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Caching at the Habitat Scale:
## Clark's Nutcracker Cache Site Selection, Part II

CLARK'S NUTCRACKERS are considered seed dispersers for more than 10 conifer species, but they're more concerned with keeping seeds out of heavy winter snow than placing them in the right habitat types. What do we know about the selective habits of resident nutcrackers, and how might they affect whitebark pine regeneration?

BACKGROUND

We investigated habitat use, caching behavior, and migratory patterns in Clark's nutcrackers in the Pacific Northwest using radio telemetry. Over 4 years (2006–2009), we captured 54 adult nutcrackers at 10 sites in the Cascade and Olympic Mountains in Washington State. We fitted nutcrackers with a back-pack style harness. The battery life on the radio tags was 450 days, and we tracked nutcrackers year-round, on foot (to obtain behavior observations) and via aircraft (to obtain point locations). We obtained more than 6,000 telemetry point locations on radio-tagged nutcrackers, and we observed more than 1,000 seed-harvest events and 655 seed-caching events.

Of nutcrackers captured in this study, we classified 20 nutcrackers as residents and 21 as emigrants wintering on our study area. Among residents, 11 had home ranges in whitebark pine stands and 9 had home ranges in ponderosa pine stands.

The future of whitebark pine is of serious concern because of the species' vulnerability to white pine blister rust, mountain pine beetle infestation, wildfires, and climate change. The Clark's nutcracker is the primary means of whitebark pine seed dispersal.
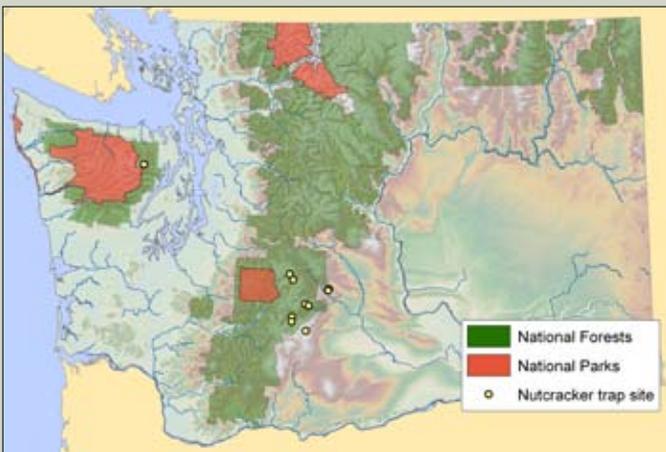
THE STUDY'S Clark's nutcracker trap sites.

What habitat types do nutcrackers select for caching?

Residents of ponderosa pine habitat and residents of whitebark pine habitat selected different habitats for caching seeds (see table, next page). Ponderosa residents selected open, park-like ponderosa pine stands for caching and rarely cached in higher elevation forest types within their home ranges, such as mixed grand fir/Douglas-fir forests. Whitebark pine residents avoided high-elevation forests such as whitebark pine and mixed subalpine fir/mountain hemlock stands, and most commonly used mixed grand fir/Douglas-fir forests or talus slopes for caching. Thus, whitebark pine residents selected one of the habitat types that ponderosa residents avoided. However, all residents were alike in selecting the lowest elevation forests available within their respective home ranges, and avoiding higher elevation habitats within home ranges.

Why did our nutcrackers avoid high-elevation habitats when caching seeds? One hypothesis is that nutcrackers selected habitats for caching based on the amount of snow likely to accumulate during the winter rather than a preference for a particular forest type. Nutcrackers retrieve most of their seed caches in winter, and sites that accumulate a lot of snow would be inaccessible during this time.

Why does it matter?

The caching behavior of nutcrackers in autumn determines patterns of regeneration in whitebark pine. This is because nutcrackers subsist year-round on pine seeds, which are produced only in autumn, so the birds need to store seeds in order to have food for winter and spring. Nutcrackers place the seeds in small "caches" of one to five seeds and, for various reasons, some caches are never retrieved. Because of this caching behavior, Clark's nutcrackers are considered seed dispersers for more than 10 conifer species in western North America. Some species, like the declining whitebark pine, rely on nutcrackers for all seed dispersal.

We wanted to know more about which specific habitat patches seed-caching nutcrackers choose in autumn, a subject that researchers have not previously studied. For example, what proportions of whitebark pine seeds are cached in high-elevation habitats, where whitebark pine can establish, and how many seeds are placed in low-elevation habitats, where seedlings will be outcompeted by other tree species?

