Temporal and energetic drivers of seed resource use by Clark’s nutcracker, keystone seed disperser of coniferous forests

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Citation: Williams, T. J., D. F. Tomback, N. Grevstad, and K. Broms. 2020. Temporal and energetic drivers of seed resource use by Clark’s nutcracker, keystone seed disperser of coniferous forests. Ecosphere 11(3):e03085. 10.1002/ecs2.3085

Abstract. Clark’s nutcracker (Nucifraga columbiana) functions as a keystone seed disperser and ecological mobile link for many western conifers. The bird is the primary seed disperser for limber pine (Pinus flexilis), which is an important seed resource for the bird. In the Southern Rocky Mountains, annual variation in limber pine cone production and growing threats, such as exotic disease, require that nutcrackers rely on additional conifer seed resources. We investigated the utilization of limber pine, ponderosa pine (Pinus ponderosa), and Douglas-fir (Pseudotsuga menziesii) as seed resources by nutcrackers to determine how temporal variation in seed production and maturation drives nutcracker seed resource and habitat use decisions. Working in Rocky Mountain National Park (RMNP) during three field seasons, we examined (1) cone production in limber pine, ponderosa pine, and Douglas-fir, and seed energy availability across the RMNP landscape; (2) timing and likelihood of nutcracker seed harvest and caching behavior for each conifer species; and (3) predictors of nutcracker visitation to the different forest stand types. Each year starting in mid- to late August, nutcrackers foraged on limber pine seeds. In 2014 and 2015, nutcrackers transitioned from limber pine to harvesting ponderosa pine seeds. In 2016, a year of low ponderosa pine cone production but exceptionally high Douglas-fir cone production, they transitioned from limber pine to Douglas-fir seeds. Cone density was a significant predictor of nutcracker counts in every negative binomial regression model in which it was used. However, the best overall model, which included interaction effects, indicated that stand type, year, and month were better predictors. We interpret these three predictors as reflecting temporal variation in patterns of cone production and maturation among the three conifers but also in habitat use by nutcrackers. In all three years of study, limber pine alone did not provide sufficient energy resources for foraging and caching, and nutcrackers used an additional conifer seed resource. With potential future limber pine losses, these other seed resources may be essential to sustain a nutcracker population. We suggest that Douglas-fir and especially ponderosa pine will serve as increasingly important food resources as limber pine declines across the montane West.

Key words: carrying capacity; Clark’s nutcracker; Douglas-fir; landscape energetics; limber pine; Nucifraga columbiana; ponderosa pine; Rocky Mountain National Park; seed resources; white pine blister rust.

Received 24 October 2019; revised 20 December 2019; accepted 6 January 2020; final version received 10 February 2020. Corresponding Editor: Paige S. Warren.

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**INTRODUCTION**

Clark’s nutcrackers (*Nucifraga columbiana*) are keystone seed dispersers: They disseminate seeds for a number of conifers throughout the mountains of the western USA and Canada (Tomback 1998, Tomback and Kendall 2001). Seed dispersal results from the tendency of nutcrackers to store conifer seeds in caches buried in mountain terrain for retrieval during periods of food scarcity (Vander Wall and Balda 1977, Tombok 1978, Hutchins and Lanner 1982). Nutcracker-mediated seed dispersal is “directed seed dispersal” and considered one of the more highly specialized examples of this syndrome (Wenny 2001). Nutcrackers frequently deliver seeds to ecologically suitable microsite safe sites that facilitate conifer seed survival and germination and influence tree distribution on the landscape (Tomback and Linant 1990, Tomback 2005). Seeds in unretrieved nutcracker caches may germinate after snowmelt or spring and summer rains, which often leads to seedling survival and forest regeneration (Tomback 1982, Tomback et al. 2001).

In late summer and fall, nutcrackers harvest conifer seeds and transport them in their sublingual (throat) pouches to cache nearby or tens of kilometers away for retrieval and consumption during winter and spring (Vander Wall and Balda 1977, Tomback 1978, Lorenz and Sullivan 2009). The dispersal services provided by nutcrackers include long-distance seed dispersal, local tree establishment after disturbances such as insect outbreaks or wildfire, ongoing forest replacement over time, and facilitating distributional changes in conifers in response to changing climate (Tomback and Linhart 1990, Tomback 2001, Tomback et al. 2001, 2011). Nutcracker seed dispersal over long distances enables small, isolated stands of pines, including limber pine (*Pinus flexilis*), to function as a metapopulation by connecting them through seed dispersal flights (Webster and Johnson 2000, Williams 2017).

Nutcrackers function as obligate seed dispersers for whitebark pine (*Pinus albicaulis*), important seed dispersers for related white pines with large, wingless seeds (*genus Pinus*, subgenus *Strobus*), and opportunistic seed dispersers for other conifer species with smaller, winged seeds (Tomback 1998, 2001, Tomback and Kendall 2001, Tomback et al. 2011). Several conifer species that are not strongly dependent on nutcrackers for seed dispersal, however, may be more important to nutcracker ecology and the stability of their populations than previously recognized. In this paper, we explore this potential role in two such species, ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*).

Studies often emphasize that nutcrackers use white pines with large, wingless seeds as preferred food resources. For example, Tomback (1978) studied nutcrackers harvesting and caching whitebark pine seeds in California, and Benkman et al. (1984) and Vander Wall (1988) described nutcrackers foraging for limber pine seeds in Arizona and Utah, respectively. Nutcrackers also forage on and disperse the large, wingless seeds of southwestern white pine (*Pinus strobus*; Benkman et al. 1984, Samano and Tomback 2003), Colorado pinyon pine (*Pinus edulis*; Vander Wall and Balda 1977), and single-leaf pinyon pine (*Pinus monophylla*; Tomback 1978, Vander Wall 1988). Each of these conifer species is an important regional food resource.

Across their range, nutcrackers also utilize conifers with smaller, winged seeds (e.g., see reviews, Tomback 1998, Tomback et al. 2011), which Schaming (2016) refers to as “alternative” seed resources. Tomback (1978) reports the harvest and caching of Jeffrey pine (*Pinus jeffreyi*) seeds following whitebark pine seed use in the eastern Sierra Nevada; Giuntoli and Mewaldt (1978) report nutcracker stomach contents including ponderosa pine and Douglas-fir seeds in addition to whitebark pine seeds in western Montana; Vander Wall et al. (1981) note nutcracker harvest of Douglas-fir seeds in Utah; Lorenz and Sullivan (2009) report use of ponderosa pine and Douglas-fir seeds in the Cascade Range, Washington; and Schaming (2016) observed nutcrackers foraging on Douglas-fir seeds in Wyoming. Nutcrackers also forage on the small, winged seeds of bristlecone pines (*Pinus longaeva* and *Pinus aristata*) throughout the Great Basin and in the southern Rocky Mountains (Lanner 1988, Torick et al. 1996). In addition to these smaller-seeded conifer species, nutcrackers have been observed foraging and caching the large, winged seeds of sugar pine in Oregon (*Pinus
Nutcrackers are energy-sensitive foragers (Tomback 1978, Vander Wall 1988, Barringer et al. 2012). Optimal foraging theory can help contextualize nutcracker seed use decisions. Factors affecting these decisions include search time, handling time, and energetic reward, all of which vary across conifer species, season, and year. Compared to the generally smaller seeds of alternative seed resources, the large, wingless seeds yield substantial energetic rewards and relatively low handling times (Tomback 1978, Vander Wall 1988). However, when seed production in these seed resources is either depleted or otherwise limited, several widely distributed alternative seed resources may be ecologically critical to provide sufficient seed production to sustain nutcracker populations over time.

