Dynamics of Finnish Starling *Sturnus vulgaris* populations in recent decades

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The development of the Finnish Starling Sturnus vulgaris population was studied, using data from 20 local populations and from the national ringing scheme extending from the beginning of the 1960s to the end of the 1980s (data for 7-26 years from each population). According to local studies, the population size started to decrease in the late 1960s, and fell to about 20% by the early 1980s. In the timing of the decrease, there were clear regional and local differences. Clutch size varied significantly among local populations (range of the means of annual means in three populations: 4.7–5.3 eggs; data from 12-21 years), but there were much greater differences in the number of fledglings (range in the same populations: 2.33–3.99 fledglings, with 3.52–4.87 for four other populations; data from 5-21 years). These differences were caused by differences in foraging habitat. According to national ringing data, brood size at the age of ringing increased significantly (by 0.04 nestlings/year) during the period of 1968-89. The mean brood size decreased towards the north. This decline seems be due to large-scale abandoning of dairy farming in southern Finland. This has resulted in losses of good foraging habitats (pastures and leys) for the Starlings, and, as consequence, to reduced reproductive success in the whole south Finnish population. The continuous increase of brood size at the age of ringing reflects the disappearance of Starlings from poor breeding habitats and the strong decrease in northern Finland.

1. Introduction

The Starling *Sturnus vulgaris* exists at the northern margin of the species' European range in most of Finland (e.g., Feare 1984), but it has been a very successful species here during this century. At the beginning of the last century Starlings were still limited to the southernmost parts of the country, but from the end of the century their numbers have increased and the



range expanded northwards up untill the second half of this century (e.g., von Haartman et al. 1963–72, Solonen 1985a).

During the 1970s, however, a considerable decline in the Starling population was documented in various parts of Finland (for overviews, see Orell & Ojanen 1980a, Solonen 1985b). This decline has continued during the 1980s. Although in the 1960s Starling densities were highest in southern than in middle Finland (von Haartman et al. 1963-72), in 1984 there were no significant differences between southern and eastern Finland, and the density in southern and eastern parts of central Finland was only twice as high as that in western parts of central Finland (Piiroinen et al. 1985). Hence, it seems that regional density differences had diminished within one decade. Most recently, field work in 1986-89 for a new breeding-bird atlas demonstrates the disappearance of Starlings from northern and northeastern Finland when compared with data from the previous atlas of 1974-1979 (Lemmetyinen 1983, Zool. Mus., Helsinki, unpubl.).

The probable causes of the population crash inspired a lively discussion (von Haartman 1978a, Järvinen & Väisänen 1978, Korpimäki 1978, Ojanen et al. 1978, Saurola 1978, Laine 1985, Solonen 1985b, 1986), but no convincing explanations were presented for the causal relationships involved. Usually it has been suggested that winter mortality has increased because of population delimitation efforts in Belgium and France (Orell & Ojanen 1980a, Laine 1985), but already Korpimäki (1978) suggested that changes in Finnish agriculture may have negatively affected the breeding environment of the Starling.

Recently Tiainen et al. (1989) proposed that changes in farming explain the decrease of the Finnish Starling population because of having decreased its reproductive success. They were thus first to point out the functional relationship between changing farming practices and declining Starling populations. In 1986, breeding success was very low in specialised cultivation areas compared with that in mixed farming areas (Tiainen et al. 1989). According to agricultural statistics, at the end of the 1960s most Finnish farms still had dairy cattle and pastures, but thereafter agriculture has greatly specialized, resulting in a major reduction in the number and percentage of cattle farms, and a respective increase in pure cereal or root crop plant cultivation (Anon. 1971, Anon. 1986, see Tiainen et al. 1989). Moreover, the cattles are kept nowadays in restricted areas near the farms, instead of being allowed to graze on large pastures.

The purpose of this paper is to examine the dynamics of Finnish Starling populations from the beginning of the 1960s onwards. We first describe patterns of population size and breeding success on the basis of sample studies from various parts of the country, and from ringing statistics. We try to evaluate the suggestion cited that the population crash is due to the decreased reproduction rate caused by changing agriculture. Other possible explanations are also discussed.

