How consistent are different estimates of long-term trends of Finnish bird populations?

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Estimates of the frequency of long-term increases in the Finnish bird fauna range from about one-third to about two-thirds, while the frequency of decreasing trends has been reported as between nil and about one-quarter. This apparent discrepancy is examined here on the basis of a simple model describing long-term population changes. The main result is that the number of increasing species can be expected to be disproportionately high in species sets that include only the most abundant species. Unexpectedly, despite the seemingly large variation among different estimates, they are largely consistent with each other. The only exception is that Järvinen & Väisänen (1977) reported the frequency of increasing species among the most abundant species (those that had more than 1.28 mill. pairs in either the 1940s or the 1970s) as about 40 %, which is significantly lower than expected. Methodological aspects and some misinterpretations in the literature are examined in some detail.

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Introduction

Several authors have tried to assess long-term trends in Finnish bird populations. The first, and still the most extensive, estimate is that by von Haartman (1973), who concluded that in recent times 34 % of the bird species breeding in Finland have enlarged their area and/or become more numerous, while 25 % have receded. The other species have either remained stable or fluctuated. In a later attempt, based on quantitative data on land birds, Järvinen & Väisänen (1977) estimated that, of the 86 most abundant land birds in the 1940s, 43 % have increased and 29 % have decreased. Further data were reported by the same authors in a later paper (Järvinen & Väisänen 1978a) and in their two data sets the proportion of species that had increased in recent decades was between 60 % and 70 %.

Especially the higher figures have been received with scepticism by Hildén (1981) and others, who claim that the proportion of increasing species is lower than reported by Järvinen and Väisänen. The following quotation (Hildén 1981:159) shows that the scepticism was merged with exaggeration: ". . . such a strong increase of *the entire bird fauna,* including species from a variety of different habitats, appears puzzling" (emphasis mine). The exaggeration is here two-fold. No estimate has suggested that the proportion of increasing species is anywhere close to 100 %, nor has any of the higher percentages reported been based on more than 26—56 species out of more than 230. It will be shown here that the latter fact has some surprising methodological consequences, which are likely to be relevant in other studies of long-term trends of bird populations. I will also compare the estimates given above using a simple model. The unexpected result obtained here is that, even if the proportion of increases in the whole bird fauna is no more than 34 %, one will easily find that 60—70 % of the currently most abundant species have recently increased.

The model

I constructed a model based on the following assumptions:

(i) The bird fauna (217 species) studied has the quantitative structure reported by Merikallio (1958) for Finland. In a very few cases I had to make a guess of the exact pair number on the basis of Merikallio's verbal account, but this concerns only rare species not discussed here. Merikallio's errors in estimating the population size of single species have little effect on the results reported below. The only crucial assumption here is that the species-abundance distribution is similar to that reported by Merikallio (1958).

(ii) The 217 species were assigned to abundance classes with limits given by even powers of 2, starting from $2^0=1$, and continuing to 2^2, 2^4, etc.

(iii) I assumed that the bird fauna then experiences quantitative changes along the lines envisaged by von Haartman (1973). So 34 % of the species in each abundance class increase, 25 % of them decrease, and the rest (41 %) are stable. The increases and decreases are of two kinds: species shift to the nearest or second nearest abundance class, equally probably. This assumption is arbitrary, and I do not suggest that bird population changes in nature are so easily classified as the model would imply. The assumption of dramatic increases among the most abundant species seems especially unlikely, but this assumption is used here only as a null model. The basic question asked is, "what are the expected frequencies of increasing and decreasing species in different samples from the avifauna, assuming that the probabilities of increase and decrease are those reported by von Haartman (1973)?"

(iv) I assumed that no extinctions will take place (Järvinen & Ulfstrand 1980), but this assumption is not crucial in this paper.

Table 1 gives the present numbers of species in the different abundance classes according to the above assumptions. A small sample of species that are now abundant includes a disproportionate number of species that have recently increased. On the other hand, a sample of species that are rare at present can be expected to include unusually many species that have recently decreased.

Judging the consistency of different estimates

There are three sets of data that can be compared with the model derived from von Haartman's (1973) percentages of increasing and decreasing species. I calculated the expected number of increasing species in samples that include all species that exceeded a certain threshold abundance either before or after the population changes. Such data were used by Järvinen & Väisänen (1978a) for two different areas (Åland and Häme). Combining the information from Tables 1 and 3 in Järvinen & Väisänen (1977) makes it possible to calculate the proportion of increasing species in their sample also, down to species that had at least 20 000 breeding pairs in Finland in either the 1940s or the 1970s.

