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THE PERIODIC INVASIONS OF GOSHAWKS

HELMUT C. MUELLER, DANIEL D. BERGER, AND GEORGE ALLEZ

ABSTRACT.—We watched for Goshawk migration each autumn in the years 1950–74. Two major invasions, composed largely of adults, were seen, one in 1962 and 1963 and the other in 1972 and 1973. The 1972 southward movement was probably the greatest in history. Comparisons of interannual fluctuations in age and sex ratios with those derived from a model population strongly suggest that major invasions of Goshawks indicate a massive reproductive failure and a precipitous decline in population, approaching 70% for 1972–73.

We suggest that the magnitude of an invasion is determined by the synchrony of the decline of prey populations in time and space, and also by the size of the Goshawk population. We hypothesize that agonistic interactions between Goshawks play an important role in producing both invasions and massive reproductive failure. Our calculations suggest that the decline in population in 1972–73 was sufficiently great that recovery will take more than 12 years of optimal reproduction. We therefore predict that several 10-year cycles will pass before we witness another major invasion of Goshawks.—*Department of Zoology and Curriculum in Ecology, University of North Carolina, Chapel Hill, North Carolina 27514 and Cedar Grove Ornithological Station, Route 1, Cedar Grove, Wisconsin 53013.* Accepted 14 January 1976.

ALMOST a decade ago two of us published an analysis of 15 years of observations of the migrations of Goshawks (*Accipiter gentilis*) along with some suggestions as to the causes of the southward movements (Mueller and Berger 1967a, 1968). We have since collected another 10 years of observations, including data on the invasion of 1972, which quite probably represents the greatest southward movement on record for this species. We now believe that we have some insights into the population dynamics of this “cyclic” species and the causes of the southward invasions.

We watched for hawk migration on 1,566 days in the autumns of 1950 through 1974 at the Cedar Grove Ornithological Station, on the western shore of Lake Michigan some 70 km north of Milwaukee, Wisconsin. A description of the region and the hawk migrations studied there can be found in Mueller and Berger (1961, 1966, 1967b). At least one of the authors was present at the station on most observation days, although a number of persons aided in the watches. As the southern boundary of the breeding range of the Goshawk is more than 100 km north of Cedar Grove (Gromme 1963, Erdman pers. comm.), all birds of this species seen at the station must have been migrants. In all, 591 Goshawks were seen and 354 of these were trapped, examined, marked with USFWS leg bands, and released.

An essentially dawn-to-dusk watch was maintained on most observation days but on days with little or no migration, the coverage 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 27 December. The earliest and latest dates we saw Goshawks were 15 September and 27 December.

ANNUAL FLUCTUATIONS IN THE NUMBERS OF GOSHAWKS SEEN

The number of Goshawks seen per autumn varied from none to 206 (Fig. 1). As the number of observation days varied greatly from year to year, simply comparing numbers seen is meaningless. To permit statistical comparisons between years, we calculated an “expected” number of Goshawks for each year in the same manner as we used in our previous paper (Mueller and Berger 1967a). The expected number for