2. Material and methods

Our basic data come from many nest-box studies on local populations conducted in various parts of Finland, which started in the 1960s or 1970s (Appendix). These studies include both southern, western and northern populations, but we have no representative sample from eastern Finland. The number of study years varied within a period of 28 years (1961–88) from 9 to 25. The study sites, as well as their regional grouping, are shown in Fig. 1.

The number of nestboxes in different study areas varied somewhat over the years, but there was always a considerable surplus of boxes available, and, as a consequence, the variation in population size was not affected by availability of boxes. In study areas 2, 4, 5 and 10 the number of boxes was lower in the first one or two years, but still not limiting for the new study populations establishing themselves. We had data on clutch size from populations 7, 9, 11 and 12 (11 and 12 combined, already in the original source), and on fledgling numbers from populations 1, 3, 6, 7, 8, 9, 11, 12, and 13 (11 and 12 combined).

The Finnish ringing statistics (Zoological Museum, Helsinki) formed another data base, from which we analysed the variation in the number of nestlings ringed in 1968–89 (cf. Saurola 1978). The number of young is not, however, fully comparable with the true number of fledglings in local studies. Especially in mar-

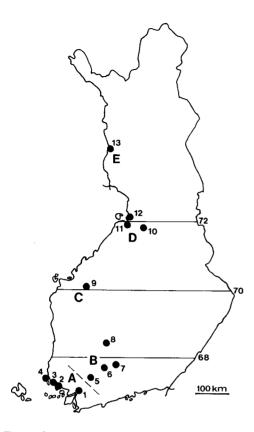


Fig. 1. Study sites and their regional grouping (for explanations for numbers and letters, see Appendix). Note that numbers 6, 9 and 12 include three, three and four actual study sites, respectively. North coordinates of Finnish national uniform grid (grid 27° E) are also shown.

ginal habitats nestling mortality may still be considerable after the age of ringing (1-2 weeks,with the nestling period lasting for 21 days; Tiainen et al. 1989).

3. Results

3.1. Population decline

The present data show that Finnish Starlings have decreased throughout the 1970s, i.e. that the decline had started in the late 1960s or early 1970s (Fig. 2). Many large local populations have now almost or completely disappeared. According to the number of nests per ten nestboxes checked

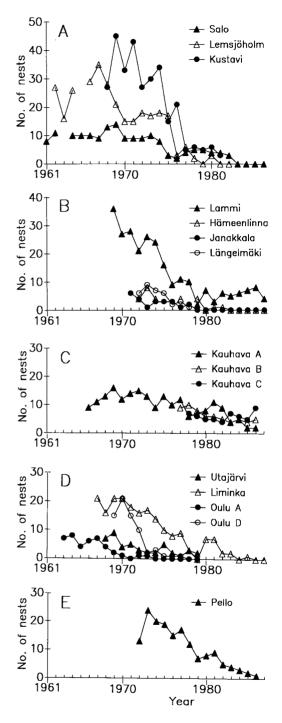


Fig. 2. Variation in number of nests in study populations.

annually in all study areas, the Finnish Starling population declined to a fifth of the 1960s in ten

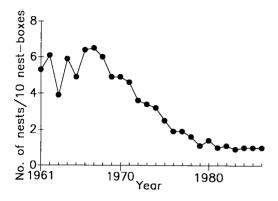


Fig. 3. Number of nestboxes occupied by Starlings per 10 boxes available in all study areas pooled.

years (Fig. 3). In the 1980s the declining trend seems to have levelled off.

There were large regional differences in the magnitude of the decline (Fig. 4). The decline has been most severe in Häme and N Ostrobothnia, where population size dropped to about one sixth or seventh in ten years, while the decline was rather small in S Ostrobothnia. The increase in SW Finland in the early 1970s is an artefact, being caused by the initiation of studies in the large populations of Kustavi and Naantali. In Häme, only one population (Lammi) was studied during the first years, and later it had many more pairs than the others (see Fig. 2). Hence here the initial decline was produced by a single study population, and need not be representative for the whole region. The decline has been severe also in the single population of N Finland, which dropped to a tenth in ten years (Fig. 2).

