCP once hourly in summer and once every

38 minutes in autumn. For home range estimation I used only focal session points that

were separated by at least 60 minutes in summer and 38 minutes in autumn.

I assessed differences in the range of summer and autumn movements by

residents and emigrants although I did not obtain enough points on emigrants to estimate

home ranges and conduct statistical tests. I also compared differences in foraging and

seed harvesting behavior for residents and emigrants. I conducted statistical tests only on

seasonal differences in space use for residents and I used 95% fixed kernels for all

hypothesis testing. I 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**

I used one-tailed paired t-tests to test the hypothesis of an increase in home range

size from summer to autumn ($P < 0.05$). I 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 UDs come from a common distribution. I computed MRPP using ordinary Euclidean distances in BLOSSOM statistical software (Cade and Richards 2000). I used ordinary Euclidean distances because they have greater power over a wider range of distributions compared to squared Euclidean distances (Zimmerman et al. 1985).

I assessed the static interaction of summer and autumn ranges by computing both the area and volume of overlap. I 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 I calculated the proportion of overlap of the summer and the autumn range ($S_{summer, autumn}$) (White and Garrott 1990). I calculated the volume of overlap of summer and autumn ranges 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. I 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. I compared the elevation of summer and autumn range centroids and used one-tailed paired t-tests to test for significant differences.

I considered residents altitudinal migrants between autumn and summer seasons 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 high elevation conifer seed sources in July and August and switched to low elevation seed sources in September and October. Rather than migrating between distinct summer and autumn ranges, nutcrackers may therefore migrate altitudinally within the autumn seed harvest season. To determine whether nutcrackers migrate altitudinally within autumn I determined the mean elevation used by individuals within each week of the seed harvest season and regressed week on mean elevation for the twelve week autumn season (6 August through 1 November). Using data from focal observation sessions I 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 high elevation whitebark pine versus low elevation ponderosa pine/Douglas-fir seed harvest seasons. I compared these mean elevations to the elevation of the summer home range centroid.

From focal observation sessions I determined the number of autumn cache and harvest events that occurred inside versus outside of the summer range. I also measured the distance between the summer range centroid (SRC) to each individual autumn seed harvest and cache event. I compared means of these distances (SRC to caches and SRC to harvest trees) to the distance between the SRC and all summer movements. I used this to assess whether nutcrackers traveled within the range of summer movements when caching and harvesting seeds in autumn. I determined distances from SRC to harvest trees and cache sites separately for whitebark and ponderosa pine. I used Mann-Whitney U-tests to test for differences in these travel distances.

I considered resident nutcrackers altitudinal migrants within autumn if (1) there was a significant decrease in mean elevation of point relocations over the course of autumn, (2) there was a significant difference in the mean elevations used for seed harvest, seed caching, and 'other' activities between the whitebark and ponderosa pine seed harvest seasons, and (3) during the whitebark pine seed harvest season nutcrackers harvested and cached seeds within the summer range, but during the ponderosa pine seed harvest season they harvested and cached seeds outside of this range.

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

CHAPTER 3

RESULTS

I captured 31 nutcrackers at three locations between 2006 and 2007; 27 adult and two juvenile nutcrackers were radio tagged. I classified five adult nutcrackers as residents and 19 adults and two juveniles as emigrants. I could not determine the migratory status of three adults because they exhibited characteristics of 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 five weeks after capture.

I counted an average of 43 ($\pm$ 38) cones on whitebark pine trees in 2006 (n = 40) and 22 ($\pm$ 27) cones in 2007 (n = 40). I did not conduct cone counts 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 on 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 through early summer. I

captured and radio tagged 21 emigrants in the spring following this large whitebark pine

cone crop and monitored their movements from April through July of 2007. During this

time emigrants ranged up to 7540 ha (100% MCP) in area and between 785 and 2118 m

in elevation (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).

I observed 181 foraging events totaling 755 minutes by emigrants (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 on communal caching

grounds (71% of observations). Emigrants foraging on germinating seedlings scrutinized

the ground surface, particularly focusing 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). I did not observe emigrants retrieving caches from memory.

