PRE-ROOSTING FLIGHT OF THE CLARK'S NUTCRACKER

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ABSTRACT.—Each summer at Tioga Pass, California, Clark's Nutcrackers participate in a nightly pre-roosting flight beginning in mid- to late July. Before sunset, nutcrackers are active on the sunlit, west-facing Mt. Dana slope. As light intensity rapidly decreases, they fly in small groups to the east-facing Gaylor Ridge slope to roost—a distance of 2 km. Gaylor Ridge is the first slope in the study area to receive sunlight at sunrise. In 1974, 1975, and 1976, the number of pre-roosting flight participants peaked at 30, 33, and 47, respectively, and dwindled to a few birds by the end of August. Irregular pre-roosting movements of nutcrackers were also observed in 1973 in the Minaret Summit area. Data on temperature and solar radiation gathered at Tioga Pass in summer 1974 suggest two explanations for this behavior: 1) nutcrackers may derive some energetic benefit by remaining in the warmest area at sunset and by roosting in the first area to be warmed at sunrise, or 2) nutcrackers may extend their activity time for foraging, feeding young, and socializing by being in the last sunlit area at sunset and in the first sunlit area at sunrise. Observations of the feeding habits and pre- and post-roosting activities of nutcrackers suggest that light intensity may be the primary factor triggering pre-roosting flights. *Received 13 April 1977, accepted 28 August 1977.*

IN the summers of 1974, 1975, and 1976, I observed an unusual behavior pattern of the Clark's Nutcracker (*Nucifraga columbiana*) at Tioga Pass, Inyo National Forest, Mono County, California. Each evening, a number of nutcrackers participated in a unidirectional pre-roosting flight—a mass movement across the valley to a roosting area. Ferdinand J. Castillo, Yosemite Park Ranger at Tioga Pass, observed this phenomenon for several summers in succession prior to my observations. Such regular flights have not been reported elsewhere for the nutcracker, although I have observed occasional and less structured pre-roosting movements of nutcrackers in the vicinity of Mammoth Mountain, Inyo National Forest, Madera County, California.

Each evening before sunset, most of the nutcrackers in the Dana Meadows vicinity of Tioga Pass were found on the west-facing Mt. Dana slope, the last terrain in the area to receive sunlight. When light intensity on the slope dropped rapidly between 1930 and 2000, nutcrackers in groups of two to five birds left the Mt. Dana side of the pass. The groups flew about 100 m above the valley, directly across Tioga Pass—a distance of 2 km—into the dense forest on the east-facing slope of Gaylor Ridge. Here I examine two factors that may be responsible for the occurrence and fixed pattern of such pre-roosting flights.

STUDY AREAS AND METHODS

Minaret Summit.—Minaret Summit, elevation 2,825 m, is 3 km northwest of Mammoth Mountain. On the summit and in the adjacent forest are mature stands of whitebark pine (*Pinus albicaulis*). Other conifers in the area include lodgepole pine (*Pinus contorta*), red fir (*Abies magnifica*), and mountain hemlock (*Tsuga mertensiana*). Approximately 1 km southeast of Minaret Summit is a ridge, 125 m in height, which is the last terrain northwest of Mammoth Mountain to receive sunlight at sunset. Part of the east slope of the same ridge is the first area to receive sunlight at sunrise.

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Tioga Pass.—At Tioga Pass data were collected in the Dana Meadows area, elevation 3,030 m, on the west-facing slope of Mt. Dana, and on the east-facing slope of Gaylor Ridge up to about 3,150-m elevation. The two slopes face each other and are aligned on an east-west axis in the study area. Both slopes are steep (approximately 40% grade) in the areas frequented by nutcrackers.

At the base of Mt. Dana are mixed stands of whitebark pine, lodgepole pine, and red fir, interspersed with meadow. Higher on the slope in the area frequented by nutcrackers are small stands of whitebark pine scattered among meadows and talus slopes. At the base of Gaylor Ridge and up to about 3,120-m elevation is a dense forest of whitebark pine, lodgepole pine, and red fir. Above the forest is a steep, 70-m slope bearing scattered whitebark pine.