Table 1 was used in the calculations. For example, if the threshold abundance is 2^{16} pairs, one must include (a) all species that now exceed this limit, (b) those 3.0 species that have decreased by one abundance class but still exceed the limit of 2^{14} pairs, and (c) those 3.0 species that have decreased by two abundance classes but still exceed the limit of 2^{12} pairs. The proportion of increases in this collection of species can be calculated easily. I then calculated confidence limits for the expected value using the binomial distribution. Fig. 1 gives the expected percentage with 2 standard deviations for all values between 10 and 100 species in the sample. Sampling here is not random but starts from the most abundant species. Moreover, successive samples are not independent, for the same reason.

Table 1. The number of species expected in different abundance classes according to the model described in the text. Five trends are possible: decreased by two abundance classes (— —), by one class (—), stable (0), increased by one class (+), or by two classes (++).

Present abundance	Recent trend					Total spp. now (before)
	--	—	0	+	++	
2^0—2^2	3.1	1.9	1.7	..	..	6.7 (4)
2^2—2^4	1.9	1.2	4.5	0.7	..	8.3 (11)
2^4—2^6	3.2	1.9	4.1	1.9	0.7	11.8 (10)
2^6—2^8	4.8	3.2	6.2	1.7	1.9	17.6 (15)
2^8—2^{10}	4.1	4.8	10.7	2.6	1.7	23.9 (25)
2^{10}—2^{12}	3.2	4.1	15.6	4.4	2.6	29.9 (38)
2^{12}—2^{14}	3.0	3.2	13.5	6.5	4.4	30.6 (33)
2^{14}—2^{16}	3.2	3.0	10.7	5.6	6.5	29.0 (26)
2^{16}—2^{18}	0.2	3.2	9.9	4.4	5.6	23.3 (24)
2^{18}—2^{20}	0.3	0.2	10.7	4.1	4.4	19.7 (26)
2^{20}—2^{22}	..	0.3	0.9	4.4	4.1	9.7 (2)
2^{22} or more	..	..	0.9	0.6	5.0	6.5 (2)
Total	25 %		41 %	34 %		217 (217)

Let us now look at the three data sets.

1. Järvinen & Väisänen (1978a) compared censuses made on Åland in 1926—27 and in 1975, and included all species that were observed at least 10 times in either of the samples. Of the 40 abundant species that could be studied, 27, or 68 %, had increased since the 1920s, which is slightly more than expected from the model but well within the limits set by 2 S.D. (Fig. 1). The percentage of decreases (20 %) was also slightly greater than expected, but the difference was not statistically significant. I conclude that these data are consistent with von Haartman's overall estimates for the entire bird fauna. It has already been pointed out by Haila et al. (1980) that long-term trends of single species in this data set and in a data set collected by von Haartman (1973, 1978) from SW Finland are very similar.

2. Järvinen & Väisänen (1978a) compared censuses made in Häme in 1936 and in 1977, and included all species that were observed at least 10 times in either of the samples. Of the 26 abundant species that could be studied, 16, or 62 %, had increased since 1936, which is slightly less than expected from the model but well within the limits set by 2 S.D. (Fig. 1). No species decreased in this sample, which is less than expected (10.0 % or 2.6 species), but not significantly so. Järvinen & Väisänen (1978c, see also 1978b) have pointed out that the trends in this data set tend to be similar to those reported generally for Finland (von Haartman et al. 1963—72), though Mikkola (1978) disputed this similarity of trends for two species.

3. Järvinen & Väisänen (1977) compared results from line transects censused in the whole of Finland in the 1940s, 1950s and 1970s. Combining information from their Tables 1 and 3 makes it possible to plot the data in Fig. 1. The percentage of increasing species is consistently within the statistical confidence limits, except that there were unusually few increases among the 12 most abundant species. In fact, Järvinen & Väisänen (1977) pointed out that the most abundant species in