Conifer species generally vary in magnitude of cone production each year and produce large cone crops only every few years (Krugman and Jenkinson 1974, McCaughey and Tomback 2001). Nutcrackers are known to emigrate long distances when all local seed resources simultaneously fail to produce (Davis and Williams 1957, 1964, Vander Wall et al. 1981). In years when nutcrackers are unable to obtain sufficient energy from large, wingless seeds, the other, energetically less-rewarding seed resources enable nutcrackers to store food for winter and early spring. The degree of reliance on alternative seed resources varies both geographically and across years (Tomback 1982, 1998, Vander Wall 1988). The smaller-seeded conifer species may help to stabilize the seed dispersal mutualisms between nutcrackers and white pines; while some mutualisms appear specific, they may persist over time only because of seed production by these other conifer species (Tomback and Linhart 1990).

Alternative seed resources may become more important as populations of the “five-needle white pines” (Pinus Subsections Strobus and Balfourianae; Gernandt et al. 2005), especially white-bark and limber pine, decline because of multiple current stressors (Tomback and Achuff 2010). These threats include mountain pine beetle (Dendroctonus ponderosae) outbreaks (Gibson et al. 2008, Logan et al. 2010); historical fire suppression (Gruell 1983, Rebertus et al. 1991, Murray et al. 2000); the occurrence of more frequent and severe wildfire (Westerling et al. 2011, Enright et al. 2015); the spread of white pine blister rust, which is caused by the introduced pathogen Cronartium ribicolae (Kearns and Jacobi 2007, Tomback and Achuff 2010); and the impacts of climate change on pine distribution (Tomback and Achuff 2010, Tomback et al. 2011). The ongoing and future loss of the large-seeded five-needle white pines increases the importance of conifer species with smaller, winged seeds for sustaining nutcracker populations.

We examined nutcracker use of limber pine, ponderosa pine, and Douglas-fir seeds and forest habitat across three field seasons in Rocky Mountain National Park (RMNP), Colorado. Nutcrackers were previously observed to use these latter two seed resources in other geographic regions, but our central goal was to determine whether these seed resources are also used in RMNP and, if so, the magnitude of cone production and seasonal timing associated with their use. Our objectives were to estimate: (1) annual cone production of the limber pine, ponderosa pine, and Douglas-fir forest communities, and the total energy each conifer species provided across the landscape in RMNP; (2) the relative numbers, timing, and likelihood of nutcrackers foraging for and caching the seeds of each conifer species each year; and (3) inter- and intra-annual predictors that influence nutcracker visitation of each forest type.

**METHODS**

**Study area**

Rocky Mountain National Park is located in northern Colorado within the Southern Rockies Ecoregion (Drummond 2012). We studied nutcrackers on the eastern slope of RMNP from mid-June to 31 October in 2014, 2015, and 2016 (Fig. 1). Using GIS layers (Rocky Mountain National Park Vegetation Layers), we determined the locations and total areal extent of ponderosa pine, Douglas-fir, and limber pine forest communities in RMNP. All three forest types are primarily located on the eastern slope of the park. Park elevations range from 2380 to 4350 m, and study stand elevations ranged from 2400 to 3400 m. Ponderosa pine and Douglas-fir forest communities within the park are contiguous...
with similar forest types outside park boundaries, extending further to the east (Fig. 1). For example, ponderosa pine (~12,000 ha) and Douglas-fir (~11,000 ha) forest communities are located within 10 km of the eastern RMNP boundary in Roosevelt National Forest. Nutcrackers thus freely entered and exited RMNP during the study (Williams 2017). Other plant communities within the park include lodgepole pine (Pinus contorta) and spruce-fir (Picea engelmannii and Abies lasiocarpa) forests, aspen (Populus tremuloides) communities, moist and dry meadows, sagebrush shrublands, riparian zones, alpine tundra, and talus slopes. Based on 10 yr of data, the average minimum January temperature in nearby Estes Park is –9°C, and the average maximum July temperature is 26°C. Estes Park receives a mean value of 13.10 inches of precipitation per year (https://www.nps.gov/romo/planyourvisit/weather.htm). These conditions reflect the climate for most ponderosa pine and Douglas-fir stands. Limber pine study stands are higher in elevation, but the broad elevational range of limber pine encompasses highly variable climatic conditions.

Field methods

Stand selection.—We selected study stands of ponderosa pine, Douglas-fir, and limber pine for cone density estimation, focal behavior surveys, and nutcracker visitation surveys. A stand is defined as a continuous forested area where one conifer species dominates. We identified stand type, also called forest (community) type, based on the dominant conifer species. We required that each study stand be more than 5.0 ha in area to accommodate assessment transects. We selected stands that are distributed across the eastern slope of the park and accessible from the park’s road or trail system by examining the GIS vegetation layers and visiting stands to determine access time and suitability. In 2014, we selected two stands of Douglas-fir, three stands of ponderosa pine, and five stands of limber pine. In 2015 and 2016, opting instead for four study stands of each stand type, we eliminated one limber pine stand and added additional stands of ponderosa pine and Douglas-fir.

We established virtual transect lines using GPS points within each stand in order to gather all survey and observational data. Transects ranged from 300 to 1000 m in length (mean = 817 m) and consisted of survey points separated by 100 m, resulting in 4–11 survey points per transect. Transects consisted of either one continuous line (10 stands), two lines (2 stands), or three lines (1 stand); thus, a transect within a study stand in three cases consisted of more than one line. We placed transects within a stand with random start points using ArcGIS whenever possible. If constrained by topography, we placed them along an accessible ridge, slope, or trail. Constraints on transect length, connectedness, and random placement resulted from small stand area or hazardous terrain.