Evidently the decrease began at somewhat different times in different regions and local populations (Figs. 2 and 4). The decline in SW Finland was the latest, starting sharply in 1975. However, there was a strong drop to about a half in the Lemsjöholm population by the late 1960s, which was followed by a new drop in 1976. In S Ostrobothnia the decline started gradually in the first half of the 1970s. In Häme there was a sharp drop in 1975, but the decline had started in the first years of the 1970s, probably even before. In N Ostrobothnia all the populations were already declining when the studies were started, and the regional decline started in the mid or late 1960s.

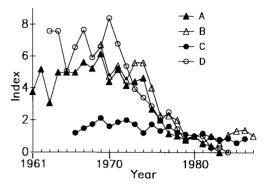


Fig. 4. Dynamics of regional Starling populations. Population in 1980 set at 1.

The Utajärvi population was the only exception; it did not decline before the 1970s. The probable time of the begin of the decrease can be pointed out only in the data of Lemsjöholm (late 1960s), Salo (mid-1970s), Kauhava (late 1970s) and Liminka (early 1970s; Fig. 2).

In some of the study areas, the population decline can be related to habitat changes (cf. Appendix). In Salo and Lemsjöholm, the declines follow the gradual overgrowth of abandoned seashore meadow pastures by tall grasses and bushes. In Lammi and Liminka, the sharp decline in the mid-1970s coincides with disappearance of leys, meadows and pastures from the close neighbourhood of the study area. All these habitat changes are due to cessation of dairy cattle breeding.

The national ringing statistics also reveal a declining trend from the peak in 1974 to the late 1970s (Fig. 5). The number of nestlings ringed is clearly higher in 1980-84 than in the late 1970s. However, these patterns are not unbiased. Ringing statistics tell us, besides about fluctuations in the number of breeding pairs, also about variations in nesting success and in ringing activity (e.g., Saurola 1978). General ringing activity in Finland increased throughout the 1960s and 1970s, which probably has flattened the pattern shown in Fig. 5 at its beginning. Furthermore, the discussion in 1978 on the Starling crash inspired new ringing activity, and some new large nest-box colonies were founded. Despite the increased interest by ringers, a new drop in the number of nestlings ringed followed in 1985 (Fig. 5).

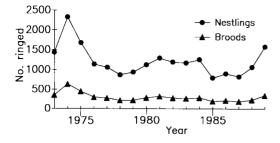


Fig. 5. Number of Starling nestlings and broods ringed in Finland in 1973-88.

3.2. Reproduction

We have clutch-size data from Lammi, Kauhava (all three populations pooled), and Liminka and Oulu (which are also pooled). Clutch size was larger in the Liminka-Oulu and Kauhava populations, and smaller in the Lammi population, than the Finnish average (5.0, n = 192; von Haartman 1969;P < 0.001 for all, t-test; Table 1). There were no significant temporal trends in clutch size in Lammi or Liminka-Oulu, but in Kauhava it increased slightly (regression coefficient for annual change = 0.026, t = 2.12, P = 0.047, df = 19). Yearly variations in mean clutch size were not synchronised between areas (Kauhava and Liminka–Oulu: r = -0.080, P > 0.10, df = 10; Kauhava and Lammi: r = 0.362, P > 0.10, df = 9; Liminka–Oulu and Lammi: r = 0.015, P > 0.10, df = 3). In addition, coefficients of variation did not differ between the areas, either (Ftests).

There were large differences in production of young between some of the study populations

(one-way ANOVA, F = 13.64, P < 0.001, df = 6, 86; Table 2). The production per nesting attempt was highest in Pello, and lowest in Liminka and, especially, in Lammi. Yearly variation in number of fledglings varied significantly more in Lammi than in any other area (P < 0.01 or 0.001, F-test for coefficients of variation; CV was also smaller in Längelmäki than in Janakkala; P < 0.05; other differences were not found). The variations were not parallel between areas; only one nearly significant correlation was found (between Janakkala and Liminka; r = 0.664, P = 0.05, df = 7). No significant temporal trends could be detected.