TABLE—Proportion of different habitat types used by seed-caching Clark's nutcrackers in the Cascade Range, Washington, and availability of habitat types within home ranges for 5 ponderosa and 5 whitebark pine residents separately

PONDEROSA PINE RESIDENTS

	Habitat type							
	Mixed low elevation		*Ponderosa pine*		*Parkland ponderosa pine*		*Burned*	
Bird ID	Used	Available	Used	Available	Used	Available	Used	Available
193	0.03	0.25	0.38	0.20	0.59	0.33	0.00	0.21
211	0.05	0.09	0.44	0.18	0.44	0.11	0.08	0.62
505	0.19	0.47	0.52	0.11	0.29	0.13	0.00	0.30
632	0.10	0.53	0.18	0.20	0.73	0.22	0.00	0.05
781	0.72	0.48	0.13	0.13	0.15	0.17	0.00	0.22

WHITEBARK PINE RESIDENTS

	Habitat type							
	Cliffs/talus		*Whitebark pine*		*Parkland whitebark pine*		*Mixed low elevation*	
Bird ID	Used	Available	Used	Available	Used	Available	Used	Available
043	0.13	0.12	0.06	0.08	0.33	0.54	0.48	0.26
312	0.00	0.06	0.00	0.07	0.00	0.23	1.00	0.64
719	0.41	0.13	0.00	0.07	0.13	0.26	0.47	0.53
746	0.50	0.32	0.37	0.28	0.03	0.06	0.11	0.34
893	0.18	0.12	0.07	0.08	0.41	0.33	0.34	0.47

Although we studied caching by 12 resident birds, we had sufficient sample sizes to look at habitat-scale selection for only 10 residents. For the habitat-scale analyses, we considered habitats selected compared to habitats available for each individual separately, requiring a sample size of at least 20 caches in the home range. Two residents had only a few caches observed in the home range and so they were not included in the habitat-scale analysis. However, since we observed some caching by these 2 birds, we did use them in the landscape-scale analyses.
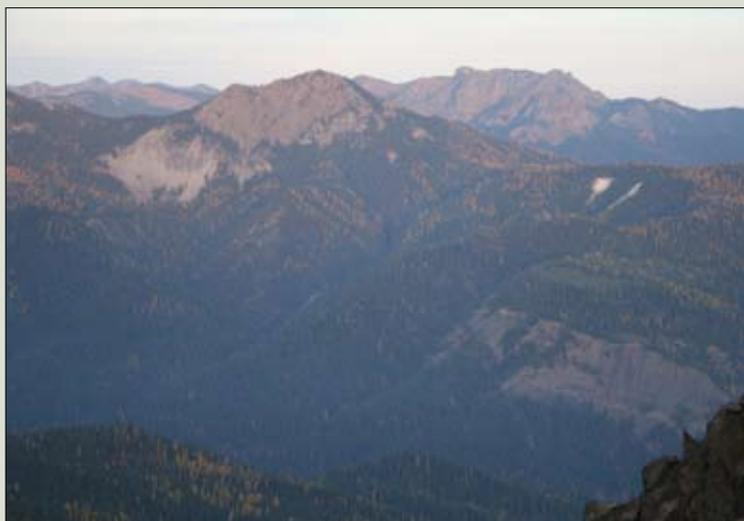
NUTCRACKERS HAVE an array of habitat types to choose from when caching, ranging from high-elevation whitebark pine stands to mid-elevation cliffs and low-elevation ponderosa pine forests.

NUTCRACKERS FIRST selected their home ranges for seed caching. Once within home range, they selected low-elevation habitats, like this ponderosa pine stand used by nutcracker #893.

CASE STUDY: Why Did Nutcrackers #043 and #211 Avoid Caching in Burns?

Nutcrackers have been thought to preferentially cache seeds in recent burns. This study provided the first opportunity to test this hypothesis using radio-tagged nutcrackers and recognized two reasons why nutcrackers might avoid burns when caching.

First, nutcrackers might avoid burns if they do not occur within their home range. In the case of nutcracker #043, there were no burns within the boundaries of its home range. Like other residents, #043 showed strong home range fidelity and rarely cached outside the home range. Thus, even though #043 traveled through burns when transporting seeds between harvest stands and the home range, the burns were never used for caching.

Second, nutcrackers sometimes choose not to cache in burns even when burns occur within the home range. In the case of nutcracker #211, burned habitat occurred within its home range, but #211 and other nutcrackers with home ranges near this burn avoided

it for caching. Among 6 radio-tagged nutcrackers and 258 seed caches, only 6 caches were placed within this burn. Most seed caches were placed in nearby living ponderosa pine forests. We suspect that nutcrackers avoided this burn because it was very open and nutcrackers caching seeds may have been vulnerable to predation.