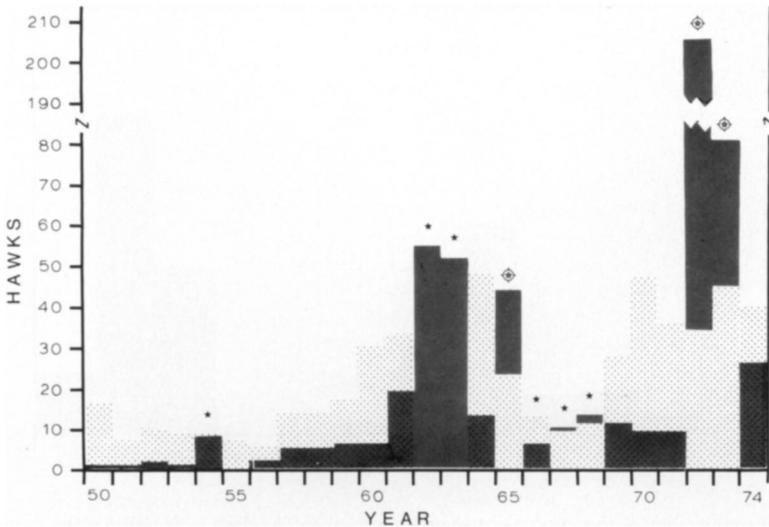


Fig. 1. The number of Goshawks observed (dark bars) and expected (light bars) for each of the years 1950 through 1974. The bars are superimposed on each other; thus, when expected exceeds observed, the dark bar covers the base of the light bar; when observed exceeds expected, the light bar covers the base of the dark bar. An encircled star at the apex of a bar indicates that observed significantly exceeded expected (Chi-square test $P < 0.05$); a star indicates that observed and expected did not differ significantly. In other years, expected significantly exceeded observed.

each calendar date was obtained by calculating the mean number of Goshawks seen on that calendar date in the years 1962 and 1963. The expected number for a given year was obtained by adding the expected values for all days of observation in that year. The years 1962 and 1963 produced the first unequivocal invasions that we saw at Cedar Grove, and the mean for the 2 years is retained as a base for comparison in this paper because of the large numbers of birds recorded as well as the extensive and continuous period of observation during these 2 years. The use of the term "invasion" in the following paragraph indicates that the number of Goshawks seen either exceeded or did not differ significantly from the numbers recorded in 1962–63.

Three of the observation years (1951, 1955, and 1956) had too few observation days to permit use of the Chi-square test. Apparently from 1950 through 1960 the only possible invasion was in 1954, and it was a small one at best (Mueller and Berger, 1967a). In 1961 the number of Goshawks seen rose almost to invasion levels, and the invasions of 1962 and 1963 followed. In 1964 the number of Goshawks dropped to a low level, and we thought at the time that we would see little of the species for the next 8 years. We were thus very surprised in the autumn of 1965 when we saw significantly more Goshawks than expected in an invasion year. In 1966, 1967, and 1968 the numbers of Goshawks seen remained high and did not differ significantly from 1962–63. It was not until 1969 that the number of birds seen declined to noninvasion levels, and this situation continued through 1970 and 1971. In 1972 we saw considerably more Goshawks than ever before, and in all probability this was the largest southward invasion in many years (see also Hofslund 1973, and the various regional accounts in *Amer. Birds*). The flight of 1973 was of considerably lesser magnitude than that of 1972 but greater than that of any other year. In 1974

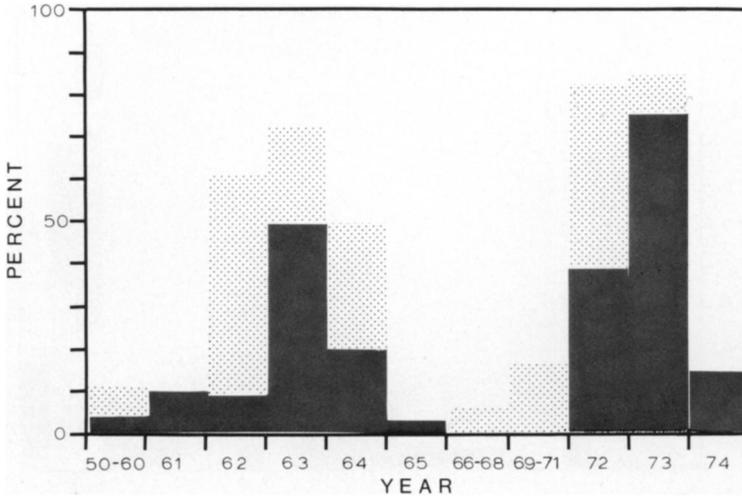


Fig. 2. Age composition of the sample of trapped Goshawks. The dark bars indicate the proportion of adult II, the light bars adult I, and the uncolored portion of the graph indicates the proportion of juvenals in the sample.

the number of Goshawks again declined to a noninvasion level. Thus Goshawks were seen in "invasion" numbers in 1954, 1962–63, 1965–68, and 1972–73.

Fluctuations in age ratios.—Examination of the plumage and molt of trapped birds permitted us to assign all but a few individuals to one of the following 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 (Mueller and Berger 1967a).