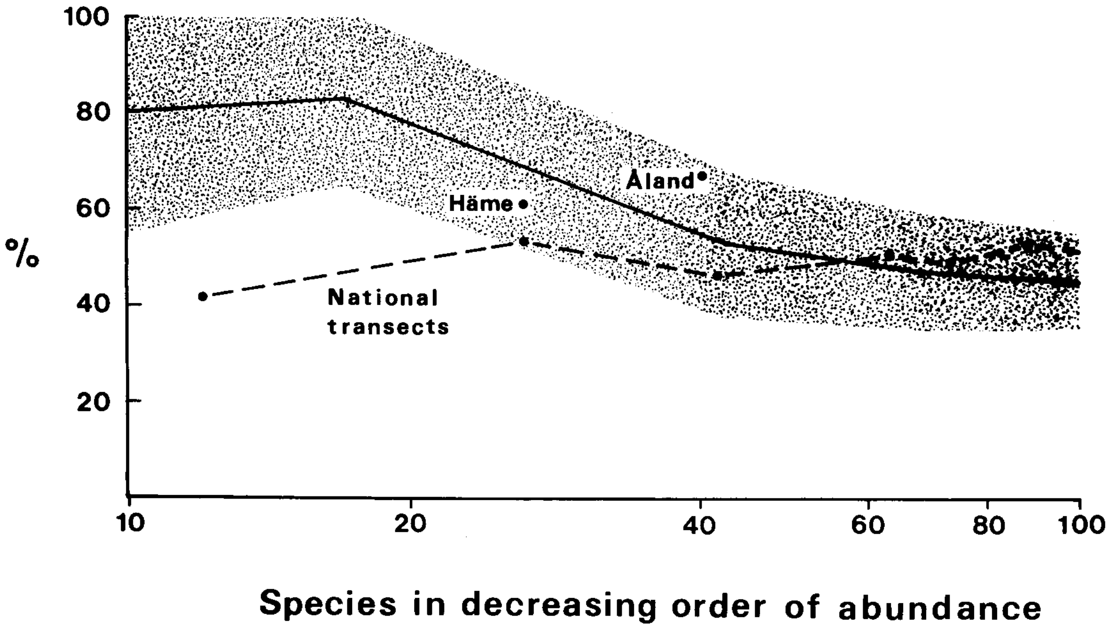

Fig. 1. The percentage of species that have increased (according to the model described in the text) as a function of the number of species included in the sample. Note that the samples here comprise the most abundant species, and species are added in decreasing order of abundance (for details, see text). The shaded area gives the 95 % confidence limits of the expected values (continuous line). Three different sets of observations are also shown; for discussion, see text.

their data tended to be stable more often than other species. The low frequency of increases among the most abundant species is perhaps merely a consequence of the unrealistic assumption in the model that drastic increases can occur even in the most abundant species in the bird fauna.

Järvinen & Väisänen (1977) also reported that, of the species that had a population of at least 160 000 pairs in the 1970s almost one in two had doubled its population or increased even more, while only five of these 56 species had decreased in recent times. Hildén (1979:141) seems to imply that this result indicates that most Finnish bird species have increased their numbers recently. This implication is also false for the reason that 56 species are less than one-quarter of the Finnish avifauna. However, calculation of probabilities from Table 1 for different data sets leads to the conclusion that the observed percentage of increasing species among the 56 most abundant species is close to the expected value. This is true even when all increases reported by Järvinen & Väisänen (1977) are included, and not only those that involved at least a doubling of the population. Moreover, the percentage of decreases is slightly greater than expected from the model. Indeed, in other species sets than the 56 most abundant species in the 1970s, Järvinen & Väisänen (1977) also consistently observed more decreases than expected from the model.

Summing up, in an avifauna that has more increases than decreases, the percentage of increasing species tends to be unexpectedly high in samples that include only the most abundant species. According to the simple model constructed, the percentages reported by Järvinen & Väisänen (1977, 1978a) are consistent with those given by von Haartman (1973). Moreover, the estimates from Åland and Häme are consistent with line-transect estimates for a similar-sized sample of species (χ^2 tests). The only noteworthy deviation is the high frequency of relatively stable populations among the most abundant species. This tendency has already been noted by Järvinen & Väisänen (1977) (see especially their Table 2). In addition to the preponderance of increases over decreases, another formal property of the model is important in creating the patterns observed. This is the fact that species-abundance distributions of birds tend to be lognormal (for Finnish birds, see Preston 1962). Lognormality is not a necessary assumption here, for the main condition is that there are many more species in the "average" abundance classes than among the very abundant species. This would be true of all avifaunas of any extent.

Concluding remarks

The methodological conclusion of this paper is best illustrated with an error that is my own. Järvinen & Väisänen (1978a) argued that their sample of species was unbiased because they compared equal-sized samples and included all species that exceeded the limit of 10 pairs in either the old (1926—27 or 1936) or the new (1975 or 1977) census. However, their claim was misleading because a sample of this kind yields a remarkably high proportion of increasing species.

Comparing the frequencies of species that have increased or decreased in different-sized samples is not straightforward but must be based on a model describing population changes. This can be illustrated by the sample of Järvinen & Väisänen (1977). Of the species that had more than 1.28 x 10^6 pairs in the 1940s or in the 1970s, more than 40 % had increased during recent decades. The percentage of increases is greater than the overall average of 34 % reported by von Haartman (1973) but nevertheless this value is highly significantly smaller than expected from the present model (Fig. 1, the only data point outside the confidence limits).

Consistency among different estimates of increasing species is naturally gratifying, as it makes it possible to view different results in the same framework. I will not discuss different interpretations here (see von Haartman 1973, 1978, Järvinen & Väisänen 1978a), especially because a book on Finnish bird population changes during recent decades is now in preparation (O. Järvinen and R. A. Väisänen). I will only call attention to one of the assumptions here, namely that the probability of increase (or decrease) is independent of abundance. In reality this assumption is incorrect for a variety of reasons:

(i) If man is a major agent in causing bird population changes in present times, one would not expect many decreases among the most abundant species. These are likely to be more tolerant than other species of the human impact, excepting man-made changes that are qualitatively new in the environment.

