



A Perplexing Puzzle: Clark's Nutcracker Whitebark Pine Seed Dispersal Effectiveness

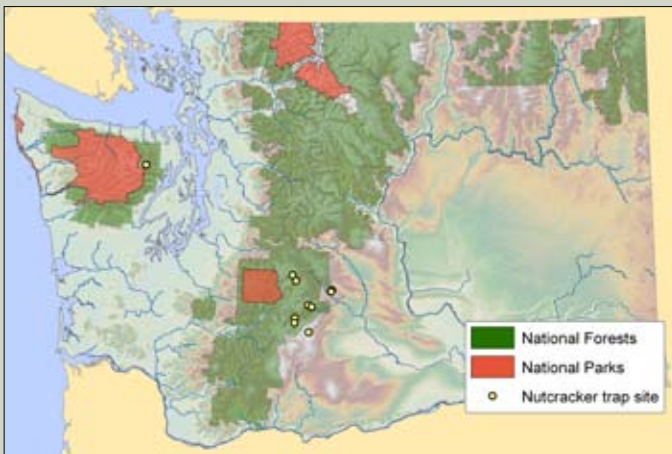
THEY CARRY seeds across landscapes, promoting the genetic diversity of whitebark and ponderosa pines. But nutcrackers often cache whitebark pine seeds in less-than-ideal habitat types and microsites. Yet, this bird and tree are considered co-evolved mutualists. So, what's up?

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 does “seed dispersal effectiveness” refer to?

Seed dispersal effectiveness refers to the number of seeds placed in locations where they can successfully mature into cone-bearing trees (Schupp 1993). Dispersal effectiveness is often considered separately for different stages of seed dispersal. For example, Clark's nutcrackers could be considered effective seed dispersers when harvesting seeds because relatively few seeds are immediately consumed. However, nutcrackers could be considered ineffective seed dispersers during winter and spring if they then consume most of the seeds previously cached.

Dispersal effectiveness is also scale-dependent. For example, we found that nutcrackers were highly effective long-distance seed dispersers, commonly transporting seeds more than 30 km between harvest trees and cache sites. However, most of the microsites that they selected for whitebark pine seed caches were in low-elevation forests or sites above ground where seedlings could not establish. Thus, nutcrackers were effective at one stage of dispersal but ineffective in another.

Why does it matter?

Seed dispersal information is important for restoring whitebark pine and assessing whether a natural regeneration approach (i.e., a restoration approach that relies entirely on Clark's nutcracker seed dispersal) is a viable restoration strategy. Information on nutcracker dispersal effectiveness is also critical for making informed decisions regarding regeneration potential within stands stressed by white pine blister rust, mountain pine beetle, or both and for predicting the response of pines to climate change.