The annual average size of Starling broods ringed in whole Finland varied between 3.56 and 4.63 with a significantly increasing trend in 1968– 89 (Fig. 6). The brood size was significantly smaller during 1968–77 (mean \pm SD = 3.8 \pm 0.17) than in 1978–89 (4.3 \pm 0.23; t = 4.94, P = 0.0001). Whether there were differences in the brood size at the ringing age between geographical zones was tested using the ringing data of 1986–89 (Table 3). Northern populations reproduced less than the southern ones (Kruskal-Wallis test, H = 3.37, P = 0.018, df = 3, 971; with pooling of the two northernmost zones, H = 4.56, P = 0.011).

4. Discussion

Besides depending on circumstances in the breeding grounds, the population size of Finnish Starlings may also depend on the conditions in wintering areas and along migration routes. Thus the decline of the Finnish Starling population may be caused by deterioration of habitats in breeding, post-breeding (including migration) or

Table 1. Overall mean clutch size and minimum and maximum annual means in local Starling populations (for Kauhava, all three study populations pooled, Liminka and the three populations of Oulu combined). N indicates total number of clutches. For minima and maxima, number of nests in parentheses. In Lammi actual annual maximum is 6, but that year there was only one nest. In Kauhava maximum occurred also in another year, and in Liminka-Oulu in four other years.

Population	Mean	SD	CV	N	Minimum	Maximum	Years
Lammi	4.7	0.66	0.14	60	4.0 (2)	5.0 (7)	12
Kauhava	5.3	1.05	0.20	291	4.9 (13)	6.0 (8)	21
Liminka-Oulu	5.3	0.87	0.17	299	4.6 (21)	5.4 (52)	13

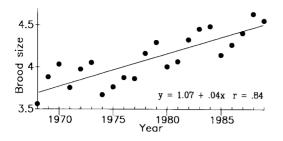


Fig. 6. Mean Starling brood size at ringing age in Finland in 1968-89. In regression, 1900 is subtracted from years.

wintering areas, resulting in decreasing production of young or in increasing mortality. Other factors with similar effects may also be involved.

Tiainen et al. (1989) suggested that the population crash has been due to a decreased reproduction rate caused by agricultural change in which the pasture and ley area has given way to cereal and root crop fields. We found the following evidence in support of this hypothesis:

- The population decline occurred at different times in different study areas. This suggests that factors affecting local populations were more important than factors affecting the whole Finnish population (e.g. changes in wintering grounds). Habitat change due to intensification of agriculture is a sudden event on the farm level, but proceeds slowly in larger areas, which accordingly may be in different stages of change.
- The Starling decline was associated with cessation of dairy farming. Where the pastures were left to develop naturally, the decline

started some years after the pasture abandonment. On the other hand, where the pastures were converted into arable fields, the decline occurred more or less immediately.

- 3) Fledgling production differed among study areas. These differences were excessive compared with clutch-size differences in Kauhava, Liminka and Lammi. Although, based on ringing data, the average brood size in the whole country increased, the number of fledglings in local study populations did not increase. This suggests that resources in the nestling period form an important factor affecting local populations. The lack of parallel temporal variation in fledgling number among populations suggests that no common factors, like weather, affected breeding success.
- 4) In southern Finland (SW Finland, Häme, and S Ostrobothnia), only poorly reproducing populations declined, while in northern Finland (N Ostrobothnia and N Finland; see Appendix) both well and poorly reproducing populations declined. This suggests that although the reproductive success of northern populations was insufficient to balance mortality, populations were supported by immigrants from southern populations.