Tree and cone density surveys.—Each year, we surveyed all study stands once between 13 June and 13 September before the cones had ripened, to estimate tree and cone density. During this time, unripe cones are easy to distinguish from old cones and large enough to observe for all three conifer species (see Results for more details). We used a distance sampling protocol to collect tree and cone density data (Buckland et al. 2001). While walking a transect, we recorded the following information for each observed tree: distance to tree from observer measured by laser rangefinder (Nikon ProStaff 550, Nikon, El Segundo, California, USA), azimuth of tree from observer on transect line measured by compass (Silva Ranger), and the number of cones observed from the transect counted using 10 × 42 mm binoculars. Information was recorded only for trees within 50 m of the transect line because cone visibility declined steeply beyond this distance. To ensure that all recorded trees were reproducively mature, we only included trees that were at least two meters in height. Because the observer stayed on the line during distance sampling, we only counted cones on the visible side of each tree canopy (a partial count). This method thus underestimates total cone density, but because we are interested in relative cone production among conifer species and years, this limitation does not affect our interpretation of distance sampling results.

In 2014, an exploratory field season, we sampled between 100 and 1000 m of each transect (median = 500 m). Based on analyses of 2014 data, we determined that sampling 100 trees per transect would be sufficient for good model fit.
Based on a chi-square test, as described in Statistical analyses) and low standard errors, and would enable us to finish one stand per field day. Sampling 100 trees per transect in 2015 required that we walk only 50–350 m of each transect (median = 200 m). We randomly selected the starting point of each survey within a transect when logistically possible (n = 7 stands). For the other five stands, stand shape or topography precluded choice. In 2015 and 2016, we also conducted a full cone count for every fifth tree (in addition to a partial count for that tree) by circling the tree and counting cones not observed from the transect. Full cone counts allowed us to estimate the proportion of cones missed by the distance sampling counts and were used for generating landscape energetics information (described in Statistical analyses).
We observed that cone infestation by insects was widespread each year in ponderosa and limber pine, and we estimated the magnitude of impact on these seed resources. Insects typically infested developing, unripe cones. Infestation was indicated by small, light-brown, or reddish-brown cones filled with frass and was likely caused by either ponderosa pine coneworms (*Dioryctria auranticella*) or lodgepole pine cone beetles (*Conophthorus contortae*) (Schoettle and Negron 2001). Infested cones were not used as seed resources by nutcrackers. During nutcracker visitation surveys, we examined 20 ponderosa pine trees in October 2015 and 20 limber pine trees in September 2016 for infestation—five trees from each stand—selecting the nearest cone-bearing tree from five haphazardly selected points per transect. We circled each tree and counted the number of healthy and infested cones to estimate the percentage of infested cones for each tree and for each conifer species as a whole.

**Focal behavior surveys.** We collected data on nutcracker behaviors related to seed foraging and caching behavior to estimate temporal trends and to compare seed use for each conifer species. Focal behavior surveys were conducted from 11 August to 31 October each year concurrent with the visitation surveys (described in Statistical analyses; 8 surveys across all years). Focal behavior surveys were conducted from 11 August to 31 October each year concurrent with the visitation surveys (described in Statistical analyses; 8 surveys across all years), commencing as we entered the stand, or after the cone counts (*n* = 8 surveys across all years). If we detected a nutcracker within ~100 m of the transect, we approached the bird and documented all foraging-related behavior, the time allocated to each behavior using a stopwatch, and the conifer species. We designated all non-foraging or non-caching behaviors, including calling, perching, preening, bill wiping, and flying, as “other.” We ceased recording a bird’s behavior when the bird flew out of view or after 10 min. If other birds were present, we turned our attention to the nearest nutcracker and began recording data. A behavior survey ceased when we collected a total of 60 min of behavior data or we exited the stand. Survey time was used to normalize the foraging observations for nutcrackers and was calculated as the duration between starting and ending a behavior survey. We did not record stand entrance or exit times (used to calculate survey time) in 2014 and several surveys early in 2015, but we estimated them based on 2015 and 2016 hiking durations between transect end points and the study stand boundary.

**Nutcracker visitation surveys.** We surveyed study stands from 11 August to 31 October each year to examine temporal trends in nutcracker numbers and presence or absence in the three forest community types. At the beginning of these surveys, cones in all three stand types were green and unripe and little used by nutcrackers, which most often harvest seeds from ripening or ripe cones (Tombak 1978, Tombak and Taylor 1987). In 2014, we completed 20 surveys in limber pine stands, 10 surveys in ponderosa pine stands, and six surveys in Douglas-fir stands. In 2015 and 2016, we completed 20 surveys within each stand type each year. We attempted to distribute surveys for each stand across the survey time period so that different stages of cone ripening were included in the surveys. In 2015 and 2016, we visited all transects at least once every other week and up to four times within a month, with rare exception.

Surveys were conducted as follows: At each point along the transect, we listened and watched for nutcrackers for 10 min and recorded the number of nutcrackers detected within the stand (if any) from either visual sightings or vocalizations within the stand. We walked two transects per day when possible, but the number of points included in each survey depended on available time and hazardous conditions encountered, including extreme weather, moose, and rutting elk (percent points completed per survey: mean = 88%, range = 18–100%).

**Statistical analyses**

*Tree and cone density and landscape energetics.*** To prepare the distance sampling data for analysis, we first calculated sighting angle (θ) for each tree relative to transect heading. We then used the distance from observer (r) to each tree to calculate perpendicular distance from transect (x) by using the equation:

\[ x = r \cdot \sin(\theta) \]  

We used Program Distance (Thomas et al. 1998) for all distance sampling analyses, because trees can be completely or partly hidden by closer trees. This program estimates the proportion of
objects not detected, which allows for more accurate estimates and confidence intervals of density. To calculate object density, Program Distance plots a histogram of the number of detected objects against $x$. A detection function, $g(x)$, is then plotted along the bin peaks in the histogram. The equation expressing $g(x)$ may be defined by one of four key functions: uniform, half-normal, hazard rate, and negative exponential. Each key function may be further defined by three series expansions: cosine, simple polynomial, and hermite polynomial. We selected the key function and series expansion based on the lowest Akaike Information Criterion (AIC) values. However, we rejected the negative exponential key function because none of the stand types should generate a spiked distribution on the histogram (Buckland et al. 2001). The remaining key functions generally estimated similar densities, with the 95% confidence intervals overlapping nearly completely. The observed number of objects ($n$) is divided by transect length ($L$) and the integral of $g(x)$ to obtain the estimate of object density. Using distance sampling, we found small differences in tree numbers for the same stand each year. Consequently, we estimated tree density across years for each stand type by using data from all stands of a forest community type each year, stratifying by stand, and using a weighted average based on stand area (Thomas et al. 1998).

We estimated cone density for each study stand each year. For each year, we also estimated cone density for each forest community type by combining data from all stands of a forest type within that year, stratifying by stand, and using a weighted average based on stand area (Thomas et al. 1998). Trees were only included in the estimates for cone density analysis if they contained at least one cone: across all years, about 42% of limber pine trees, 40% of ponderosa pine trees, and 57% of Douglas-fir trees lacked cones. We examined the histogram and left-truncated the data if bins near the transect contained few trees and right-truncated the data if there were a few distant trees (Buckland et al. 2001). We evaluated model fit with a chi-square goodness-of-fit test, which compares the expected histogram values of the model to the observed histogram values. Large test statistic values would indicate that the models are significantly different from the observed data and are a poor fit.

