Winter ecology and partial migration of the Goldcrest *Regulus regulus* in Finland

OLAVI HILDÉN

HILDÉN, O. 1982: *Winter ecology and partial migration of the Goldcrest* Regulus regulus *in Finland.* — Ornis Fennica 59:99—122.

The paper is based mainly on results of the Finnish winter bird censuses made in the period 1956/57 to 1981/82 and on monthly censuses made during six winters along a standard route in southernmost Finland.

The proportions of residents and migrants in the population are about equal. The departure of the migrants takes place from late August to early November, the arrival from late March to mid-May. The winter quarters lie in Central and Southern Europe. Juveniles clearly predominate among the migrants and males outnumber females. In the northern part of the breeding range the population is completely migratory, the proportion of residents increasing towards the south.

Wintering Goldcrests unite in social groups of 2—5 individuals, which stay within fixed territories of some hectares. In the study area in S Finland, the mean group size remained stable throughout the winter and from year to year. The flock bonds began to loosen in March, when males started singing. In November-January, 64 % of the Goldcrest groups were associated with tits and/or treecreepers, in February-March 53 %. Food, feeding techniques and roosting are described.

In southernmost Finland, winter mortality between November and March averaged c. 70 %, with wide annual variation. North of 64°N the mortality was roughly 85 %, and for the entire Finnish population c. 75 %. Mortality was highly significantly correlated with the mean temperature of January or January-February, but not with the February temperature alone. Precipitation in January-February, added as a second independent variable to the temperature, somewhat improved the correlation. Low winter temperatures and snow cover on the branches are assumed to affect the birds indirectly, mainly through food shortage. Comparison of the autumn and spring totals of Goldcrests ringed at the Lågskär bird observatory suggests that the winter losses among the migrants are about as high as among the residents.

Winter mortality in the resident section shows only a slight influence on the numbers of Goldcrests remaining in the country the next autumn. This is due to the masking effect of other factors: losses in the migrant section, breeding success and, above all, density-dependent regulation of the proportion of migrants. This regulation is assumed to result from a social hierarchy, established through aggressive behaviour among the birds in autumn, the dominants remaining resident and the subdominants leaving. The possibility cannot be excluded, however, that genetic differences exist in the disposition to migrate.

Olavi Hildén, Zoological Museum, University of Helsinki, P. Rautatiekatu 13, SF-00100 Helsinki 10, Finland

Introduction

The Goldcrest *Regulus regulus* is one of the partial migrants of Finland, some individuals moving out of the country for the winter and others staying here throughout the year. The proportions of residents and migrants in the numerous breeding population are about equal. Consequently, the species is both one of our commonest winter birds and also one of the dominant passage migrants at our coastal bird observatories. This dimorphism in the migratory strategy is remarkable, particularly when one considers that the Goldcrest is the smallest bird in Northern Europe and a genuine insectivore. Moreover, its closest relative, the more southerly distributed Firecrest *R. ignicapillus,* is a completely migratory bird in Central Europe in spite of the much milder winters prevailing there, and the more distantly related *Phylloscopus* species are all long-distance migrants.

All this raises many challenging questions for an ecologist. How can the minute, 5-gram bird tolerate the harsh winter conditions in the north, where it is faced with short days, severe cold and limited food supply? How heavy are the losses in the wintering section of the population and do they vary much from year to year, with the severity of the winter? How do the numbers of migrants surviving the winter compare with those of the residents? Why do some individuals migrate while others remain as residents, and how is the balance between the two adaptations preserved?

Palmgren (1936) first realized the many interesting questions involved in the winter ecology of the Goldcrest. As a result of regular line-transect counts of Goldcrests during one and a half years, he found that the population was greatly reduced in both winters. Palmgren's study was followed by several others on the survival of wintering Goldcrests in Finland (Klockars 1936, Bergroth & Bruun 1939, Lehtonen 1948), which also revealed extremely high winter losses (80—90 %). This poses the problem of why the resident section of the population is not quickly eliminated by natural selection (cf. Lack 1954, p. 114).

The papers cited above were based on data from only one or two winters. Nowadays, our knowledge of Finnish winter birds is far better than it was a few decades ago, thanks to the annual winter bird censuses. The results so far published have shown that the winter mortality of Goldcrests varies from year to year much more than was formerly realized: in some winters most birds succumb, but in others up to 80 % survive the worst period from late December to early March (e.g. Hildén & Mikkola 1968, Hildén & Koskimies 1969, Sammalisto 1974).

In this paper the chief focus is on the seasonal, annual and geographical variation in the winter mortality of the Goldcrest, and its dependence on ambient temperature and other factors. The winter ecology and migration of the species are considered in so far as they relate to the main problem. Finally, population regulation and maintenance of the strategy of partial migration are discussed.

Material and methods

Finnish winter bird censuses. Annual counts of winter birds in Finland (between 26 December and 10 January) were started in winter 1956/57. The main objectives of the censuses are to obtain a reliable picture of the range and abundance of the different species wintering in Finland, and to monitor the annual and long-term changes in their occurrence. On my initiative, a late-winter count (about 25 February — 10 March) was added to the programme some years later, from 1960 onwards in the Helsinki region and from 1966 in the whole country, mainly to measure the losses of birds during the coldest period of the year. In 1976 a late-autumn count (about 1—15 November) was also added, to document more completely the changes in range, numbers and habitats of birds in the course of the winter. The censuses are organized by the Zoological Museum at the University of Helsinki.

The counts are made along fixed routes, which average c. 11 km in length, and all the birds observed are noted. The total length of the routes has been around 6000 km in midwinter, and 4000 km in both other censuses. In the southern half of Finland the routes cover all parts of the country fairly well. The two-week census period guarantees that most census takers can choose a day with favourable weather. The results are recorded on standardized forms, and later they are punched for data processing. In the computer analysis, the occurrence of each species is given as the number of individuals per 10 route kilometres. Geographical differences can be studied by dividing the country into zones or squares (for details, see Koskimies 1966, Hildén & Koskimies 1969, Sammalisto 1974, 1977a, 1977b, 1978, 1979, 1980, 1981).

Regrettably, for technical reasons the unique material of the Finnish winter bird censuses cannot be processed by computer at the moment. Hence, the Goldcrest analysis presented below had to be confined to smaller, manually collected samples. One is from the Helsinki region (mid-winter vs. late-winter), the other from a broader zone covering the whole of Finland south of 61°N (late-autumn vs. mid-winter). For the rest of the country, only the reports by Hildén & Koskimies and Sammalisto (see above) were available, together with some zonal analyses up to 1975/76 made by P. Munne. A detailed geographical analysis of mortality pattern could therefore not be undertaken.

Calculation of the mortality. Mortality has been derived simply from the percentages of birds surviving between two counts. Munne (1973) has shown that the routes censused at the turn of the year may differ considerably in their distribution among the various habitats from those censused two months later. The proportion of forest routes in the countryside, in particular, is usually much lower in the late-winter counts. This will affect the mean density of Goldcrests along the routes in the two censuses. Therefore, the mortality in the Helsinki region has been calculated only from the routes included in both censuses. The same procedure has been followed in comparing the late-autumn and mid-winter counts in southernmost Finland. The data for the whole of the country, however, include all routes and are thus less reliable.

Special censuses in Kirkkonummi. To collect more detailed data on Goldcrest abundance, flock size, association with tits, size of the home range, timing of the mortality, etc., I censused a 5.2 km route twice every month from November to March during six winters (1971/72 to 1976/77) at Kirkkonummi, c. 30 km west of Helsinki. For the whole of its length the route ran through coniferous forests of varying age, in places mixed with deciduous trees. To facilitate recording, it was marked with numbered tags at intervals of 100 m. The census was made on foot or on skis, starting soon after sunrise and usually lasting about 4 hours. In addition to Goldcrests, all tits *(Parus major, P. caeruleus, P. montanus, P. cristatus, P. ater, Aegithalos caudatus)* and Treecreepers *Certhia familiaris* were counted within 50 m on both sides of the transect. Flocks were included in full even if only some of the birds were inside these limits. Often it was necessary to follow the flock outside the strip to obtain its size. The number of Goldcrests in each group was determined as accurately as possible, which could take up to 15—20 minutes. Occurrence of song was always noted down.

Suitability of the Goldcrest for censuses. Only a few species can be counted sufficiently reliably for evaluation of their winter mortality (Hildén & Koskimies 1969). The Goldcrest is one of these, for the following reasons:

(1) It is sufficiently abundant to make the effects of chance on numbers seen more or less negligible.

(2) It does not perform movements during the winter. After the termination of the autumn migration in early November, the Goldcrest is completely sedentary spending the whole winter within a fixed group territory (p. 103).

(3) It does not switch from one type of habitat to another, depending on the food supply, but keeps strictly to coniferous forests.

(4) The Goldcrest is easy to observe and count owing to its almost continuous contact calls and habit of feeding conspicuously at the tips of branches. In addition, Goldcrest flocks are more coherent than the mixed-species

parties of tits and thus easier to count accurately.

(5) The behaviour of the Goldcrest does not change much in the course of the winter. Unlike the tits, which may be very silent and inconspicuous during the darkest time at the turn of the year, especially on cold days, Goldcrests can be detected almost equally easily by their calls from November to February-March. The onset of song varies with the temperature: if the weather is mild, the first males can be heard delivering a continuous, weak subsong in early February and full song at the end of the month, but if the weather remains cold, song is not heard before March. In most years, the first males are already singing during the late-winter count, at least in southernmost Finland, which makes them more conspicuous than in mid-winter. Hence, the calculated survival values are likely to be somewhat too high. The onset of song also explains why the censuses in Kirkkonummi usually yielded slightly higher numbers in March than in February.

General winter ecology

Migrants and residents. Departure of migrant Goldcrests from Finland takes place from late August to early November, with a peak in late September and early October. By the time of the late-autumn census, migration is almost over; at the bird observatories of Signilskär and Lågskär, for instance, only 1.3 % of the Goldcrests ringed during 14 seasons (N = 12450) were caught after 31 October. Similarly, arrival of the spring migrants does not commence until a couple of weeks after the late-winter count; at Lågskär the first sightings during the years 1969 to 1979 have ranged from 10 March to 7 April, averaging 25 March. The passage is usually heaviest around mid-April, but late migrants are seen in the archipelago until mid-May. Hence, all the Goldcrests counted in the three successive censuses in each winter belong to the resident section of the population.