On the basis of these findings we suggest that both local and regional processes have been important in the dynamics of local Starling populations. The whole south Finnish population has become less productive because of habitat changes. During the process of habitat deteriora-

Population	Mean	SD	CV	Minimum	Maximum	Years
Salo	4.03	0.685	0.17	2.7 (3)	5.3 (4)	21
Längelmäki	3.52	0.306	0.09	3.1 (7)	3.8 (6,9)	5
Janakkala	4.01	0.844	0.21	2.0 (2)	5.3 (12)	12
Lammi	2.33	1.006	0.43	0.0 (2)	5.0 (3)	14
Kauhava	3.99	0.648	0.16	2.8 (17)	5.2 (10)	20
Liminka	3.30	0.613	0.19	2.6 (7)	4.7 (3)	14
Pello	4.87	0.634	0.13	4.0 3)	5.8 (4)	7

Table 2. Mean, and minimum and maximum of annual means of fledgling numbers in ten of the Starling populations (the three populations in Kauhava pooled), calculated for all nests where laying was completed. For minima and maxima, number of nests in the particular year in parenthesis.

tion there have been fewer and fewer effectively producing local populations in southern Finland. At the same time there have been fewer immigrants to north Finnish populations. In the following we discuss various points in greater detail.

4.1. Changes in breeding habitats

Breeding habitats of Starlings have changed considerably during recent decades in Finland. Along with the modernization and intensification of agriculture, the amount of meadows, pastures, and leys has drastically decreased in southern Finland (Solonen 1985b, Tiainen et al. 1985, 1989). Starlings prefer to forage in such shortgrass habitats (Dunnet 1955, Tinbergen 1981).

Besides reducing breeding success, changes in the agricultural environment may be followed by local disappearance of Starlings due to decreasing suitability of habitats. With the decreasing number of settlers, the poorest breeding habitats were first left unoccupied both in Lammi and Kustavi (T. Solonen, P. Saurola & J. Tiainen, unpubl., R. Lemmetyinen & R. Tenovuo, pers. comm.). Although the Starling has disappeared from many areas earlier occupied by dense populations, a sparse population still inhabits some though not all parts of the SW-archipelagoes (L. von Haartman, pers. comm., R. Lemmetyinen & R. Tenovuo, pers. comm.).

Such diminishing regional density differences (based on data in von Haartman et al. 1963–72, and Piiroinen et al. 1985) can be understood on the basis of habitat changes, which have been most drastic in southernmost Finland. Large-scale habitat changes have not taken place in eastern parts of central Finland at all. In western parts of

Table 3. Zonal variation in mean brood size of Finnish Starlings at ringing age in 1986-89. Zonation based on national uniform grid coordinates (see Fig. 1).

Zone	Mean	Variance	Ν
66–68	4.54	1.269	660
68–70	4.38	1.803	162
70–72	4.24	1.590	146
72	3.57	2.286	7
All	4.46	1.426	975

central Finland, habitats have changed, but not to as great a degree as in the south (e.g., Ylimaunu & Siira 1985). Accordingly, in more traditional farmland habitats, the density is similar to that of other parts of southern and central Finland.

4.2. Breeding success in different habitats

Breeding success of the Starling varies among colonies and localities (Tenovuo & Lemmetvinen 1970, Gibo et al. 1976, Korpimäki 1978, Ojanen et al. 1979, Feare 1984). It seems probable that spatial variation could be due to habitat quality. Tiainen et al. (1989) studied the breeding success of Starlings in various agricultural environments in Lammi in 1986, and found pronounced differences. In the most traditional mixed-farming areas, where besides cereal fields, there were also pastures and leys, 70-90% of the hatched Starling eggs produced fledglings, whereas in areas of cereal and sugar beet monocultures the corresponding proportion was only 20-30%. The differences were particularly due to nestling mortality in nestboxes fouled with wet faeces, a phenomenon probably connected with the quality of the nestling food. Kluyver (1933) and Tinbergen (1981) found that faeces became wet when nestlings were fed with tipulid larvae instead of the preferred noctuid larvae. O'Connor & Shrubb (1986) found also that nestling mortality rate was higher in arable land than in grassland.

The brood size was low until 1977, but thereafter it has been increasing (Fig. 6). This coincides with the sharp decline in the whole Finnish population. As the clutch and brood sizes of the Starling vary between different habitats, this pattern of increase is most probably a result of Starlings' disappearance from unproductive habitats, or the fact that ringing activities have ceased there. Another possibility would be that the remaining breeding population has responded to reduced density by increasing its reproductive effort. This explanation was suggested by Wallin et al. (1983) for Kestrels Falco tinnunculus in Sweden which have shown reduced adult survival and increased brood size during the last four decades. We can rule out this possibility because in own local populations studied brood size did not increase at the same time as the population size decreased. On the other hand, breeding and foraging habitats of Starlings have changed, so that fledgling production has probably decreased considerably in many localities and areas (Figs. 2 and 4). At present, only a small proportion of farmland seems to make up productive breeding areas in southern Finland.