Of the birds trapped, the proportion of adults (of both classes) is less than 20% except for the years 1962–64 and 1972–73, when it exceeded 50% (Fig. 2). Thus juvenals predominated in noninvasion years and in the peculiar years of 1965–68, and adults were trapped in numbers only in the invasions of 1962–63, the following year, and the invasions of 1972–73.

Fluctuations in sex ratios.—We measured the wing and tail of all Goshawks we trapped, and the considerable sex-dimorphism of the species enabled us to determine the sex of each bird (Mueller and Berger 1968). During the years 1950–71 we trapped more than two juvenal males for every juvenal female, which is a significant departure from a 1:1 sex ratio (Table 1). The male-to-female ratio was greater than 1 in each of these years, but only in 1965 was the sample size (35) and the sex ratio disparity great enough (3.4) to achieve statistical significance. In 1972 and 1973 we trapped more juvenal females than males, although the ratio did not differ signifi-

TABLE 1
SEX RATIOS (MALES PER FEMALE)

	Juvenal	Adult I	Adult II
1950–71	2.21 ¹	1.14	1.44
1972–73	0.92 ²	0.68	0.56 ^{1,2}
Total	1.88 ¹	0.82	0.69

¹ Differs significantly from 1:1, Chi-square test, $P < 0.05$.

² Differs significantly from the ratio for 1950–71.

TABLE 2
MEAN WEIGHTS OF GOSHAWKS

	Juvenal		Adult I		Adult II	
	♂	♀	♂	♀	♂	♀
1950-71	807 (8) ¹	1,016 (15)	890 (17)	1,084 (32)	944 (17)	1,189 (30)
1972-73	807 (18)	987 (17)	916 (15)	1,132 (17)	906 (13)	1,144 (12)
Difference	0	+29	-24	-48	+38	+45
P (t test)	1.00	0.28	0.25	0.17	< 0.05	0.18

¹ The standard error of the mean is given in parentheses.

cantly from unity, but did differ significantly from the sex ratio of 1950-71. In 1974 we caught 11 juvenal males and only 1 juvenal female, a ratio that differs significantly from unity. The sex ratio of both classes of adults was also dominated by males in the years 1950-71 but did not differ significantly from unity. In 1972 and 1973 we trapped more than three adult females for every two males but only in the adult II class does the ratio depart significantly from unity and from the ratio for 1950-71.

Fluctuations in body weight.—The weights of Goshawks are extremely variable and show a tendency to increase during the autumn. In our previous paper we found no significant difference between the weights of juvenals taken in invasion and noninvasion years (Mueller and Berger 1968). The number of adults taken in noninvasion years was, and remains, insufficient for such a comparison (93% of all adults trapped were taken in 1962-63 and 1972-73). In the present paper we have grouped all of the weights of birds taken prior to 1972-73 and compared them with the weights of birds taken during this invasion (Table 2).

Fluctuations in the time of migration.—It is difficult to characterize briefly the interannual differences in the chronology of Goshawk migration. Too few birds are seen even in a good year, and the weather has an effect on the number of hawks seen on a given day, although less so far for the Goshawk than for most other species (Mueller and Berger 1961, 1967b). In view of these problems, we have again grouped the data and simply used the median date of occurrence as a measure of the timing of migration. The median date of occurrence for all Goshawks seen in 1972-73 was 27 days earlier than the median for 1950-71, a difference that seems to be significant (Table 3). The birds that were trapped, and for which the age and sex were determined, show considerable differences in timing. In 1972-73 juvenals arrived slightly earlier than in previous years. Both sexes of adult I came through considerably earlier as did the adult II males but not the adult II females, which arrived only 8 days earlier in 1972-73 than in previous years.