Emigrants also foraged in other parts of the study area on insects and ponderosa pine

Table 1. 100% minimum convex polygon range size (ha) of and range of elevations (m) used by migrant nutcrackers.

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

[a] Nutcrackers were aged as either juvenile (hatch-year) or adult (after hatch-year) according to Mewaldt (1958) and A=adult and J=juvenile.
[b] [1] denotes a nutcracker that was depredated (043[1] and 621[1]) or shed its tag (220[1]) and the same tag was later fitted to a second nutcracker within the same year (621[2] and 220[2]).

Table 2. Daily use of different elevations by emigrant nutcrackers on the study area during summer 2007. Whitebark pine typically occurred in stands between 1640–1890 m and ponderosa pine dominated between 700–1440 m.

Emigrant nutcracker	Date	Daily change in elevation (m)	Daily maximum elevation (m)	Daily minimum elevation (m)
043[1]	15 May	236	1762.66	1526.74
	23 May	-385	1826.67	1441.40
	1 June	290	1740.10	1449.63
107	1 June	582	1620.32	1038.15
	12 June	435	2036.37	1601.11
	14 June	-70	2001.01	1931.21
240	23 May	170	1919.63	1749.25
	29 May	79	1871.78	1792.83
382	15 May	-66	1783.08	1717.24
	5 June	-196	1621.54	1425.55
422	31 May	-231	1655.67	1424.94
	1 June	-18	1638.60	1620.32
	14 June	69	2003.76	1934.57
	18 June	36	2060.45	2024.48
	23 June	-153	2118.06	1965.35
	26 June	-134	1496.57	1362.15
	2 July	106	2036.98	1931.21
483	23 May	-40	1316.13	1276.50
505	28 May	-504	1854.40	1349.96
	12 June	-191	1835.20	1644.70
	13 June	-52	1756.56	1704.14
	21 June	-203	1693.77	1490.78
529	23 May	239	1528.57	1289.91
	1 June	-22	1800.45	1778.81
	7 June	25	1696.21	1671.22
591	15 May	301	1852.57	1552.04
	22 May	-44	1780.64	1736.75
	14 June	-151	2058.31	1907.13
	18 June	97	2033.02	1935.78
733	15 May	36	1798.32	1762.66
	23 May	235	1640.43	1405.43
	28 May	-447	1626.11	1178.97

Table 3. Number (proportion) of independent foraging events and total time (proportion) spent foraging for different 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 personal 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

seeds retained in cones from the previous autumn's cone crop. When engaged in prolonged searches and foraging on ponderosa pine seed 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 a six week period 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 between 157 and 737 ha (100% MCP) (Table 4) and between 957 and 1841 m elevation. I observed 140 foraging events by residents totaling 432 minutes and they predominately foraged on insects in their summer home range (Table 3). I 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. I did not observe residents visiting or engaging in prolonged searches on communal caching grounds. Residents foraged only singly or in small groups of two to ten individuals and this contrasted markedly with the characteristically large and vocal flocks of emigrants. Composition of resident summer home ranges varied. All home ranges contained ponderosa pine and

Table 4. Summer and autumn home range size estimates (ha) of resident Clark's Nutcrackers. 95% kernel estimates most accurately depicted space use by all nutcrackers and were used for all analyses.

Resident nutcracker	Season	n	50% Kernel Estimate	95% Kernel Estimate	99% Kernel Estimate	95% Minimum Convex Polygon	100% Minimum Convex Polygon
Whitebark pine residents							
043	summer	36	12.32	157.00	245.64	139.18	157.36
043	autumn	122	109.52	732.91	1838.80	1747.65	4478.10
893	summer	34	48.93	547.02	940.71	664.02	737.04
893	autumn	127	245.62	1356.88	3150.09	3652.91	5411.73
719	summer	30	25.56	197.72	267.19	117.80	154.56
719	autumn	82	32.89	317.90	712.12	400.41	835.89
Ponderosa pine burn residents							
211	summer	31	31.11	473.68	628.43	353.45	356.98
211	autumn	67	144.95	962.16	2389.99	1140.16	1631.48
505	summer	29	15.88	216.22	385.34	207.26	306.67
505	autumn	34	88.43	1028.66	2113.76	9468.30	11464.46

Douglas-fir seed sources and three out of five home ranges also contained whitebark

pine. Two home ranges were located within a four-year-old mixed severity burn in an

open ponderosa pine stand with a southwesterly aspect.