The Goldcrest is a night migrant. According to more than one hundred ringing recoveries, migration from Fennoscandia is directed to the southwest, mainly to Germany, the Netherlands, Belgium, England and northern France, and sometimes as far as southern France, Spain and Italy (Österlöf 1966, Saurola 1978, Hanssen 1981). The recoveries also show that the migrants include both juveniles and adults, although the juveniles clearly predominate. Contrary to the general rule among partial or irregular migrants, males outnumber females: on average 58 % of the Goldcrests ringed at the Finnish bird observatories have been males (cf. Hildén 1974). About the same percentage has been obtained in Denmark (Österlöf 1966), Poland (Busse & Machalska 1969) and France (Frelin & Cornillon 1974).

The winter range of the Goldcrest in Finland is considerably more southern than the breeding range (Fig. 1). This implies that the population in the northernmost part of the breeding range is completely migratory. The proportion of residents evidently increases towards the south, since there is a marked increase from north to south in the winter densities, whereas the latitudinal difference in breeding densities is much smaller (Fig. 2). However, the possibility cannot be directly disproved that part of the Goldcrests wintering in Finland are short-distance migrants from more northern regions.

Habitat and territory size. The Goldcrest is one of the few birds present throughout the year in Finland that does not show any change in its habitat preference between the breeding and non-breeding season. It invariably frequents coniferous forest, both spruce and pine stands or mixed spruce-pine woods.

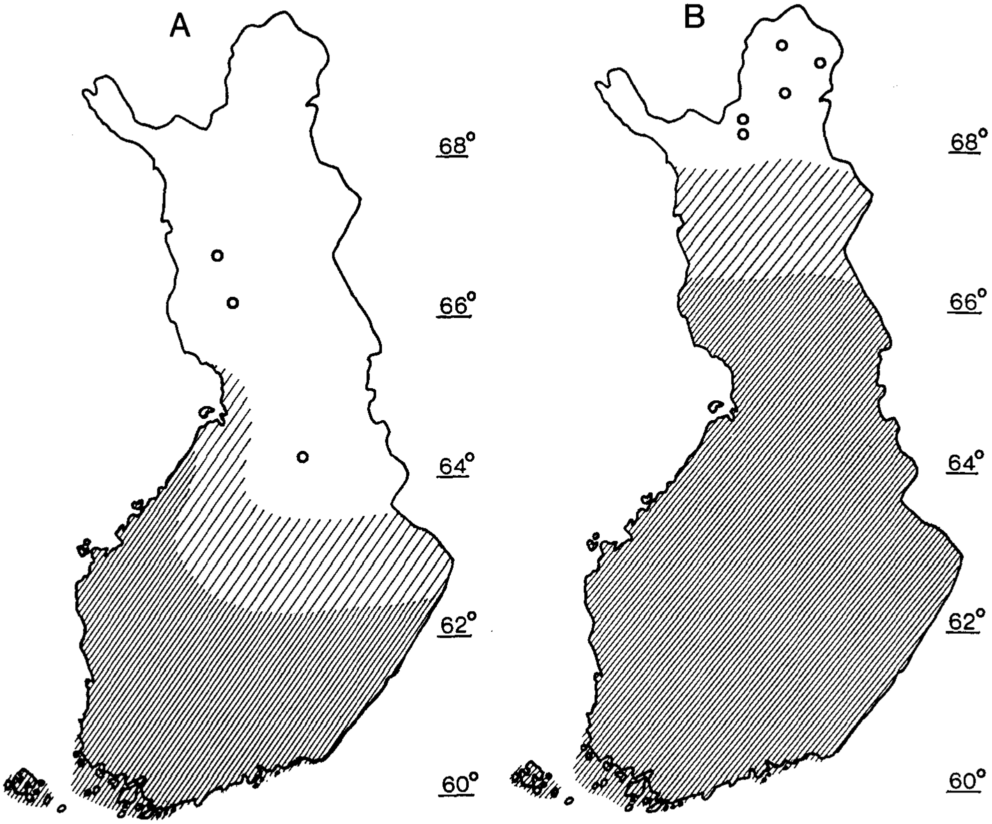

FIG. 1. The winter range of the Goldcrest (A) according to Finnish winter bird censuses in 1960/61—1971/72, as compared with its breeding range (B) based on the Finnish Bird Atlas project in 1974—79. Dense hatching = recorded in more than 50 % of the samples, sparse hatching = recorded in less than 50 % of the samples, open circles = occasional observations outside the regular range.

In my censuses in Kirkkonummi, Goldcrests were often found at nearly the same places along the route during each count. This suggested that they stayed within restricted areas throughout the winter. In fact, special studies, partly made by marking birds, have shown that Goldcrests are highly stationary, each small group having a fixed winter territory, 1.5—12 ha in size, which does not overlap with the territories of neighbouring flocks (Nöhring 1959, Hogstad 1970, 1982, Thaler 1973). Within this range the birds move around the whole day seeking for food, often along the same routes following the edges of different habitats. The group territory system of the Goldcrest and its biological significance seem to be essentially the same as those described in the Willow Tit *Parus montanus* and Crested Tit *P. cristatus* (Ekman 1979, Ekman et al. 1981).

Flocking behaviour. Wintering Goldcrests unite in small social groups. In my area, the mean size of a "Goldcrest unit" in 1971—77 was 2.44 (N = 371), 2—3 birds being the most common unit (74.4 %) and single birds (13.2 %) occurring about as frequently as parties of 4—5 individuals (12.4 %). No groups larger than 5 birds were recorded in the censuses, but on other winter excursions in the same area I have occasionally encountered 6 or 7 Goldcrests in one flock. There was no reduction in the monthly mean group size from November to February (range 2.42 to 2.54), and only a slight decrease in March (2.11), when the flocks start breaking up. Nor were there any significant annual differences in the mean group size (range 2.21 to 2.66). This suggests that surviving group members may join neighbouring groups to maintain the flock size, which would imply some reorganization of territories.

In other areas, Goldcrests may form larger winter groups. In southern Norway the flocks consists of 3—9 individuals (mean 4.57) during the early winter months, but are reduced to 2—4 individuals (mean 2.82) by January-February (Hogstad 1970, 1982). In Austria, wintering Goldcrests keep in groups of 3—7, usually 4—5 individuals, without showing any seasonal or annual changes in flock size (Thaler 1973). In both countries the groups are reported to be more coherent on cold days, whereas in mild weather some flock members often detach themselves from the others, even for hours. I have also witnessed many times that a group of Goldcrests suddenly splits into two parts, or is joined by new birds, probably ordinary members of the flock that have left it for a while. Such temporary breaking up of the group may, of course, give a false impression of the real flock size, and this fact has probably somewhat reduced the mean size obtained for the unit in my material, as two thirds of the counts were taken on days with temperatures higher than —5°C (cf. Hogstad 1982).

As is commonly known, Goldcrests often consort with tits and Treecreepers. In my observations, 64 % of the Goldcrest units were associated with tits and/or Treecreepers in November-January (N = 302), and 53 % in February-March (N = 101). Attachment to the mixed flocks seemed to be rather loose, and it frequently happened that the Goldcrests left or joined the flock during the time I was counting the birds. This is also reported by Hogstad (1970) and Thaler (1973). The association may last from a few minutes to several hours, but cannot be permanent, as the tits move faster than the Goldcrests.

Depending on the ambient temperature, flock bonds begin to loosen in March, when the males also start singing and chasing each other. At the same time at least some of the Goldcrests form pairs, as the proportion of units containing two individuals clearly increased, from an average of 42 % in November-February to 65 % in March. Breeding territories are also established from March onwards, but how far males may move to do this is not known (cf. p. 118). Probably most pairs nest within, or close by, the group territory with which they are familiar. This has been shown to be the rule in the Willow Tit and Crested Tit (Ekman 1979), and evidence for the same system in the Goldcrest was presented by Nöhring (1959) in Germany.

Food and feeding. Even in wintertime, the Goldcrests feed exclusively

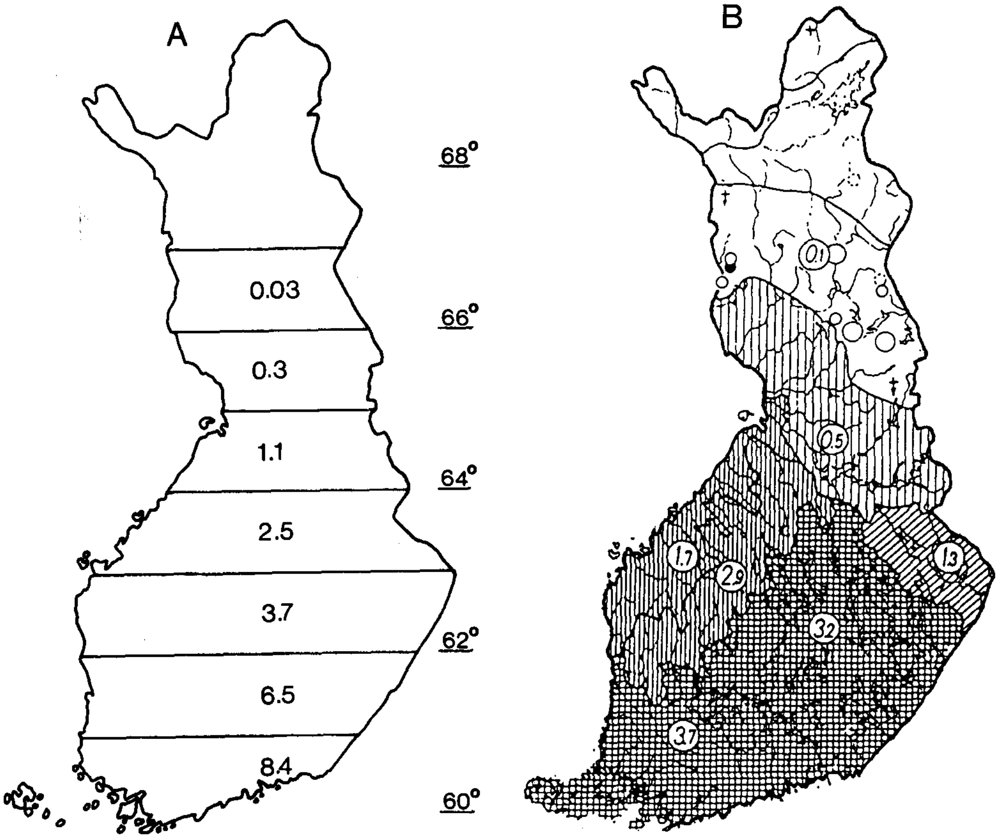

FIG. 2. A. Average densities (ind./10 route km) of Goldcrests in the latitudinal zones of Finland, according to the mid-winter censuses in 1960/61—1975/76. — B. Breeding densities (pairs/km^2) of Goldcrests in the zoological regions of Finland, according to Merikallio (1958).