Observations on the behavior patterns of nutcrackers prior to roosting, at roosting sites, and immediately after roosting, were made in the subalpine habitats of Minaret Summit and Tioga Pass in 1973 and 1974, respectively. Intermittently throughout the summers of 1974, 1975, and 1976, I censused the number of nutcrackers participating in the nightly flights at Tioga Pass from a point adjacent to the Yosemite National Park entrance station.

I recorded daily temperatures and solar radiation using meteorographs (WeatherMeasure model M701) and actinographs (WeatherMeasure model R401) with 7-day chart recorders. One of each instrument was set on the ground, the meteorographs in vented housings, at 3,150-m elevation on both the Gaylor Ridge and Mt. Dana slopes. The instruments were placed just upslope of the trees where nutcrackers usually perched or roosted. As a result, the recorded data approximated the conditions that the birds experienced when perched on treetops at sunrise or sunset.

Results

Summer Timetable and Food Habits

An evaluation of the factors responsible for the occurrence of pre-roosting flights at Tioga Pass and other pre- and post-roosting activities must consider several aspects of the biology of the nutcracker in the eastern Sierra Nevada, which I describe in detail elsewhere (Tomback 1978). In the south-central region, the majority of nutcrackers overwinter and nest below subalpine elevations. After young fledge, family groups of nutcrackers migrate to subalpine habitat. By mid-July, the numbers of nutcrackers at subalpine elevations peak. Throughout the summer there are three principal sources of food for nutcrackers: 1) insects and spiders, 2) stores of whitebark pine seed made by the birds the previous summer, and 3) seeds from unripe and partially ripe cones of the whitebark pine. The availability of the latter food source varies from year to year; in 1973 the cones were first harvested on 19 July, but in 1974 no seed was taken until 2 August. Many juvenile nutcrackers are fed by adults until late August when whitebark pine cones are ripe and seed storage begins. This occurred about 29 August in 1973 and 25 August in 1974. After whitebark pine seed has been harvested and stored, most nutcrackers descend to lower elevations in late September to harvest and store the seed of the Jeffrey (*Pinus jeffreyi*) and piñon (*P. monophylla*) pines.

Pre- and Post-roosting Behavior

Minaret Summit.—In 1973 the whitebark pine in the forest on and adjacent to Minaret Summit had an abundant crop of cones, which attracted between 35 and 50 nutcrackers, mostly in family groups, into the area. On 31 July, 2, 9, and 13 August, I observed the pre-roosting behavior of nutcrackers. Each evening until dark nutcrackers participated in two activities: 1) adults harvested whitebark pine seed and fed juveniles, which perched nearby and constantly gave hunger calls (vocalization terminology from Mewaldt 1956); and 2) for periods of several minutes at a time, nutcrackers assumed treetop perches and vocalized, most often using the regular call.

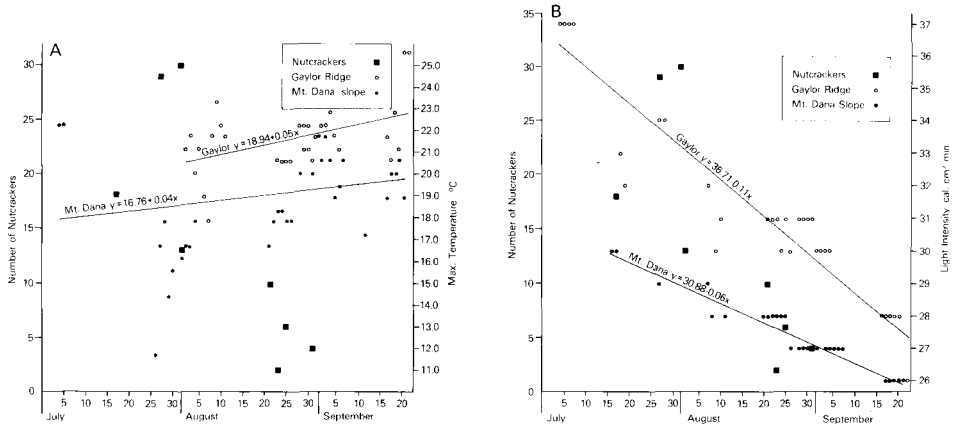

Fig. 1. Variation in the numbers of nutcrackers participating in pre-roosting flights: A) vs. maximum temperature; and B) vs. light intensity. Recorded on both Gaylor Ridge and the Mt. Dana slope from July through September 1974.