Three home ranges were on a ridgeline that contained mixed whitebark pine and

mountain hemlock on northerly aspects and ponderosa pine, Douglas-fir, and grand fir on

southerly aspects. All five resident 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. I 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, WA (approximately 120°15' W, 48°6'

N). Itracked 591 only during the whitebark pine seed harvest season. It ranged over 274

km^2 in August and crossed Lake Chelan to Domke Lake (approximately 120°36' W,

48°10' N) before its radio signal was lost on 5 September. I assumed it continued

wandering and left the Washington Cascades because I did not relocate it on two flights

and nine hours of aerial tracking in mid-September. Because of logistical constraints,

between 22 August and 5 September I only obtained relocation data on five days and

seed harvest and caching data on two days. I 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 250 km^2 and between mid-elevation

transitional forest types at 1354 m and high elevation whitebark pine stands at 2123 m. I

did not observe it retrieve its caches before emigrating and to my 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, WA (approximately 120°53' W, 47°29' N) and ranged over 175 km^2 (100% MCP) during the whitebark pine seed harvest season (August 16 to September 14). It moved between ponderosa pine stands at 721 m and whitebark pine stands at 1974 m during this time. It was not logistically possible to watch seed harvesting and caching by 505 at all times because it was harvesting and pouching seeds on near vertical cliffs. I estimated using triangulations that nutcracker 505 was traveling between 600 and 1700 m between harvest trees and caching grounds. After September 14 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. Whitebark pine seeds were harvested at 2075 m elevation and Douglas-fir and ponderosa seeds were harvested 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 throughout autumn. There were considerable differences in the size of areas that residents ranged over when harvesting seeds. One individual was never observed traveling more than 4 km from its

home range center whereas another individual traveled upwards of 29 km and ranged over 115 km^2 for seed harvesting purposes (Table 4). All five residents harvested ponderosa pine seed but only four also harvested whitebark pine seed and three additionally harvested Douglas-fir seed. I observed 215 whitebark pine seed harvest events by four resident nutcrackers, 225 ponderosa pine seed harvest events by five nutcrackers, and 16 Douglas-fir seed harvest events by three nutcrackers. I observed four resident nutcrackers place a total of 205 seed caches; 108 whitebark pine seed caches by two nutcrackers and 97 ponderosa pine/Douglas-fir seed caches by four nutcrackers. Residents harvested whitebark pine seeds at high elevations both individually and in loose flocks of up to 100 individuals. When harvesting low elevation ponderosa pine seed 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. I also observed that resident nutcrackers harvested, transported, and cached seeds purposefully and often in a rather hasty manner. 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 harvest stands where they filled their sublingual pouches for up to 80 minutes. Once pouches were full or nearly full they departed from the harvest stand and flew off in the direction of the summer range. Within 5 to 25 minute, these same individuals were observed flying into the summer range with full sublingual pouches and where I observed them caching seeds. After caching seeds for 20 to 40 minutes, 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 residents could fill their pouches in the harvest stand.

Residents: Statistical Analyses for Altitudinal Migration Between Summer and Autumn

I obtained 503 summer and 1582 autumn point locations from residents and I used 190 and 432 point relocations for estimating summer and autumn home ranges, respectively. Area-observation curves reached an asymptote with 25 points for the summer season and 45 points for the autumn season. 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). Home range size of all residents increased in autumn ($t_4 = 4.4$, $P_{one-tailed} = 0.006$) and the UDs 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 ($S_{summer, autumn} = 0.75 \pm 0.17$) (Table 5). The volume of overlap of summer on autumn ranges was 0.70 ± 0.22 and 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 ± 274 m) and autumn range centroids (1426 ± 383 m) ($t_4 = 1.3$, $P_{one-tailed} = 0.14$).