(ii) New species in the avifauna are by definition species that increase, but at the beginning of their expansion they must belong to the lowest abundance classes.

(iii) Species that have decreased owing to persecution or adverse habitat changes and are now rare may have experienced these negative effects over a long period. Such species may therefore be particularly frequent among the lower abundance classes.

Of these points, (i) and (iii) make the model presented above somewhat too conservative, while point (ii) acts in the opposite direction. At this stage of knowledge, it is not possible to evaluate the combined effect of these conflicting tendencies. At the specific level, assessment of consistency among different estimates poses no problems. In contrast, the use of frequencies of increasing or decreasing species as synthetic indices of overall trends requires considerable caution: similar estimates from two different data sets may be inconsistent with each other, while two very different estimates may nevertheless be consistent.

Note added in proof. After this paper was submitted, Hildén & Koskimies (1984) concluded that in their data set (1973—82) there were fewer increases and more decreases than in the data set of Järvinen & Väisänen (1977). However, when equivalent data sets are compared, no statistically significant difference emerges (Järvinen & Väisänen 1984).

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Selostus: **Ovatko eri arviot runsastuneiden ja taantuneiden lajien osuudesta yhdenmukaisia?**

Eri yhteyksissä on arvioitu, että Suomen linnustoon kuuluvista lajeista viime aikoina runsastuneiden osuus vaihtelee suunnilleen kolmanneksen ja kahden kolmanneksen välillä. Taantuneiden osuus eri tutkimuksissa on vaihdellut nollasta noin yhteen neljännekseen lajeista. Arvioiden yhteensopivuuden testaaminen edellyttää, että vertailupohjaksi rakennetaan malli, jonka avulla voidaan arvioida runsastuneiden ja taantuneiden lajien suhteelliset osuudet erilaisissa lajijoukoissa. Kirjoituksessa rakennetaan tällainen malli; tärkeimmät olettamukset ovat, että linnuston runsausjakauma vastaa Merikallion (1958) esittämää ja että runsastuneita ja taantuneita lajeja on kaikissa runsausluokissa von Haartmanin (1973) esittämät prosenttiosuudet. Täsmällinen runsausjakauma ei ole mallin kannalta kovin kriittinen olettamus, paitsi että joka tapauksessa joudutaan olettamaan, että huippurunsaita lajeja ja huippuharvinaisuuksia on suhteellisen vähän keskirunsaisiin lajeihin verrattuna. Tämä lienee totta kaikkien vähänkään suurempien alueiden lintufaunoissa.

Olennaiset tulokset on esitetty kuvassa 1. Vaaka-akselilla on tutkittu lajimäärä. Lajit on otettu mukaan näytteeseen runsausjärjestyksessä, joten esim. 20 lajia merkitsee, että näytteeseen kuuluu ao. faunan 20 runsainta lajia. (Täsmälleen ottaen: runsautta arvioitaessa on otettu huomioon joko ennen linnuston muutoksia tai näiden tapahduttua todettu parimäärä, kumpi näistä vain on suurempi.) Pystyakselilla on mallin mukaan odotettu runsastuneiden lajien määrä tilastollisin luotettavuusrajoin (rasteri). Järvisen & Väisäsen (1977) havainnot valtakunnallisista linjalaskennoista sekä heidän havaintonsa (1978a) Ahvenanmaalta ja Kalelan tutkimusalueelta Hämeestä sopivat kaikki yhteen odotettujen arvojen kanssa. Ainoa poikkeus on, että 12 runsaimman lajin joukossa Järvinen & Väisänen (1977) totesivat odotettua vähemmän runsastuneita lajeja. Taantuneita lajeja koskevat johtopäätökset ovat samansuuntaiset: ei tilastollisia eroja, joskin valtakunnallisissa linjalaskennoissa taantuneita lajeja todettiin joka näytekoossa hiukan odotettua enemmän.

Kuvan 1 jossakin määrin odottamattoman tuloksen selittää, että lintufaunassa runsastumisia on ollut keskimäärin enemmän kuin taantumia (von Haartman 1973) ja että eniten lajeja on keskirunsaiden lajien luokissa (näistä siirtyy runsaiden lajien puolelle paljon enemmän runsastuneita lajeja kuin suhteellisen harvoista huippurunsaista lajeista tapahtuu taantumia).

Myös Hildénin & Koskimiehen (1984) esittämät arviot runsastujien ja taantujien osuuksista sopivat hyvin yhteen vuonna 1977 esittämiemme lukujen kanssa (ks. Järvinen & Väisänen 1984).

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