At sunset on 31 July and 13 August I observed group movements of nutcrackers that were similar to the pre-roosting flights at Tioga Pass. Beginning at 1915, when light intensity began to drop rapidly, nutcrackers in groups of two to seven flew southeast onto the sunlit, west slope of the nearby ridge. Edited excerpts from my notes of 13 August illustrate the pre-roosting activities of the nutcrackers on the sunlit slope:

1920. Adult and two juveniles are perched on the top of a whitebark pine near the base of the west slope of the ridge. As the sun drops and the shadow travels up the slope, the three nutcrackers leave their perches and fly upslope. The adult and juveniles land on top of another whitebark pine; the adult harvests seed while juveniles beg. Both juveniles leave the tree and execute wild flying maneuvers.

1925. Juveniles are fed by adult at the top of a red fir.

1935. (Sun drops below Minarets). Adult and juveniles move higher upslope onto the sunny, steep face. Other nutcrackers are already present. There is a constant exchange of the regular call and restless flying from treetop to treetop by the nutcrackers. Groups of nutcrackers select high, exposed perches, often with several birds in the same tree. Perches are well above neighboring trees—at least 20 m high—and usually on red fir and mountain hemlock. Several nutcrackers use the shrill call.

1945. Nutcrackers continue to move upslope into sunlight as shadow creeps upward. Light is fading quickly. A nutcracker is perched on a whitebark pine cone, harvesting seed. Some nutcrackers have reached the top of the west slope where they perch briefly, vocalizing, and then fly east over the top of the ridge and out of sight. A few nutcrackers remain perched in treetops below the summit, where they will probably roost.

2000. Light has faded from the slope. No nutcrackers are on the exposed perches. A few distant vocalizations are heard, and then no movements or calls.

On 1, 2, 9, 13, and 29 August, I observed the activities of nutcrackers at roosting sites on the east slope of the ridge near Minaret Summit and at Minaret Summit directly after the arrival of nutcrackers from roosting areas. The sequence of sunrise activities can be summarized as follows:

0550. The sun is below the horizon, but the first light is touching the treetops on the east slope of the ridge.

0600. The first nutcracker call is heard.

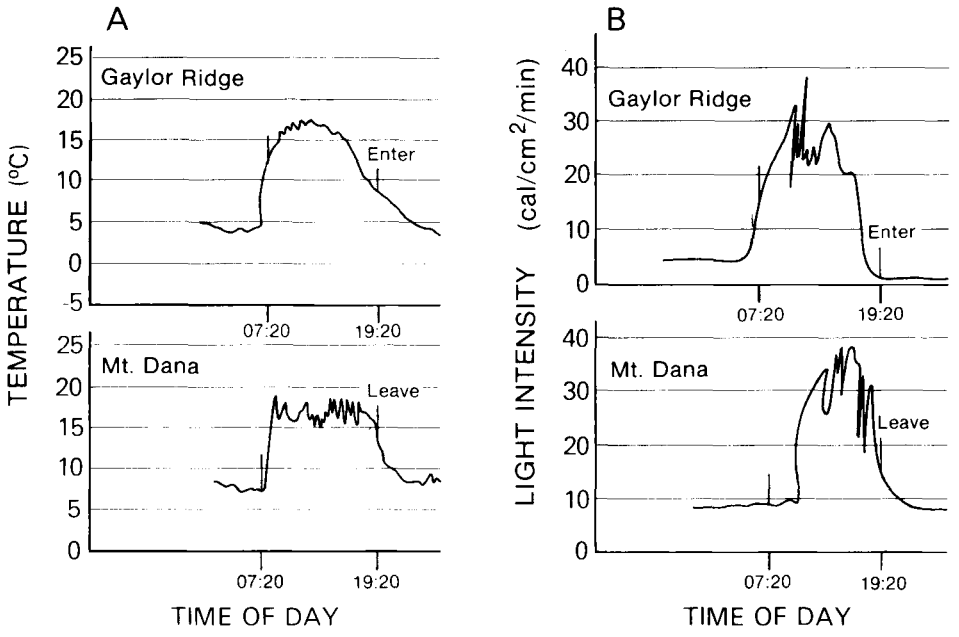

Fig. 2. A comparison of pre- and post-roosting temperature (A) and light intensity (B) for the east-facing Gaylor Ridge slope and the west-facing Mt. Dana slope in relation to the pre-roosting flight of 17 July 1974.

0605. The sunlight on the slope is gaining intensity. Several nutcrackers begin vocalizing—primarily the regular call. Nutcrackers are perched in sunlit treetops while calling.

0610. The first nutcracker flies into the Minaret Summit area.

0620–0635. More nutcrackers fly into the area in groups of two to eight birds, some nutcrackers vocalizing in flight. At Minaret Summit and in the adjacent forest, many nutcrackers perch in treetops and vocalize, using both the regular and shrill calls. Some birds begin to harvest seed while juveniles give hunger calls.

Tioga Pass.—In 1974, pre-roosting flights at Tioga Pass began about 17 July, and the number of participants peaked by the end of July with 30 birds (Fig. 1). In 1975, pre-roosting flights began about 22 July and peaked about 10 August with 33 nutcrackers. On 2 August 1976, a peak number of 47 nutcrackers participated in pre-roosting flights.

From 16 July to 16 September and 4 July to 16 September 1974, I measured the ambient temperature and light intensity at 3,150 m on both the Gaylor Ridge and Mt. Dana slopes to correlate these factors with changes in nutcracker activity. Daytime maximum temperature recorded at Tioga Pass ranged from 16° to 25°C, and nighttime minimums ranged from 1° to 9°C.

Using the charts from 17 July (Fig. 2A and B), it can be seen that by 0720, the temperature on the east-facing slope of Gaylor Ridge—where nutcrackers roosted—had risen to about 12°C about 1 h after sunlight had illuminated the slope, whereas at the same time of day the temperature on the west-facing Mt. Dana slope remained at its nighttime low. It appears that nutcrackers roosted in the first area warmed by the rising sun. By 1920, when light intensity had dropped to zero on Gaylor Ridge, some sunlight still remained on the Mt. Dana slope where nutcrackers were found. Between 1920 and 2000, as light intensity rapidly dropped on Mt. Dana, nutcrackers flew to the Gaylor Ridge slope to roost.

On nine evenings—17 and 27 July, 1, 2, 21, 23, 25, and 31 August, and 18 September—I observed the pre-roosting behavior of nutcrackers. As in the Minaret Summit area in 1973, nutcrackers participated in two types of activities each evening: 1) some adults foraged and fed juveniles until the young became independent at the end of August; and 2) nutcrackers perched in treetops and vocalized—primarily the regular call. Foraging birds occasionally flew to a high perch and vocalized. On Gaylor Ridge after the pre-roosting flight, most of the nutcrackers participated in the second activity until they went to roost. When pre-roosting flights declined at the end of August, some nutcrackers roosted at the base of the Mt. Dana slope, where they also perched in treetops and vocalized at sunset.

The following sequence of pre-roosting activities comes from my field notes of 17 July:

1910. Sunlight is gone from the top of Gaylor Ridge. The entire Mt. Dana slope and a portion of the valley floor are sunlit. At the base and on the Mt. Dana slope, nutcrackers are perched in treetops and vocalizing or flying excitedly from perch to perch.

1920: One nutcracker leaves the Mt. Dana area and flies across the valley into the dense forest on Gaylor Ridge. The valley floor is now in shadow. Many nutcrackers on the sunlit slope are vocalizing.