on animal food: insects, their eggs, larvae and pupae, and spiders. Stomach analyses of birds collected in autumn have shown caterpillars, aphids, psyllids and spiders to form the main part of their food (Palmgren 1932), and sight observations have witnessed that wintering Goldcrests take a large variety of invertebrates, ranging from minute springtails (Collembola) to 2-cm-long moths (Thaler 1973). The significance of spiders seems to increase during the winter: in 21 gizzards analysed in S Norway they constituted 45 % of the prey items in October but almost 80 % in January-February (Hogstad 1982).

Goldcrests, tits and Treecreepers occupy different feeding niches or use different feeding techniques (Palmgren 1932, Haftorn 1956, Gibb 1960, Thaler 1973, Alatalo 1981). The Goldcrest forages mainly at the tips of coniferous branches, particularly among the hanging twigs of spruce branches, which it examines by continuous flitting and frequent hovering in a hummingbird-manner, not by hanging upside down as is frequently done by the tits. As shown by Palmgren (1932) in his classical study, the differences in locomotion techniques and feeding site preferences between the Goldcrest and the tits are mainly due to differences in the functional anatomy of their legs. The preferred feeding heigth above the ground, the tree species visited most often, and the average speed of movement of the flock are largely dependent upon the weather (Hogstad 1970, Thaler 1973, own observations), and the foraging sites and feeding postures also vary with the ambient temperature (Alatalo 1982).

Due to its small size, the Goldcrest has a high metabolic rate, which necessitates a high intake of food per unit weight. Individuals held in large outdoor cages in January ate 6—7 g insects daily, i.e. more than their own weight (Thaler 1973). On cold days the food intake could be 2—3-fold the body weight (Thaler 1979). To obtain the necessary amount of food during the short winter day, Goldcrests devote "nearly 100 %" (Gibb 1954, 1960) or "more than 90 %" (Thaler 1973) of their daily activity time to feeding even in Central Europe, where the daylight period is much longer than in Finland. Fasting for as short a time as one to two hours is sufficient to cause detrimental effects (Thaler 1979).

Roosting. Where and how a bird spends its night is of crucial importance during the long cold nights of the northern winter. Many energy-saving adaptations, both physiological and behavioural, have been evolved. The most peculiar feature in the roosting habits of the Goldcrest is that the entire group sleeps in close feather contact, forming a "compact globe" (Nöhring 1959, Thaler 1979), thus reducing the heat loss. The same strategy is used, for instance, by the Long-tailed Tit *Aegithalos caudatus* (e.g. Nakamura 1962, Riehm 1970) and the Treecreepers *Certhia brachydactyla* and *C. familiaris* (Löhrl 1955, Thielcke 1959).

According to Nöhring (1959), Goldcrests choose their roost wherever the group happens to be at the critical moment at dusk, whereas the birds studied by Thaler (1973) used a permanent roost. This was a tall spruce, where the birds spent the night in a very dense part of the foliage. Interestingly, two or three groups from different territories assembled in this roost each evening, and separated again in the morning. Whether all the birds slept together could not be ascertained. Contact sleep occurred only during nights with temperatures below —10°C or in heavy snowfall and wind, whereas Nöhring (1959) did not notice any dependence upon the temperature. Observations in an outdoor aviary showed that the birds did not become torpid (Thaler 1973).

Many birds are known to roost in the snow because of its good thermo-insulation. An observation in Finland shows that even Goldcrests may do this: on 9 December 1973, three Goldcrests were seen flying at sunset into a hole in the snow, c. 20 cm in breadth, 10 cm in depth and with an entrance 5 cm in diameter. As the birds went directly to the hole, they had evidently used it earlier (Lagerström 1979). How commonly this roosting behaviour occurs in the Goldcrest deserves to be studied.

Winter mortality

Finnish winter bird censuses. Since 1976, information on the mortality during the early half of the winter

TABLE 1. Numbers of Goldcrests recorded on the same census routes in late-autumn (1—15.11.) and mid-winter (26.12.—10.1.) during six winters in southernmost Finland (60—61°N). The mortality is calculated from the percentages of birds surviving from the first to the second count.

Winter	No. of routes	Late-autumn	Mid-winter	Mortality (%)
1976/77	85	1404	1230	12
1977/78	85	744	475	36
1978/79	73	474	329	31
1979/80	81	534	397	26
1980/81	81	902	783	13
1981/82	82	1629	1066	35

can be obtained from the late-autumn counts. The number of Goldcrests on the census routes in southernmost Finland decreased each year during November-December, the mortality ranging from 12 to 36 % and averaging 25.4 % (Table 1).

Mortality during the coldest period of the winter, in January-February, can be calculated from data collected in the Helsinki region since 1959/60 (Table 2). The year-to-year variation in mortality has been much more pronounced than during the early half of the winter, in part due to the longer period. It ranges from 12 to 95 % and averages 48.4 %.

By combining the above materials, the total winter mortality can be estimated. The mean survival during November-December was 0.746 and during January-February 0.484. Thus, the overall survival was 0.746×0.484 = 0.361, corresponding to a mortality of 64 %. As the detectability of Goldcrests improves somewhat in late winter, the true long-term mean winter mortality must be a little higher, probably about 70 %.

This value applies to southernmost Finland, where the winter is mildest. The results published by Sammalisto (1977a, 1978, 1979, 1980, 1981) suggest that north of the 64th parallel the mortality during November-December may be much heavier, roughly 63 %. This was to be expected as winter comes much earlier to these latitudes than to southernmost Finland. Hard frosts are not uncommon as early as December, and the day is much shorter. For the intervening zone, 61—64°N, the mortality during November-December is also likely to be somewhat higher than in the zone 60—61°N. During January-February, on the other hand, there seems to be little variation in mortality between the zones, except for the northernmost. The mean mortality values for 1966/67 to 1975/76 calculated from the densities (ind./10 route km) within each zone are:

TABLE 2. Numbers of Goldcrests recorded on the same census routes in mid-winter (26.12.—10.1.) and late-winter counts (25.2.—10.3.) during 23 winters in the Helsinki region. The mortality is calculated from the percentages of birds surviving from mid-winter to late-winter.

Winter	No. of routes	Mid-winter	Late-winter	Mortality (%)
1959/60	11	133	17	87
1960/61	9	124	54	56
1961/62	12	269	215	20
1962/63	13	162	27	83
1963/64	15	67	58	13
1964/65	15	175	108	38
1965/66	20	175	8	95
1966/67	16	73	8	90
1967/68	18	134	8	94
1968/69	19	218	96	56
1969/70	16	120	24	80
1970/71	20	69	61	12
1971/72	25	325	222	32
1972/73	20	236	186	21
1973/74	22	342	176	49
1974/75	17	296	186	37
1975/76	29	311	241	23
1976/77	30	390	135	65
1977/78	32	132	69	48
1978/79	20	113	28	75
1979/80	22	104	80	23
1980/81	25	278	213	23
1981/82	25	344	114	67

60—61°	61—62°	62—63°
48.0	46.0	40.6
63—64°	64—65°	Average
45.6	58.7	48.7

Judging from the above figures, the total winter mortality north of the 64th parallel should average roughly 85 %, but more data are needed. In the worst winters (1965/66, 1966/67, 1967/68 and 1969/70), all the Goldcrests in this region succumbed. As the population density is low in the northern parts of the winter range (Fig. 2), the higher mortality there does not have much influence on the total Finnish winter population. For January-February, the mortality rate for the whole country has been 53.3 % (mean of 1965/66 to 1980/81), as compared with 51.4 % for the Helsinki region during the same period. As the difference is probably somewhat larger during November-December, the total winter mortality for the Finnish Goldcrest population may average about 75 %.

Censuses in Kirkkonummi. Table 3 gives the monthly numbers of Goldcrests recorded on my census route during six winters. The overall survival was very good, and only in winter 1976/77 were the numbers much reduced. There was considerable variation between the winters, e.g. hardly any decline from November to December in 1971, 1972 and 1975 but a substantial reduction in 1973 and 1976. The apparent increase during the same period in 1974 must be due to differences in the detectability of the birds: Goldcrests, and also tits and Treecreepers, were exceptionally silent during the two November counts that year.

Better detectability also explains the slight increase in numbers from February to March, when the birds begin to call more intensively and the males start singing (p. 102). The February values thus give a better indication of the winter survival. As some mortality had probably occurred before the first censuses in November, we may conclude that, on average, about 50 % of the Goldcrests spending the winter in Kirkkonummi survived to the spring during these six winters. This is remarkably good wintering success, much better than the long-term average for southern Finland, and attributable to the fact that the first four winters of this period were exceptionally mild and the two following ones only moderately cold. The result obtained is in good accordance with those from the Helsinki region (Table 2): during the same winters an average of 62 % of the Goldcrests survived from midwinter to late-winter, which is exactly the same value as in Kirkkonummi from December to February!