From the cone densities, we roughly estimated the total amount of seed energy on the RMNP landscape provided by each of the three conifer species as follows. We obtained full tree cone counts for each conifer species by year by plotting full cone counts against partial counts (from transects) for each conifer species, combining 2015 and 2016 data, and using linear regression to plot a line of best fit, with a $y$-intercept of zero (Appendix S1: Fig. S1). For each conifer species, we multiplied the slope of the line by the number of cones observed from the transect for every tree to obtain a total cone estimate for each tree. We then analyzed these data using the same Program Distance protocol described above. The amount of seed energy on the landscape represented by each of the three tree species was estimated as the number of cones per hectare times the total hectares of each forest type in RMNP times the number of seeds per cone times the energy (kJ) per seed. Total hectares of each forest type were obtained using the ArcGIS vegetation layers. The number of seeds per cone and the energy per seed came from the literature (see Table 2 for references).

**Nutcracker foraging patterns.**—To examine the time sequence for nutcracker foraging on different conifer species, how many days they foraged on each conifer species, and the timing of transition between conifer species, we displayed conifer seed use data graphically for each year by pooling foraging observations into 10-d bins. Within each bin, we summed observed foraging time across all birds for each conifer species, summed the survey time for each conifer species, and divided foraging time by survey time.

We selected the odds ratio test to compare the likelihood of nutcrackers using the seeds (foraging or caching) of a specific conifer species to the odds of using the seeds of another conifer species (Rita and Komonen 2008). We performed the tests with R (version 3.24, R Core Team 2016) as follows. For each year, we summed the number of birds within forest community types observed using seeds and not using seeds (those marked as other) for each of the three seed resource conifer species. Conifer species was not assigned by the stand type being surveyed, but rather by the conifer species selected by the nutcracker within that stand type. For example, if a bird foraged on an isolated limber pine tree within a ponderosa
pine stand, the assigned conifer species would be limber pine. If a bird’s behavior was other, we used the stand type being surveyed or (if part of a flock) utilized by the bird’s flockmates. Tests were run for a given conifer species for a given year only if we observed nutcrackers using the seeds of that conifer. In four cases, the conifer seeds used by nutcrackers could not be identified to species and were omitted from analyses.

Nutcracker visitation patterns.—Each year, we pooled nutcracker presence/absence data into 10-d bins to estimate forest community use changes over time, beginning 11 August and ending 31 October. Within each bin, we calculated the percentage of surveys with detections for each stand type. We plotted the results on a time-series graph with 10-d bins to show relative visitation changes over time, assuming detection probability for a given stand type remains the same.

We also analyzed nutcracker occurrence with generalized linear models fitted using the R package glmmTMB (Magnusson et al. 2017). The response variable in our models was the number of nutcrackers detected per transect. Explanatory variables used in the models were stand type (a factor with three levels: limber pine, Douglas-fir, and ponderosa pine), cone density (the log of the number of cones per hectare for a given year, estimated from Program Distance), cone ripeness (a factor with two levels: unripe and ripe), year (a factor with three levels: 2014, 2015, and 2016), and month (a factor with three levels: August, September, and October). Initially, we also included transect (a factor with 13 levels identifying the different transects) as a random intercept term in the models to account for the repeated visits to each transect. We subsequently left transect out of the models because its variance was estimated to be zero, and thus, it did not explain count variation.

Because nutcrackers often aggregate (group together), we allowed for potential overdispersion by using a negative binomial model. An offset, the logarithm of the number of points in the transect, was included to account for variable survey effort. We found, via a score test for overdispersion (Hilbe 2014), that the nutcracker counts were indeed overdispersed, so we modeled them using negative binomial regression (Young and Young 1998).

Negative binomial regression is available in two versions (Hilbe 2011, 2014). In the traditional version, called NB2 regression, the variance \( \sigma^2 \) of \( Y \) has a quadratic relationship with the mean, \( \sigma^2 = \mu + \alpha \mu^2 \). In the alternative version, called NB1 regression, it has the linear relationship \( \sigma^2 = \mu + \alpha \mu = (1 + \alpha) \mu \). We fit both versions to the nutcracker counts but found that NB2 models generally fit the data better, according to the AIC value. Counts of biological organisms sometimes contain substantially more zeros than would be expected for a variable following a negative binomial distribution. When this is the case, a zero-inflated negative binomial regression (ZINB) model is appropriate. However, we found no evidence of excessive zeros, and standard NB2 models fit the data better than ZINB models, as indicated by AIC. All of the models we report are traditional NB2 models that differ by the explanatory variables they include.

We compared models using the AIC criterion. Because AIC only evaluates the relative qualities of two or more models, not their absolute qualities, we also assessed individual models using chi-square goodness-of-fit tests (Hilbe 2014).

RESULTS

Tree and cone density, cone infestation, landscape energetics, and ripening phenology

Tree density varied greatly across stands and within each stand type as follows: limber pine—64 to 654 trees per ha, ponderosa pine—120 to 203 trees per ha, and Douglas-fir—152 to 1,086 trees per ha (Table 1). Other conifer species were present at low-to-moderate density within the stands: Engelmann spruce and subalpine fir were present in limber pine stands, and lodgepole pine was present in limber pine and Douglas-fir stands. Ponderosa pine woodlands were most often pure stands. The estimated tree densities only apply to the focus conifer species within each stand.

Each year, we observed different patterns of cone productivity among the three conifer species. In 2014, cone production was relatively low for the three conifer species, ranging from 180 to 690 cones per ha (Fig. 2A). The average cone number per tree (visible side) ranged from 0.4 to 5.0 cones. In 2015, limber pine and Douglas-fir again produced low cone numbers, ranging from 200 to 810 cones per ha (Fig. 2B), with stand...
averages of 0.4 to 2.0 cones per tree, but ponderosa pine cone density was high—an estimated 6,830 cones per ha (Fig. 2B)—with a stand average of 51 cones per tree. In 2016, cone density for limber and ponderosa pine ranged from 510 to 850 cones per ha (Fig. 2C), with an average of 2 to 4 cones per tree. Douglas-fir cone density was an estimated 48,830 cones per ha (Fig. 2C), with an average of 97 cones per tree. Thus, limber pine had comparatively low cone production in all three years, while ponderosa pine and Douglas-fir each experienced one highly productive cone year during the study.

