

SHORT COMMUNICATIONS

Wilson Bull., 99(2), 1987, pp. 240–243

Brood division and postnesting behavior of Flammulated Owls.—The Flammulated Owl (*Otus flammeolus*) is widely distributed in the montane forests of western North America (Bent 1938). The owl is insectivorous (Ross 1969) and is presumed to be migratory in the northern part of its range (Balda et al. 1975). Little is known of the nesting behavior of this species, especially during the postfledging period. Here, we present the postfledging behavior of adults and young and describe the occurrence of brood division in Flammulated Owls.

Study area.—The study was conducted on a 452-ha area of the Manitou Experimental Forest, Teller County, in central Colorado. Elevation of the study tract was 2700 m. Forests consisted of old-growth stands (>200 years) of ponderosa pine (*Pinus ponderosa*) mixed with Douglas-fir (*Pseudotsuga menziesii*) (58% coverage of the total area), young (<100 years) stands of Douglas-fir mixed with blue spruce (*Picea pungens*) (27% of the area), mature (100–200 years) stands of quaking aspen (*Populus tremuloides*) mixed with blue spruce (11%), mature aspen stands (>75 years) (3%), and meadow (1%). The understory vegetation and topography of the study tract were described by Reynolds et al. (1985). Also included are observations of a single pair of Flammulated Owls (MN1-83) that nested in similar habitat 52 km north of the study tract.

Methods.—Five families of owls (2 in 1982; 3 in 1983) were studied from the time the young left the nest in late July until we lost contact with the owls or until they left the area in October. Four adult males were equipped with backpack or tail-mounted transmitters, and 2 adult females and 6 of 14 young were equipped with backpack transmitters within one day of fledging (Reynolds and Linkhart 1984). Although all members of brood subgroups (see below) were not radio-tagged, 7 of 10 subgroups had at least 1 member (adult or fledgling) with a transmitter. Although the effects of transmitters on adults and young were unknown, affixing transmitters did not lower the annual return rate of adult males to the study tract, or the nesting success of radio-tagged pairs (Linkhart et al., in review). The movements and behavior of three families were monitored until the young were lost or killed by predators (1–12 nights after fledging). Two families were monitored until the owls left the study tract in the late summer and fall. Of the four other families that were studied, three were lost immediately after fledging (radio failure), and all of the fledglings of one pair were lost to a Sharp-shinned Hawk (*Accipiter striatus*) before we began postfledging monitoring. The nightly postfledging behavior of families was observed for a total of 24 h in 1982 (35% between 20:00–22:00 h MST; 35% between 22:00–24:00 h; 17% between 24:00–02:00 h; 13% between 04:00–06:00 h), and a total of 42 h in 1983 (27% between 20:00–22:00 h; 49% between 22:00–24:00 h; 7% between 24:00–02:00 h; 17% between 04:00–06:00 h). Movements and day roosts were determined by locating radio-tagged owls with a portable radio receiver and hand-held yagi antenna. Families of owls were observed continuously for 1–3 h at a time.

Results.—Mean brood size of the 5 families was 2.8 young (1 of 2 young, 4 of 3 young). Fledging of all young occurred within 1 h after sunset, and all broods fledged over 2 nights. Each of the 5 broods had divided into 2 subgroups by the third night after the first young fledged; 1 subgroup being tended only by the male and the other only by the female. However, because 2 adult females could not be captured, we were unable to continue monitoring their subgroups. In both of these situations, the broods involved had undergone the initial stages of brood separation—brood subgroups were separated by a minimum of 80 m, and the adults of both were strongly, if not completely, associated with their respective subgroups. Brood subgroups consisted of single owlets or siblings that left the nest the same night. There

was no pattern in which a parent associated with a specific subgroup; in 3 broods, the first bird to fledge was tended by the female, and in the other two, the first to fledge was tended by the male. The sex of fledglings was not determined.

Subgroups dispersed from their nests in different directions, and subsequent contact between them was not observed during the remainder of the fledgling dependency period. A typical example of the process of division was as follows: The 1 young of A10-82 brood (3 young) that fledged on 23 July formed 1 subgroup, and the remaining 2 young, which fledged on the following evening, formed the second subgroup. We observed this family for 2 h beginning at sunset (20:18 h) on 23 July. The female tended the first fledgling immediately after it left the nest (21:05 h). She continued, however, to assist the male in feeding the two young that remained in the nest. During the 2 h period, the male delivered (21:45 h) only one prey item to the single fledged young, considerably less than a nightly mean of 9.9 deliveries/h males at this and 12 other nests made during the nestling period (Reynolds and Linkhart, in press). Three nights later, the male was feeding only the 2 young that fledged on 24 July and was not assisted by the female. These 2 subgroups remained within 50 m of each other for six nights after fledging, at which time the female and her subgroup disappeared.

During the first 2 weeks after fledging, the day-roost trees of brood subgroups and tending adults were close together, and during the first week after fledging, these roosts were within 100 m of their nests. To demonstrate this general pattern, we present the distances between the day roosts of A4-83 male and his single fledgling. During the first 13 days after fledging, the distance between their day roosts was less than 35 m ($\bar{x} = 18 \pm 14$ m [SD], range = 0–32, $N = 9$), after which the distance began to increase daily. During the next 20 days, the mean distance between day roosts was 227 ± 146 m (range = 0–585, $N = 18$). The mean distance to the nest from the roosts of the male during the first seven days (23–29 July) was 47 ± 27 m (range = 14–74, $N = 5$). After the first week and through the remainder of the postfledging period, subgroups moved to 250–800 m from the nest. During this period, the fledglings and the adult of 1 subgroup wandered through the home ranges of several adjacent pairs. Throughout the postfledging period, the distance between day roosts of members of a subgroup was small, and they often roosted in the same tree (see below).

