Do Clark's Nutcracker (*Nucifraga columbiana*) life history traits predict the efficacy of their seed dispersal services?

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Background

A major challenge in conservation is predicting species range shifts in the face of climate change, particularly in mountainous regions (Parmesan and Yohe 2003, Linck 2025). Models built on historic data to project future distributions are widely used to forecast change but can under-or overestimate shifts by ignoring relevant species functional traits like dispersal ability (Dobrowski *et al.* 2011). To better understand population dynamics of whitebark pine (*Pinus albicaulus*) and other conifers in western North American forests, studies on seed disperser movement may provide a mechanistic link to explaining range shifts and species persistence.

Clark's Nutcrackers (*Nucifraga columbiana*) are a seed-eating bird species found across western North America that have been described to eat and disperse seeds of 13 conifer species (Schaming *et al.* 2024). During the fall, when cone crops are ripe, the birds cache seeds in the ground for later retrieval during resource limited times (Tomback 1982). Nutcrackers have a unique mutualism with the federally threatened whitebark pine, a slow-growing, long-lived conifer found in high elevation mountainous regions across the western United States and southwestern Canada; the birds are the most effective dispersers of whitebark pine using their specialized bill to pry open the tree's indehiscent cones and caching more seeds than they require to sustain themselves in a given year (Tomback 1982, Arno and Hoff 1989). Models project an 80% reduction in climatically suitable habitat for whitebark pine by the end of the century (Parks *et al.* 2025) but assume no change in nutcracker behavior even though a reduction in caching of whitebark pine by nutcrackers could lead to cascading impacts for both populations (McLaren *et al.* 2023). Nutcracker dispersal is also thought to be responsible for the unexpected encroachment of Jeffrey pine (*Pinus jeffreyi*), a competitive mid-elevation conifer, into the California subalpine (Safford 2025). A better understanding of nutcracker seed dispersal patterns would improve our ability to predict the future of western forests; however, knowledge gaps remain about bird movement patterns and habitat associations across the year because of the mountainous locations where they live, their highly mobile lifestyle, and their unreliable detectability by typical songbird surveys (Lorenz and Sullivan 2010, Schaming and Sutherland 2020).

Tracking studies of nutcrackers have provided great insight into the bird's ecology. As nutcrackers feed their nestlings seeds cached the preceding fall, nutcracker dispersal patterns have been proposed to be linked to their breeding home range (Lorenz and Sullivan 2009, Lorenz *et al.* 2011). However, within populations, there may exist individuals with different life history strategies: resident or migrant birds that exhibit latitudinal and/or altitudinal migration patterns tracking available pine resources throughout the year (Tomback 1977, Vander Wall 1988, Lorenz and Sullivan 2009). The seed dispersal patterns of the facultative migrants remain poorly understood largely due to challenges associated with tracking these individuals in mountainous terrains (Lorenz and Sullivan 2009). Additionally, no consensus has been reached on nutcrackers' breeding site fidelity, life history strategy, fidelity, or the environmental factors that drive these behaviors (Schaming *et al.* 2024). Understanding nutcracker life history strategy is important as it may influence seed dispersal patterns.

Objectives

For my dissertation, I plan to leverage new technologies and in-field observations to investigate nutcracker movements across elevational and forest composition gradients in the Sierra Nevada Mountains (the Sierra), to better understand the roles these birds may play in shaping the future of California's subalpine forests. For a population of Clark's Nutcrackers in California's eastern Sierra I will ask these questions:

1. Are nutcracker annual movements linked to breeding habitat?

2. Do individual birds exhibit multiple life history strategies across years?

3. Does nutcracker movement ecology predict the effectiveness of an individual's seed dispersal services?

I hypothesize that annual movement will predict disperser efficacy. My study will provide new information on the seasonal movements of nutcrackers in the Sierra, their degree of nomadism and site fidelity within and across years, and the environmental factors that drive these behaviors. I will also advance knowledge on the nesting habits of Clark's Nutcrackers in the Sierra, of which there are few records (Schaming *et al.* 2024), and the efficacy of digital VHF tracking technologies in mountainous regions.

Study Plan and Methods

To study nutcrackers' annual movements, my collaborators and I will capture birds following methods in Schaming (2016) during the winter and spring of 2027 at the UC Davis Reserve Valentine Camp (~7900-8500 ft, Mono Co.) and at nearby locations around Mammoth Mountain (~9,000 to 11,053 ft) on Inyo National Forest Land in the southern Sierras. As nutcrackers are highly mobile and not likely to be recaptured, we will equip adult birds with Cellular Tracking Technologies (CTT) BlūBird digital VHF tags that share location information through not only traditional hand-held Yagi antennas, but also Motus-enabled towers, CTT nodes, and "passively listening" smart phones, increasing the number of times a location can be gathered on the bird. CTT nodes will be erected at high points across the study areas, taking advantage of nearby ski resorts to allow for year-long high-elevation monitoring of bird movement. Unlike traditional VHF tags and satellite GPS tags, these digital VHF tags will provide potential for us to track birds throughout the year and across years with the potential for a high frequency of daily detections. They will also ensure that if birds leave the study area, they can be tracked via passive detections through smartphones.

