BRISTLECONE PINE AND CLARK'S NUTCRACKER: PROBABLE INTERACTION IN THE WHITE MOUNTAINS, CALIFORNIA

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ABSTRACT.— Many bristlecone pines in the White Mountains, California, are members of multistem clumps. We propose that these clumps have arisen by multiple germinations from seed caches of Clark's Nutcracker, as occurs in several other pine species. The commonness of nutcrackers and their caching of singleleaf pinyon seeds in the study area provide supporting evidence. Other vertebrates appear unlikely to be responsible for the stem clumps. Seed burial may be required to establish regeneration on these adverse sites where bristlecone pine attains great longevity.

Clark's Nutcracker (Corvidae: *Nucifraga columbiana* Wilson) disperses seeds and establishes seedlings of Colorado pinyon (*Pinus edulis* Engelm.), singleleaf pinyon (*P. monophylla* Torr. & Frém.), limber pine (*P. flexilis* James), and whitebark pine (*P. albicaulis* Engelm.) (Vander Wall and Balda 1977, Tomback 1978, Lanner and Vander Wall 1980). Nutcrackers remove seeds from cones, hold them temporarily in a sublingual pouch, and subsequently cache them in the soil as a winter and spring food resource. Despite a marked preference for the large wingless seeds of the above-mentioned species, nutcrackers sometimes harvest as well the smaller winged seeds of ponderosa pine (*P. ponderosa* Laws.), Jeffrey pine (*P. jeffreyi* Grev. & Balf.), and even Rocky Mountain Douglas-fir (*Pseudotsuga menziesii* var. *glauca* [Beissn.] Franco) (Giuntoli and Mewaldt 1978, Tomback 1978). Seeds left unretrieved frequently germinate as groups of seedlings that develop into distinctive tree clumps in which the number of stems reflects the number of seeds per cache. High frequencies of multiple stem clumps, as opposed to single stems, characterize limber and whitebark pine, and greatly exceed clumping in winged-seeded conifers not cached by nutcrackers (Lanner 1980). Clark's Nutcracker is the only reliable agent of seed dispersal and seedling establishment of whitebark pine, other animals lacking the capability of serving these functions (Hutchins and Lanner 1982). The similarity of fauna in whitebark and limber pine forests suggests it is the most effective disperser and establisher of limber pine as well.

Great Basin bristlecone pine (*P. longaeva* D. K. Bailey) has relatively small winged seeds (USDA Forest Service 1974). Peattie (1953) reported that nutcrackers harvest seeds of *P. aristata* Engelm., under which name he included what has since been segregated as *P. longaeva*. Vander Wall and Balda (1977) stated that *P. aristata* seeds were eaten by nutcrackers, but probably not stored unless local pinyon and limber pine seed crops had failed. In this paper we present evidence that nutcrackers not only eat bristlecone pine seeds, but they also store them in the soil, thus causing establishment of seedlings.

METHODS

The study area is the Ancient Bristlecone Pine Forest, a dedicated botanical area within the Inyo National Forest in the White Mountains, California. We made observations 23 July and 30 September–3 October 1982 in the Schulman Memorial Grove (3030–3150 m) and the Patriarch Grove (3425 m). Both areas have substrate of light gray to white dolomitic limestone that frequently forms a pavement of small fragments. Bristlecone pine is the predominant tree species. Limber pine occurs sporadically in both groves but does not reach tree size in the Patriarch Grove. The most common shrubs are of the genera *Artemisia* and *Ribes*, but the ground is mostly bare of vegetation (Fig. 1).

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Fig. 1. An ancient bristlecone pine stem clump growing on dolomite in the Patriarch Grove.

Three 20 x 50 m transects were laid out in each grove, through typical forest cover. Data recorded for each tree in each transect were species, diameter class (<1 cm, 1–10 cm, >10 cm at breast height), and number of independent stems in contact at the root collar. The transects sampled east, northeast, west, northwest, and south aspects.

Diurnal vertebrates were identified and counted during 29.25 hr in the Schulman and Patriarch Groves and in a limber pine woodland nearby at 3000 m. A "visit" is an episode in which an individual animal was observed in (bird) or at the base of (mammal) a bristlecone pine tree; or, in the case of the lower woodland, a limber pine tree.

RESULTS

Stem clumps were common among trees of both species and of all diameter classes, at both groves. All the limber pines were members of multistem clumps. Bristlecone pine was more highly clumped in the Patriarch Grove than in the Schulman Grove (Table 1). Though one would intuitively expect larger and therefore older trees to have fewer stems per clump due to attrition, no such relationship was detectable in the data. It is suggested by Forest Service interpretive signs in the Patriarch Grove that the multistem habit of bristlecone pines there is due to the rooting of prostrate branches (i.e., layering); but close examination of clumps disclosed no evidence of such an origin.