During the first 5 nights after fledging, adults foraged in the vicinity of the fledglings and delivered food to them every 1–5 min during the first hour after sunset and more sporadically later in the night. By 7–10 nights after leaving the nest, fledglings made attempts to glean insects from the ground. During this latter period, fledglings followed adults during foraging trips, which gradually increased in distance and duration as the flight capabilities of fledglings improved. Fledglings ceased moving by about 22:00 h, but the adults continued to feed them. Just before dawn, additional, although less extensive foraging movements involving the fledglings took place. These culminated with owls going to roost approximately one-half hour before sunrise. Fledglings begged for food 5–15 times/min during early evening and morning foraging periods, but vocalized less frequently during the middle of the night. Food-begging ceased altogether when owls went to roost.

By 20–25 nights after fledging, adults spent little time in the vicinity of fledglings during the night and only occasionally provisioned them with food. By 25–32 nights after fledging, the young were no longer provisioned with food and only occasionally gave food-begging vocalizations while foraging. After independence, fledglings continued to forage most intensively in the early evening (between 20:30–22:00 h). Subgroup members foraged within 50 m of each other and gleaned insects from the crowns and trunks of live trees, from snags, and from the ground. By the middle of the night, foraging occurred at irregular intervals. A second intensive foraging bout occurred in the last 2 h before dawn.

We monitored 2 brood subgroups (separate families) until the young dispersed from the

study tract. Two fledglings of A15-82 were last observed on 28 August, 35 nights after fledging. Both transmitters may have failed on this night, but the foraging and flight capabilities of the fledglings and subsequent wide searches for the owlets suggested that they dispersed from the study tract. Moreover, mean distance between the day-roost trees of these 2 fledglings for 3 days prior to 28 August ($\bar{x} = 98 \pm 46$ m, range = 61–150, $N = 3$) was considerably more than the distance between their day roosts prior to 25 August ($\bar{x} = 5 \pm 6$ m, range = 0–14, $N = 13$). Radio contact with a second subgroup (single fledgling of A4-83) was lost 33 nights after fledging (25 August). This owlet flew well and was foraging successfully.

One adult male (A4-83) was monitored into the fall. This male was last observed on 12 October and had increased in body weight by 20% during the 23 days from 13 September (56.5 g) to 6 October (67.5 g). Also, during the last 5 days of his residence, the male changed his day-roosting behavior by abandoning his favored roosts during the previous month (all within his nesting home range) for roosts that were increasingly farther from his home range and toward the southwest.

Discussion.—Brood division, in which part of the brood is tended by the male and part by the female, is best known in precocial birds (e.g., Tuck 1972, Simmons 1974, Horsfall 1984). Recent studies of altricial birds (e.g., Smith and Merkt 1980, Moreno 1984, McLaughlin and Montgomerie 1985) indicate that brood division may be common in birds with biparental care. Our results are the first to demonstrate brood division in strigiforms.

Within altricial species where brood division occurs, its establishment appears to require varying amounts of time after fledging. Flammulated Owl fledglings passed through what we term a “brood separation phase,” in which the fledglings gradually separated but continued to be tended by both adults. What has been variously termed as stable brood division (McLaughlin and Montgomerie 1985), complete division of labor (Smith 1978), or simply brood division (Edwards 1985) occurred when, perhaps due to the increasing distance between brood subgroups, each adult becomes conditioned to associate with a single subgroup (see Smith 1978). Published accounts indicate that for Song Sparrows (*Melospiza melodia*), the “brood separation phase” lasts 5 days (Smith and Merkt 1980), for Northern Wheatears (*Oenanthe oenanthe*) 3–8 days (Moreno 1984), for Eurasian Blackbirds (*Turdus merula*) 0–10 days (Edwards 1985), and for Prairie Warblers (*Dendroica discolor*) (Nolan 1978) and Lapland Longspurs (*Calcarius lapponicus*) less than 1 day (McLaughlin and Montgomerie 1985). In Flammulated Owls, brood separation began with the fledging of the first young in a brood, and brood division had occurred by two nights after the fledging of the last young.

McLaughlin and Montgomerie (1985) reviewed five possible benefits of dividing broods: (1) minimizing losses to predators, (2) increasing foraging efficiency, (3) helping young learn to forage, (4) facilitating differential dispersal of the sexes, and (5) promoting sexual imprinting and mate choice. In Flammulated Owls, we suspect that brood division might reduce predation on the young. First, food begging of the fledglings was frequent, and more pronounced (facilitated) when fledglings were in the same area. Dividing broods into small segments might reduce vocalizations and possibly losses to nocturnal predators. Second, because owlets in subgroups day-roosted close to one another (making them more obvious), and all known cases of predation on owlets occurred during the day, losses of whole broods could be reduced by dividing and separating broods. Alternatively, brood division may simply be the result of the timing of fledging. Because the broods we studied fledged over two nights, the limited mobility of the owlets during the evening of fledging may have forced them to associate with siblings that left the nest the same night (see also Smith and Merkt 1980). Whether brood division occurs in broods all of whose members fledged in the same night is unknown.

Acknowledgments.—We thank J. Jeanson for help with field work and G. Crouch, P.

Edwards, E. Forsman, R. King, P. Lehner, W. Mannan, J. Marks, C. Marti, C. Meslow, M. Ryan, and F. Samson for helpful comments on the manuscript.

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Wilson Bull., 99(2), 1987, pp. 243-252

Species-area relationships of winter residents in isolated woodlots.—The number of bird species breeding within woodlots or using woodlots temporarily during migration is strongly correlated with woodlot area (e.g., Martin 1980, Ambuel and Temple 1983, Blake 1986).