TABLE 3. Monthly numbers of Goldcrests recorded on a 5.2 km-long census route counted twice each month during six winters in Kirkkonummi, S Finland.

Winter	Nov	Dec	Jan	Feb	Mar
1971/72	46	40	28	26	33
1972/73	48	40	36	34	37
1973/74	55	33	31	24	23
1974/75	32	47	49	35	46
1975/76	60	64	43	34	40
1976/77	66	39	9	9	15
Total	307	263	196	162	194
In %	100	86	64	53	63

Factors affecting mortality

Temperature. The high winter mortality of the Goldcrest is generally believed to result from insufficient cold-hardiness, due to its small body-size and energy-demanding foraging behaviour. Indeed, during the severest winters the population has been nearly exterminated (e.g. Hildén & Mikkola 1968, Hildén & Koskimies 1969, v. Haartman et al. 1963—72). However, the relationship between the mortality and ambient temperature has never been tested with a sufficiently large material, nor has it been ascertained which temperature parameters are the most crucial.

As the data from the mid-winter and late-winter censuses in the Helsinki region cover 23 years (Table 2), the long-term relations between mortality and temperature can be tested reliably. The mortality during January -February is correlated with a variety of different temperature parameters, as follows:

- Mean temperature in January $r = 0.739^{***}$
- Mean temperature in February $r = 0.365$ n.s.
- Mean temperature in January-February $r = 0.638^{**}$
- Sum of daily mean temperatures below —10°C in January $r = 0.686^{***}$
- The same in February $r = 0.456^{*}$
- The same in January-February $r = 0.732^{***}$

The mean temperature in January thus gives the highest correlation and explains 54 % of the annual variation in mortality in a linear regression model. The regression is depicted in Fig. 3A. In contrast, the mean temperature of February does not correlate significantly with the mortality, but low February temperatures have some effect.

The corresponding material for November-December is confined to six years (Table 1), so it is understandable that no significant correlation between mortality and temperature can be found. The data from my census route in Kirkkonummi (Table 3), however, suggest a clear relationship between mortality and low temperatures. The three years (1971, 1973 and 1976) with substantial losses from November to January were the coldest during the six-year period, with temperatures below —10°C occurring as early as November-December. In contrast, the two years (1972 and 1975) in which only slight mortality occurred during the early winter were mild, and in 1974, when no decreases in the numbers of Goldcrests were noted, the temperatures remained exceptionally high throughout November-December.

The effect of temperature on winter mortality can also be tested by comparing the density of Goldcrests in February-March with the severity of the winter. During the 16 winters (1966—81) when late-winter counts have been taken in Finland, the density of Goldcrests in the whole country has varied between 0.4 and 6.4 individuals per 10 route kilometres. The density values are highly significantly correlated with the winter cold in Jyväskylä, which lies in about the middle of the species' winter range ($r = 0.831^{***}$; Fig. 3B).

Snow cover. The effect of snow cover on mortality is very difficult to analyse. The amount of snow on the branches may be decisive, but there are no statistics about this. The precipitation or the depth of snow on the ground are not reliable measures of the snow cover on the branches, as heavy winds or temperatures above zero cause most of the snow to fall off. On the other hand, wet snow which freezes afterwards may stay for a long time on the foliage.

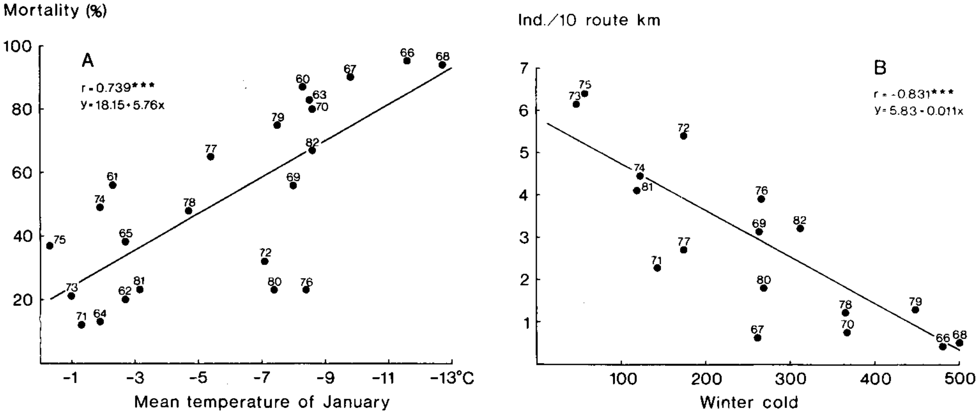

FIG. 3. The relationship between the winter mortality of the Goldcrest and ambient temperature in Finland. — A. Mortality in January-February in the Helsinki region during 23 winters (1959/60—1981/82) compared with the mean temperature of January. — B. Density in late-winter counts in the whole country during 16 winters (1966—81) compared with the winter cold in Jyväskylä (= sum of daily mean temperatures below —10°C in December-February).

Probably for these reasons, no correlation was found between Goldcrest mortality and the precipitation or snow depth in January-February. But added as a second independent variable to the temperature, precipitation somewhat improved the coefficient of determination: e.g., the mean temperature and precipitation in January together explained 59 % of the annual variation in mortality. A corresponding increase in the coefficient of determination can also be shown for February and January-February.

For biological reasons, the snowiness of the winter must have a marked effect on the survival of Goldcrests. A thick snow cover on the branches reduces the available feeding area to a small fraction of its maximal extent, and also shades the snow-free parts of the foliage, thus making foraging more difficult. After heavy snow falls, the spruces may look like white candles (Fig. 4) and feeding sites are restricted to narrow, dark crevices and hollows between the thick snow layers. Such a "Christmas card" landscape may prevail for weeks in central and especially northern Finland, where storms and temperatures above zero are rare in winter. Hence, the correlation between mortality and abundance of snow would probably be clearer in the northern parts of the Goldcrest's winter range. In S Norway, Hogstad (1982) found a significant correlation between the winter mortality of Goldcrests and the precipitation.

Food supply. There are large annual fluctuations in the stock of invertebrates hibernating in the tree foliage and providing the main food supply for the tits and Goldcrests (Gibb 1960, Jansson & v. Brömssen 1981). Field-experiments showed that the birds can consume from a quarter to more than a half of the winter stock of their preferred food items (Gibb 1960, Askenmo et al. 1977, Jansson & v. Brömssen 1981). This suggests that at times they are faced with food shortage. The crucial significance of food

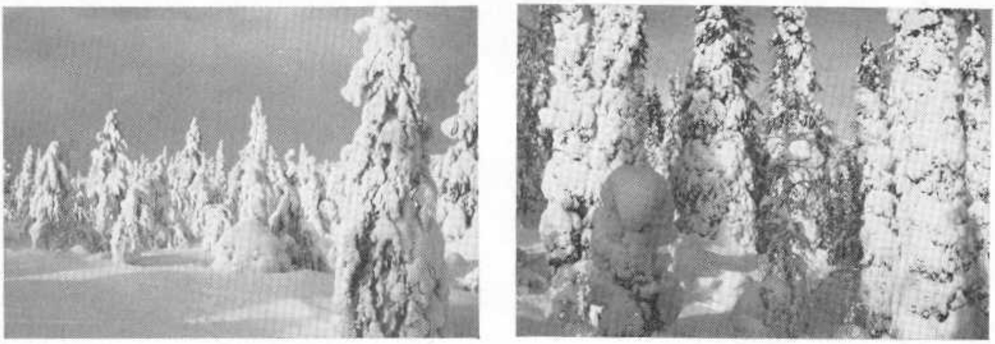

FIG. 4. In northern Finland spruces are often covered by thick snow for weeks (left), but after heavy falls of snow "Christmas card" landscapes may occur in southern Finland as well (right). A thick snow cover on the branches makes foraging difficult for the Goldcrest. — Photo M. Rautkari.

to the winter survival was proved convincingly in colour-ringed populations of Willow Tits and Crested Tits (Jansson et al. 1981).

All this implies that the food supply is one of the factors influencing winter survival in Goldcrests. In fact, Hogstad (1982) considers their high winter losses to be mainly caused by food shortage. This is also supported by the findings by Gibb (1960), that the numbers of Goldcrests were closely associated with the invertebrate stock on branches and that the population decreased more markedly in winters when food was short. The significance of the food factor, however, is dependent on temperature and snow cover: low temperatures increase the need for food, and snow covering the branches impedes foraging. It is noteworthy that food-searching Goldcrests use hovering, the most energy-consuming foraging method, less frequently in falling temperatures (Alatalo 1982).

Population density. If food limits the numbers of Goldcrests in winter, then population density should also have some significance. In itself, however, this factor does not seem to have much effect, since in the mild winters of 1971/72 to 1975/76 the Goldcrests survived very well in spite of especially high densities (cf. Fig. 5). Population density is likely to affect survival only in combination with poor availability of winter food, i.e. during spells of adverse weather or when food is scarce.

Predation. The Sparrowhawk *Accipiter nisus*, the Pygmy Owl *Glaucidium passerinum* and the Great Grey Shrike *Lanius excubitor* are in practice the only predators likely to kill Goldcrests in winter. According to my experience, their predation is insignificant. All are scarce winter birds in Finland, and only the Pygmy Owl frequents coniferous forests. In an analysis of the autumn and winter food of the Pygmy Owl in central Finland, Kellomäki (1966) found only two Goldcrests among 343 prey animals. The corresponding figures in material from northern Finland (64—65°N) were two out of 147 (Kaakinen & Mikkola 1972). Hence, predation cannot play any noteworthy part in the annually varying winter mortality of the Goldcrest.

Discussion

Survival of residents. In southernmost Finland the mortality of Goldcrests from early November to early March averages c. 70 %, but the annual differences are very pronounced. In severe winters more than 90 % succumb, in mild winters less than 30 %. In the northernmost parts of the winter range, north of the 64th parallel, the losses are higher, probably roughly 85 % on average.

