Mortality rates of some Finnish Passerines

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Introduction

It is possible to calculate the annual mortality or survival rates of birds e.g. from reported recoveries of ringed birds or by studying the colour-marked population of a species which returns regularly to the same nesting site. The former method has been used about twenty-five years (LACK 1943 a, b, c) and the latter about forty years (BURKITT 1926, NICE 1937 etc.).

For this paper I have calculated from ringing data annual mortality rates for 19 Passerine species. Because it is evident that the recoveries which form the basis of the calculations do not always represent an unbiased sample for the whole population I have made special efforts to select the recoveries used in order to get as unbiased mortality rates as possible.

Materials and methods

The material used in this paper has been assembled from the ringing reports of Department of the Bird-Ringing at Helsinki University and I have also had access to some unpublished recoveries of this institution.

Species for which at least twenty useful recoveries were made during no more than fifteen years (up to 1965 or 1966) were chosen for the present analysis. Irruptive species (Waxwing (*Bombycilla garrulus*), Redpoll (*Acanthis flammea*), and Siskin (*Carduelis spinus*)) were neglected. Whether only pullus or certain other age groups were also taken into account, was determined according to the number of recoveries.

The likelihood of a bird being found every year was tested by a χ^2-test, and in one instance a correction was made.

As the starting day of the survival calculations I have used the first of January after ringing (see FARNER 1955).

The annual recoveries were tabulated according to HALDANE's (1955) example. In nearly every case I first used all recoveries as combined material and then the recoveries were selected according to the way in which the bird was found. These criteria were not the same for every species. The reasons are presented under the title of the species in question. The following grouping of recoveries was used:

A. All recoveries, except those controlled at the ringing place after having been ringed there as adults. The combining of killed birds and birds found dead is justified if the size of the population is stable, the annual mortality of adult birds is not dependent on age (see MARTIN-LÖF 1961) and if the probability of recovery is as great at all phases of a bird's life (after the first of January).

By neglecting controlled adults I have tried to eliminate the error that is caused by the human factor: it is evident that a ringer reports more regularly the control of a very old bird than that of a bird that was ringed the preceding year (in former years there were no detailed guides for reporting a ringer's own controls). It is also a common situation that a ringer is active for some years during which time he gets several controls but then his enthusiasm wanes, and then the probability of getting old recoveries by this means is slight (see v. HAARTMAN 1951). For this reason reports of all controlled birds should perhaps be ignored. I have, however, in order to obtain more material, included in this group those controls obtained from birds ringed as nestlings or young because their dispersal means controls are often obtained from more than one ringer.

B. All recoveries except those reported by a ringer. This practice has been used only with the Great Tit (*Parus major*) and the arguments are presented under this title.

C. Birds reported as found dead during the whole year plus those controlled in their breeding areas (birds ringed as adults, and controlled later have been ignored for the reasons presented under A). The intention of this practice is to try to exclude the effects of different wintering areas and the effect of possible different hunting and reporting activities by man upon young and older birds. This method was chosen for those species where method A gave rather high mortality figures and it was suspected that first year birds possibly migrate to a greater extent to southern Europe where they are caught for food. When we use only those recoveries mentioned at the beginning of this paragraph the possible over-representation of those year classes caught in southern Europe decreases. This method assumes that man is not an important cause of death. This probably holds true for (nearly) all the Passerines dealt with here.

D. All birds found dead. This practice has been used only for the Magpie (*Pica pica*) under which title the reasons for this practice have been explained.

The annual survival rates (100 — mortality per cent) and their standard errors have been calculated by HALDANE's (1955) method which corrects the bias caused by the fact that some recoveries will probably still be reported from those year classes which I have treated in this paper.

The stability of adult mortality has been tested by a χ^2-test.

All calculations have been carried out using a programmed desk-top computer.

Results

The calculated mortality rates are given in Table 1. In the following survey I have presented the arguments for the selection of the recoveries and compared the results with some previous ones.

Motacilla alba. The annual mortality rate is 48±6.5 %. There are not enough recoveries for a more detailed analysis.

Turdus pilaris. The annual mortality rate based on all recoveries is 65±3.2 %. Because this value seems surprisingly high I selected those recoveries in accordance with the method C. The mortality rate based on this data is 61±5.1 %. This points to that the annual mortality rate of the Fieldfare is rather high and that young birds probably migrate more than adults. Because many recoveries were the result of shooting it is possible that this also increases the proportion of young unexperienced birds and thus the apparent annual mortality rate, too.