Why do our conclusions differ so much from convention? Among the possible reasons:

1. Past studies did not formally examine selection (that is, they did not quantify use compared to availability), so results might not be directly comparable because of different methodologies;

2. Nutcrackers might be sensitive to fire history or other landscape features of burns (such as burn size, aspect, or slope) when caching and the burns in our study lacked some other unmeasured feature important for caching;

3. With a small sample size of 12 resident nutcrackers, this study might not have captured individuals that were representative of the population; and

4. Resident and emigrant nutcrackers might have different caching preferences (we studied habitat-scale selection by resident nutcrackers only).

IN AUTUMN 2007, nutcracker #043 transported whitebark pine seeds over this burn enroute to its home range.

NUTCRACKER #211 was one of six nutcrackers with a home range that contained this mid-elevation ponderosa pine burn. All nutcrackers avoided this burn for caching.
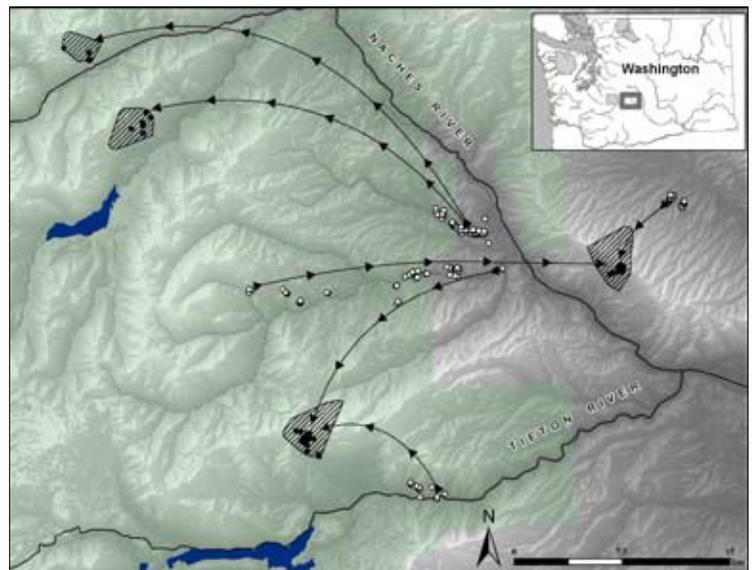
NUTCRACKER #043 headed for its home range with a pouch full of whitebark pine seeds (right) and map showing its whitebark pine seed transport flights in autumn (above). Nutcracker #043 harvested seeds near 2 high-elevation whitebark pine burns, but all seeds were transported from these areas, through the burns, and to the unburned home range for caching (arrows depict the direction of seed transport flights from harvest stands to cache sites within the home range).

THE BOTTOM LINE: MANAGER'S PERSPECTIVE

Why did we study nutcracker cache site selection?

In this study, we modeled nutcracker cache site selection rather than nutcracker caching preferences.

Studies of preference in animals compare the selection of habitat types when all types are equally available and animals have free choice among them. Preference is nearly impossible to study under natural conditions because we cannot ensure that all habitats are equally available to animals. For example, a nutcracker might prefer open meadows for caching compared to a closed-canopy forest, but if predation risk is higher in the open meadow, then it will not be used. Most studies of animal preferences must be conducted in controlled, laboratory settings.

In studies of selection, on the other hand, which is what we chose to do, researchers obtain a sample of used habitats for each individual and compare it to the availability of that habitat. (The term "selection" refers to habitats that are used in large proportion to their availability, whereas "avoidance" means that the habitat type was used less commonly than would be expected compared to availability.) When testing for site selection, it is important to obtain an unbiased sample of used habitats, which can be accomplished using telemetry such as we did because animals are equally likely to be detected in all habitat types. (Strictly observational studies can introduce bias when animals are more easily detected in some habitats than others.) Studies of animal habitat selection make no inferences to the preferences of animals.

FURTHER READING

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

Lorenz, T.J.; Sullivan, K.A.; Bakian, A.V.; Aubry, C.A. 2011. Cache-site selection in Clark's nutcracker (*Nucifraga columbiana*). *Auk.* 128(2): 237–247.

Manly, B.F.J.; McDonald, L.L.; Thomas, D.L.; McDonald, T.L.; Erickson, W.P. 2002. Resource selection by animals. 2ⁿᵈ ed. London: Kluwer Academic Publishers.

ADULT NUTCRACKER fitted with a radio tag prior to release.

SNOW ACCUMULATION in 3 habitat types during the nutcracker breeding season (March and April): from left to right, a low-elevation ponderosa pine stand, mid-elevation mixed forest, and high-elevation whitebark pine stand. Within home ranges, nutcrackers selected habitat types that accumulated the least amount of snow, presumably to enable easy access to cache sites in winter. Thus, ponderosa pine stands were selected over mixed forests, which were selected over whitebark pine stands.