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)[1]	Proportion of summer range overlapped by autumn range ($S_{summer, autumn}$)[2]	Volume of intersection of summer on autumn ranges ($VI_{summer, autumn}$)[3]	Volume of intersection of autumn on summer ranges ($VI_{autumn, summer}$)
043	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

[1] $AO = \dfrac{summer \cap autumn}{summer \cup autumn}$ (Siedel 1992)

[2] $S_{summer, autumn} = \dfrac{summer \cap autumn}{summer}$ (White and Garrott 1990)

[3] $VI = \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \min(\hat{f}_{summer}(x,y), \hat{f}_{autumn}(x,y))\,dxdy$ (Siedel 1992, Millspaugh et al. 2004)

**Residents: Statistical Analyses for Altitudinal
Migration Within Autumn**

Nutcrackers shifted their seed harvest 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, 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 low elevation areas as autumn progressed.

The regression of elevation on week had a poor fit however, because as autumn progressed nutcrackers only shifted their seed harvest efforts to low elevations. They continued to use high elevations for all other activities (Fig. 2, Fig. 3). I 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) ($t_1 = -18.1$, $P_{one-tailed} = 0.02$) 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) versus ponderosa pine/Douglas-fir seeds (1773 ± 13 m) ($t_1 = 1.6$, $P_{one-tailed} = 0.19$).