Turdus philomelos. The annual mortality rate is 54±6.1 %. There are not enough recoveries for a more detailed analysis. LACK (1946) has given a value of 47 % for British birds.

Turdus iliacus. Using all recoveries a value of 57±3.5 % is arrived at. This figure seems rather high but selecting recoveries on the basis of method C gives nearly the same value, 58±5.7 %. So the annual mortality rate of this efficiently reproductive species (TYRVÄINEN 1969) probably is high.

Turdus merula. All recoveries give a value of 59±6.4 % and those of the method C 58±6.5 %. So the annual mortality rate seems to be rather high. For British birds the annual mortality rate was 40 % (LACK 1946).

Phoenicurus phoenicurus. The annual mortality based on all recoveries is 51±10.0 % which is a little lower than that calculated by RUIJTER (1941) 56 %.

Erithacus rubecula. The annual mortality rate based on all recoveries is 76±4.7 %. This is so high a figure that there is probably some source of error, possibly different wintering areas of year-old birds and older birds. However, it is impossible to test this on Finnish material because there are not enough recoveries of birds found dead. The mortality rate of British Robins is 62 % according to LACK (1943 d).

Muscicapa striata. The most peculiar figure in the calculations of this paper is the mortality rate of the Spotted Flycatcher, 28±9.9 %. It is very low but I cannot find any reasonable source of error that would cause this figure. The only way I know in which the Spotted Flycatcher deviates from other Passerines is in its ascendant moult of primaries (DIESSELHORST 1961) but it is very difficult to discover any connection between these two facts. The reproductive biology of this species does not seem to deviate from

TABLE 1. Annual mortality rates of some Finnish Passerine birds. For methods, see text. (*Eräiden suomalaisten varpuslintujen vuosikuolevuudet. Menetelmät selitetty tekstissä.*)

Species *Laji*	Method *Menetelmä*	Recoveries used *Käytetyt löydöt*		Mortality % *Kuolevuus*	Deviation from stable adult mortality rate. *Poikkeama tasaisesta aikuiskuolevuudesta*		
					χ^2	f	P
Motacilla alba	A	all	57	48± 6.5	2.28	4	0.75—0.50
Turdus pilaris	A	pull & juv	202	65± 3.2	2.33	3	0.75—0.50
"	C	all	90	61± 5.1	1.39	3	0.75—0.50
Turdus philomelos	A	pull & juv	64	54± 6.1	0.47	2	0.90—0.75
Turdus iliacus	A	pull & juv	210	57± 3.5	0.09	3	>0.99
"	C	all	73	58± 5.7	3.08	3	0.50—0.10
Turdus merula	A	pull & juv	50	59± 6.4	2.01	3	0.75—0.50
"	C	all	49	58± 6.5	1.43	3	0.75—0.50
Phoenicurus phoenicurus	A	all	30	51±10.0	0.34	2	0.90—0.75
Erithacus rubecula	A	all	91	76± 4.7	0.51	3	0.95—0.90
Muscicapa striata	A	pull & juv	28	28± 9.9	1.04	4	0.95—0.90
Ficedula hypoleuca	A	pull & juv	123	64± 4.3	0.21	2	0.90—0.95
"	C	all	89	63± 5.0	1.80	3	0.75—0.50
Parus major	B	all	157	44± 3.7	3.40	6	0.90—0.75
Emberiza citrinella	A	all	32	46± 9.4	4.35	3	0.50—0.10
Fringilla coelebs	A	all	133	52± 4.0	4.93	4	0.50—0.10
"	C	all	78	43± 5.8	2.57	4	0.75—0.50
Chloris chloris	A	all	43	43± 8.3	0.94	3	0.90—0.75
Pyrrhula pyrrhula	A	all	59	47± 6.4	1.87	5	0.90—0.75
Passer domesticus	A	all	31	64± 7.4	2.04	3	0.75—0.50
Sturnus vulgaris	A	pull & juv	195	53± 3.2	3.02	4	0.75—0.50
"	C	all	128	46± 4.4	2.22	5	0.90—0.75
Corvus corone	A	pull & juv	313	47± 2.3	5.77	5	0.50—0.10
Corvus monedula	A	pull	137	35± 3.2	6.34	6	0.50—0.10
Pica pica	A	pull	100	61± 4.3	4.67	3	0.50—0.10
"	D	all	44	57± 6.8	2.04	3	0.75—0.50

that of other small Passerines (see SUMMERS-SMITH 1952) but the population dynamics varies according to first-year mortality, too, and this is not known for this species.