From the preceding, it seems evident that changes in agricultural habitats have had adverse effects on the reproductive success of Finnish Starlings, though these effects are not directly demonstrable by means of the present data.

4.3. Habitat changes in wintering grounds

Finnish Starlings overwinter in The Netherlands, Belgium, northern France and England (Saurola 1978, Fliege 1984). Habitats have considerably changed also along the migration routes and in the wintering grounds. As a result of intensification of agriculture in western and central Europe, birds' foraging conditions on fields have deteriorated in many ways (Bezzel 1982, 1985, de Molenaar 1983, Steen 1983, O'Connor & Shrubb 1986, Potts 1986). However, the intensification of agriculture there seems not to have resulted in such abrupt habitat changes that could explain the recent deep crash of the Finnish breeding population (Feare 1984).

4.4. Adult mortality

Short-term population crashes can often be explained by some exceptional winters, but a longterm decline must be due to more permanent factors, of which increased adult mortality is one. In the 1970s, the ring-recovery data did not indicate that the annual mortality of Finnish Starlings had increased from that of earlier decades (Saurola 1978). However, it seemed possible that production of young was not sufficient to compensate for mortality, which might explain the population decline. In a third of the Starling recoveries, where the cause of death was known, the birds were killed by man (Saurola 1978). However, most of even those Starlings which man has killed are probably not found, or at least the rings recovered are not returned. This makes estimation of changes in adult mortality more uncertain.

In France and Belgium, because the birds considerably damage various fruit crops, massive efforts to limit population size have been made by means of blowing up and poisoning enormous flocks of Starlings (Tahon 1980, Feare 1984). The long-term population decline of Finnish Starlings could be due to such continuous mass destruction of wintering flocks. Tiainen et al. (1989), however, challenged the possibility that winter mortality of Finnish Starlings had greatly increased because of such population limitation efforts. In France, where these efforts were started only after the crash of the Finnish breeding population, only about 2% of the winter population was killed (Douville et al. undated). In Belgium destruction efforts were carried out before migrants arrived (Stevens 1982, Clobert & Leruth 1983).

Starlings are sensitive to many agricultural pesticides (Schafer 1972, Schafer et al. 1983). Their use has dramatically increased both in breeding and wintering grounds since the early 1950s (for summaries, see Solonen 1985b, O'Connor & Shrubb 1986), which might have increased Starling mortality. However, there was not any dramatic increase in the use of pesticides in the 1970s and 1980s, when Starlings declined in Finland (Markkula 1990). Moreover, the breeding populations have not declined in west-ern Europe despite greater amounts of pesticides used there in agriculture (Feare 1984).

Probably we get only a very few ring-recoveries of the birds killed in these ways. Thus, the estimates of mortality and causes of death based on ringing statistics may be somewhat misleading. With the present data we are not able to exclude the possibility of increased adult mortality.

4.5. Conclusion

The Finnish population of the Starling did not crash uprubtly in mid-1970s, as has often been interpreted, but the decline started at different times in different regions and in different places within regions. Our results support the hypothesis put forward by Tiainen et al. (1989). They suggested that the decline is due to lowered reproductive output of the whole Finnish population, which results from lowered reproductive success in many localities. This in turn is due to agricultural habitat changes which are the result of large-scale displacement of animal husbandry with specialised cereal and root crop cultivation. No data are available which would support explanations according to which the population decrease would be due to increased winter mortality.