1930. One nutcracker leaves the valley near the base of Mt. Dana and flies into the Gaylor Ridge forest.

1940. Two nutcrackers leave the Mt. Dana slope and land in treetops just below the instrument station on Gaylor Ridge. The nutcrackers in the forest on Gaylor Ridge are calling constantly.

1950. The base of the Mt. Dana slope is in shadow. Nine nutcrackers, in associations of twos and threes, leave the Mt. Dana slope and fly into the dense forest on Gaylor Ridge.

2000: The lower slope of Mt. Dana, including the instrument station, is in shadow.

2005. Three nutcrackers leave the Mt. Dana slope and fly into the dense forest on Gaylor Ridge.

2015. The shadow has rapidly reached timberline.

On 28 June, 19 July, 3 and 22 August, and 23 September, I observed the post-roosting behavior of nutcrackers on Gaylor Ridge. On 24 August, I observed the post-roosting behavior of nutcrackers at the base of Mt. Dana. Nutcrackers engaged in the following activities on Gaylor Ridge at sunrise throughout the summer, including the period before and after pre-roosting flights. In the dense forest and on the whitebark pine trees on the upper slope, nutcrackers perched in treetops and vocalized frequently; a few nutcrackers foraged and fed young. At the base of Mt. Dana, nutcrackers also perched in treetops and vocalized, although their activities were not as prolonged; birds left the Mt. Dana roosting area as early as 0615. The following material is from my field notes of 3 August:

0615. Top of Gaylor Ridge is sunlit. There are intermittent nutcracker calls from the dense forest on Gaylor Ridge.

0630. The forest is sunlit down to about 3,075-m elevation. In the sunlit area, a nutcracker flies from treetop to treetop. Now, several nutcrackers take treetop perches and vocalize. Four nutcrackers are perched on whitebark pines and vocalize on the upper slope of Gaylor Ridge. One nutcracker leaves its perch and flies across the valley towards the Mt. Dana side. Hunger calls and the "gurgling" sounds of young nutcrackers being fed come from the sunlit forest area. One nutcracker flies north along the ridgetop. Mountain Bluebirds (*Sialia currucoides*) are now flycatching and Mountain Chickadees (*Parus gambeli*) are foraging.

0648–0700. Nutcrackers are still present near the top of Gaylor Ridge, vocalizing. Notes terminate here.

My observations on 22 August, after the number of participants in pre-roosting flights had declined, suggested that morning sunbathing was important at this time of year for several species of birds and mammals, including the nutcracker, Moun-

tain Bluebird, cony (*Ochotona princeps*), Alpine Chipmunk (*Eutamias alpinus*), and Golden-mantled Ground Squirrel (*Spermophilus lateralis*).

Correlation with Temperature and Light Intensity

The behavior patterns described in the previous section suggest that variations in temperature and/or light intensity within each study area may be related to pre- and post-roosting activities of nutcrackers. An examination of changes in both of these environmental factors in relation to the onset and decrease of pre-roosting flights at Tioga Pass may lend insight into the phenomenon.

If pre- and post-roosting activities are in response to temperature, then some energetic benefit may be derived by nutcrackers from this behavior. In this case, a record of daily minimum and maximum temperatures throughout the summer may indicate that a period of low daytime and/or nighttime temperatures corresponds to the occurrence of pre-roosting flights. Sunbathing under these conditions may fulfill some energetic requirements for the species. If pre- and post-roosting activities are in response to light intensity, the onset and peak of the flights should occur during the period of greatest solar radiation.

A regression analysis of minimum summer temperature vs. date in 1974 for each slope at Tioga Pass did not show a significant correlation. Regression analyses of maximum temperature vs. date showed significant correlations, i.e. an increase in temperature throughout the summer ($r = 0.490$, $.001 < P < .01$, and $r = 0.332$, $P < .05$, for the Gaylor Ridge and Mt. Dana slopes, respectively) (Fig. 1A). For both the Gaylor Ridge and Mt. Dana slopes, regression analyses of solar radiation vs. date in 1974 showed highly significant negative correlations; solar radiation decreased throughout the summer ($r = -0.943$, $P < .001$, and $r = -0.969$, $P < .001$, respectively) (Fig. 1B). Therefore, as the number of nutcrackers participating in pre-roosting flights decreased, maximum temperatures rose and light intensity decreased.

