SOME OBSERVATIONS AND COMMENTS ON THE PERIODIC INVASIONS OF GOSHAWKS

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THE periodic invasions of the Goshawk (*Accipiter gentilis*) into the northern United States are well known. A summary of pertinent data and an analysis of the phenomenon have been published by Keith (1963). The relative paucity of quantitative observations on Goshawk population cycles prompted this publication, which summarizes approximately comparable observations of migration, including at least one invasion, for 15 consecutive years, and provides information on the age structure of the migrant population.

Observations of Migration

Observations of hawk migration were conducted on 953 days in the autumns of 1950 through 1964 at the Cedar Grove Ornithological Station, located on the western shore of Lake Michigan some 40 miles north of Milwaukee, Wisconsin. At least one of the authors was present at the station on most observation days, although a number of persons aided in the observations. The southern boundary of the known breeding range of the Goshawk is more than 90 miles north of Cedar Grove (Gromme, 1963). In all, 177 Goshawks were observed, and 106 of these were trapped, examined, marked with leg bands issued by the U. S. Fish and Wildlife Service, and released. An essentially dawn-to-dusk watch was maintained on most observation days; however, on days with little or no migration the observations often became sporadic.

The number of observation days per autumn varied from 22 to 125 with a mean of 63 days. The earliest observation date in any year was 3 August; the latest, 26 December. The number of hawks observed per day during autumn at Cedar Grove varies considerably, largely as a function of the weather (Mueller and Berger, 1961). A deliberate attempt to select for good weather conditions, and hence a greater probability of large numbers of hawks, was made on 80 of the 953 observation days. The distribution of this observational bias is such that it is difficult to determine the median dates of occurrence of Goshawks in autumn. No other calculation or conclusion presented in this paper was appreciably affected by the observational bias. The earliest and latest dates on which we observed Goshawks were, respectively, 17 September and 16 December. The peak in the movement of juvenals appears to be in late October, and that of adults, in late November.

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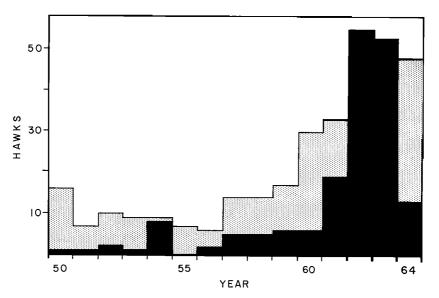


Figure 1. The numbers of Goshawks observed (dark bars) and expected (stippled bars) for each of the years 1950 through 1964.

The number of Goshawks observed per autumn varied from none to 55 with an obvious peak in occurrence in 1962 and 1963 (Figure 1). To permit statistical comparisons, an "expected" number of Goshawks was calculated for each year. This was done by calculating the mean number of Goshawks observed per calendar date in 1962 and 1963. The expected number per year for each of the other 13 years was then considered to be the sum of the calculated means for those dates upon which observations were made. In three of the observation years (1951, 1955, and 1956) the expected values are too small for statistical comparison. In most other years the number of Goshawks observed differed significantly (at the 95 per cent level) from the expected value. This was true except for 1954, when there may have been an invasion somewhat similar to 1962–1963 (see below), and for 1961, in which year the difference was almost significant ($X^2 = 3.77$, p < .06). The 1961 flight of Goshawks can be regarded as a prelude to the invasion of 1962 and 1963.

Observations From Other Localities

A survey of the literature revealed little in the way of observations of Goshawk populations or movements for the years 1950 through 1964. A perusal of the regional reports in *Audubon Field Notes* (1950–1964) for the northeastern and mid-western United States and adjacent parts of Canada yielded only the information that observations from Duluth, Min-

nesota, rather clearly indicated an invasion in 1963, and that Goshawks were "more frequent than usual" or occurred in "unusual numbers" at various localities in 1953, 1954, 1955, 1957, and 1962. Counts of Goshawks published in the Hawk Mountain Sanctuary Association "News-letter to Members" (1950–1964) indicated three nearly equal peaks (81 to 89 birds seen) in the years 1954, 1957, and 1961. The next highest count was only 33 Goshawks, recorded in the autumn of 1962. The number of hawks and owls destroyed per year by the Division of Predator Control of British Columbia reached a peak in 1954 (Keith, 1963: 52). Thus, the observations from other localities suggest that 1954 may have been an invasion year for Goshawks, as suggested by our data. On the other hand, the data from other localities also suggest an invasion in 1957, a year which our data indicate to be a non-invasion year.