As birds caught late in the season tend to be heavier in weight than those caught

TABLE 3
MEDIAN DATES OF OCCURRENCE

Observed birds (all)	Trapped birds						
	Juvenal		Adult I		Adult II		
	♂	♀	♂	♀	♂	♀	
1950-71	13 Nov	24 Oct	27 Oct	13 Nov	29 Nov	17 Nov	13 Nov
1972-73	17 Oct	17 Oct	17 Oct	17 Oct	17 Oct	19 Oct	5 Nov

TABLE 4
AGE COMPOSITION AND POPULATION CHANGE (IN %)¹

Young per successful pair	Juvenal	Adult I	Adult II	Population change
3.5	57	17	26	+16
3.0	53	17	30	+9
2.3	46	16	38	0
2.0	42	16	42	-4
1.0	28	11	61	-17
0.5	16	7	77	-23
0.1	4	1	95	-29

¹ These calculations assume a population at equilibrium with 75% of the population breeding successfully and annual mortality rates of 65% for juvenals and 30% for adults.

earlier, a comparison of Tables 2 and 3 is in order. The early movement of the adult II males in 1972-73 appears at first glance to explain the significantly lower body weight than in previous years, but both sexes of adult I migrated early in 1972-73 and their weights were higher than in previous years (although the differences were not statistically significant).

Prey populations.—Although Goshawks prey upon a wide variety of birds and mammals, the snowshoe hare (*Lepus americanus*) and the Ruffed Grouse (*Bonasa umbellus*) may well constitute a very important part of the diet of these hawks, particularly in winter, because no other common prey animals of comparable size exist throughout much of the Goshawk's normal range and habitat. The populations of both these prey species exhibit marked fluctuations, with peaks occurring approximately at 10-year intervals (Keith 1963). We have previously shown that the invasion of 1962-63 correlated quite well with population declines in Ruffed Grouse and snowshoe hare (Mueller and Berger 1967a).

The available data indicate that snowshoe hares continued to decline from their 1961 peak through 1965 in Alberta, then rose in 1966-67 and continued to rise to a well-defined peak in 1971. Numbers sharply declined in 1972. Ruffed Grouse populations showed a similar fluctuation as did populations of Spruce Grouse (*Canachites canadensis*) and Sharp-tailed Grouse (*Pedioecetes phasianellus*) (Keith MS). The annual reports of the Game Branch of the Department of Mines, Resources and Environmental Management of the Province of Manitoba indicate that Ruffed Grouse population trends in this province were similar to those of Alberta. Fragmentary data from the province of Ontario on both Ruffed Grouse and snowshoe hare suggest a picture similar to that of the other provinces. The Small Game and Waterfowl Harvest Index for Wisconsin indicates a low in Ruffed Grouse populations in 1965-68, a rise to a peak in 1971, and sharp declines in 1972 and 1973 (see also Janssen 1973). In all, the Goshawk invasions of 1972-73 correlate extremely well with a crash in Ruffed Grouse and snowshoe hare populations over what appears to be quite a wide area. The synchrony in population declines between the two prey species and between localities seems to be considerably greater than it was for 1962-63.

DISCUSSION

We believe that our data on migrant Goshawks can be used to obtain a reasonable approximation of population fluctuations of the species in eastern North America. The age ratio existing in a population is the result of reproductive success and the

mortality rate of each age class. If we know reproductive and mortality rates, we know the age ratios in a population. Unfortunately, knowledge of age ratios alone gives us only the end result of the combination of reproduction and mortality and, further, age ratios obtained from migrants may not be representative of the entire population. The age ratios obtained from migrants can be informative if we have a reasonable idea of what age ratios are possible in a population. We have no information on the population dynamics of North American Goshawks, but the species has been extensively investigated in Europe. All of the European studies have been summarized by Glutz et al. (1971) except the one by Haukioja and Haukioja (1970). We propose to use this information to construct a simple population model in which mortality rates are kept constant and the reproductive rate is varied (Table 4), and then to compare age ratios obtained from the model with those we observed in migrants, and finally, to estimate the yearly changes in population.

We first present data that support the assumptions made in the model. We assume that 75% of the birds will breed successfully. It would appear that most Goshawks usually attempt to breed each year, unlike many species of *Buteo* and other large raptors. Goshawks often breed in the juvenal plumage. Looft (in Glutz et al. 1971) reported that juvenal males occurred in 6.7% and juvenal females in 9.7% of the nesting pairs observed. We were unable to find any other quantitative statements of the incidence of breeding by juvenals, but a number of other workers use such modifiers as "often" or "not infrequent" and several authors report successful breeding pairs in which both male and female were in the juvenal plumage.

