In their discussion of the Northern Three-toed Woodpecker (*Picoides tridactylus*), Bailey and Niedrach (1965:507) stated: "This species, with the Downy (*Picoides pubescens*) and Hairy (*P. villosus*) Woodpeckers, was a great help in the preservation of the forests in western Colorado threatened by the destructive bark beetles in 1939." They went on to quote a statement by Noel D. Wygant regarding this event: "In some of the large outbreak centers, woodpeckers built up a population as heavy as a pair per acre."

Since 1939, numerical responses of picids to insect infestations have been noted repeatedly. For example, Blackford (1955) reported a large increase of woodpeckers, especially *P. tridactylus*, during the fall and winter following a forest fire in a Douglas-fir (*Pseudotsuga menziesii*) and Ponderosa Pine (*Pinus ponderosa*) forest in Montana. Presumably, the woodpeckers were responding to increased populations of prey species, particularly boring beetles. Woodpeckers had declined to normal numbers by March, however, and did not re-invade during the following cold season.

The observed population increases of Northern Three-toed, Hairy, and Downy woodpeckers in apparent response to bark beetle (*Dendroctonus* spp.) infestations in Colorado are of special significance. Most published reports have dealt with outbreaks of the Spruce Bark Beetle (*D. rufipennis* Kirby) in Engelmann Spruce (*Picea engelmannii*) stands in subalpine spruce-fir forests (Hutchinson 1951, Yeager 1955, Knight 1958, Amman and Baldwin 1960, Baldwin 1960, Koplin 1969 and 1972, Koplin and Baldwin 1970). Although three widely separated areas were discussed in these papers, five major similarities are evident:

(1) The woodpeckers that responded to bark beetle epidemics were *P. tridactylus*, *P. villosus*, and *P. pubescens*, in decreasing order of abundance.

(2) The increases in population were most significant in the non-breeding season, although some higher breeding densities were noted in large, long-term (panepidemic) areas. That is, immediate responses resulted from aggregation or immigration.

(3) Bark beetle adults and larvae formed the major winter food source for the three picids in infested areas (67-99 percent of stomach contents).
Woodpecker activity resulted in 45-98 percent decreases in beetle survival. Beetle mortality was related to predation by picids or to freezing, desiccation, parasites, and insect predators following removal of bark by picids.

Secondary infection by other boring beetles, such as *Pityophthorus occidentalis* and *Ips pilifrons*, may affect trees weakened by *Dendroctonus* attack. Secondary borers likely lead to increased intensity and duration of woodpecker response.

The 1975 and 1976 Audubon Christmas Bird Counts in Boulder, Colorado, have provided tentative evidence of a similar invasion by *Picoides* woodpeckers in response to an increasingly severe outbreak of the Pine Bark Beetle (*D. ponderosae*). This outbreak has affected Ponderosa Pine primarily in overcrowded stands characterized by reduced vigor and, presumably, decreased resistance to attack.

The apparent response of picids to the Pine Bark Beetle is indicated by two major trends. The first trend is the expansion of *P. tridactylus* into montane pine from higher subalpine spruce-fir, where it normally occurs (Bailey and Niedrach 1965, Bock and Bock 1974). Indeed, 1975 and 1976 mark the first recorded occurrences of *P. tridactylus* on Boulder Christmas Bird Counts. We have observed this picid in other bark beetle-infested stands of Ponderosa Pine throughout the Front Range. Perhaps this niche expansion should be expected, since three-toed woodpeckers are generally regarded as opportunistic, irruptive species (Blackford 1955, Bock and Bock 1974).

The second trend is the increase in numbers of Hairy and Downy woodpeckers during winters since 1972, when the outbreak reached major proportions. Christmas Bird Count data must be analyzed carefully because of yearly differences in the number of observers and the distances covered; however, these difficulties can be overcome to some extent through careful interpretation. Other factors influencing raw data are count-day weather, amount and types of habitat covered, and general expertise of the participants. However, we do not feel that the latter two factors have varied markedly in recent years, and our own experience suggests that counts of picids are less affected by weather than counts of most species. Nevertheless, augmentive data are always desirable, and we have therefore surveyed Ponderosa Pine woodlands west of Boulder repeatedly since the 1976 Christmas Bird Count.

During the 25-year period 1951-1976, there was a close correlation between numbers of observers and numbers of *Picoides* on Christmas Bird Counts. From 1972 to 1976, however, observers in Boulder increased 308 percent, while *Picoides* increased by 589 percent. A similarly disproportionate rise in picid observations is shown by comparing the ratio of *Picoides* observed to party miles. From 1951 through 1971,
The average ratio was 0.04, with a high of 0.11 in 1965 and 1967 and a low of 0.02 in 1963. During the 1972-1976 interval, this ratio averaged 0.14, having increased to 0.20 in 1975 and 0.23 in 1976. Thus, since the bark beetle outbreak began, numbers of *Picoides* have increased nearly twice as fast as observers, and approximately 3.5 as many have been seen per party mile as during the previous twenty years.

Of course, the relative amount of suitable habitat surveyed each year would also affect Christmas Count findings. Unfortunately, habitat proportions were not recorded between 1956 and 1972. Even when habitat proportions were noted, however, the data were not organized to show how many woodpeckers were observed in each habitat type, and valid comparisons are therefore not possible.

Although detailed habitat utilization data are not yet available for the Boulder area, the preference of picids for bark beetle-infested areas during 1976-77 was inarguable. Of 48 Hairy and Downy woodpeckers observed in our study area on the western flanks of South Boulder Peak, none was seen in an uninfested area. Moreover, uninfested areas (more than one-half of the total) were essentially devoid of woodpeckers, except for the ubiquitous Common Flicker (*Colaptes auratus cafer*). This clumped distribution has been repeatedly observed in the area since the 1976 Christmas Bird Count. Indeed, clumping was so extreme that on three occasions we observed two Hairy and two Downy woodpeckers working diligently in one infected tree. Similar behavior was reported by Baldwin (1960) and Koplin (1969).

Initial increases in woodpecker populations result primarily from immigration. This immigration could result from purposeful aggregation by picids in the areas of heavy infestation, or it could merely represent prolonged stays by picids that normally drift through during postbreeding wandering and migration. Whether *Picoides* populations increased by aggregation or drift, they apparently did so in response to the increased winter food supply. Certainly, dead or dying “beetle” trees present a highly visible cue to woodpeckers of high concentrations of insect prey.

Koplin (1972) and Koplin and Baldwin (1970) reported 50- to 85-fold increases in woodpecker abundance in Spruce Bark Beetle outbreaks during winter, while breeding population responses have varied from no increase in limited outbreaks to a 6- or 7-fold increase in the 1939-1952 panepidemic (Koplin 1972). The limited rise in breeding densities is not surprising, because (1) woodpeckers are territorial and probably would not tolerate excessive crowding, and (2) bark beetles are apt to be a more significant food resource during the winter, when other prey species are less abundant or less accessible. Otvos (1965) suggested that Hairy Woodpeckers may be highly dependent on bark beetles during winter.
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No increases of breeding densities in the Front Range have been reported during the present bark beetle epidemic, but it is only now reaching the extent of the 1939-1952 panepidemic, and continued surveys will be necessary to determine adequately the extent and duration of the apparent population expansion. Intensive logging activities designed to control the bark beetle presently are underway and may reverse this trend before it reaches its full potential.

LITERATURE CITED


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