During September 1975, I attempted to determine whether Clark's Nutcrackers would respond to an artificial source of heat or heat plus light at sunrise. Two nutcrackers were maintained in separate compartments of an outdoor aviary at 2,150-m elevation. Either a 250 W red or 250 W clear reflector heatlamp (General Electric R 40/10, radiation peaking between 0.5 to 4.0 microns; R 40/1, radiation peaking between 0.3 and 5.0 microns, respectively) was placed above one perch in each compartment. At sunrise, after a timer switched on the lamps, I noted the relative time spent by each nutcracker on an irradiated perch. Results were inconclusive; the nutcrackers showed no preference for the perches under lamps.

Discussion

The timing of the onset and peak of pre-roosting flights at Tioga Pass may in part relate to the fact that the population of nutcrackers does not reach a maximum at subalpine elevations until sometime during the month of July. The numbers of nutcrackers at subalpine elevations decrease throughout September and October, after the period of whitebark pine seed storage.

The elevation, the east-west orientation, and the short distance between the two slopes in the Dana Meadows vicinity may be factors in the regular occurrence of pre-roosting flights at Tioga Pass. By remaining in the sunlight in the evening at Mt. Dana and roosting on Gaylor Ridge, nutcrackers may be utilizing late evening/

early morning higher temperatures and/or light intensities. Pre- and post-roosting movements by nutcrackers in other montane areas may also be in response to one or both of these factors.

THERMOREGULATION

As nutcrackers engage in pre- and post-roosting activities, they may be utilizing the warmth from the first and last sunlight of the day. During these activities, nutcrackers spend much of their time on exposed, sunlit perches. The utilization of solar radiation by birds to warm the body, and thereby reduce caloric intake, has been documented for several species, including the Roadrunner (*Geococcyx californianus*) (Ohmart and Lasiewski 1971), the Turkey Vulture (*Cathartes aura*) (Heath 1962), the Brown-headed Cowbird (*Molothrus ater*) (Lustick 1969) and the White-crowned Sparrow (*Zonotrichia leucophrys*) (Morton 1967).

For nutcrackers, the reduction of caloric intake may be an important factor for the following reasons: 1) until juveniles become independent in late August, parent nutcrackers must forage for food for both themselves and their young; and 2) in order for parent nutcrackers to obtain enough food for themselves and their young, their foraging efforts must be continuous. The extraction of seed from unripe cones requires much physical effort. In 1975, I obtained mean values for the rates at which nutcrackers extracted seed from unripe, partially ripe, and ripe whitebark pine cones, respectively: one item per 31 ± 16 s, one item per 21 ± 10 s, and one item per 7 ± 3 s (Tomback 1978). Thus, before whitebark pine cones are completely ripe, foraging behavior requires greater effort and may be energetically costly.

If pre-roosting flights occur for energetic reasons, one or more of the following explanations may account for the decrease in participants throughout August: 1) as cones ripen, less effort is required to extract seed; 2) when cones are ripe, juveniles obtain their own food; and/or 3) maximum temperature tends to increase throughout the summer (Fig. 1A). The increase in daytime temperature throughout August and September, coupled with the availability of ripening pine seed, may gradually obviate the necessity for sunrise/sunset sunbathing.

Several contradicting observations suggest that the thermoregulation hypothesis may not entirely explain pre-roosting flights and other pre- and post-roosting activities of nutcrackers: 1) in the Minaret Summit area in 1973, nutcrackers left their roost shortly after arousal without prolonged sunbathing; 2) on 22 August, when the importance of sunbathing had, in theory, declined, nutcrackers as well as a number of other species of birds and mammals on Gaylor Ridge appeared to sunbathe after sunrise, and 3) captive nutcrackers did not sunbathe in response to an artificial radiation source during chilly mornings (however, this should not rule out the possibility they will sunbathe after sunrise under natural conditions).