PREY POPULATIONS IN THE BREEDING RANGE

Goshawks prey on a wide variety of birds and mammals, including the Ruffed Grouse (*Bonasa umbellus*) and the snowshoe hare (*Lepus americanus*). Both of these prey species exhibit marked fluctuations of populations, with peaks occurring approximately at 10-year intervals (Keith, 1963). Although the extent to which Goshawks depend on snowshoe hares and Ruffed Grouse for sustenance has not been demonstrated, relatively good indices of abundance are available for these two prey species and these invite comparison with indices of Goshawks.

Indices and estimates of the kill of Ruffed Grouse for Wisconsin, Michigan, Minnesota, Manitoba, Saskatchewan, Alberta, and British Columbia declined from 1953 to 1954. The estimates and indices then showed little change through 1957 (Keith, 1963: 32, 36). Kill indices for snowshoe hare in Wisconsin and Michigan reached a low in 1955. The kill index for Minnesota showed less variation in these years, reaching a poorly defined low in 1957 (Keith, 1963: 39). Thus, there is some evidence of declines in Ruffed Grouse and snowshoe hare populations which would correlate with a presumed Goshawk invasion in 1954, but there is little evidence of declines of prey populations in 1957. We suspect that there may have been a greater than normal movement of Goshawks in 1954, but we do not think that the flight attained the proportions of the invasion of 1962 and 1963.

Snowshoe hare populations in Alberta were at a peak in 1961. Great numbers died in northern Alberta late in the winter of 1961–62. In the summers of 1963 and 1964 hares were generally scarce throughout Alberta (L. B. Keith, pers. comm.). On Manitoulin Island, Ontario, the population peak in hares was reached in 1959, and there was a sharp fall in the population of the eastern part of the island by the winter of 1961 (Newson

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and de Vos, 1964). In Michigan the decline in hare populations began in 1960–1961 (Bookhout, 1963). Thus, the invasion peak of Goshawks in 1962 and 1963 was preceded by a marked decrease in snowshoe hare populations through much of central Canada. Speirs (1939) noted that the cyclic invasions of Goshawks into the Toronto region usually occurred about one or two years after the peak in populations of snowshoe hares in the Hudson Bay watershed.

The annual reports of the Game Branch of the Department of Mines and Natural Resources of the Province of Manitoba indicate that Ruffed Grouse were present in above-average numbers there in the fall of 1961. There was a crash decline in grouse populations in the winter of 1962–63 and a continued decline in the winter of 1963–64. Estimates of the kill of Ruffed Grouse, given in the annual reports of the Department of Natural Resources of the Province of Saskatchewan, were high in the autumns of 1957 and 1958. There was a precipitous drop in the estimated kill in 1959. The annual kill rose slowly from the low of 1959 to a moderate level in 1961, and then declined slowly in 1962 and 1963 to almost the level of 1959. Thus, the 1961–63 invasion of Goshawks was preceded, one to several years, by a general decline, from a peak, of the populations of snowshoe hares and Ruffed Grouse.

Recoveries of Banded Birds

The extent to which the Goshawk migrates is poorly known. We examined the records of all known recoveries of Goshawks banded in North America in an effort to learn more about the migrations of this species. As of January, 1965, there were 39 recoveries of Goshawks banded at localities other than Cedar Grove. Only 4 of these were more than two degrees of latitude distant from the place of banding, a fact suggesting that most Goshawks do not usually migrate or wander appreciable distances.

All Goshawks seen at Cedar Grove were migrants, and it is not surprising that band recoveries indicated considerable movement for those birds banded and released at Cedar Grove (Table 1). Of the 10 recoveries of Goshawks banded in autumn at Cedar Grove, 8 were recovered in the same autumn or following winter; 4 of these 8 were from non-invasion years and were recovered south of Cedar Grove, except for 1 bird which apparently died near Cedar Grove shortly after banding (Table 1). The other 4 birds were banded and recovered during invasion years. Of these, 1 was recovered to the west-southwest and 3 to the north (Table 1). These limited data suggest that the movements in invasion are less southward oriented than in non-invasion years.