The trend of increasing mortality towards the north can be explained by three main factors. First, the winter is longer and colder in the northern parts of the range. Second, the foliage is covered by more snow and for longer periods in the north. Third, the winter day is shorter in the north; between Helsinki and Oulu, for instance, the greatest difference in daylength (at Christmas time) is 2 hours and 20 minutes. These factors determine the northern boundary of the species' winter range, which lies about 500 km to the south of the corresponding limit of the breeding season (Fig. 1).

As expected, the winter temperature proved to be the most important factor correlated with mortality. Hence the poor correlation of the February temperature with mortality may at first appear strange. In part, it is spurious and arises from the masking effect of the January temperature: mild weather in February will not allow high overall winter survival if preceded by a cold January. This happened several times during the study period, which naturally weakens the correlation between mortality and February temperature.

But in part the poor correlation reflects the fact that hard frosts in February-March are not as destructive as in December-January. This holds not only for the Goldcrest but also for most other species. The main reason is that the daylength, and thus the time available for feeding, has begun to increase; in Helsinki, for example, the daylight period is more than three hours longer in mid-February than at Christmas, and the difference is even greater further north. For a small bird with a high metabolic rate, this change in the ratio of feeding to roosting time must be of crucial importance (cf. Evans 1969). Therefore, I cannot agree with Haftorn (1976) and van Balen (1981) that the later unfavourable conditions occur in the winter, the stronger is their impact. This may be so in Central Europe, where the daylength changes less during the winter, but not in Northern Europe.

Some additional factors contribute to the reduction in the mortality rate of Goldcrests in late winter. First, the individuals left are likely to be the most resistant. Second, the snow begins to drop from the trees as sunshine becomes stronger, and new snow falls less frequently than in midwinter. Third, the higher day temperatures make invertebrates more mobile; spiders, dipterans and springtails are commonly seen on the snow in mild weather. This may more than counterbalance their reduced number.

Low winter temperatures affect the birds indirectly, or at least in combination with other factors, especially food shortage (cf. Gibb 1960, Berndt & Frantzen 1964, Hildén & Koskimies 1969, v. Haartman 1973, van Balen 1981, Källander & Karlsson 1981, Svensson 1981). Low ambient temperatures increase a bird's daily energy requirements and often reduce the availability of food, which makes it more difficult for the bird to store enough energy during the few daylight hours to survive the long winter night. The density of available food for Goldcrests is also dependent on the stock of invertebrates in the tree foliage and the snow cover on the branches. These factors modify the effect of temperature on mortality and explain why the correlation is not linear.

Survival of migrants. A basic question with respect to the evolution of partial migration is how the winter mortality of the migrants compares with that of the residents. How high are the losses during migration and in the winter quarters, and do they vary considerably from year to year?

These questions are not easy to answer. From the number of Goldcrests found dead at lighthouses during the autumn and spring migration, it should be possible to get a rough idea of the mortality during winter. In total, 1135 Goldcrests were collected at Danish lighthouses during 1891—1939; of these 91.3 % were from the autumn and only 8.7 % from the spring (Österlöf 1966). According to this ratio, less than 10 % of those leaving Fennoscandia return; but this result may exaggerate the mortality. First, most victims at the lighthouses are killed during foggy or drizzling nights, and such weather occurs more frequently in autumn than in spring. Second, accidents are more likely to happen during the first journey of the inexperienced juveniles, and this may also increase the proportion of autumn deaths at lighthouses.

Alternatively, the autumn and spring totals of Goldcrests ringed at bird observatories can be compared. The location of the bird observatory is important: it should be such that the chances of intercepting birds on the autumn and spring migration routes are about equal. Of the Finnish bird stations, Lågskär in Åland is the most suitable, lying on the open sea about as far from the Finnish as from the Swedish coast and along a migratory pathway used heavily by birds in both autumn and spring. Moreover, Lågskär has been manned almost regularly throughout the migration seasons, and the ringing effort has been kept about constant.

TABLE 4. Ringing totals of Goldcrests at the bird observatory of Lågskär, Åland, in 10 springs compared with the corresponding totals of the preceding autumns.

Autumn		Spring		Per cent
1968	500	1969	65	13.0
1971	1080	1972	180	16.7
1972	1175	1973	286	24.3
1973	1809	1974	450*	24.9
1974	1549	1975	700	45.2
1975	3250	1976	525	16.2
1976	2535	1977	298	11.8
1977	1603	1978	322	20.1
1978	1192	1979	134	11.2
1979	400*	1980	162	40.5

* The station was not manned the whole season; the numbers of birds missed have been estimated using the mean seasonal distribution of migrants.

Table 4 shows the ringing totals of Goldcrests at Lågskär for ten springs, compared with the totals for the preceding autumns. The numbers caught while returning in spring have constituted 11 to 45 % (average 22.4 %) of those trapped while departing in autumn. How accurately this ratio reflects the true winter survival is not known, however. When anyone spring is compared with the preceding autumn, considerable error may arise from the unpredictable weather conditions: the stopping of migrants to rest on isolated islands, like Lågskär, is highly dependent on the weather, and often the greater part of a season's ringing total is trapped on a few favourable days. The most extreme values for the ratio of spring to autumn catches may partly result from this factor. But in the long run, the days with particularly favourable weather are probably about evenly distributed between the autumn and spring, so the 10-year average should not be biased systematically. A more serious source of error could arise if there was a consistent difference between autumn and spring in the tendency of birds to stop and rest on isolated islands. In general, one might expect this tendency to be higher in autumn, when the inexperienced juveniles depart on their first journey. In this case, the survival values obtained would be somewhat too low.

I have also obtained ringing statistics for Goldcrests from the island of Heligoland in West Germany (D. Moritz in litt.). In the 1960s and 1970s, the ratio of spring totals to preceding autumn totals averaged 13.2 % (range 0 to 39 %). But the numbers ringed at Heligoland are much smaller and less predictable than at Lågskär, varying between 9 and 243 in autumn and between 0 and 29 in spring. The ratio obtained is thus not as reliable as that for Lågskär.

Although some uncertainty attaches to the above calculations, two general conclusions can be drawn. First, mortality among the migrants is high. It was estimated above that the mortality of Goldcrests wintering in Finland averages 75 % from November to March. The ringing statistics from Lågskär suggest that the corresponding value for the migrants between October and April may be almost 78 %. As this value could be somewhat too high, the losses for both sections of the population are of the same order of magnitude. Second, the annual variation in mortality is considerably lower than that of the residents. The mortality of migrating Goldcrests is also high compared with that of some other partial migrants: for the Great Tit *Parus major*, Blue Tit *P. caeruleus* and Bullfinch *Pyrrhula pyrrhula*, the annual ringing totals at Lågskär in spring have corresponded to 25—65 % of the preceding autumn totals (Hildén 1978).

A consistently high annual mortality among migrant Goldcrests is not unexpected. Being a rather slow flyer of very small size, the Goldcrest must be very susceptible to adverse weather when crossing the Baltic and the North Sea (e.g. Thaler 1979, p. 21). It may also be less well adapted physiologically and behaviourally to long-distance migration than the regular migrants. Large numbers of Goldcrests often gather on ships during nights when visibility is poor, which suggests a weak ability to maintain flight direction. Being a bird of mature spruce forests, the Goldcrest is also particularly exposed to predators when resting in open terrain with low bushes and scattered trees. In the outer archipelago, for instance, I have frequently seen Goldcrests taken by Sparrowhawks and Great Grey Shrikes. Finally, the migrants do not always succeed in escaping from harsh winter weather, since at times this extends throughout Western and Central Europe. In Britain, for example, the species was practically exterminated in the hard winter of 1916/17, and suffered again in the winters of 1939/40 and 1940/41 (Hosking & Newberry 1946). Even in normal winters the numbers of Goldcrests in

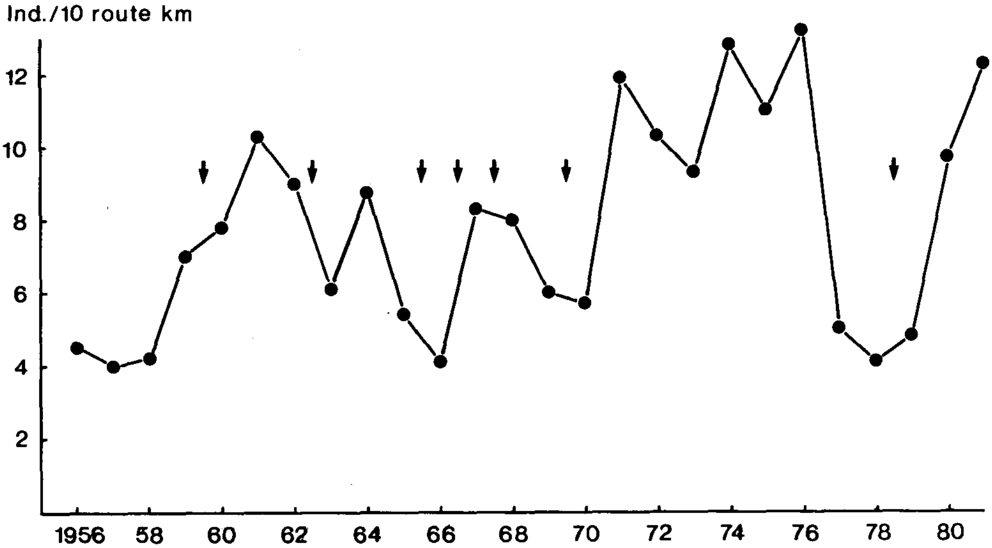

FIG. 5. Annual fluctuations of Goldcrest densities in southernmost Finland (south of 61°N) at the turn of the year during 26 winters (1956—81). The arrows indicate winters with particularly heavy mortality (75 % or more during January-February).

Britain decline by a quarter between November and February (Gibb 1960).

Regulation of the winter population. Fig. 5 depicts the annual fluctuations in the densities of Goldcrests in southernmost Finland at the turn of the year. The variation between 4.0 and 13.2 individuals per 10 route km cannot be considered especially high when compared with the wide annual fluctuations in the winter mortality. How is the size of the winter population controlled, and to what extent is it affected by the mortality in the preceding winter?