Although the number of cones per hectare is lower for limber pine, the energy provided per limber pine seed is more than 10 times the energy provided by a Douglas-fir seed, and more than twice the energy of a ponderosa pine seed (Table 2). For limber pine, cone densities across years ranged from 800 to 1400 cones per ha, and yearly energy across the RMNP landscape ranged from $4.5 \times 10^8$ to $8.0 \times 10^8$ kJ. For ponderosa pine, estimates of cone density ranged from 700 to 9600 cones per ha, and yearly energy available from seeds ranged from $1.4 \times 10^9$ to $1.9 \times 10^9$ kJ. Estimates of Douglas-fir cone densities ranged from 300 to 92,900 cones per ha, and the energy from seeds ranged from $1.6 \times 10^7$ to $4.3 \times 10^9$ kJ. Thus, despite relatively lower cone production, the energy provided each year by limber pine across the landscape represented a considerable food resource. For Douglas-fir, despite the low energetic value of its seeds, the species represented an important energy resource in high cone production years because of its greater number of cones per tree, high tree density, and larger area occupied.

Cone infestation by insects was extensive for limber and ponderosa pine. In 2015, for the 20 ponderosa pine trees we examined, 53% of the cones were affected. Percent cone infestation per ponderosa pine tree ranged from 8% to 97%. For the 20 limber pine trees we examined in 2016, 79% of the cones showed infestation by cone insects, and infestation for individual limber pine trees ranged from 0% to 100%. We excluded a portion of the infested limber pine cones in the distance sampling cone counts (for cone density estimates), because some infestation could be detected by June or July. For the cones included in distance sampling cone counts (and therefore Program Distance), we now estimate that 57% of these limber pine cones were also infested. Cone infestation occurred in all three years of the study for both tree species, but we did not alter cone density estimates based on infestation.
because infestation data were not collected for all stands and all years. Each conifer species studied followed a different cone opening (and seed development) phenology. Cone opening and seed maturation entails the transition from unripe cones with closed scales, protecting developing seeds with incompletely formed seed coats, to cones with scales separating from the cone core, to cones with fully open cone scales and mature seeds with fully hardened seed coats. Unripe limber pine cones are green, and, as cones ripen from late August to early September, they turn brown and scales begin opening; scales open fully in early September. Unripe Douglas-fir cones are green or purple; they ripen, turning brown, and open from mid- to late September. Unripe ponderosa pine cones are green, turn brown with
ripening, and open from late September to early October. Nutcrackers preferred to forage for seeds just as cone scales were starting to open, exposing the seeds.

**Nutcracker foraging and caching behavior in relation to cone phenology and visitation**

We observed differences in the timing and behavior of nutcracker foraging both by conifer species and by year. General observations are as follows: Nutcrackers began foraging on unripe limber pine cones as early as 7 August, as indicated by cones with conspicuous damage, that is, red-brown exposed core contrasting with the unripe green color of the closed scales. Birds yanked off cone scales with their bill and foraged on the developing seeds but were not caching seeds this early. To remove seeds from a closed, resinous cone, nutcrackers either perched on a cone in the tree, stabbing the side or top of the cone to access seeds, or removed a cone and carried it to a rock, branch, or fallen tree for support. Once limber pine cones began opening (scales pulling away from the cone core), nutcrackers foraged for seeds from cones in trees and transported seeds in their throat pouch to caching sites. Birds cached seeds nearby in the ground, or in cracks or holes within a log, rock, or tree, or flew off with full pouches to cache elsewhere. Birds primarily foraged alone, in pairs, or in small groups of 3–5 birds, but one larger flock of about 10 birds was observed to forage for limber pine seeds.

Nutcrackers began foraging on unripe ponderosa pine cones as early as 1 September, using their bill to rip off cone scales and remove seeds. Once ponderosa pine cones began ripening, nutcrackers simply removed seeds from open scales. Nutcrackers detached the seed wing from each seed by either shaking the seed or rubbing it against a tree branch. Birds then pouched seeds, and either cached seeds nearby or flew out of view to cache elsewhere. Most birds foraged alone or in groups ranging from 2 to 6 birds. One large group of 40–50 birds was observed to cache seeds in a ponderosa pine woodland, with some birds also foraging. For Douglas-fir, we observed birds forage in groups of 2–5 for seeds in trees by September 22—within 10 to 15 d after cones had begun to ripen. We later observed nutcrackers in flocks of up to 15 birds forage on the ground for Douglas-fir seeds that had blown out of cones. Prior to placing Douglas-fir seeds in their pouches, birds removed the seed wings, which detached easily, by shaking the seeds or rubbing them quickly on the ground or a branch. We observed several birds pouch Douglas-fir seeds and then cache the seeds within 20 m of the seed source tree.

Annual differences in foraging behavior were apparent: In 2014, when cone crops were relatively small for all three conifer species, we observed nutcrackers forage only on the seeds of limber pine and ponderosa pine (Fig. 3A). That year, nutcrackers first harvested seeds from limber pine cones in late August and continued through September. As limber pine seeds were depleted, nutcrackers transitioned to ponderosa pine seeds in early October. At the end of October in the Estes Cone limber pine study stand, we watched a group of five nutcrackers raid red squirrel (*Tamiasciurus hudsonicus*) middens and remove intact, closed limber pine cones.

In 2015, ponderosa pine experienced a large cone crop, and nutcrackers foraged primarily on limber and ponderosa pine seeds (Fig. 3B). Nutcrackers harvested seeds from limber pine cones from late August through September and began foraging on ponderosa pine cones in early September, one month earlier than in 2014. The ponderosa pine cones at this time were largely unripe, requiring considerable effort to extract seeds.

In 2016, Douglas-fir experienced high cone production and ponderosa pine low cone production. Nutcrackers foraged first on limber pine seeds until late August and then foraged exclusively on ripe Douglas-fir seeds (Fig. 3C). This is the only year of our study in which nutcrackers harvested and cached Douglas-fir seeds and did not harvest ponderosa pine seeds, but also foraged on limber pine seeds weeks prior to cone ripening.

As described, we observed nutcrackers utilize seeds from two conifer species each year, but the odds of use were not always equal. In 2014, we observed that only about half the nutcrackers within ponderosa pine study stands foraged for ponderosa pine seeds, while the majority of birds within limber pine study stands foraged for limber pine seeds (Table 3). The odds of nutcrackers using limber pine seeds in 2014...
were 4.96 (95% confidence interval [CI]: 1.30–18.84) times higher than the odds of nutcrackers using ponderosa pine seeds. In 2015, with ponderosa pine’s large cone crop, nutcrackers favored the ponderosa pine, and the odds of nutcrackers using ponderosa pine seeds were 3.13 (95% CI: 1.34–7.34) times greater than the odds of nutcrackers using limber pine seeds. In 2016, when we observed nutcrackers harvesting Douglas-fir seeds for the first time, the odds of nutcrackers using these seeds were 2.38 (95% CI: 0.81–6.98) times the odds of nutcrackers using limber pine seeds. A significant difference in foraging odds is inferred when confidence intervals exclude 1.0.

