blackbirds may thus protect or improve the yield of some agricultural crops.

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LIMBER PINE SEED HARVEST BY CLARK'S NUTCRACKER IN THE SIERRA NEVADA: TIMING AND FORAGING BEHAVIOR

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The preferred seed sources for the Clark's Nutcracker (*Nucifraga columbiana*) in the Sierra Nevada of California are the whitebark (*Pinus albicaulis*), Jeffrey (*P. jeffreyi*), ponderosa (*P. ponderosa*), and singleleaf piñon (*P. monophylla*) pines (Tomback 1977). Nutcrackers prefer these species because: 1) the seeds are large and easily harvested, 2) the trees are locally abundant, and 3) the timing of cone ripening and/or opening allows sequential exploitation of the seeds of two or more pine species (Tomback 1977).

Nutcrackers harvest and store limber pine (*P. flexilis*) seeds in the San Francisco Mountains of north-central Arizona (Vander Wall and Balda 1977). As we report here, nutcrackers also harvest and store limber pine seeds in the Sierra Nevada. Like the other preferred seeds, those of the limber pine are large, the pine is locally abundant (although patchy in distribution), and most of the cones open after the peak of whitebark pine seed harvest by nutcrackers. In the Sierra Nevada, limber pine occurs from Mono Pass southward, primarily on the eastern slope, in stands less than 3 km across (Sudworth 1908, Griffin and Critchfield 1972).

On 5, 6, and 16 September 1979 we watched nutcrackers harvest and store limber pine seeds in the southern Sierra Nevada, Onion Valley, Inyo Co. (2,700 m elevation). Our observation point was above Independence Creek, about 1 km below the Kearsarge Pass trailhead, and about 0.2 km south of the Onion Valley road. Here, limber pine is scattered over the steep north- and south-facing valley walls, interspersed with foxtail pine (*P. balfouriana*) and red fir (*Abies magnifica*). New cones were plentiful on all three conifer species. On 5 and 6 September, limber pine cones were in various stages of ripening, both among trees and, to a lesser extent, on individual trees. Half the cones or more were entirely green, highly resinous, and completely closed. The others were partly brown and opening, with scales extending to various degrees from the cone core. Open, brown cones of the previous year remained on most limber pines.

At 15:30 on 5 September, we observed an adult nutcracker harvest seeds for 15 min from the top of a limber pine tree on the north-facing slope above Independence Creek. On 6 September from 15:00 to 17:00, we watched two nutcrackers on the same north-facing

slope harvest and store limber pine seeds. The birds would land on an open cone, search quickly through the scales, and occasionally extract a seed. The seed was rattled between the mandibles to test for edibility (Tomback 1977, Vander Wall and Balda 1977) and placed in the sublingual pouch. Each bird moved rapidly around a tree and went from tree to tree, without any apparent search pattern. It was evident, however, that birds were selective; both nutcrackers returned to two particular trees several times. One nutcracker with a bulging sublingual pouch flew to a rock wall, landed on a ledge barren of vegetation, and stored one or more caches of seeds in a vertical fissure. It then flew to a second fissure where it repeated the process.

On 16 September we returned to this site from 14:00 to 17:00. All limber pine cones were now pale brown and fully open. Nutcrackers were more numerous and active than on our earlier visit. At least five individuals were harvesting and storing limber pine seeds on the north-facing slope and also on the ridge top. At 14:05 a nutcracker began foraging directly below us in one tree preferred by nutcrackers on 5 and 6 September. After landing on each cone, the bird methodically searched through the scales at the sides and top. The nutcracker extracted only one or two seeds from any cone before moving on. After 12 min of foraging the bird flew to the creek to drink and then spent about 5 min searching through three limber pines. The nutcracker then flew eastward to the rock wall and out of sight.

The increase in nutcracker activity from early to mid-September in the limber pine stands of Onion Valley may be attributed to the diminishing supply of whitebark pine seeds at subalpine elevations (Tomback 1977) and the increased availability of ripe limber pine cones. We observed 100 or more nutcrackers harvest and store whitebark pine seeds from 1 to 5 September 1979, along the Kearsarge Pass trail in the Independence Creek drainage above Onion Valley (Inyo Co.) and around the Kearsarge Lakes (King's Canyon National Park, Fresno Co.), elevations 3,050 m to 3,605 m. Stands of whitebark pine were prevalent throughout the drainage and around the Kearsarge Lakes. Whitebark pine cones were abundant, yet most of them showed signs of foraging by nutcrackers and other vertebrates (Tomback 1977), suggesting that the whitebark pine seed harvest had already peaked.

The limber pine seed foraging behavior of nutcrackers early in September suggests how cone ripening affects the timing of seed source utilization. Nutcrackers bypassed the closed cones and examined and reexamined the open cones. Tearing into closed cones requires more effort than does searching through newly opened cones, which should still bear a number of seeds. We propose that the nutcracker is an optimal forager. Presented with a choice of seeds, a nutcracker should select the one with the shortest search and/or handling time (Krebs 1978). As whitebark pine seeds are depleted and search time increases, and as more limber pine cones open, at some point it may be equally, and then more, efficient for nutcrackers to harvest and store limber pine seeds in a year when the cone crop is good.

Nutcrackers in the San Francisco Mountains harvest and store seeds from closed limber pine cones (Vander Wall and Balda 1977). The difference in limber pine seed harvesting behavior between the nutcrackers in the San Francisco Mountains and those in the Sierra Nevada, at least as observed in 1979, may relate in part to the widespread occurrence of whitebark pine in the Sierra Nevada. Whitebark pine, a highly preferred seed source (Tomback 1977), does not occur in the San Francisco Mountains. There, nutcrackers preferentially harvest and store seeds from closed limber pine cones and closed Colorado piñon pine (*P. edulis*) cones. The seeds of other pines may be taken later (Vander Wall and Balda 1977).

In the central eastern Sierra Nevada, nutcrackers harvest and store Jeffrey pine seeds after the supply of whitebark pine seed has declined. The birds prefer to take seeds from Jeffrey pine cones with partly extended scales rather than from cones with closed scales or fully extended scales (Tomback 1977). This reduces the effort required to remove seeds but also improves their chances of selecting a cone with a nearly full complement of seeds.

We offer two reasons, not necessarily mutually exclusive, why the nutcrackers we observed in early September restricted their foraging in limber pine to open cones and why they spent so little time on each cone. Possibly, 1) after harvesting and storing whitebark pine seeds, nutcrackers habitually forage through newly opened limber pine cones rather than harvest seeds from depleted whitebark pine cones or closed limber pine cones or 2) limber pine cones were so abundant in 1979 that birds obtained seeds most efficiently by foraging through open cones. These hypotheses may be tested as follows: if nutcrackers still prefer open limber pine cones in years of low limber pine cone productivity and moderate-to-good whitebark pine cone productivity, the first explanation is supported. However, following a whitebark pine cone crop failure, we predict that nutcrackers will at least initially harvest seeds from closed limber pine cones and thereby maximize the total number of seeds obtained.

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