The arrows in Fig. 5 indicate winters with particularly heavy mortality (75 % or more in January-February). After such crashes, the population of the following winter was clearly smaller only in 1963 and 1966, remained at about the same level in 1960, 1968, 1970 and 1979, and was clearly higher in 1967. It is thus difficult to see any correlation between the population density in one winter and heavy winter mortality the preceding year. On the other hand, the very high densities during the early 1970s coincide with successive winters of low mortality. The correlation between the abundance of the Goldcrest and the mortality during the preceding winter is presented in more detail in Fig. 6. Although not distinct, the correlation is nevertheless significant ($r = -0.590^{**}$).

The slight effect of the winter mortality on the size of the Goldcrest population in the following winter may appear strange. One would have expected much lower densities in the late 1960s, for instance, when the severe winters almost completely destroyed the wintering population, and continuously increasing densities during the early 1970s, when the residents survived extremely well. Moreover, the breeding population of the Goldcrest is known to fluctuate in accordance with the coldness of the winters.

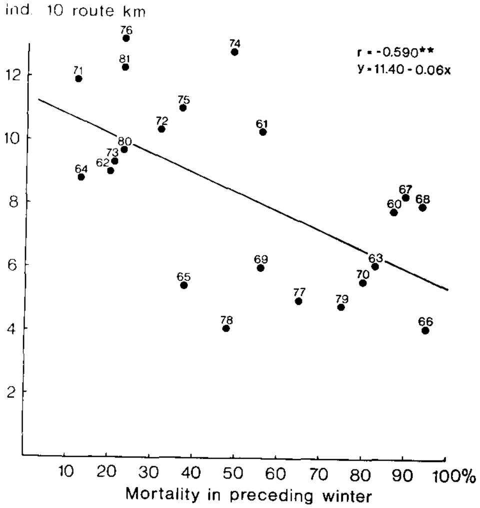

Fig. 6. The relationship between the density of Goldcrests in southernmost Finland (south of 61°N) at the turn of the year and mortality during the preceding winter.

Thus, the Finnish population grew during the warm period in the 1930s (Merikallio 1946), and in 1949—56 the population changes corresponded closely to the mean temperatures of the preceding winters (Siivonen 1956). In the province of Häme, the population in 1956 hardly reached 10 % of that in the previous summer, after an extremely cold winter (P. Linkola in v. Haartman et al. 1963—72).

Clearly, there must be additional factors which influence the numbers of Goldcrests present at the turn of the year in Finland and which may mask the effect of the winter mortality. At least the following can be listed:

(1) Losses in the migrant section. The migrants also experience varying mortality, and the winter losses in this section of the population need not parallel those among the residents.

(2) Breeding success. The reproductive potential of the Goldcrest is the highest among the northern passerines. It frequently, perhaps regularly, rears two broods, which partly overlap in time (Palmgren 1932, Haftorn 1978a, 1978b, Thaler 1979), and each clutch contains 8—12 eggs (v. Haartman 1969, Haftorn 1978a). This exceptionally high reproductive rate enables the population to compensate for even heavy winter losses during a single breeding season, if nesting is successful. This was confirmed in 1967 and 1968 in Häme (P. Linkola in v. Haartman et al. 1963—72). Differences in the weather conditions and in the abundance of nest predators during the breeding season are likely to cause considerable fluctuations in the annual numbers of offspring produced (cf. Thaler 1979, p. 21).

(3) Proportions of migrants. At the bird observatory of Lågskär, the ringing efficiency has been kept about constant since 1971. In Fig. 7 the autumn totals of Goldcrests ringed at Lågskär in 1971—81 have been compared with the densities in the winter population during the same period. It shows convincingly that the numbers of migrants have fluctuated more than those of the residents. When the population was very high in the early 1970s, due to exceptionally mild winters, the density of the residents stayed within narrow limits, while the number of migrants grew manyfold. After the decline of the population, on the other hand, the number of migrants dropped more steeply than that of the residents. In other words, there seems to be an upper limit to the density of the population staying for the winter, which causes heavy fluctuations in the migrant section.

(4) Mortality during the early winter. The density values in Fig. 5 refer to numbers present at the turn of the year. By this date, considerably

mortality may have occurred in some years, and this may further mask the effect of the previous winter on the population. At the beginning of the winter season, in early November, the annual differences are likely to be smaller, as is suggested by the fairly stable numbers recorded during six years in Kirkkonummi (Table 3) and in S Norway (Hogstad 1982).

Migration strategy. The mechanism suggested above implies that the proportion of migrants is determined by the numbers present in autumn. The same proximate factor has been shown to be decisive in many irruptive species, high densities releasing emigrations (e.g. Hildén 1977). In fact, there is only a difference of degree between partial migrants, such as the Goldcrest, and irregular migrants of the invasion type. While the populations of the invasion species emigrate only in certain years, often at long intervals, when they have produced a large surplus, emigration is an annual phenomenon in the Goldcrest.

The Goldcrest is rather exceptional among the partial migrants of Finland in that by early autumn the migrant and resident sections of the population are both numerous. In fact, of the passerines, the only species showing similar proportions of migrants are the Hooded Crow *Corvus corone cornix*, Jackdaw *C. monedula*, Yellowhammer *Emberiza citrinella* and Greenfinch *Carduelis chloris*. However, during the winter, these species are almost completely dependent on food sources provided by man, so the proportion leaving before the winter must have been much larger in past centuries when the country was more sparsely inhabited. All the other partial migrant species in Finland are either mainly migratory (e.g. *Sturnus vulgaris, Fringilla coelebs, Turdus merula*), or mainly sedentary (e.g. *Parus major, P. caeruleus, Certhia familiaris).*

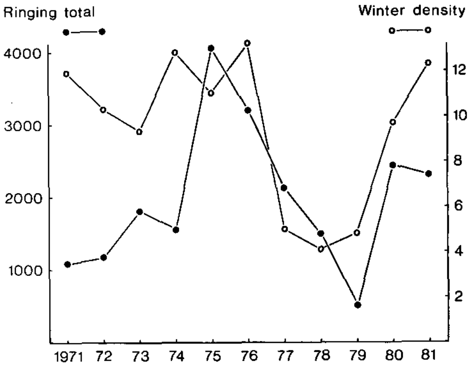

FIG. 7. Autumn totals of Goldcrests ringed at the Lågskär bird observatory in 1971—81 (black dots), compared with the densities of the mid-winter population in southernmost Finland (south of 61°N) during the same period (open dots).

In partial migrants, as well as in regularly migratory species with two or more categories of individuals (differing in the directions they take, their wintering regions or other characteristics of migratory behaviour), genetic differences are usually assumed to be involved (e.g. Lack 1943—44, Österlöf 1966, v. Haartman 1968, Berthold 1982). For a species like the Goldcrest, with about equal proportions of migrants and residents in the population in most autumns, evolution of such a situation implies two genotypes of nearly the same fitness. Indeed, the winter mortality among both sections was found to be about equal, which might be thought to give some support to the theory of a genetic programming of migratory behaviour. But, fitness involves both survival and reproduction, and in partial migrant species, as pointed out by v. Haartman (1968, 1978), residents have several advantages over migrants with respect to breeding performance. They have access to the best territories and best nest sites, which increases their chances of obtaining a mate and improves their breeding success. Furthermore, they can start nesting earlier in spring and thus have more time to lay replacement and second clutches. They may also attain sexual maturity at a younger age (Berthold 1964). Consequently, residents most probably achieve a higher reproductive rate than migrants.

These advantages probably hold for the Goldcrest, too. The resident males start singing in February-March, several weeks before arrival of the first migrants. At the same time, winter flocks begin to break up, pair bonds are formed and breeding territories are established. The late-winter population is small compared with the breeding population later in spring, in some years only a minute fraction, and there are optimal habitats available for all the survivors. A general rule in habitat selection by birds is that the best territories are occupied first and then, with increasing population density, the less suitable ones in decreasing order of quality (Hildén 1965). Consequently, the residents will take possession of the best territories and the migrants make do with what is left (cf. also Wallgren 1956).

I followed this sequence of events for Finnish Goldcrests, particularly in the spring of 1982. The wintering population was much reduced, and on long skiing trips in early March I could not find a single Goldcrest in the surroundings of my home and only a few farther away. But after mid-March, before the arrival of migrants, singing males had occupied the scattered optimal territories containing old, tall spruces, the same sites that had been inhabited regularly in previous years. These territories included two on my own property, where I had not seen Goldcrests for several weeks, which suggests that the males may move around over some distance in search of the best territories.

The above reasoning implies a higher fitness among resident than migrant Goldcrests, given that they have similar mortalities, and contradicts the theory of two genotypes with overall equal selective advantage. Another fact that proves difficult to reconcile with an entirely genetic theory is the relatively stable number of Goldcrests remaining in the country each autumn, in spite of the wide annual fluctuations in winter mortality. No such difficulties emerge, however, if we assume that the partial migration in this species is regulated by a phenotypic density-dependent mechanism.

Such a mechanism could result from a social hierarchy among the birds, the dominants (mainly adults) remaining resident and the subdominants (mainly juveniles) leaving. This mechanism, operating over shorter distances, is found in many sedentary species in which most of the adults stay within restricted areas throughout the year, while the juveniles disperse during their first autumn (e.g. *Parus montanus* and *P. cristatus:* Ekman 1979). The irregular movements of irruptive species can be explained on the same basis (e.g. *Aegithalos caudatus:* Hildén 1977). It seems unnecessary to postulate a different mechanism, based on genetic polymorphism, in the Goldcrest. Nor does it accord with the facts.

In all the above categories — sedentary species, irruptive birds and partial migrants — both sedentary and migratory behaviour are likely to enhance individual survival under certain circumstances. The advantages of remaining resident were discussed above; these are available to the dominants. The subdominants, on the other hand, would not be successful in competition with the dominants, so, for them, moving to other areas is the better strategy. In this way the population is dispersed over a much wider geographical area in winter, which reduces intraspecific competition and is advantageous to individuals of all ranks.