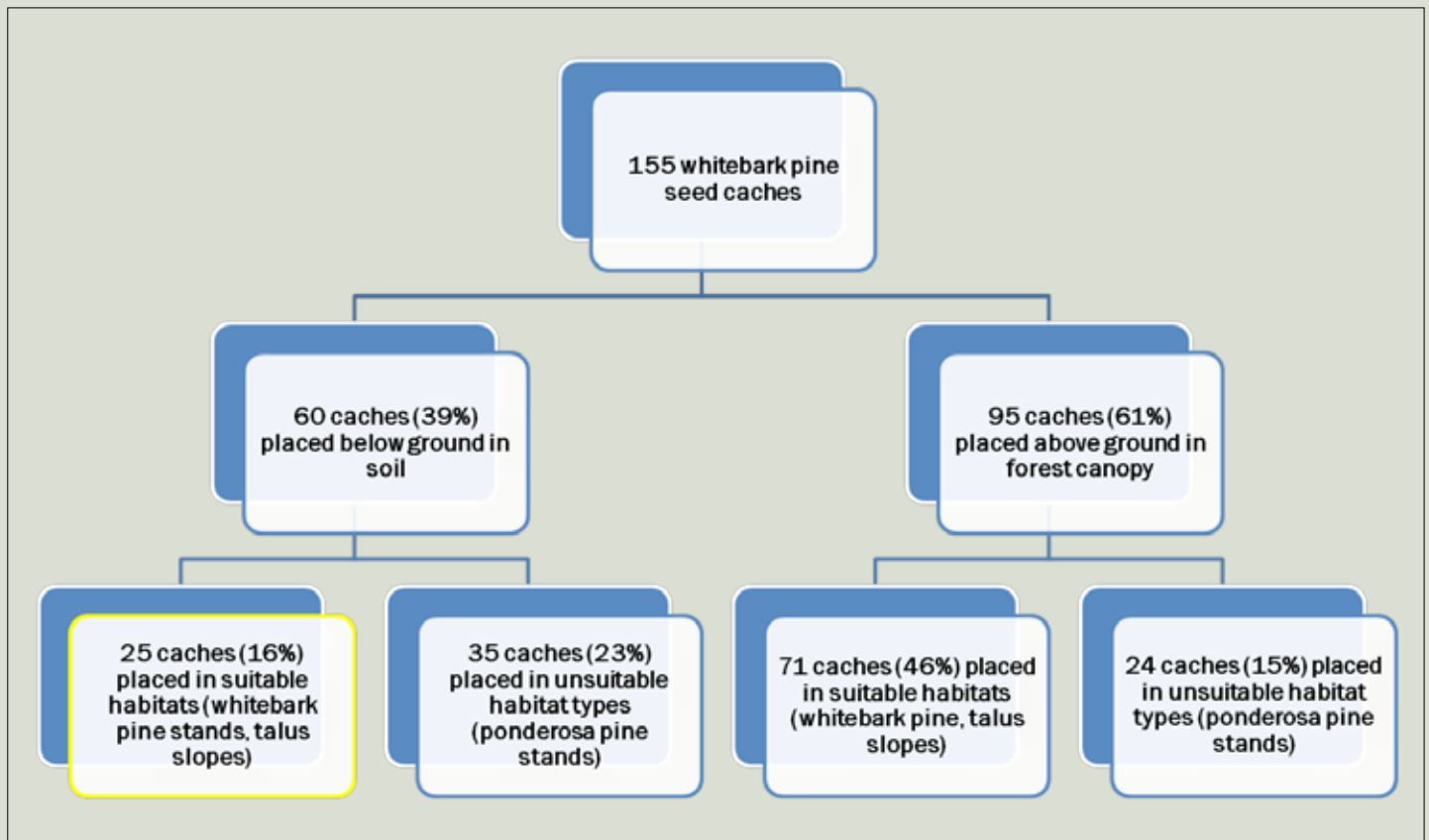
How did we measure nutcracker seed dispersal effectiveness?

We first used radio telemetry to follow resident (non-migratory) nutcrackers to their personal cache sites. We then measured landscape-scale, habitat-scale, and microsite-scale features of each site. We related our observations of nutcracker site selection to what is known about seed germination and seedling establishment in whitebark pine.





NUTCRACKERS ARE the only known mechanism of seed dispersal for whitebark pine, but they cache many seeds in unfavorable locations. For example, whitebark pine seeds may be cached in ponderosa pine forests, and ponderosa seeds in whitebark pine stands. In the photo above (left), a whitebark and ponderosa pine sapling are growing out of the same site in a transitional Douglas-fir forest—neither tree is likely to survive to reproductive maturity. At a microsite scale, many caches may be placed above ground, where germination is impossible, such as this whitebark pine cache being placed by nutcracker #719 in a mountain hemlock (above right).



SCHEMATIC DIAGRAM showing scale-dependent seed dispersal effectiveness of Clark's nutcrackers in this study. All told, only 16 percent of all whitebark pine seed caches ($n = 199$ caches) were placed in locations suitable for the establishment of cone-bearing, adult whitebark pine trees. The remaining 85 percent were placed in sites unsuitable for seed germination, such as tree bark or branches, or habitats unsuitable for seedling maturation, such as low elevation ponderosa pine stands.

Were nutcrackers in this study effective seed dispersers for whitebark pine?

At the landscape scale, yes.

Prior to this study, the maximum recorded seed dispersal distance for whitebark pine seed transport was 12.5 km, and the maximum nutcracker seed transport distance (for any kind of pine seed) ever reported was 22 km (reviewed in Tomback 1998). Using radio telemetry, we found that long-distance seed transport was common. For example, among 12 resident nutcrackers in this study, 5 transported seeds farther than 12.5 km and 3 transported seeds farther than 22 km. For ponderosa pine, the seed shadows of trees—the area of ground on which the seeds fall—growing in the center of our study area encompassed 523 km², and seeds were transported up to 26 km east, 33 km northwest, 26 km west, and 21 km south of seed harvest trees. These results suggest that nutcrackers have the potential to affect genetic diversity in ponderosa and whitebark pines more than previously thought and that they are effective long-distance seed dispersers.