In addition to passive detections via CTT node infrastructure and recreating smart phone users, I plan to track individuals using a handheld VHF Yagi antennae during the spring breeding season to locate nests. I will monitor the success of nests and band nestlings as I am able to. During the summer, we will erect a grid of evenly spaced CTT nodes across the study area to increase the likelihood of detection during the summer and fall. During the nutcrackers' cone harvest and caching season, a team of undergraduate researchers and I will conduct focal observations on tagged individuals to ensure sufficient location fixes and to pair behaviors with location data. In collaboration with Forest Service staff in the Inyo National Forest, we will conduct surveys on forest composition, conifer phenology, pine tree cone abundance, and presence of white pine blister rust (*Cronartium ribicola*) across the wider study area as potential variables to explain nutcracker movement.

I will use seasonal boundary definitions (e.g., breeding season, preharvest season, harvest season, etc.) and methods described in Schaming (2016) to describe seasonal habitat selection and home range estimates. I will compare the extent of home range between each season and across years using methods

described in Lorenz and Sullivan (2009) and appropriate autocorrelated kernel density estimation techniques (Silva *et al.* 2022). I will quantify the efficacy of dispersal services by comparing individual home ranges and movement patterns to seasonal foraging patterns to determine if birds are dispersing conifer seeds within areas where they are climatically suited to grow. Lastly, I will check for bias in data associated with cellphone users and assess effectiveness of tags in mountainous regions.

Literature Cited

Arno, SF, and RJ Hoff. 1989. *Silvics of whitebark pine (*Pinus albicaulis*).* USDA Forest Service General Technical Report INT-GTR-253. https://doi.org/10.2737/INT-GTR-253 .

Dobrowski, SZ, JH Thorne, JA Greenberg, HD Safford, AR Mynsberge, SM Crimmins, AK Swanson. 2011. Modeling plant ranges over 75 years of climate change in California, USA: temporal transferability and species traits. *Ecological Monographs* 81:241-257.

Interagency Conservation Strategy Team. 2020. *An Interagency Conservation Strategy for* Pinus albicaulis *(Whitebark Pine) in California*. Sacramento, CA, USA.

Linck, EB. 2025. What is an elevational range? *American Naturalist* 206:299-317.

Lorenz, TJ, and KA Sullivan. 2009. Seasonal differences in space use by Clark's Nutcrackers in the Cascade Range. *Condor* 111:326-340.

Lorenz, TJ, and KA Sullivan. 2010. Comparison of survey methods for monitoring Clark's Nutcrackers and predicting dispersal of whitebark pine seeds. *Journal of Field Ornithology* 81:430-441.

Lorenz, TJ, KA Sullivan, AV Bakian, and CA Aubry. 2011. Cache-site selection in Clark's Nutcracker (*Nucifraga columbiana*). *Auk* 128:237-247.

McLaren, TH, DF Tomback, N Grevstad, MB Wunder, W Wehtje, LE Walker, and DW Smith. 2023. Clark's Nutcracker forest community visitation: whitebark pine maintains a keystone seed disperser. *Ecology and Evolution* 13:e10813.

Parks, SA, KL Hefty, JF Rushing, SA Goeking, DF Tomback, SM Hood, JC Toney, DL Harrell, J Lindstrom, CE Naficy, MR Slaton, BS Soderquist, and EJ Taylor. 2025. Whitebark pine in the United States projected to experience an 80% reduction in climatically suitable area by the mid-21st century. *Environmental Research Letters* 20:104012. https://doi.org/10.1088/1748-9326/adfcef.

Parmesan, C, and G Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421:37-42.

Safford, HD. 2025. New elevation records for Jeffrey Pine (*Pinus jeffreyi* A. Murray bis & al.). *Madroño* 72.

Schaming, TD. 2016. Clark's Nutcracker breeding season space use and foraging behavior. *PLoS ONE* 11:e0149116.

Schaming, TD, and CS Sutherland. 2020. Landscape- and local-scale habitat influences on occurrence and detection probability of Clark's Nutcrackers: implications for conservation. *PLoS ONE* 15:e0233726.

Schaming, TD, DF Tomback, and TJ Lorenz. 2024. Clark's Nutcracker (*Nucifraga columbiana*), version 2.0. In *Birds of the World* (ND Sly, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.clanut.02.

Silva, I, CH Fleming, MJ Noonan, J Alston, C Folta, WF Fagan, and JM Calabrese. 2022. Autocorrelation-informed home range estimation: a review and practical guide. *Methods in Ecology and Evolution* 13:534-544.

Tomback, DF. 1977. The behavioral ecology of the Clark's Nutcracker (*Nucifraga columbiana*) in the Eastern Sierra Nevada. Ph.D. dissertation, University of California, Santa Barbara, CA, USA.

Tomback, DF. 1982. Dispersal of whitebark pine seeds by Clark's Nutcracker: a mutualism hypothesis. *Journal of Animal Ecology* 51:451-467.

Vander Wall, SB. 1988. Foraging of Clark's Nutcrackers on rapidly changing pine seed resources. *Condor* 90:621-631.