High numbers in autumn cause part of the population to emigrate through the medium of aggressive behaviour (e.g. Kalela 1954a, 1954b, Berndt & Henss 1967, Hildén 1977). This has been observed to occur in the Goldcrest also. During the period November to March, Hogstad (1982) noticed supplanting attacks and chasings within the flocks mainly in the first part of November. This could lead to establishment of a social dominance hierarchy. Thaler (1979) also mentions autumn fights among Goldcrests.

I must stress, however, that a density-dependent hypothesis should not be extended to cover all partial migrants. In other species, whether individuals stay or leave may be a more direct response to the prevailing food supply or temperature, with food shortage and low temperature being most effective in releasing emigration. For mainly migratory species, in which only a small fraction of the population regularly overwinters on the breeding grounds, two genetic types may provide the most appropriate explanation. Neither do I exclude the possibility that genetic differences exist in the disposition to migrate amongst individual Goldcrests — but the main mechanism nevertheless seems to operate phenotypically, through behavioural responses.

As a consequence of the strategy of partial migration, individual Goldcrests cannot be particularly well adapted to either the sedentary or the migratory way of life. For instance, migrants would certainly benefit by longer, more pointed wings, but this wing shape would not be suited to residents wintering in the north. Similarly, better cold-hardiness would be definitely of survival value for the residents, but probably not for the migrants. Hence, evolution produces adaptations which are compromises between the selective pressures.

Acknowledgements. I am most grateful to Jan Ekman, Peter Evans, Lars von Haartman and Olav Hogstad, who kindly read the first draft and made valuable suggestions for its improvement. The final manuscript benefitted greatly from their help. I also thank Jukka Haapala and Jörgen Palmgren for compiling data from the winter bird censuses and ringing statistics, Dieter Moritz for his data from Heligoland, and Pekka Vakkari for statistical treatment of the material. The work of the assistants was financed by a grant from Societas Scientiarum Fennica.

Selostus: **Hippiäisen talviekologia ja osittaismuutto Suomessa**

1. Kirjoitus perustuu talvilintulaskentoihin, Lågskärin lintuaseman rengastustilastoihin ja tekijän omiin laskentoihin Kirkkonummen vakioreitillä kuutena talvena. Kuolevuus on arvioitu suoraan peräkkäisten laskentojen yksilömääristä, mikä menetelmä soveltuu hippiäiseen erityisen hyvin.

2. Muuttava ja talvehtiva kannanosa ovat suunnilleen yhtä suuret. Poismuutto Keski- ja Etelä-Eurooppaan tapahtuu elokuun lopusta marraskuun alkuun, paluu maaliskuun lopusta toukokuun puoliväliin. Nuoret ovat selvänä enemmistönä muuttajissa, ja koiraita on keskimäärin 58 %. Lajin talvialue Suomessa on huomattavasti eteläisempi kuin pesimisalue (kuva 1), mikä osoittaa kannan kokonaisuudessaan muuttavan asuinalueen pohjoisosista. Täältä talvehtijoiden osuus kasvaa etelään päin (kuva 2).

3. Talvehtivat hippiäiset liittyvät 2—5 yksilön parviksi, jotka pysyttelevät muutaman hehtaarin reviireissä läpi talven. Kirkkonummen laskennoissa "hippiäisyksikön" keskikoko pysyi suunnilleen samana vuodesta toiseen (2.21—2.66) sekä marraskuusta helmikuuhun (2.42—2.54); maaliskuussa se vähän pieneni laulukauden ja parinmuodostuksen alettua. Marras-tammikuussa 64 % hippiäisyksiköistä oli tiaisten ja/tai puukiipijöiden seuraan liittyneinä, helmi-maaliskuussa 53 %.

4. Lähinnä kirjallisuustietojen pohjalla tarkastellaan hippiäisten talviekologiaa. Ravinto käsittää yksinomaan selkärangattomia, etenkin hämähäkkejä, ja päivittäinen ravinnontarve on tammikuussa 6—7 g, kovalla pakkasella huomattavasti enemmän. Tämän hankkimiseksi hippiäiset käyttävät lähes 100 % valoisasta ajasta ruokailuun, ja jo parin tunnin paasto voi olla kohtalokas. Lämmönhukan pienentämiseksi hippiäiset yöpyvät kyljitysten tiiviinä höyhenpallona.

5. Eteläisimmässä Suomessa kuolleisuus marras-joulukuussa on keskimäärin 25 % (taul. 1), tammi-helmikuussa 50 % (taul. 2). Kokonaiskuolleisuus talven aikana on keskimäärin n. 70 %, hyvin suurin vuosittaisin eroin; esim. leutona jaksona 1970-luvulla talvikuolleisuus Kirkkonummella oli vain 50 %. Talvialueen pohjoisosissa keskimääräinen kuolleisuus on n. 85 % ja koko talvikantamme osalta n. 75 %.

6. Talvikuolleisuus on hyvin merkitsevästi riippuvainen talven kylmyydestä (kuva 3). Sademäärä tammi-helmikuussa, lisättynä toisena riippumattomana muuttujana lämpötilaan, parantaa korrelaatiota jonkin verran. Alhaiset lämpötilat ja paksu lumi oksilla (kuva 4) vaikuttanevat pääasiassa epäsuorasti, lisäämällä ravinnontarvetta ja vaikeuttamalla ruokailua. Lopputalvesta kovat pakkaset eivät enää ole yhtä kohtalokkaita, koska päivä on jo huomattavasti pitempi.

7. Lågskärillä rengastettujen hippiäismäärien perusteella 11—45, keskimäärin 22.4 % syksyllä Suomesta lähteneistä yksilöistä palaa keväällä (taul. 4). Muuttajien talvikuolleisuus lienee siten samaa luokkaa kuin talvehtijoiden. Suuri kuolleisuus johtuu lajin alttiudesta säätuhoille ja vihollisille muuttomatkoilla.

8. Talvehtimaan jäävän kannanosan suuruus ei ole vaihdellut kovin paljon 26 vuoden aikana, huolimatta kannan tuhoutumisesta eräinä talvina lähes kokonaan (kuva 5). Talvehtijoiden määrän melko vähäinen riippuvuus edellisen talven kuolleisuudesta (kuva 6) johtuu osittain siitä, että tämä tekijä peittyy muuttotappioiden ja pesimätuloksen vaikutusten alle. Viime kädessä talvikannan otaksutaan määrytyvän tiheydestä riippuvan säätelymekanismin avulla: kun lintuja on paljon, suhteellisesti suurempi osa muuttaa, ja päinvastoin. Tätä tukee se, että muuttajien määrä näyttää vaihtelevan enemmän kuin talvehtijoiden (kuva 7). Säätelymekanismi perustunee sosiaaliseen hierarkiaan, joka syntyy lintujen aggressiivisen käyttäytymisen tuloksena: dominantit (lähinnä vanhoja) jäävät talvehtimaan ja subdominantit (lähinnä nuoria) lähtevät muuttamaan. Teoria ei kuitenkaan sulje pois mahdollisuutta perinnöllisistä eroista muuttovalmiudessa.

References

Alatalo, R. V. 1981: Interspecific competition in tits Parus spp. and the Goldcrest Regulus regulus: foraging shifts in multispecific flocks. — Oikos 37:335—344.

Alatalo, R. V. 1982: Effects of temperature on foraging behaviour of small forest birds wintering in northern Finland. — Ornis Fennica 59:1—12.

Askenmo, C., A. v. Brömssen, J. Ekman & C. Jansson 1977: Impact of some wintering birds on spider abundance in spruce. — Oikos 28:90—94.

van Balen, J. H. 1981: Population fluctuations of the Great Tit and feeding conditions in winter. — *In* H. Klomp & J. W. Woldendorp (eds.): The integrated study of bird populations, pp. 143—164. Amsterdam/Oxford/New York.

Bergroth, S. & H. Bruun 1939: Bidrag till kännedomen om vinterfågelbeståndet i Åbo-traktens skogar (Zusammenfassung: Zur Kenntnis des Wintervogelbestandes in den Wäldern der Gegend von Åbo). — Ornis Fennica 16:41—45.

Berndt, R. & M. Frantzen 1964: Vom Einfluss des strengen Winters 1962/63 auf den Brutbestand der Höhlenbrüter bei Braunschweig. — Ornithol. Mitt. 16: 126—130.

Berndt, R. & M. Henss 1967: Die Kohlmeise, Parus major, als Invasionsvogel. — Vogelwarte 24:17—37.

Berthold, P. 1964: Über den Fortpflanzungszyklus südwestdeutscher Stare (Sturnus vulgaris L.) und über bedingende Faktoren der Brutreife beim Star. — Vogelwarte 22:236—275.

Berthold, P. 1982: Genetic basis of bird migration. — Ornis Fennica 59, suppl. (in press).

Busse, P. & J. Machalska 1969: Instability of sex composition of migrating Goldcrests (in Polish with English summary). — Notatki Ornitol. 10:21—31.

Ekman, J. 1979: Coherence, composition and territories of winter social groups of the Willow Tit Parus montanus and the Crested Tit P. cristatus. — Ornis Scand. 10:56—68.

Ekman, J., G. Cederholm & C. Askenmo 1981: Spacing and survival in winter groups of Willow Tit Parus montanus and Crested Tit P. cristatus — a removal study. — J. Anim. Ecol. 50:1—9.

Evans, P. R. 1969: Ecological aspects of migration, and pre-migratory fat deposition in the Lesser Redpoll, Carduelis flammea cabaret. — Condor 71:316—330.

FRELIN, C. & B. CORNILLON 1974: La migration d'automne du Roitelet huppé (Regulus regulus) et du Roitelet triple bandeau (Regulus ignicapillus) au col de la Goléze. — Oiseau 44:291—307.

GIBB, J. 1954: Feeding ecology of tits, with notes on Treecreeper and Goldcrest. — Ibis 96:513—543.