None of 21 banded Goshawks which were two or more years old and

Banding date	Recovery date	Recovery location	Distance (in miles) and direction
24 October 1954	21 July 1957	Marinette Co., Wisconsin	125 N
18 October 1957	20 December 1957 ²	Cedar Grove	0
25 October 1957	28 December 1957	Cook Co., Illinois	110 S
26 September 1958	9 October 1958	Adams Co., Illinois	300 SW
17 October 1960	13 December 1960 ³	Laurel Co., Kentucky	500 SSE
20 October 1961	12 November 1961	Oconto Co., Wisconsin	95 N
31 October 1961	22 December 1962 ³	St. Joseph Island, Ontario	265 NE
21 November 1962	25 December 1962	Sauk Co., Wisconsin	125 WSW
22 November 1962	19 December 1962 ³	Brown Co., Wisconsin	80 NNW
2 November 1963	21 January 1964 ³	Manitowoc Co., Wisconsi	n 45 NNE

 TABLE 1

 Recoveries of Goshawks Banded at Cedar Grove¹

¹ All were banded as Juvenals except the one banded on 22 November 1962, which was an Adult I.

² Bird had been dead for some time.

³ Date of letter of notification.

only 1 of 27 which were one year old were recovered within four months of the time of banding. Of 58 banded juvenals, 6 were recovered within this time period, suggesting considerably higher mortality rates for juvenals than for adults.

Two of the Goshawks banded at Cedar Grove were recovered more than a year after banding. Both of these recoveries were from localities within the breeding range of the species. When one considers the low density of human population within the Goshawk's breeding range and the concomitant low probability of band recoveries, these two recoveries suggest that many Goshawks do return to the breeding range after invading the south.

Age Composition of the Invading Population

All adult Goshawks trapped at Cedar Grove had two generations of feathers in their plumage. The difference in color between juvenal and adult feathers permitted us to place trapped birds into three age classes: Juvenals, birds in the juvenal plumage and hence less than one year old; Adult I, birds obtaining their first adult (basic) plumage and hence slightly more than one year old; and Adult II, birds obtaining their second or subsequent adult (basic) plumage and hence two or more years old. We think that adult Goshawks may be slightly more difficult to trap than juvenals. Our sample may thus be biased, but the bias probably does not vary from year to year and thus does not markedly influence the conclusions presented in this paper.

In the 11 years prior to 1961, 89 per cent of the 27 Goshawks trapped were juvenals (Figure 2). In 1961, 92 per cent of the 11 birds trapped

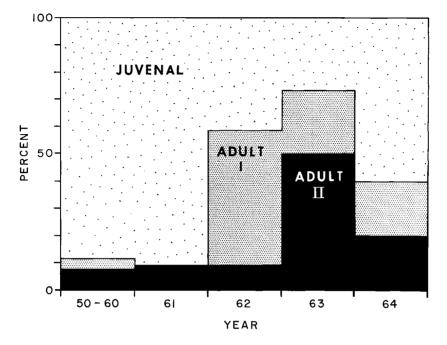


Figure 2. Age composition of the sample of trapped Goshawks.

were in the juvenal plumage (Figure 2). Of the 32 birds trapped in 1962, 50 per cent were in the Adult I class, and 50 per cent of the 26 birds trapped in 1963 were in the Adult II group (Figure 2). Thus, the following percentages of birds taken had hatched in 1961: in 1961, 92 per cent; in 1962, 50 per cent; in 1963 up to 50 per cent (some birds in the Adult II group in 1963 could have hatched prior to 1961). Thus, it would appear that many, if not most, of the Goshawks involved in the invasion of 1961–63 had hatched in 1961. Our attempt to explain this phenomenon follows later.