In 26.25 hr of animal observations, 11 species of birds and 2 of mammals were observed in or at the base of bristlecone pines. The following species are omitted from Table 2 because they are not considered possible dispersers or establishers of bristlecone pine: White-breasted and Pygmy Nuthatches, Dark-eyed Junco, White-crowned Sparrow, Hairy Woodpecker, Mountain Chickadee, and Common Flicker. None of these species is reported to cache seeds in the soil. Of the remaining 6 animals considered possible dispersers or establishers, nutcrackers made 88% of the visits to bristlecone pines (Table 2). We saw no seeds actually being harvested from cones of bristlecone pine, which were then beginning to open. There was, however, a high level of harvesting activity by nutcrackers on singleleaf pinyons and limber

TABLE 1. Stem clumping in bristlecone and limber pines on transects in the Ancient Bristlecone Pine Forest, White Mountains, California. Asterisk (*) indicates significant difference between groves (a = .05, Newman-Keuls multiple mean test).

	Schulman Grove		Patriarch Grove	
	Bristlecone	Limber	Bristlecone	Limber
n (trees)	76	5	122	27
n (clumps)[1]	48	2	45	7
trees/clump, $\bar{x} \pm$ s.d.	1.6 ± .9*	2.5[2]	2.7 ± 2.1*	3.9 ± 1.8
trees/clump, range	1–4	2–3	1–11	2–7
percent multi-stem clumps	46	100	69	100

[1]A clump includes single stems as well as multiples.
[2]Insufficient data for S.D. computation.

pines nearby, even though their cones also were mainly closed. On many occasions nutcrackers were seen caching seeds in the study area, but the five caches that were excavated (four in the Patriarch Grove, one in the Schulman Grove) contained only seeds of singleleaf pinyon. Cones of 50 bristlecone pines from each grove showed no damage of the type often caused by nutcrackers (Lanner 1980).

DISCUSSION

The high frequency of stem-clumping among bristlecone pines (46–69%) cannot reasonably be attributed to the generally random seed-rain resulting from wind dispersal. It compares with the following clumping frequencies of wingless-seeded pines known to be dispersed and established by nutcrackers: limber pine in Logan Canyon, Utah, 53–68%; and whitebark pine in Togwotee Pass, Wyoming, 47% (Lanner 1980). These figures are conservative as indices of nutcracker activity because they exclude (a) caches consisting of one seed only and (b) multiseed caches in which only one germinant survives to be counted. Fritts (1969) found 34% of bristlecone pines in his White Mountain quadrats to be multistemmed. The clumping frequency of limber pine in both groves (100%) and the observations of nutcracker activity there conclusively show that nutcrackers cache seeds in the very areas where clumped bristlecones occur. The transport of singleleaf pinyon seeds to high elevations where seedling survival is doubtful has also been noted in Utah (Lanner and Vander Wall 1980). It may have the ultimate effect of selecting genotypes adapted to these high-elevation conditions.

The much greater density of Clark's Nutcracker in both groves, compared to that of other possible dispersers, further supports the hypothesis that nutcrackers establish bristlecone pine seedlings. Pinyon jays are known to cache pinyon pine seeds in groups (Vander Wall and Balda 1981), but their small numbers suggest a minor role here. Scrub jays seldom cache seeds in groups (Vander Wall and Balda 1981), so are unlikely to be responsible for stem clumps. Though ravens, chipmunks, and golden-mantled ground squirrels are possible dispersers, our recent study (Hutchins and Lanner 1982) has shown such a role highly improbable for them. Also, ground squirrels were not seen in the Patriarch Grove, where clumping was most common. The effect of nocturnal rodents was not measured here, but is probably very minor (Abbott and Quink 1970, Hutchins and Lanner 1982).

The texture of the substrate in both groves is morphologically similar to that of a communal caching site described by Lanner and Vander Wall (1980). Though bristlecone pine distribution in the White Mountains has been attributed largely to the moisture-holding qualities of the substrate (Wright and Mooney 1965), it is possible that the cache-site preference of nutcrackers is also a significant factor.

Our inability to observe nutcrackers harvesting and caching bristlecone pine seeds did not surprise us in view of the availability of the larger limber pine and singleleaf pinyon seeds nearby. The nutcrackers obtained these seeds by tearing up the unopened cones, as they often do (Lanner 1980) with these species. Whether they also demolish the hard, bristly, closed cones of bristlecone pine is unknown. We found no such cones on the ground.

Though some investigators have called attention to the fact that the most ancient of the old bristlecone pines are found on the most adverse sites (Schulman 1954, 1958, LaMarche 1969, Wright and Mooney 1965), they have not addressed the question of how

TABLE 2. Frequency of visits by potential seed dispersers in and adjacent to Ancient Bristlecone Pine Forest, White Mountains, California, 30 September–3 October 1982.

	Schulman Grove	Patriarch Grove	Limber Pine Woodland
Observation time, hours	15.5	10.75	3.0
	Visits per hour of observation		
Clark's Nutcracker	7.0	3.7	25.7
Pinyon Jay	0	.2	0
Scrub Jay	.1	0	0
Raven	.1	.2	.7
Chipmunk	0	.6	0
Golden-mantled ground squirrel	.5	0	0