Ficedula hypoleuca. The annual mortality rate based on all recoveries is 64±4.3 %. Because this is much higher than the value published by v. HAARTMAN (1951), 50 %, I have calculated the values by method C but this gave practically the same result, 63±5.0 %. This, however, is not surprising because the wintering areas of this species are outside Europe (VOOUS 1960).

Parus major. For this species large amounts of controls are obtained by ringers because the species is very common and very easily caught. The practice has been that only controls some years old are reported by ringers and so I consider the recoveries reported by ringers to be a biased sample. When we use other recoveries we get an annual mortality rate of 44±3.7 %. This is less than that of PLATTNER & SUTTER's (1947), 46 %, or KLUIJVER's (1951), 49 %.

Emberiza citrinella. The annual mortality rate based on all recoveries is 46±9.4 %. Most recoveries of this species, as of the Great Tit, Greenfinch (*Chloris chloris*), and Bullfinch (*Pyrrhula pyrrhula*), come from birds ringed as adults and later found dead, or controlled outside their ringing parish. Because they practically never migrate to areas where they are caught for food but remain in areas where the human standard of living is about the same I regard these figures as rather reliable.

Fringilla coelebs. The annual mortality rate based on all recoveries is 52±4.0 %. Because old males are known not to migrate so far south as young (DEELDER 1949) I assume that the value calculated on the basis of recoveries of the method C is a more real one. The value obtained by this method, 43±5.8 % accords well with this expectation. The annual mortality rates given by BERGMAN (1939) and ANVÉN & ENEMAR (1957) are lower.

Chloris chloris. The annual mortality rate based on all recoveries is 43±8.3 % (see the Yellowhammer).

Pyrrhula pyrrhula. Because the Bullfinch migrates some years much more than others and the probability of recovery is thus some years much higher than the others ($\chi^2 = 22.7$, $f = 9$, $P < 0.01$) the annual numbers of recoveries were weighed. The annual mortality rate is 47±6.4 % (see the Yellowhammer).

Passer domesticus. The House Sparrow learns to shun traps and nets very quickly (SUMMERS-SMITH 1963, NORTH 1968). That is why no controls have been taken into account in the material of "all recoveries". This gives the apparent mortality rate of 64±7.4 %. This is probably too high because many Sparrows are reported as shot. The annual mortality rate based on birds found dead is lower but is based on very few recoveries.

Sturnus vulgaris. The annual mortality rate based on all recoveries is 53±3.2 % and that based on recoveries made on the basis of method C 46±4.4 %. This indicates that young age classes of Starlings migrate probably farther south than adults and/or are more vulnerable to hunting by man. Because man is probably not an important cause of death I regard the latter value as more reliable especially for older year-classes. KLUIJVER (1935) has calculated an annual mortality rate of about 50 % for Dutch Starlings and COULSON (1960) 52.8±1.0 % for British ones.

Corvus corone. The annual mortality rate based on all recoveries is 47±2.3 %. A more detailed analysis is in preparation.

Corvus monedula. The annual mortality rate based on all recoveries is 35±3.2 %. Because most recoveries are of birds not shot, I regard the value as a rather good one.

Pica pica. The annual mortality rate based on all recoveries is 61±4.3 %. The annual mortality rate based on those found dead only is 57±6.8 %. This points to that Magpies shot by man are not an unbiased sample of the whole population. There are many recoveries from the first year and if we neglect these by taking as the starting day of the annual mortality rate the first of January of the second year we get a value of 47±7.9 %. This probably means that it is difficult to shoot elder birds and I am inclined to regard this latter figure as a rather good estimate of the mortality rate for breeding birds.

Possible correctness of the assumptions

The assumptions, which HALDANE's (1955) formula presupposes, are that the size of the population is stable, the annual adult mortality rate is stable, and the possibility of recovery is as high during one phase of an adult birds's life as another. If these assumptions are true it is also permissible to combine the data referring to birds killed and birds found dead. A method for combining the mortality rates derived from birds killed and those found dead is presented elsewhere (HAUKIOJA & HAUKIOJA 1970). This is not necessary if man is not an important cause of death and the former assumptions hold true.

It is very difficult to know exactly whether the size of the Finnish populations of the species dealt with in this paper are stable or not. During recent years it is evident that only the Blackbird has expanded its range to a large degree. This is why I chose only recoveries of this species made during the last ten years for the present analysis in order to minimize possible error.