**Nutcracker stand visitation and predictors**

Nutcrackers were observed in all forest types in all three years, even with low cone production (Fig. 4). Spatial changes in nutcracker detections were coincident with phenology of cone ripening for the three conifer species. The percentage of surveys with detections in part reflected the relative magnitude of cone production each year, especially for limber and ponderosa pine. Peak detections generally occurred during cone opening. In 2014 and 2015, the percentage of nutcracker surveys with detections in limber pine peaked during September 11–20, but in 2016 peaked during August 21–31. In all three years, the percentage of surveys with detections in

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**Fig. 3.** Nutcracker foraging timeline in (A) 2014, (B) 2015, and (C) 2016. Time observed foraging (in seconds) is summed across all birds and divided by survey time (in min) within forest types for each 10-d bin; reported units are observed foraging sec per survey min. A different scale is used in 2015 compared to 2014 and 2016. Arrows indicate the average cone ripening dates across three years for each conifer species.
Table 3. Odds ratios calculated for 2014, 2015, and 2016.

| Year | Conifer species | No seed use | Seed use |
|------|----------------|-------------|----------|
| 2014 | Limber pine    | 8           | 34       |
|      | Ponderosa pine | 7           | 6        |
| 2015 | Ponderosa pine | 16          | 59       |
|      | Limber pine    | 17          | 20       |
| 2016 | Douglas-fir    | 10          | 19       |
|      | Limber pine    | 15          | 12       |

Notes: The numbers reflect total counts of nutcracker seed use per year across all months and all surveys of stands, sorted by stand type and observed activity. Seed use includes foraging and/or caching. Odds ratios indicate the odds of nutcracker use of ponderosa pine or Douglas-fir seeds compared to the odds of nutcracker use of limber pine seeds. The odds ratios of limber pine seed use relative to ponderosa pine seed use for 2014 = 4.96 (95% confidence interval [CI] = 1.30–18.84). The odds ratios of ponderosa pine seed use relative to limber pine seed use for 2015 = 3.13 (95% CI = 1.34–7.34). The odds ratios of Douglas-fir seed use relative to limber pine seed use for 2016 = 2.38 (95% CI = 0.81–6.98).

For Douglas-fir stands, detections increased in early October in 2014 and 2015; and in 2016, visitation was high from mid-September through early October.

We developed negative binomial regression models to examine which explanatory variables predict nutcracker counts (Table 4; Appendix S1: Table S1). With interaction effects excluded, stand type and cone density were significant influences on nutcracker counts, whereas year, month, and cone ripeness were not (Table 4). The main effects model with the lowest AIC value included only stand type and cone density. Cone density and year were confounded (because cone density changed across years). Models containing both variables had high AIC values, indicating an inferior model, and are not reported. Likewise, cone ripeness and month were confounded (because ripeness changed over months), and models containing both variables had high AIC values and are not reported.

By comparing models that include interaction effects, we found that the model with the lowest AIC value had stand type, year, and month but excluded cone density and ripeness (Table 4; Appendix S1: Table S1). However, cone density appeared to influence nutcracker counts, because it is significant as an interaction effect with stand type in all models that include both variables. Furthermore, in the lowest AIC model, a redistribution from year to year of nutcrackers across stand types is indicated by the statistically significant year by stand type interaction, and the model-predicted redistribution is consistent with the observed patterns of cone production across the three conifer species (Table 5). More precisely, the predicted numbers of nutcrackers in ponderosa pine for 2015 are relatively high, but they are low for 2016. Likewise, the predicted numbers in Douglas-fir for 2016 are relatively high.

Cone ripeness was not significant in any model. However, the interaction between stand type and month in the lowest AIC model indicates a redistribution of nutcrackers across stand types by month, and the redistribution indicated by the model is consistent with the observed pattern of cone maturation (Table 5). In particular, the model-predicted counts in limber pine for October are low across all years, and those in ponderosa pine for September and October are high. We found no indications of model inadequacy in the negative binomial regression models using the chi-square goodness-of-fit tests (at the 0.05 significance level).

In summary, models suggest that nutcrackers responded to cone density differently for each conifer species (Fig. 5, Table 5). Nutcrackers always visited limber pine stands regardless of cone availability. Visitation to limber pine stands occurred earliest in the season, but afterward nutcrackers tended to remain at lower elevations in the other stand types, likely resulting in low detections in limber pine overall. Limber pine cone density was also relatively consistent across years, but a bumper cone year could alter this visitation trend. Nutcrackers were strongly responsive to changes in ponderosa pine cone availability, indicating that these seeds were an important resource during high cone production years. Nutcrackers, however, were most commonly present within Douglas-fir stands, and changes in Douglas-fir cone density did not greatly affect nutcracker counts on average.

**Discussion**

Our objectives for this study were to examine annual cone production in limber pine, ponderosa pine, and Douglas-fir forest communities; estimate the total seed energy provided by the
conifer species across the landscape in RMNP; and determine the yearly use of these conifers as seed resources and as habitat by Clark’s nutcracker. Across three years, the conifer species provided markedly different levels of seed energy because of differences in energy per seed, annual cone production, and areal extent of stand type. Each year, two seed resources were utilized by nutcrackers as seeds ripened. Most cone density estimates for the three conifer species were below or near 1,000 cones per ha, which we are defining as relatively low cone production, although we do not know the maximum that each conifer can produce (Fig. 2). Limber pine produced a low cone crop every year. While we never observed a large cone crop from this conifer, limber pine can produce a bumper crop approximately once every two to four years (Krugman and Jenkinson 1974). Comparing the total energy estimates from Table 2, low cone production for limber pine (4.5 \times 10^8 to 8.0 \times 10^8 total kJ) resulted in 3.2–5.7 times more potential food energy in RMNP than low cone production in ponderosa pine (1.4 \times 10^8 total kJ) and 28.1 to 50.0 times more energy than low cone production in Douglas-fir (1.6 \times 10^7 total kJ). In contrast, high cone production in ponderosa pine (1.9 \times 10^9 total kJ) resulted in 2.4–4.2 times more energy than provided by a low cone crop of limber pine, and high cone production in Douglas-

Fig. 4. Nutcracker visitation in (A) 2014, (B) 2015, and (C) 2016. For each 10-d bin, surveys are pooled by stand type, and the total number of surveys with detections of nutcrackers within the survey stand is divided by the total number of surveys; both visual and auditory detections are included. Arrows indicate the observed time of cone ripening for each conifer species.
indicate statistically significant effects (at the 0.05 level) using a chi-square likelihood ratio test. All models also include the log of the sampling effort as an offset. The number of terms in the model (not including the intercept or offset) is p. AIC, Akaike Information Criterion.