In European studies nest losses ranged from 14 to 47% with a mean of 32%, but we believe that most of these figures are too high for American birds because many of the losses of eggs or young in Europe are the result of human interference. The study with the 47% nest losses presented an itemization of the cause of destruction; 84% of the losses were caused by humans (Sperber, in Glutz et al. 1971). Few North American Goshawks nest as close to human habitation as do the European birds, and nests are much more difficult to find in the American wilderness than in the often managed forests of Europe. In most of the Goshawk range in North America we also lack the professional game managers, the pigeon fanciers, and the farmers with free-ranging domestic fowl, all of whom persecute the Goshawk in Europe. Further, renesting after loss of eggs, or even young, appears to be common. Thus, an estimate of 75% successful breeding is probably a conservative one.

The five European studies of mortality rates in the Goshawk (Glutz et al. 1971), when averaged, show a mortality rate of 69% for the first year and an average of 32% per year for subsequent years. As many of the losses are at the hand of man, perhaps these percentages are somewhat too high for North American birds, but we have chosen to be conservative and use estimates of 65% for juvenals and 30% for adults, figures close to the European averages.

Utilizing the above estimates for nesting success and mortality rates as constants, we can now let the number of young produced per pair vary and, in Table 4, produce estimates of the age composition of the population and the annual change in population. The model is, of course, an oversimplification. Undoubtedly mortality rates and the percentage of birds breeding vary, as well as clutch size and the number of young produced. Varying several parameters simultaneously would result in an extremely complicated table and would not appreciably increase its utility for our purposes. Varying the percentage of birds breeding would simply change the number of birds produced per pair and for our purposes it does not matter whether 75% of all pairs

breed successfully, each producing two young, or if 38% of the pairs breed successfully, each producing four young; the end result would be the same. Varying the mortality rates could change the model considerably. For example, if mortality rates are appreciably lower than assumed in our model, then we are overestimating negative population changes and underestimating positive population changes. Changing the mortality rates of juvenals would have little effect on our usage of the model as decreased reproduction has the same effect, but changing adult mortality ratios would affect not only population size but also age ratios.

With the above reservations in mind, we will now compare the age ratios of the model (Table 4) with those we obtained at Cedar Grove (Fig. 2).

The mean clutch size of the Goshawk in 8 separate European studies ranged from 3.51 to 3.64 with an overall average of 2.43 young fledged per successful nest (Glutz et al. 1971). Thus 3.5 young per successful nest would seem to be a high estimate of maximum possible production. From this we can see that the percentage of juvenals in the population probably cannot exceed 50%, certainly not in the population existing in the autumn when considerable juvenal mortality would have already occurred. Yet in all but the years 1962–64 and 1972–73, more than 80% of the birds we captured were juvenals. It is obvious that in most years a much higher proportion of the juvenals migrate than do the adults.

We believe that interactions with older Goshawks induce younger birds to emigrate when prey populations are too low, or Goshawk populations too high, to support the entire Goshawk population within the normal range of the species. The percentage of adult I birds observed at Cedar Grove in 1962 and 1972 was about 3 times as great as in any model population. We believe that this indicates that older adults displace younger adults when conditions in the breeding range can no longer provide support for all adults. Adult II birds migrate in numbers only when prey populations are very low, as in 1963 and 1973. We hypothesize that agonistic interactions drive younger birds into regions that are marginal or insufficient for Goshawks during all but years of very high prey populations. These birds are faced with insufficient food, particularly after many species of potential avian prey begin to migrate, and we think that they begin to wander. The displacement of younger birds by older birds is the only reasonable explanation for the marked fluctuations in age ratios at Cedar Grove.

We have previously indicated that there may have been a small invasion in 1954. Both the samples of birds seen and of birds captured are too small for rigorous analysis, but the age ratio of only one adult I bird to 5 juvenals suggests that few adults moved in 1954, and as we will see below, this is further evidence that no major invasion occurred. In the remaining years through 1960 both the total number of Goshawks (Fig. 1) and the percentage of adults was very low (Fig. 2), typical of noninvasion years. In 1961 the number of birds seen increased dramatically but the ratio of adults remained low. We suggest that a combination of reasonably high Goshawk populations and declining prey populations was forcing an increased number of juvenals southward.