The Goshawk lays only two to five eggs and rears but a single brood each year (Bent, 1937: 128). Hickey (1952: 85) found that the annual mortality rate in Marsh Hawks (*Circus cyaneus*) was 59 per cent in the first year and averaged 30 per cent in subsequent years. Mebs (1964: 191) found that the annual mortality rate in the Buzzard (*Buteo buteo*) was 51 per cent in the first year (from the time of fledging), 32 per cent in the second year, 29 per cent in the third year, and averaged 19 per cent for subsequent years. In the absence of pertinent data, and in view of the above mortality rates, we estimate the annual mortality rate of Goshawks to be 50 per cent for juvenals and 25 per cent for adults. These estimates of mortality rates, along with an estimate of young fledged per pair per year, enable us to hypothesize the population structure in a given year. For example: if all Goshawks, including juvenals, in a given year produce four young per pair, the autumn population would be 33 per cent adults (the former juvenals now being Adult I's) and 67 per cent juvenals. Onefourth of the adults and one-half of the juvenals would die before autumn of the next year. Of the population of adult birds existing in a given autumn about 57 per cent would be Adult I and 43 per cent Adult II. If three young per pair had been fledged, 50 per cent of the adult population would be Adult I. If two young per pair had been fledged, 40 per cent of the adult population would be Adult I. The percentages of juvenal and Adult I birds in all of the above calculations would be reduced if some of the Goshawks did not breed until they were more than one year old. In 1961, 92 per cent of the birds trapped were juvenals, markedly in excess of the maximum of 67 per cent predicted by the above model. In 1962, 85 per cent of the adults were Adult I, again considerably exceeding the prediction of a maximum of 57 per cent by the model. The population of invading birds thus contained a higher proportion of young birds, both juvenals and first-year adults, than one would reasonably expect to occur in the total population of Goshawks.

Hypothesis: Cause of the Invasions

We propose that the Goshawk population increased along with the prey populations, both reaching a peak in the summer of 1961. The dense population would have resulted in increased agonistic encounters between Goshawks. The incidence of social interactions would further increase when the beginnings of a prey decline in the autumn of 1961 may have caused resident hawks to expand winter territories. A portion of the population, unable to find suitable wintering areas within the breeding range of the species, would thus be forced to emigrate southward. Since Goshawks presumably are largely permanent residents, the juvenals, without an established home range or territory, would probably be the first to be displaced.

We think, as evidence from band recoveries has suggested, that most of the invading Goshawks return to the breeding range. The young birds, in their search for a breeding territory would presumably be buffeted about a great deal by the older, established birds and either prevented from breeding or forced to settle in poor or unsuitable breeding areas. A high incidence of agonistic encounters might in itself exert a disruptive influence on the breeding success of Goshawks of all ages.

Continued declines in prey populations and increased social interactions between Goshawks in the summer of 1962 may have resulted in

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markedly reduced production of young. With the onset of winter, the departure of migratory birds, and the hibernation of some of the mammals, the availability of prey would be further reduced. A greater proportion of the total population of Goshawks would thus be forced to emigrate in the autumn of 1962 than in 1961. Iuvenals constituted only a small portion of the invading population in 1962 presumably because few had been produced in the summer of 1962. As in 1961, younger birds would be forced by the older, established birds to disperse, but in 1962 most of the vounger birds were first-year adults. Continued declines of prey and continued agonistic encounters between members of a still relatively dense population of Goshawks again would result in low production of young in the summer of 1963. A large proportion of the total Goshawk population presumably again emigrated southward in the autumn of 1963. Because of presumed low reproductive success in 1962 and 1963, there were few juvenals and first-year adults in the population, and many of the migrants were thus two-year-old adults.

Several studies offer indirect evidence which supports portions of this hypothesis. Craighead and Craighead (1956: 35) found that population densities of hawks in winter appear to be largely a function of prey availability, whereas (pp. 227, 257) the population densities during the breeding season appear to be independent of the size of the prey population, and that young hawks establishing a range for the first time apparently are buffeted about by established nesting birds. Cade (1955) found that adult Sparrow Hawks (*Falco sparverius*) maintain winter territories while young birds apparently do not. Perhaps the same is true of Goshawks.

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SUMMARY

Observations of hawk migration near Cedar Grove, Wisconsin, in the autumns of 1950 through 1964 revealed an invasion of Goshawks in the years 1961 through 1963. The invasion was preceded by decreases in populations of snowshoe hare and Ruffed Grouse in central Canada and the upper Great Lakes area. Most of the invading birds were hatched in 1961. We hypothesize that older, established birds displaced younger, poorly established birds from a range that could not support large wintering populations of Goshawks.

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