Pooling observations for all resident nutcrackers, mean elevation for seed harvest observations was 1814 ± 55 m for the whitebark pine season ($n = 3$ residents) and 1025 ± 528 m for ponderosa pine/Douglas-fir season ($n = 5$ residents). Mean elevation for seed caching observations was 1750 ± 7 m for the whitebark pine ($n = 2$ residents) season 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,
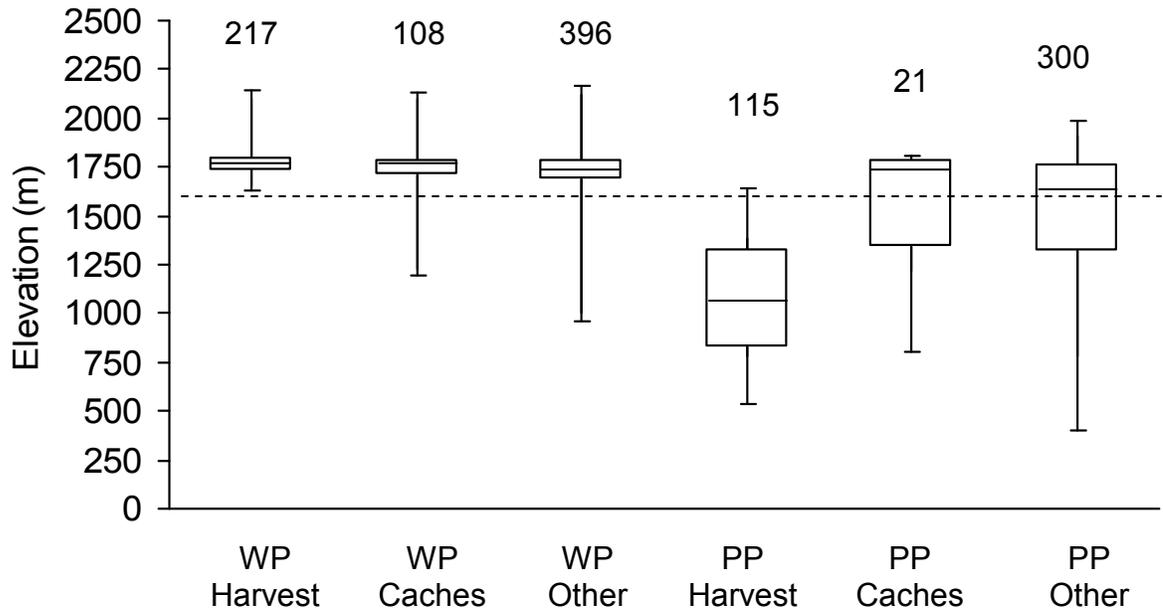
Figure 2. Elevation (m) used for seed harvest, seed caching, and other activities during the whitebark (WP) and ponderosa (PP) pine seasons by three adult Clark's Nutcrackers with a summer home range in a whitebark pine stand. Observations of activities are pooled for all nutcrackers. The rectangle represents interquartile range, the center line inside represents median, and the whiskers represent minimum and maximum values. Numbers above individual box plots indicate sample sizes and dashed line indicates mean elevation of summer home range centroid.
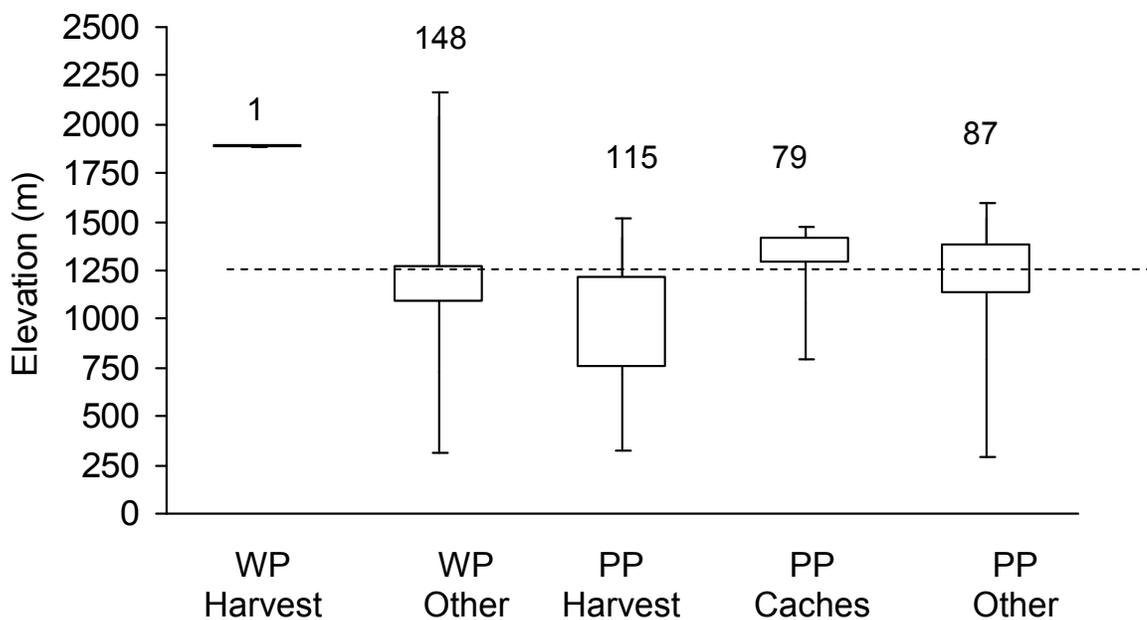
Figure 3. Elevation (m) used for seed harvest, seed caching, and other activities during the whitebark (WP) and ponderosa (PP) pine seasons by two adult Clark's Nutcrackers with a summer home range in a ponderosa pine burn. Observations of activities are pooled for both nutcrackers. The rectangle represents interquartile range, the center line inside represents median, and the whiskers represent minimum and maximum values. Numbers above individual box plots indicate sample sizes and dashed line indicates mean elevation of summer home range centroid.

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 ($t_4 = 1.6$, $P_{one-tailed} = 0.09$). In relation to the summer range centroid (SRC), whitebark pine seeds were harvested 205 ± 338 m above the SRC whereas ponderosa pine/Douglas-fir seeds were obtained 507 ± 301 m below the SRC. There was much less variability in the elevations nutcrackers used for caching seeds and they cached all seeds at nearly the same elevation as their SRC. On average whitebark pine seeds were cached 17 ± 9 m below the center of the SRC and ponderosa pine/Douglas-fir seeds 31 ± 41 m above the center of the SRC.