In 1962 the percentage of juvenals trapped at Cedar Grove (Fig. 2) is about what we would expect in a stable population (Table 4). But we have argued above that juvenals are displaced by adults and hence are overrepresented in our sample. This argument is strengthened by the fact that adult I birds were at least three times as common in migration in 1962 as is possible in any model population. Adult II birds were only about one-third as abundant as is possible in any model population,

indicating that not all of them were migrating and that they were displacing adult I birds as well as juvenals. If we make the conservative assumption that juvenals are no more overrepresented in our sample than were the adult I birds, we can then divide our percentage of juvenals observed by 3, arriving at an estimate of no more than 13% in the 1962 population. This is indicative of a reproductive rate of less than 0.5 young per successful nesting pair (or survival of 0.5 young per nesting pair); in short, either reproduction was extremely poor in 1962 or nestling and early juvenal mortality was extremely high. This low reproductive rate indicates a population decline of at least 25%, even without increased mortality of adults.

In 1963, 23% of the Goshawks trapped were adult I, about 3 times as great as the 7% predicted in a population that produced only 0.5 young per nesting pair in the previous year. If we again assume that the juvenals are similarly overrepresented in our sample, we end up with an estimate of 9% juvenals in the population, about 0.3 young produced per nesting pair, and a further population decline of more than 25%. Inferences from age ratios in 1962–63 thus suggest a population decline of at least 40 to 50%, without any increase in the mortality of adults. Adult II birds were again probably underrepresented in our sample, as a population producing 0.3 young per nesting pair would be expected to have about 85% adult II birds, and we observed only 50%. This suggests that a reasonable number of adults remained in the north.

We are reluctant to produce quantitative estimates based on the relatively small sample of birds caught in 1964, but we can perhaps make some qualitative statements. The proportion of adult I birds is again much higher than predicted in a population with low reproduction in the previous year, suggesting conditions similar to 1962–63, including poor reproduction and continued population declines. The only positive change is that the percentage of adult I birds exceeded that of adult II, suggesting that conditions had ameliorated sufficiently to permit a large proportion of adult II birds to winter in the north.

Our calculations, thus, leave us with very low reproductive rates for 3 years and a severe population decline, which makes it difficult to explain the appearance, in 1965, of significantly more migrant Goshawks than predicted for an invasion year. The situation is further complicated by the fact that more than 95% of the migrants were juvenals. This suggests good reproduction and a sufficient amelioration of conditions to permit essentially all adults to remain in the north. Yet the available data indicate that Ruffed Grouse and snowshoe hares were at their lowest in 1965. We suggest that by 1965 Goshawk populations had declined sufficiently to permit most of the remaining birds to occupy optimal territories, sufficient to permit successful breeding and even wintering by adults, but that the juvenals were forced to emigrate. It may be that food is not as important a limiting factor for successful breeding as it is for winter survival, since in summer the prey populations are greatly augmented by the presence of migratory birds plus small mammals which are unavailable in winter because they are in hibernation or living under the snow. We also continue to believe, as we stated in our 1967a paper, that high populations of Goshawks and low prey availability result in an unstable social situation which helps disrupt reproduction. Thus it appears that the breeding success of 1965 was due to low populations of Goshawks, allowing for optimal habitat utilization. We believe that the same explanation holds for the years 1966–68, except that populations of Ruffed Grouse and snowshoe hare began to rise, permitting more juvenals, as well as adults, to winter in the north.

By 1969 prey populations were quite high; successful breeding and overwinter

survival probably became possible on "marginal" territories, and we saw few migrant Goshawks in the years 1969–71.

Between 1971 and 1972, Ruffed Grouse and snowshoe hare populations crashed and an extraordinarily large southward movement of Goshawks resulted, with only 17% of the birds being juvenals. In itself, the relatively small number of juvenals trapped indicates very poor reproduction in 1972. The percentage of adult I birds trapped is 2.5 times that which can be expected in any population. If we make the conservative assumption that juvenals are similarly overrepresented in our sample, then we get an estimate of 7% juvenals in the population, about 0.2 young surviving per nesting pair, and a population decline of more than 25%, even without any increased mortality of adults.