The stability of the adult mortality rate has been tested in accordance with normal practice by a χ^2-test (Table 1). In no instance has the assumpted stability of an adult mortality rate proved to be wrong but it may be stressed that the test does not prove that the assumption is right, either. That this assumption is not quite right for all species is pointed to by the fact that for both *Corvus*-species dealt with here, the value of P is at a level of 0.5—0.1 and if the rise of the mean life expectation with adult age is a real phenomenon then the Corvidae are evidently most likely to show it.

That the probability of recovery of all adult birds is as great is probably one of the greatest weaknesses of the recovery method. It is probable that young birds are more easily shot than old, experienced ones, but whether this vulnerable period stretches over the first of January, which is the starting day of the calculations in this paper, is another thing. This possibly happens at least with the Hooded Crow (in prep.) and the Magpie. For most other species dealt with here the situation probably is not so except for those species which migrate in their first winter farther south than in following years. An attempt to correct this source of error has, however, been made by using selected recoveries according to method C.

If the probability of finding birds varies with different years the yearly numbers of recoveries have to be weighed. Only with two species did this prove to be evident. These species were the Bullfinch and the Redwing. The former are ringed in Finland mainly as adults or juveniles during autumn and winter and so the annual numbers of ringed Bullfinches have been comparable during the whole of the time which was used in the calculations and annual recoveries were weighed. Redwings, however, have generally been ringed as nestlings during the whole calculation period but annual numbers of netted adults, who generally have a higher recovery percentage, have increased greatly during this time. Because the annual numbers of ringed Redwings are not comparable and there are no published ringing numbers of nestlings and adults from different years I have not weighed the recoveries of this species.

Ring wear has been regarded as the most important factor affecting apparently high mortality rates. Ring wear has been studied especially on long-lived birds and the loss of rings may affect results even before the fifth year (LUDWIG 1967). On species studied in this paper the loss of rings is probably a less important source of error because Passerine birds seldom live very long.

A possible bias which favours young birds in the recovery data is that at some places hunting by man is more intensive than at others. This will be important if shooting or killing is an important cause of death and if birds show site-tenacity during the shooting period and empty territories (or areas in general) are filled by newcomers, in general mainly young birds. This bias probably has no great effect on the birds dealt with in this paper. Species of Corvidae may again form an exception.

A fact which probably can affect an apparently high mortality rate occurs if the trapping methods used for catching adults and juveniles for ringing are age (or experience) selective. The bias caused by this can probably be corrected by comparing the rates from later years of those birds ringed as nestlings and those ringed as adults. This, however, demands large amounts of data.

Discussion

Theoretically, the recovery method should give at least as real mortality rates as the colour marking method because it is not dependent on one investigator or one study area and at least those birds ringed as nestlings form an unbiased sample of the whole population at a later stage of life. It is, however, another thing to get enough recoveries to represent an unbiased sample. Because the recovery method is based only on *reported* rings it is evident that birds killed by man are over-represented and on the other hand birds dying in densely inhabited areas are the most likely to be found. The latter bias is difficult to eliminate but an effort has been made to eliminate the former by selecting the recoveries used. The selection method, of course, has always to have a sound biological basis in order to avoid a situation where a student seeks such figures which give a presupposed result.

Most assumptions mentioned in the preceding chapter favour the over-representation of young year-classes and so a higher annual mortality rate than the true one. GROSSKOPF's (1964) conclusion that mortality rates calculated by the recovery method are higher than those arrived at by studying colour marked populations of long-lived birds is therefore not astonishing.

It is worth mentioning that the mortality calculations based on colour marked populations have their own sources of error, too. The fact that all birds are not found although they have survived is the first possible bias. Certain procedures may be adopted to correct this and so it is possible to overcome this difficulty. Another bias which may be rather great but in another direction and is almost impossible to correct is that many population studies of colour ringed birds are conducted in the species' optimum habitats. If we bear in mind that territory establishment often seems to be rather laborious for a bird it is probable that the strongest individuals are found in the best habitats. So it is possible that the mortality values found in population studies are somewhat lower than for the species as a whole.

Nearly all mortality values calculated in this paper fall within the limits mentioned by FARNER (1955) for Passerine birds (40—70 %). Only the values for the Robin, the Spotted Flycatcher and the Jackdaw fall outside these limits. The high mortality rate of the Robin may well be only an apparent one and be caused by different wintering areas during the first and later years. It is more difficult to interpret the low value found for the Spotted Flycatcher but the value for the Jackdaw seems to be rather reasonable.