LIGHT INTENSITY

The pre- and post-roosting activities of nutcrackers, including flights, may be in response to light intensity. Two benefits may be gained by effectively "prolonging" daylength. First, nutcrackers may begin foraging earlier in the day and continue later into the evening, an important factor for birds with young. Observations in the Minaret Summit and Tioga Pass study areas indicate that some nutcrackers with young do forage immediately after arousal and until the last light at sunset. Second, nutcrackers may utilize the first and last light for social interaction. This theory is

especially plausible because the most prominent nutcracker behavior patterns at sunrise and sunset are vocalizations and the tendency for the birds to take high, exposed perches. The most important effect of vocalizations and visual display may be to attract together all members of a family group before and after roosting. Also, vocalizations and visual display before pre-roosting flights may gather together a number of nutcracker family groups for the trip to the roosting area. Two major benefits may be gained by roosting in family groups and larger aggregations:

1) Defense against predation. This may be especially important for juvenile nutcrackers, which are inexperienced. The Red-tail Hawk (*Buteo jamaicensis*), Cooper's Hawk (*Accipiter cooperii*), Prairie Falcon (*Falco mexicanus*), and Goshawk (*Accipiter gentilis*) frequent the subalpine habitat and elicit alarm reactions from nutcrackers. On three occasions in the Mammoth Mountain area I observed groups of nutcrackers pursue Cooper's Hawks. On 17 September 1975, an immature Cooper's Hawk twice crashed into an outdoor aviary containing two experimental nutcrackers; this "impetuous" behavior is characteristic of young Cooper's Hawks (Brown and Amadon 1968). By restricting evening activities to the better-lit areas, nutcrackers may facilitate predator detection. Maximizing the numbers of nutcrackers roosting in a particular area may increase the probability that a bird of prey will be spotted and may decrease the probability that a particular individual will be selected as the prey.

2) Information on food location. During the time whitebark pine cones are ripening, roosting in an aggregation may allow many nutcrackers to benefit from the knowledge of a few. Among different stands of trees, there is differential ripeness in cones (Tomback 1978). Individual nutcrackers with knowledge of foraging areas that have the ripest cones may set off from the roost soon after sunrise. Nutcrackers lacking such information may follow those first individuals. Ward and Zahavi (1973) have proposed the transfer of food information to be the main function of communal roosts for many species.

Nutcracker vocalizations and plumage coloration are well-suited to attracting individuals together. According to my field experience, the regular call carries over a kilometer in distance, even during high wind. The plumage of a perched nutcracker is conspicuous: black wings and light face against a medium gray body. A nutcracker vocalizing while perched on a sunlit, exposed treetop is easily located. In flight, a nutcracker also shows high contrast plumage: a series of white secondaries against otherwise black wings and white rectrices bordering black rectrices. Flying nutcrackers are easy to track against sky or forest.

If the pre-roosting flights at Tioga Pass are the consequence of nutcrackers maximizing foraging time, gathering together family group members, and maximizing the number of nutcrackers roosting together, then the following factors may account for the decrease in pre-roosting flight participants at the end of August: 1) when cones finally ripen, adults no longer feed their young and family groups break up; 2) when most whitebark pine cones are ripe, food information transfer is no longer necessary; 3) when juveniles are independent they may be more experienced and less vulnerable to predation. (Birds of prey may begin migrating out of subalpine habitat in August, which would decrease predation pressure on nutcrackers); and 4) solar radiation decreases throughout the summer (Fig. 1B). The quality of light is noticeably weaker in September. Therefore, the levels of light intensity may not be high enough at sunrise and sunset for nutcrackers to forage and interact socially on the Mt. Dana slope.

In regard to the previous discussion, light intensity may be the major physical factor underlying the occurrence of pre-roosting flights at Tioga Pass and the occurrence of pre- and post-roosting activities of nutcrackers in all montane areas. However, we cannot rule out that some energetic benefit may also be derived from these behavior patterns. A physiological study of the nutcracker's ability to acclimate to the wide range of yearly temperatures in the Sierra Nevada would certainly lend insight to this phenomenon.

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