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Selostus: Kottaraisen kannankehitys Suomessa viime vuosikymmeninä

Kottaraisen kannankehitystä 1960-80-luvuilla tutkittiin 20 paikallispopulaatiosta saadun aineiston (7-26 vuotta; Kuva 1 ja Appendix) sekä rengastusaineiston perusteella. Aiemmin on esitetty, että maamme kottaraiskanta olisi romahtanut jyrkästi lyhyessä ajassa heti 1970luvun puolivälin jälkeen. Väheneminen on kuitenkin alkanut eri aikoihin eri populaatioissa (Kuva 2) ja eri alueilla (Kuva 4). Kanta oli vähentynyt suunnilleen viidennekseen 1980luvulle tultaessa siitä, mitä se oli ollut 1960luvun lopulla (Kuvat 3 ja 4). Kuvan 4 mukaan väheneminen on ollut Etelä-Pohjanmaalla vähäisempää kuin muilla alueilla; sitä onko kyseessä yleisempi eteläpohjalainen ilmiö vai johtuuko tämä tutkittujen populaatioiden tavallista suotuisammista ympäristöistä, ei aineistomme perusteella voi ratkaista.

Myös rengastusaineisto osoittaa kannan vähentyneen (Kuva 5), mutta aineiston tulkinta ei ole ongelmatonta, koska rengastusmäärät riippuvat rengastajien määrästä, joka kasvoi koko 1960-luvun ajan ja vielä 1970-luvun alkupuolella, ja aktiivisuudesta, joka todistettavasti lisääntyi 1970-luvun lopulla kottaraisen kohdalla erityisesti.

Kottaraisen lisääntymistulos vaihteli suuresti tutkittujen paikallispopulaatioiden välillä. Erot keskimää iisessä pesyekoossa olivat vähäisempiä kuin poikuekoossa (Taulukot 1 ja 2). Erityisesti Lammin biologisen aseman populaatio erottuu heikkotuottoisena; siellä myös poikastuoton (lentopoikasia/pesä) vuosittainen vaihtelu on selvästi suurempaa kuin muissa tutkituissa populaatioissa (Taulukko 2, sarake CV).

Tulokset tukevat Tiaisen ym. (1989) esittämää ajatusta, jonka mukaan kottaraisen väheneminen johtuu pesimäaikaisen elinympäristön muuttumisesta lajille epäsuotuisaksi. Paikallisten populaatioiden pesimistuloserot ja vähenemisen ajoittuminen näyttävät selittyvän elinympäristön laatueroilla ja muutoksilla (keskeistä on laitumien häviäminen karjatalouden väistyessä).

Rengastusaineiston perusteella kottaraisen keskimääräinen poikuekoko (rengastusikäisiä poikasia/pesä) on kasvanut roimasti 22 viime vuoden aikana (Kuva 6). Tulos voidaan tulkita seuraavasti: Poikuekoko oli tarkastelujakson alussa niin pieni, että se ei ylläpitänyt kantaa. Tästä oli seurauksena pesimäkannan väheneminen ja häviäminen huonotuottoisista ympäristöistä. Tästä on puolestaan ollut seurauksena keskimääräisen poikuekoon kasvu. Jossain vaiheessa poikastuotto tullee jälleen olemaan riittävä ylläpitämään tietyn kokoista pesimäkantaa.

Sanottu selittää senkin, miksi kottarainen on vähentynyt myös Pohjois- ja Keski-Suomessa, missä karjatalouden harjoittaminen ei ole vähentynyt. Taulukko 3 osoittaa, että kottaraisen lentopoikasten määrä vähenee etelästä pohjoiseen. Tämä tukee ajatusta, että pohjoiset populaatiot eivät kykenisi omalla poikastuotollaan ylläpitämään itseään, vaan olisivat riippuvaisia eteläisistä populaatioista saatavasta täydennyksestä.