In 1973 the percentages of all age classes are about what we would expect in a population with a reproductive rate of 0.5 young per pair. The reproductive rate was probably lower than this, and we expect that the population decline exceeded 30%, probably by a considerable margin. But if we assume that our sample of migrants was nearly representative of the population and if we adhere to previous assumptions, then we must conclude that essentially the entire population of Goshawks abandoned the breeding range and migrated south in 1973. We saw considerably fewer Goshawks in 1973 than in 1972, and this alone can be interpreted as a tremendous decrease in the population. Indeed, our calculations based on age ratios suggest a decline of more than 50% over the 2 years, without assuming increased adult mortality. But, as shown below, evidence from sex ratios of migrants indicates increased mortality of adults in 1972–73. In 1974 we observed a reasonable number of Goshawks, of which 85% were juvenals, suggesting at least fair reproduction but conditions which did not permit all birds to overwinter in the north.

Our data thus show two major invasions of Goshawks, each lasting 2 years (1962–63 and 1972–73) and each composed largely of adults. We have suggested that at least a considerable fraction of the entire Goshawk population emigrated during these invasions. In addition we observed greater than expected numbers of Goshawks in 5 more years (1954, 1965–68) but these movements were largely of juvenals, suggesting that most of the adults were able to remain in the north.

For each of the years 1950–71, males predominated in the sex ratio of juvenals and the overall ratio was more than two males to each female. We believe that this indicates that the larger females displace the smaller males from the breeding range during fall and winter, much as the adults displace juvenals, but under conditions insufficiently harsh to cause appreciable displacement of adults. The sex ratio of adults taken before 1972 did not differ significantly from unity, although more males than females were trapped (Table 1). The shift in sex ratios in 1972–73 was dramatic: for the first time in 23 years the sex ratio of juvenals fell below 1:1 (Table 1) and, although the observed ratio did not differ significantly from unity, it differed significantly from the ratio of previous years. This suggests that virtually all juvenals migrated in 1972–73. The sex ratio of adults changed from one that did not differ from unity in 1950–71 to one dominated by females in 1972–73. However, the change is statistically significant only in the adult II birds. We believe that most of the adults (of both classes) moved southward in 1972–73 and that the reduction in adult II males represents mortality. We suggest that established adults are reluctant to abandon territories and that females can dominate males in agonistic encounters. We further suggest that the combination of these factors resulted in increased mortality of males in the unusually severe conditions existing in the breeding range in the

autumns and winters of 1972–73. This hypothesis is supported by the facts that adult II males captured in migration were significantly lighter in weight and that the reduced number of males migrated earlier than in previous years and, for the first time, earlier than the females. We believe this indicates that the males that might have migrated late in the season simply did not survive. Adult II birds constituted most of the population in 1973 and if we accept our observed sex ratio of one female to 0.56 males as a conservative estimate of the sex ratio in the population, then we are left with the conclusion that about half of the females would be unable to breed in 1974. Further, if we conservatively assume that all increased mortality was suffered by males, we end up with an estimate that more than 20% of the Goshawks that normally would have survived succumbed in 1972–73. This additional mortality leads us to a revised estimate of population decline of approximately 70% between 1971 and the spring of 1974. The unprecedented sex ratio of 11 juvenal males to one juvenal female observed in the 1974 migration, and the suggested considerable overwintering of juvenal females in the north, was probably made possible mainly by the great decline in Goshawk populations rather than by great increases in prey.