At the habitat and micro-site scales, maybe not.

Fifty-eight percent of whitebark pine seed caches were placed in the whitebark pine zone or on talus slopes. The remaining seeds were placed in the ponderosa pine zone, where seedlings are

unable to mature into adult trees.

Thus, most whitebark pine seeds were placed in favorable habitats, so nutcrackers were fairly effective seed dispersers at a habitat scale.

However, habitat-scale caching directly influenced microsite scale caching. When caching whitebark pine seeds in high elevations, nutcrackers placed very few seeds in the soil (16 percent) compared to when caching in low elevations, where 48 percent of seed caches were placed in soil. When caching at high elevations, nutcrackers placed most seed in above-ground caches in the forest canopy, presumably to enable access to those caches during winter—but seeds placed in trees cannot germinate. Even when seeds were cached below ground in whitebark pine stands, most were cached in full sun or in forest litter, where McCaughey and Weaver (1990) found that germination success can be low.

Overall, the landscape-scale and habitat-scale effectiveness of nutcrackers was compromised at the microsite scale. Furthermore, even when seeds were cached by nutcrackers in below-ground sites and in suitable habitats, not all of these were placed in microsites favorable for seed germination and seedling survival. Thus, the actual effectiveness of nutcracker seed dispersal in our study is undoubtedly lower than suggested by our analyses.



NUTCRACKER DISPERSAL effectiveness refers to the numbers of seeds placed in sites that result in mature cone-bearing trees. Effective seed dispersal begins with nutcrackers harvesting seeds in autumn and only ends 20–30 years later, when those seeds have developed into cone-bearing trees.

Why are migratory nutcrackers more effective than residents at dispersing seeds?

Nutcrackers that inhabit regions with many cone-producing trees may never have to migrate over the course of their lifetime, while nutcrackers that occupy regions with few cone-producing stands may migrate in most years. Resident birds transport seeds back to their home range, so if home happens to be in a low-elevation ponderosa pine zone, their cached whitebark pine seeds will not germinate. Migratory nutcrackers, on the other hand, appear to wander throughout autumn, winter, and spring unless they find productive pine stands for settling. They do

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not show home range fidelity when caching, and they are more likely than residents to cache seeds in the same stand that they harvest from. This suggests that in a cone-producing whitebark pine site, migratory nutcrackers may be more effective seed dispersers than residents.

THE BOTTOM LINE: MANAGER'S PERSPECTIVE

How can nutcrackers be “ineffective” seed dispersers if they are whitebark pine mutualists?

We found that nutcrackers rarely cached seeds in habitats and microsites where whitebark pine would be able to germinate and mature. Therefore, nutcrackers appeared to be ineffective seed dispersers for whitebark pine. This conclusion is perplexing, and seemingly contradictory, since nutcrackers are known to be co-evolved mutualists for whitebark pine. It raises the question of why whitebark pine would have co-evolved with a potentially ineffective seed dispersal mechanism.

This question can partly be answered by considering the reproductive strategy of whitebark pine trees. An individual whitebark pine tree produces tens or hundreds of thousands of seeds during each mast year—a year of high seed production across a large geographic area. Given the longevity of whitebark pine trees, an individual may live through a hundred or more mast years. From the perspective of a whitebark pine tree, it needs only to have one of these seeds survive to reproductive maturity in order to be evolutionarily fit. Whitebark pine trees produce copious amounts of seeds over the course of a lifetime, so despite high rates of predation and largely ineffective seed dispersal, some seeds are able to survive into mature trees.

FURTHER READING

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Nicholas Ernst

A NUTCRACKER searching for emerging whitebark pine germinants in July, just after snowmelt.



EMIGRANT NUTCRACKERS, like the flock shown here in a ponderosa pine stand, may be more effective seed dispersers than residents because they are more likely to cache seeds in the same stand that they harvest from, rather than transport the seeds to distant home ranges.

FOR FURTHER INFORMATION

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