GIBB, J. 1960: Populations of tits and Goldcrests and their food supply in pine plantations. — Ibis 102:163—208.

v. HAARTMAN, L. 1968: The evolution of resident versus migratory habit in birds. Some considerations. — Ornis Fennica 45:1—7.

v. HAARTMAN, L. 1969: The nesting habits of Finnish birds. I. Passeriformes. — Comm. Biol. Soc. Sci. Fennica 32:1—187.

v. HAARTMAN, L. 1971: Talgmespopulationen på Lemsjöholm (Summary: The population of the Great Tit at Lemsjöholm). — Lintumies 8:7—9.

v. HAARTMAN, L. 1978: Lintujen muuton evoluutio. — *In* O. HILDÉN, J. TIAINEN & R. VALJAKKA (eds): Muuttolinnut, pp. 238—253. Helsinki.

v. HAARTMAN, L., O. HILDÉN, P. LINKOLA, P. SUOMALAINEN & R. TENOVUO 1963—72: Pohjolan linnut värikuvin. — Helsinki.

HAFTORN, S. 1956: Contribution to the food biology of tits, especially about storing of surplus food. Part IV. — K. Norske Vidensk. Selsk. Skr. 4:1—54.

HAFTORN, S. 1976: Variation in body weight, wing length and tail length in the Great Tit Parus major. — Norw. J. Zool. 24: 241—271.

HAFTORN, S. 1978a: Energetics of incubation by the Goldcrest Regulus regulus in relation to ambient air temperatures and the geographical distribution of the species. — Ornis Scand. 9:22—30.

HAFTORN, S. 1978b: Cooperation between the male and female Goldcrest Regulus regulus when rearing overlapping double broods. — Ornis Scand. 9:124—129.

HAFTORN, S. 1982: Parental care of nestlings by the Goldcrest Regulus regulus. — Ornis Fennica 59:123—134.

HANSSEN, O. J. 1981: Migratory movements of Scandinavian Goldcrests Regulus regulus (L.). — Fauna Norv. Ser. C, Cinclus 4:1—8.

HILDÉN, O. 1965: Habitat selection in birds. A review. -- Ann. Zool. Fennici 2: 53—75.

HILDÉN, O. 1974: Finnish bird stations, their activities and aims. — Ornis Fennica 51: 10—35.

HILDÉN, O. 1977: Mass irruption of Long-tailed Tits Aegithalos caudatus in Northern Europe in 1973. — Ornis Fennica 54:47—65.

HILDÉN, O. 1978: Vaelluslinnut. — *In* O. HILDÉN, J. TIAINEN & R. VALJAKKA (eds.): Muuttolinnut, pp. 157—180. Helsinki.

HILDÉN, O. & K. MIKKOLA 1968: Katsaus Helsingin talvilinnustoon 1967/68 (Summary: A review of the winter bird fauna in the Helsinki district in 1967/68). — Lintumies 4:35—43.

HILDÉN, O. & J. KOSKIMIES 1969: Effects of the severe winter of 1965/66 upon winter bird fauna in Finland. — Ornis Fennica 46:22—31.

HOGSTAD, O. 1970: Movements of winter flocks of Goldcrests, Regulus regulus (L.). — Nytt Mag. Zool. 18:33—39.

HOGSTAD, O. 1982: Flock size, territoriality, food and mortality of the Goldcrest, Regulus regulus, during winter. — Unpubl. manuscript.

HOSKING, E. J. & C. W. NEWBERRY 1946: More birds of the day. — London.

JANSSON, C. & A. v. BRÖMSSEN 1981: Winter decline of spiders and insects in spruce Picea abies and its relation to predation by birds. — Holarct. Ecol. 4:82—93.

JANSSON, C., J. EKMAN & A. v. BRÖMSSEN 1981: Winter mortality and food supply in tits Parus spp. — Oikos 37:313—322.

KAAKINEN, K. & H. MIKKOLA 1972: Varpuspöllön syys- ja talviravinnosta Oulun seudulla ja Kainuussa 1962—1971. — Kainuun linnut 2:78—79.

KALELA, O. 1954a: Über den Revierbesitz bei Vögeln und Säugetieren als populationsökologischer Faktor. — Ann. Zool. Soc. 'Vanamo' 16(2):1—48.

KALELA, O. 1954b: Populationsökologische Gesichtspunkte zur Entstehung des Vogelzuges. — Ann. Zool. Soc. 'Vanamo' 16 (4):1—30.

KELLOMÄKI, E. 1977: Food of the Pygmy Owl Glaucidium passerinum in the breeding season. — Ornis Fennica 54:1—29.

KLOCKARS, B. 1936: Försök till kvantitativ undersökning av vinterfågelbeståndet (Zusammenfassung: Versuch einer quantitativen Untersuchung des Wintervogelbestandes). — Ornis Fennica 13:139—147.

KOSKIMIES, J. 1966: Kymmenen vuotta talvilintulaskentaa. — Suomen Luonto 16: 3—8.

KÄLLANDER, H. & J. KARLSSON 1981: Population fluctuations of some North European bird species in relation to winter temperatures. — Proc. Second Nordic Congr. Ornithol. 1979:111—117.

LACK, D. 1943—44: The problem of partial migration. — Brit. Birds 37:122—130, 143—150.

LACK, D. 1954: The natural regulation of animal numbers. — Oxford.

LACK, D. 1968: Bird migration and natural selection. — Oikos 19:1—9.

LAGERSTRÖM, M. 1979: Goldcrests Regulus regulus roosting in the snow. — Ornis Fennica 56:170—172.

LEHTONEN, L. 1948: Über die Wintervogelfauna von Gross-Helsinki. — Ornis Fennica 25:1—18.

LÖHRL, H. 1955: Schlafgewohnheiten der Baumläufer (Certhia brachydactyla, C. familiaris) und anderer Kleinvögel in kalten Winternächten. — Vogelwarte 18: 71—77.

MERIKALLIO, E. 1946: Über regionale Verbreitung und Anzahl der Landvögel in Süd- und Mittelfinnland, besonders in deren östlichen Teilen, im Lichte von quantitativen Untersuchungen. I. Allgemeiner Teil. — Ann. Zool. Soc. 'Vanamo' 12(1): 1—140.

MERIKALLIO, E. 1958: Finnish birds, their distribution and numbers. — Fauna Fennica 1—181.

MUNNE, P. 1973: Tiaisten (Parus spp.) runsausvaihteluista ja levinneisyydestä talvilintulaskentojen perusteella. — Manuscript, Dept. Zool., Univ. Helsinki.

NAKAMURA, T. 1962: Roosts and roosting behaviour of Long-tailed Tits (in Japanese with English summary). —
エナガの塒と就塒行動 17:109—122.

NÖHRING, R. 1959: Über das Verhalten von Regulus regulus während der Wintermonate. — J. Ornithol. 100:252—253.

PALMGREN, P. 1932: Zur Biologie von Regulus r. regulus (L.) und Parus atricapillus borealis Selys. Eine vergleichend-ökologische Untersuchung. — Acta Zool. Fennica 14:1—113.

PALMGREN, P. 1936: Über den Massenwechsel bei Regulus r. regulus (L.). — Ornis Fennica 13:153—159.

RIEHM, H. 1970: Ökologie und Verhalten der Schwanzmeise (Aegithalos caudatus L.). — Zool. Jb. Syst. Bd. 97:338—400.

SAMMALISTO, L. 1974: The status of the Finnish winter bird census. — Ornis Fennica 51:36—47.

SAMMALISTO, L. 1977a: Talvikauden laskennat 1976—1977 (Summary: The winter bird census in 1976—1977). — Ornis Fennica 54:127—132.

SAMMALISTO, L. 1977b: Twenty years of the Finnish winter bird census. — Pol. Ecol. Stud. 3(4):199—205.

SAMMALISTO, L. 1978: Suomen talvilinnut 1977—78 (Summary: Finnish winter birds in 1977—78). — Ornis Fennica 55:164—170.

SAMMALISTO, L. 1979: Talvilintulaskennat 1978—79 (Summary: The winter bird census in Finland in 1978—79). — Ornis Fennica 56:163—168.

SAMMALISTO, L. 1980: Talvilinnut laskennassa 1979—80 (Summary: Winter birds in the census 1979—80). — Ornis Fennica 57: 167—172.

SAMMALISTO, L. 1981: Talvilintujen laskenta Suomessa 1980—81 (Summary: Census of the Finnish winter birds in 1980—81). — Ornis Fennica 58:167—174.

SAUROLA, P. 1978: Arvokkaat hippiäislöydöt (Summary: Foreign recoveries of Goldcrests Regulus regulus ringed in Finland). — Lintumies 13:121—126.

SIIVONEN, L. 1956: The correlation between the fluctuations of Partridge and European hare populations and the climatic conditions of winters in South-West Finland during the last thirty years. — Pap. Game Res. 17:1—30.

SVENSSON, S. 1981: Populationsfluktuationer hos mesar Parus, nötväcka Sitta europaea och trädkrypare Certhia familiaris i södra Sverige (Summary: Population fluctuations in tits Parus, Nuthatch Sitta europaea, and Treecreeper Certhia familiaris in South Sweden). — Proc. Second Nordic Congr. Ornithol. 1979:9—18.

THALER, E. 1973: Zum Verhalten überwinternder Goldhänchen (Regulus r. regulus (L.)) in der Umgebung Innsbrucks (Nordtirol: Österreich). — Ber. nat.-med. Ver. Innsbruck 60:167—182.

THALER, E. 1979: Das Aktionssystem von Winter- und Sommergoldhähnchen (Regulus regulus, R. ignicapillus) und deren ethologische Differenzierung. — Bonner Zool. Monogr. 12:1—151.

THIELCKE, G. 1959: Über Schlafgewohnheiten des Gartenbaumläufers (Certhia brachydactyla) und des Waldbaumläufers (Certhia familiaris). — J. Ornithol. 100: 25—38.

WALLGREN, H. 1956: Zur biologie der Goldammer, Emberiza citrinella L. — Acta Soc. Fauna Flora Fennica 71(4):1—44.

ÖSTERLÖF, S. 1966: Kungsfågelns (Regulus regulus) flyttning (Summary: The migration of the Goldcrest (Regulus regulus)). — Vår Fågelvärld 25:49—56.

Received May 1982