We have presented a number of hypotheses concerning what happened in the breeding range of the Goshawk to produce the fluctuations we noted in migration at Cedar Grove. Support for some of these ideas is provided by Sulkava (1964), who conducted an 11-year study of breeding Goshawks in Finland. Populations of species preyed upon significantly by Goshawks declined precipitously between 1955 and 1956, and the mean clutch size of Goshawks decreased from 3.2 to 2.0. Prey populations remained low through 1959, but the clutch size of Goshawks increased to 3.5 in 1957, 3.9 in 1958, and 4.0 in 1959. Prey populations were considerably higher in 1960–62, but the clutch size of 4.0 was not exceeded. Average brood size (of half-grown young) showed a similar trend, although the range of variation, 2.2 to 3.3, was not as great. Considerable numbers of Goshawks died in the winter of 1956 and the 1957 population was reduced; Sulkava suggests that the losses of Goshawks through death and emigration enhanced the food situation for those that remained, permitting successful breeding in spite of low prey populations. Except for its emphasis on emigration, this explanation is quite similar to the one we have offered for Goshawks in North America in the years 1965–68. We have shown that it is unnecessary to postulate permanent emigration to produce drastically lowered populations.

Sulkava may have overlooked one extremely interesting item in his data. In central Europe the Goshawk attempts to breed every year, regardless of prey abundance (Uttendorfer 1952, Sulkava 1964, Glutz et al. 1971), but in 1956 many Goshawks in Finland apparently did not try to breed. In one study area 18 nests were occupied in 1955, but only 2 in 1956. In 1957 “most” of the 18 nests were again occupied. This suggests that dispersal of the breeding population is not a factor in increasing breeding success and offers indirect support for our hypothesis that interactions between wandering birds and established birds may disrupt reproduction. After the population was reduced in 1956, birds on established (and presumably adequate) territories were able to breed without interference in 1957. Thus the very low reproductive rates that we estimated for North American Goshawks in 1962–63 and 1972–73 seem reasonable; most birds simply did not breed.

We have argued that adults displace juvenals, that females displace males, and that adult males cannot compete with females in a very harsh winter. Indirect support for these arguments is provided by accounts of violent conflicts between hawks. Brüll (1964) saw one Goshawk kill another in a conflict over food and also

witnessed a number of fights between Buzzards (*Buteo buteo*) in winters of severe food shortage, some of which ended in the death of one of the participants (see also Brogmus 1966). Linkola (1957) and Sulkava (1964) reported considerable Goshawk mortality during harsh winters and low prey availability in Finland. We have also argued that increased agonistic encounters might disrupt breeding at times of high Goshawk populations and low prey densities. The above accounts can be taken as an indication that violent conflicts can occur. In addition Schnurre (1956) reported a territorial fight between 2 males that lasted more than 10 minutes.

We have suggested some rather drastic population declines in Goshawks during the invasions of 1962–63 and 1972–73. How many years will it take for the population to recover from these crashes? Using the calculations and assumptions of Table 4, it would take about 7 years for the 1964 population to recover its 50% loss, if just slightly more than 3 young were produced per successful pair. Sulkava (1964) found average brood sizes of 3.3 during a 2-year period of population recovery following a decline. If our calculations and speculations are anywhere near correct, it is possible that the 1971 Goshawk population had recovered to the level existing in 1961, but the 1972 population could not have been appreciably larger than that of 1962; only the proportion of the population that migrated was different.

If we accept our estimate of a 70% reduction in populations of Goshawks in 1971–73 and the high reproductive rate of slightly more than 3 young per successful pair mentioned above, it will take more than 12 years for Goshawk populations to return to the 1971 level. The unbalanced sex ratio adds several years to this estimate. Maximum reproductive rates probably will not be maintained as the Goshawk population increases and prey populations decline during the next cyclic low. We therefore predict that the Goshawks will require several 10-year cycles to regain population levels existing in 1971.

It is extremely difficult to evaluate past accounts of Goshawk abundance and invasions. From a thorough search of the literature, we guess that the 1962–63 invasion was the greatest since at least 1935 and that the invasion of 1972 was greater than any since 1926–27, and quite probably the greatest on record. Speirs (1939) and Keith (1963) noted that Goshawk invasions occur at approximately 10-year intervals, and our data support this observation. Bent (1937) and Keith (1963) noted that adults are common in invasions but are otherwise rarely seen, a phenomenon that our data show most clearly. No one previously seems to have noted that each Goshawk invasion lasts 2 years, as both recent invasions have, although one can see indications of this in the list of dates of invasions given by Bent (1937). Perhaps only those invasions of greater magnitude last for 2 years.

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