### Table 5. Predicted numbers of nutcrackers per transect per sampling occasion by year, stand type, and month using the lowest AIC model from Table 4 (Model 9 in Appendix S1: Table S1).

| Forest type     | 2014  | 2015  | 2016  |
|-----------------|-------|-------|-------|
| Limber pine     |       |       |       |
| August          | 3.2 (2.9) | 1.3 (1.1) | 3.6 (5.1) |
| September       | 3.9 (4.2) | 3.9 (4.6) | 6.0 (5.0) |
| October         | 1.0 (1.2) | 2.3 (1.9) | 1.6 (1.9) |
| Douglas-fir     |       |       |       |
| August          | 11.2 (21.0) | 3.2 (3.6) | 13.2 (7.1) |
| September       | 3.4 (2.4) | 2.5 (1.5) | 5.6 (6.9) |
| October         | 3.2 (2.2) | 5.3 (5.8) | 5.3 (5.0) |
| Ponderosa pine  |       |       |       |
| August          | 4.6 (3.9) | 3.2 (3.6) | 1.5 (1.8) |
| September       | 6.2 (6.1) | 10.8 (11.0) | 2.8 (2.9) |
| October         | 3.3 (3.0) | 13.2 (13.0) | 1.6 (1.4) |

**Notes:** Predicted values are obtained by taking the appropriate sum of model coefficients, which gives \(\log(\mu/k)\), where \(\mu\) is the expected nutcracker count and \(k\) is the sampling effort (number of survey points) on a transect, then exponentiating and multiplying by \(k = 10\) (corresponding to a transect with 10 survey points). Values in parentheses are the actual mean numbers of nutcrackers observed (adjusted to a sampling effort of \(k = 10\) in cases where fewer or more than that were actually sampled). Limber pine cones ripen from August to early September; Douglas-fir cones ripen from mid- to late September; and ponderosa pine cones ripen from late September to early October. Limber pine had comparatively low cone production in all three years, while ponderosa pine experienced a highly productive cone year in 2015 and Douglas-fir a highly productive cone year in 2016. AIC, Akaike Information Criterion.

Fig. 5. Counts of nutcrackers detected along a transect versus log of cone density by stand type. Lines obtained from the fitted negative binomial regression model number 7 in Appendix S1: Table S1, averaged over the three months across all years.

fir (4.3 × 10^9 total kJ) resulted in 5.4–9.6 times more energy than low production in limber pine. These comparisons do not account for insect infestation. If our estimates of cone infestation by insects are accurate and applied in every year, total usable energy across the RMNP landscape provided by limber and ponderosa pine during our study would be about half of what we report here.

Landscape energetics can be used to estimate a carrying capacity for nutcrackers in RMNP, based only on conifer seed resources, although nutcrackers will take other food types not considered here (Giuntoli and Mewaldt 1978, Tomback 1978). Assuming that the maximum energy requirement for one nutcracker across an entire year is 76,500 kJ (extrapolating calculations from Tomback 1982), limber pine within RMNP could support between 5882 and 10,458 nutcrackers with a low cone crop. Ponderosa pine could support between 5882 and 10,458 nutcrackers with a low cone crop. Ponderosa pine cones ripen from late September to early October. Limber pine had comparatively low cone production in all three years, while ponderosa pine experienced a highly productive cone year in 2015 and Douglas-fir a highly productive cone year in 2016. AIC, Akaike Information Criterion.
available to granivorous birds and mammals that forage on the forest floor. Other granivorous species may compete intensively with nutcrackers for seeds within cones. Cone insects alone could reduce the availability of seeds by half across the park. We observed insect infestation in all limber and ponderosa pine stands that we visited on the east slope. Cutting and storage of cones by red squirrels, a ubiquitous and efficient seed predator, is well-documented (Siepielski and Benkman 2007). Considering these competitors, as well as other songbirds and mammals that also forage on conifer seeds, nutcrackers only access a portion of each seed crop and their actual carrying capacity is likely to be considerably lower.

Nutcrackers are considered energy-sensitive foragers, and landscape energetics impact the foraging decisions of nutcrackers and their choices of conifer species as seed resources each year (Tombback 1978, Vander Wall 1988). Limber pine was the only seed resource that nutcrackers used every year, even though limber pine had relatively low cone production, its stands are relatively small and scattered, and it comprises the smallest forested area of the three conifer species on the landscape in RMNP. Its large seed size resulted in high total energy across the landscape. In addition, ripening or ripe limber pine seeds are available at an important time in summer—after most cached seeds from the previous fall have been retrieved (Tombback 1978, Vander Wall and Hutchins 1983) but prior to seed ripening of other conifer species. The seeds of the heavily armored ponderosa pine, like the closely related Jeffrey pine (Tomback 1978), may be energetically costly to remove from unripe cones this early in the summer. Nutcrackers searched widely for limber pine seeds, since we frequently observed them to forage on isolated limber pine trees in stands of other forest types. This suggests a landscape-level approach to seed utilization by nutcrackers, in contrast to stand-based decisions. For whitebark pine, which has similar morphology to limber pine and large, wingless seeds, previous work suggests that the probability of stand visitation or seed harvest by nutcrackers increases as cone production increases (McKinney et al. 2009, Barringer et al. 2012), but Barringer et al. (2012) suggested that foraging decisions may occur at a landscape rather than stand level, as modeled by McLane et al. (2017). In this study, cone production by limber pine and ponderosa pine was generally higher than in many whitebark pine stands assessed by McKinney et al. (2009) and Barringer et al. (2012).

Nutcrackers were observed to forage intensively on ponderosa pine seeds for two out of three years. The odds of nutcrackers foraging on ponderosa pine seeds were lower compared to limber pine seeds during the low ponderosa pine cone crop year. This is unsurprising, considering ponderosa pine’s smaller energetic reward during lower cone production compared to limber pine. However, during ponderosa pine’s higher cone production, the odds of a nutcracker using ponderosa pine seeds were greater compared to limber pine. Nutcrackers foraged on Douglas-fir seeds only during the year with high cone production.

While the importance of each conifer species to nutcrackers as a food resource appears to vary each year, we suggest that over time each conifer species plays an important role in maintaining nutcracker populations in RMNP and, by extrapolation, across much of the Colorado Front Range and beyond. Limber pine is the most important food resource in RMNP because of its seemingly consistent cone production, large seeds, and earlier ripening of seeds. Ponderosa pine may be more important for maintaining nutcracker numbers over time than Douglas-fir, given that Douglas-fir seeds were not used by nutcrackers in years with low cone production, whereas ponderosa pine seeds were. Also, nutcrackers were observed to forage on ponderosa pine seeds for a longer period in the fall compared to Douglas-fir seeds; and, ponderosa pine generally experiences moderate to high cone production years more frequently than Douglas-fir (Krugman and Jenkinson 1974, Hermann and Lavender 1990). However, when Douglas-fir experiences a mast cone year, it provides a critical energy source for nutcrackers later in fall after limber pine seeds are depleted, especially if ponderosa pine fails to produce cones.