During both the whitebark and ponderosa pine seed harvest seasons, 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 SRC and within the range of summer movements. For example, I observed that in summer nutcrackers were detected on average 0.6 ± 1.4 km from the SRC. This distance was not different from the average distance traveled between the SRC and autumn caching relocations ($n = 5$, $U = 1.0$, $P = 0.27$), although it was significantly less than the average distance between the SRC and autumn harvest relocations ($n = 5$, $U = 2.5$, $P = 0.01$) (Fig. 4).

Overall, caches were located closer to the birds' SRC (1.1 ± 0.5 km) than 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 SRC, and ponderosa pine
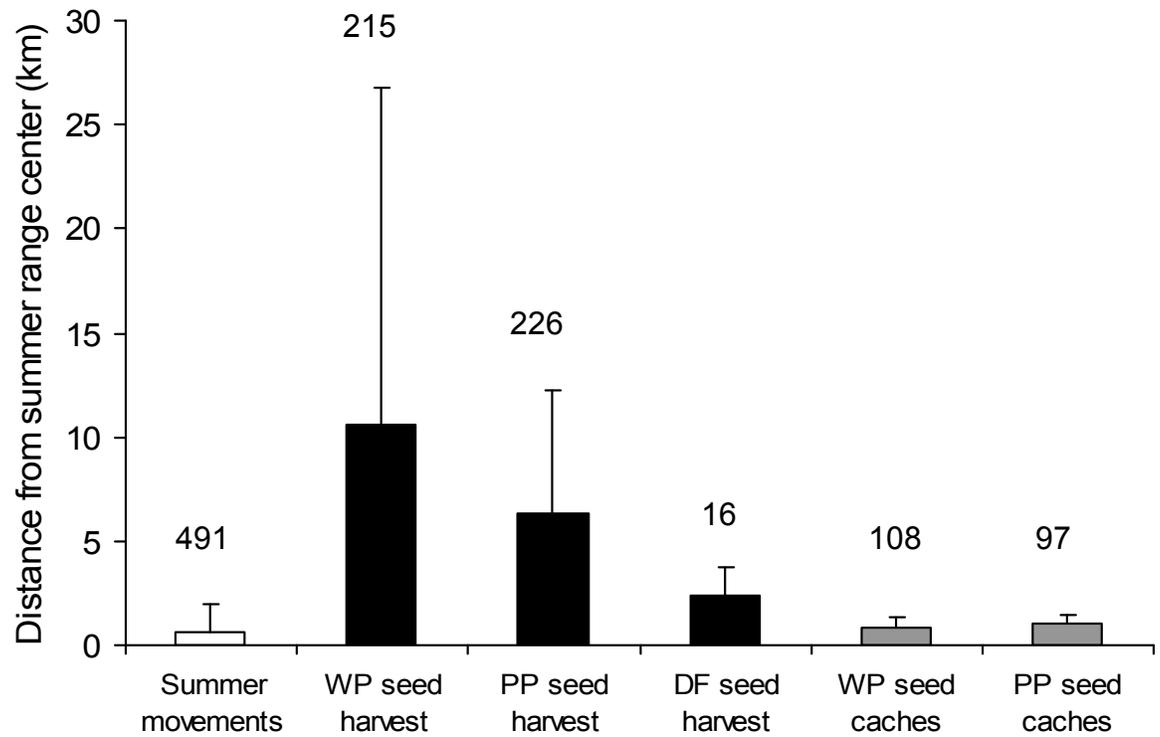
Figure 4. Mean distances traveled (km) by resident Clark's Nutcrackers from summer home range center to all summer movements and all autumn whitebark (WP), ponderosa (PP), and Douglas-fir (DF) seed harvest and caching events. Data are pooled for all five residents. Bars represent means ± SD and numbers above bars represent sample sizes.

and Douglas-fir seeds up to 25.5 (6.3 ± 6.0 km) and 3.8 (2.4 ± 1.3 km) km from their

SRC, 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 SRC. Thus, irrespective of

the distances and elevations required to transport seeds, resident nutcrackers in my study

placed seed caches of all tree species either within or very close to their summer home

range.