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Appendix. Study sites and years, number of nestboxes and sources of data

A — SW coastal Finland and archipelago (SW Finland)

- (1) Salo 1961–87; 12–15 boxes in a manor house park (1 ha) surrounded by large arable fields (cattle breeding ceased in 1959). Starlings foraged on park lawns and the abandoned pastures over a distance of 0.5 km on sea bay shore meadows (until the end of the 1970s, when they were overgrown by tall grasses and bushes) (von Knorring 1978, and pers. comm.).
- (2) Naantali 1969–1972 and 1979; 50 boxes in 1969, 95–100 boxes in 1970–1972, 22 boxes checked in 1979; pastures and sea shore meadows in the immediate vicinity of most of the boxes (Peussa 1972, R. Lemmetyinen & R. Tenovuo, pers. comm.).
- (3) Lemsjöholm 1962–87; originally 47 boxes, at the end of the 1970s 29 boxes, later fewer, around arable fields. Sea shore meadow pastures until 1957 when cattle keeping ceased, except for a single meadow where cattle pastured until the early 1970s (von Haartman 1973, 1978a, 1978b, and pers. comm.).
- (4) Kustavi 1968–81, 42 boxes in 1968, 67 boxes in 1969, 76–83 boxes in 1970–1974 and 1976, 50–53 boxes in 1975 and 1979, 23–33 boxes in 1977, 1978, 1980, and 1981 on 15 islands in three different archipelagic zones. Starlings foraged on shore meadows and fucus wracks (Lemmetyinen & Tenovuo 1970, and pers. comm.).

B — Häme

- (5) Tammela 1980–87; 27 boxes (7 in 1980) in two farm yards in the immediate neighbourhood of pastures (P. Andsten, pers. comm.).
- (6) Janakkala, three study plots in similar habitats (P. Andsten, pers. comm.).
 - (i) Janakkala A 1971–87; 7–9 boxes in a manor house yard. Nearest pastures more than 500 m away.
 - (ii) Janakkala B 1982–87; 16 boxes (6 in 1982) at forest edge of a field, used also as a pasture.

(iii) Hämeenlinna 1972-86, 8-11 boxes in forest patches in cereal fields, beef cattle pastured in the neighbourhood.

- (7) Lammi 1969–87; 120 boxes in the park of the biological station and in the nearby forest bordered by arable fields. Nearest pastures at a distance of 300–600 m, grass leys in the immediate neighbourhood until the mid-1970s (P. Saurola, T. Solonen & J. Tiainen, this study).
- (8) Längelmäki 1978–87; 16 boxes in a farm yard. Pastures in the immediate neighbourhood (P. Andsten, unpubl.).
- C S. Ostrobothnia
- (9) Three study plots in similar habitats (Korpimäki 1978, this study).
 - (i) Kauhava A 1966-87; 11-24 boxes in a farm yard, where cattle farming ceased in 1981.
 - (ii) Kauhava B 1977-87; 13-16 boxes in a farm yard with pastures in the vicinity.
 - (iii) Kauhava C 1978-87; 10-12 boxes in a farm yard with surrounding pastures.
- D N. Ostrobothnia
- (10) Utajärvi 1968–79; 10–12 boxes in an area of fields and pastures, no detailed data on habitat development (Ojanen et al. 1978, Orell & Ojanen 1980a, 1980b).
- (11) Liminka 1967–87; 30 boxes in an area of fields and meadows, pastures in the immediate neighbourhood up to 1976 (4 ha) and 1977 (1 ha), since 1977 the nearest pastures at a distance of 0.8 and 1.0 km (Hirvelä 1977, and pers. comm., Ojanen et al. 1978, Orell & Ojanen 1980a, 1980b).
- (12) Four study plots which were combined in the original source (Ojanen et al. 1978, Orell & Ojanen 1980a, 1980b). In two kinds of habitats as follows:

(i) Oulu A 1963–79; originally 12, in last years 6 boxes in gardens of an old suburb (including small fields) near the centre of the town.

(ii) Oulu B 1963-79; originally 50, in last years 15 boxes in a large park in the town centre.

(iii) Oulu C 1963–67 and 1977–79; 15 boxes in the 1960s, 7 in the 1970s in farmland consisting of small fields surrounded by forest, no obvious habitat changes during the period.

- (iv) Oulu D 1971-75; 10-12 boxes in a farm and a small woodlot surrounded by fields (Alatalo 1975).
- E ---- N. Finland
- (13) Pello 1972–87; about 100 boxes originally in the neighbourhood of dairy cattle farms numbering ca. 10 in 1970, 3–4 in 1980, and none in 1987 — instead there is now a horse pasture which is used by the Starlings for foraging (Halonen 1979, and pers. comm.).