Although the odds ratio analyses indicate that annual variation in cone production affects nutcracker seed use decisions, the regression models suggest that stand type and cone density alone are not the best predictors of nutcracker visitation within a stand (Table 4). The top model, which incorporated interaction effects, included
temporal variables (month and year) rather than cone variables (cone density and ripeness). We suggest that temporal variables comprehensively capture seasonal changes in seed availability across the landscape for each conifer species, year-to-year variation in this pattern, and habitat use information that is not related to food. Thus, the summer and early fall spatial movements by nutcrackers may not be predicted by a simplistic model of cone production but rather by a model that reflects other habitat uses. In fact, regression model results combined with field observations suggest that there are different explanations for nutcracker utilization of each conifer community type.

Although limber pine was an important food resource for nutcrackers, it may be less important as forest habitat. Nutcrackers were consistently present in limber pine stands by mid- to late summer, when cones were ripening or ripe; but, after seed depletion, they were found primarily at lower elevations in ponderosa pine and Douglas-fir forests—probably because of ripening seed resources but possibly also in response to changing weather conditions. In late September and October, nutcracker detections were relatively high in Douglas-fir forests across years, although nutcracker counts were particularly elevated during the year with high cone production by Douglas-fir (Fig. 5, Table 5). This suggests that nutcrackers primarily utilize Douglas-fir forests as habitat and not as a conifer seed resource, although they will also harvest and cache Douglas-fir seeds during a mast year. Douglas-fir stands support higher tree densities in general (Table 1), and the trees have dense foliage, which together may provide better shelter from wind and snow.

Detection probability may well differ among habitat types, and perhaps with each study stand, but nutcrackers vocalize frequently and loudly, which signals their presence—even in dense Douglas-fir stands. We originally used occupancy analysis for nutcracker visitation data but found that occupancy of stands was 1.0 for all forest types (MacKenzie et al. 2002).

Whereas nutcrackers were present in ponderosa pine forests only later in the season, this was strongly dependent on cone production. Ponderosa pine was the only species in which nutcracker detections changed significantly with changing cone density (Fig. 5), with minimal detections during a poor cone crop (as in 2016) and frequent detections during mast years (as in 2015). This suggests that nutcrackers use ponderosa pine mainly during years of good cone production, but otherwise prefer Douglas-fir forests as late-season habitat. Thus, the relative use of each forest type may also change each year. Since year was rarely significant by itself in our models but was often significant as an interaction effect with month and with stand type, this implies that the population size did not change much across years, but detections were just redistributed each year by month and forest stand type.

The importance of ponderosa pine and Douglas-fir seed resources for nutcrackers has been noted in previous studies. For example, Giuntoli and Mewaldt (1978) observed that nutcrackers foraged on the seeds of both species in Montana, and Lorenz and Sullivan (2009) observed nutcrackers utilize both conifer species for food in the Cascade Range of Washington. Schaming (2016) observed nutcrackers in Wyoming preferentially use Douglas-fir forests as habitat during the breeding season, and she described the importance of this species as a food resource to nutcrackers in this region. As five-needle white pines experience mortality from blister rust and other disturbances, ponderosa pine and Douglas-fir may become critical food resources across much of the range of the nutcrackers.

Our observations of nutcracker seed use are under conditions of comparatively low limber pine mortality from the mountain pine beetle outbreaks during the preceding 15 yr and no observed mortality from white pine blister rust in RMNP. In 2018, however, surveys in RMNP documented blister rust cankers on 51 of 368 surveyed trees in one stand (B. Verhulst, personal communication), indicating that the disease is now established in the park and losses of limber pine are anticipated. Given that we have detected nutcrackers in all study stands each year, determined that they may travel 12 km straight-line distance or more within and outside the park (Williams 2017), and observed them to forage on isolated limber pine trees within stands of other forest types, we conclude that nutcrackers potentially travel widely across the park, moving long distances to find seeds. Even with high mortality...
from blister rust, nutcrackers may be able to search for, forage on, and cache a portion of the limber pine seeds produced each year within and beyond the boundaries of RMNP.

**Conclusions**

Nutcrackers have previously been observed to forage for Douglas-fir and ponderosa pine seeds in several geographic regions, and our investigation clarifies the major temporal and energetic drivers influencing the use of these two seed resources. Clark’s nutcrackers harvested and cached limber pine seeds in every year of our study. At a landscape scale, low cone production in limber pine provided several times the energy resource of low cone production in ponderosa pine or Douglas-fir. However, in all three years, limber pine alone did not provide sufficient energy resources for foraging and caching, and nutcrackers utilized an additional conifer seed resource. We found that nutcrackers transitioned to foraging for either ponderosa pine or Douglas-fir seeds after depleting limber pine seeds. Also, at a landscape energetics scale, large cone crops of ponderosa pine and Douglas-fir provided significant energy resources to nutcrackers. Although all three conifers were utilized for their seeds, nutcrackers did not use them equivalently as a food resource or equally as habitat. Limber pine and ponderosa pine stands appeared to be utilized primarily as seed resources, whereas Douglas-fir was more frequently used as habitat.

The potential for limber pine mortality from white pine blister rust over time in RMNP implies that nutcrackers will rely more heavily on ponderosa pine and Douglas-fir. By understanding how nutcrackers utilize conifer seed resources in a system not yet heavily impacted by blister rust, we can understand the implications of declining limber pine numbers. Fewer limber pine trees may result in lower nutcracker carrying capacity, which would have adverse ecological impacts on conifer species that benefit from their seed dispersal services, such as Rocky Mountain bristlecone and Colorado pinyon pine (Tombback and Kendall 2001, Tombback et al. 2011). Given that ponderosa pine and Douglas-fir are the most widely distributed alternative seed resources across the nutcracker’s range, and white pine blister rust is spreading through the range of Rocky Mountain five-needle white pines (Tombback and Achuff 2010), the results of this study could apply broadly across the montane West.

**Acknowledgments**

This project was funded by a Bailey Research Fellowship, awarded by the Rocky Mountain Conservancy, to Tyler J. Williams in 2015, and a Research, Education, and Conservation Grant awarded by the Denver Field Ornithologists to Tyler J. Williams in 2015 and 2016; we are grateful to both organizations for their support. We thank Paul McLaughlin and Scott Esser of Rocky Mountain National Park for help with logistics and permits. All work with Clark’s nutcrackers was approved under the University of Colorado Denver IACUC protocol #88314(06)1c. Michael Greene and Michael Wunder provided invaluable advice concerning project organization and data analysis. We are also indebted to numerous University of Colorado Denver undergraduate students, Rocky Mountain National Park volunteers, and to Amber Williams, for field assistance. Furthermore, we thank the graduate students in the Department of Integrative Biology at the University of Colorado Denver for helpful discussions of this work in progress. Finally, we are deeply grateful for the support offered by loved ones throughout this project. The authors declare no conflict of interest. Tyler J. Williams and Diana F. Tombback designed the study; Tyler J. Williams collected field data; Tyler J. Williams, Nels Grevstad, and Kristin Broms analyzed data; Tyler J. Williams, Diana F. Tombback, and Nels Grevstad wrote the paper.

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