CHAPTER 4

DISCUSSION

Resident Clark's Nutcrackers in this study 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 high elevation (1640–1890 m) whitebark pine seeds in early autumn or low elevation (700–1440 m) ponderosa pine/Douglas-fir seeds in late autumn. 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 residents in this population do not migrate altitudinally at any time during the year. Overall, my inferences are limited because of small sample sizes. However, this study is the first to demonstrate that nutcrackers in one population in the Cascade Range are nonmigratory and that summer ranges of residents may represent the core of year-round space use.

While residents did not migrate altitudinally in this study, they did use space differently between summer and 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 in this study 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. I observed residents transporting seeds up to 29.2 km from harvest stands to cache sites. My 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, Hutchins and Lanner 1982, Vander Wall 1988, Dimmick 1993). While 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). This study is the first to show that residents 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, long distance seed transport was common in this study. For example, the average seed transport distance for whitebark pine in this study (10.6 km) was nearly as great as the previously reported maximum seed transport distance for whitebark pine (12.5 km) (Tomback 1978). I feel that long distance seed transport may be underreported in the literature since past studies relied on visual observations of seed transport and were unable to continuously track individuals 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 over-winter and breed. Even through large amounts of energy might be expended during autumn for seed transport, nutcrackers are typically

not food limited during autumn 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 additionally enhance their fitness if they cache seeds within their own, familiar, year-round home range. This is because individuals are cognizant of how to best find food and evade predators in their home range.

Although I did not test hypotheses regarding space use by emigrant nutcrackers my results suggest that like residents, emigrants do not exhibit altitudinal migration. During both summer and autumn emigrants moved over large geographic areas compared to residents and over a range of elevations that encompassed both whitebark and ponderosa pine cover types. In both seasons emigrants frequently moved between ponderosa and whitebark cover types in one day and there was no trend in movements by emigrants either upslope in summer or downslope in autumn. Space use by emigrant nutcrackers in my study was complex and was poorly described by altitudinal migration.

Collectively my results show that there are differences in space use between residents and emigrants. As such, my results provide the first empirical support for a model of differential space use by resident and emigrant nutcrackers first proposed by Vander Wall et al. (1981). As predicted by Vander Wall et al. (1981) all residents in my study occupied home ranges in which several species of large-seeded conifer were available within seed transport distance. In autumn, they harvested seeds from many sources although they demonstrated fidelity to the summer home range for all other activities, especially seed caching. I 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. I suggest that these individuals originate from home ranges in landscapes that are less diverse such that seed production is not consistent enough between years 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 in conifer stands where food availability is very high 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. I do not know the locations of the natal ranges of emigrant nutcrackers radio tagged in my study because I have no data on their movements prior to their capture in spring 2007. I therefore have no information on whether emigrants in my study originally occupied landscapes without multiple seed sources. However I observed that radio tagged emigrants ranged widely in autumn compared to residents. In late autumn, I observed that one emigrant settled in a location where three species of conifer were producing cones. Additionally, I 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.

I observed seed harvest and caching by two emigrants in autumn. Before settling they cached seeds in harvest stands although these seed cache were not retrieved before they emigrated from the area. Despite the apparent wasted energy, emigrants have very little to lose by caching seeds in harvest stands as they travel but possibly much to gain. The energy expended to cache seeds in the harvest stand is fairly minimal since seeds are not transported long distances. Emigrants would benefit from placing the seeds in personal caches because these seeds are thus made unavailable to other seed predators in the harvest stands. As predicted by Vander Wall et al. (1981), emigrants travel on a regional scale to locate the most productive harvest stands. 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 a more productive stand of conifer is located, an emigrant could readily settle. Under these circumstances a winter home range would be established and seeds cached previously in other regions would be abandoned.

Clark's Nutcrackers in my study did not migrate altitudinally. A portion of my study 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 boundary although seeds were cached 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 further investigate differences in space use by resident and emigrant nutcrackers.

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 caching decisions by nutcrackers is becoming increasingly important as 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. These results show that seed dispersal by nutcrackers in some populations is affected by multiple factors, such as migratory status and the position of the summer home range relative to autumn seed sources. Ultimately, nutcracker caching decisions affect community composition in many forests in western North America, and whitebark pine ecosystems in particular. I 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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