I think it is unnecessary to speculate too much about different mortality rates between different populations because many comparisons had to be made between figures derived by different methods and between populations whose migratory habits may be quite different and this may affect not only the survival of birds but also the reliability of calculated results.

The testing of those values found with the known rate of reproductivity is, of course, recommended (see FARNER 1955) but in this paper I have neglected it because, besides a knowledge of the rate of reproductivity of the species, it also presupposes that the first-year mortality rate (including that of fledglings) is known. This generally has to be calculated by some indirect method and is generally determined by using the adult mortality rate. It is evident that the calculations are wrong if the known rate of reproductivity is clearly too low for the calculated adult mortality rate, assuming a moderate first-year mortality but if it is not so, as is probably the case with nearly all the species in this paper, it proves very little.

I think that with short-lived Passerines the method based on recoveries is rather good, see e.g. the mortality values calculated for the Great Tit, the Yellowhammer, the Greenfinch, and the Bullfinch for which the assumptions presented above are probably the best. For nearly all species dealt with here further analysis of population dynamics based on ringing data requires a huge amount of field work in bird ringing and especially nestlings of common species from which it is possible to get enough recoveries for detailed analyses need to be ringed. Careful studies of people who report and do not report bird rings in different parts of the area where the species investigated •live are probably also necessary. This is perhaps at least as important as the former.

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Summary

For this paper the annual mortality rates of 19 Passerine species were calculated from Finnish ringing recoveries. The calculations were made if at least twenty useful recoveries of the species were accumulated during no more than fifteen years. In order to get as true a picture as possible of the mortality values of whole populations and not only of those specimens recoveried, special care was paid to selection of the recoveries.

The calculated values are given in Table 1. They fall, with three exceptions (the Robin, the Spotted Flycatcher, and the Jackdaw), within the common limits of Passerine mortality (40—70 % per year). The figure of the Robin is probably biased because there were not enough recoveries to correct possible differences arising from the different wintering areas of old and young individuals. The low mortality rate of the Spotted Flycatcher (28 %) needs closer study but the value of the Jackdaw (35 %) seems rather reasonable. The mortality rates of the thrushes as well as the Pied Flycatcher are higher than in previous studies. Probably the most unbiased values (43—47 %) are those of the Great Tit, the Yellowhammer, the Greenfinch, and the Bullfinch. For these species the assumptions of the formulas used (stable populations, stable adult mortality rate, stable probability of recoveries from all age-classes) are probably the most tenable.

The most valuable data for determining the population dynamics of birds according to ringing materials are obtained by ringing large numbers of nestlings of common birds. Exact knowledge of those people who report and do not report recoveries are also needed.

Selostus: **Eräiden suomalaisten varpuslintujen vuosikuolevuus.**

Kirjoituksessa on laskettuna 19 varpuslintulajin vuosikuolevuus suomalaisten rengaslöytöjen perusteella. Mukaan on otettu lajit, joista enintään viidentoista vuoden aikana (vuoteen 1965—1966 mennessä) on kertynyt vähintään kaksikymmentä käyttökelpoista löytöä. Laskelmissa on erityistä huomiota kiinnitetty löytöjen valikointiin mahdollisimman todellisen kuvan saamiseksi, ei vain löytyneistä yksilöistä, vaan koko populaatiosta.

Laskelmien tulokset on esitettynä taulukossa 1. Saadut tulokset sattuvat kolmea lajia (punarinta, harmaasieppo, naakka) lukuunottamatta varpuslinnuille normaaleihin vuosikuolevuusarvoihin (40—70 %). Punarinnan korkea vuosikuolevuus on mahdollisesti vain näennäinen, koska eri ikäisten yksilöiden ehkä erilaisia

talvehtimisalueita ja täten erilaista löytymistodennäköisyyttä ei pienten löytömäärien vuoksi pystytty korjaamaan. Harmaasiepon alhainen vuosikuolevuus (28 %) kaipaa lisäselvittelyä, mutta naakan 35 % lienee varsin lähellä todellista. Rastaiden, samoin kuin kirjosiepon vuosikuolevuusarvot ovat korkeammat kuin aikaisemmissa tutkimuksissa. Ainakin suureksi osaksi talvehtivien talitiaisen, keltasirkun, viherpeipon ja punatulkun vuosikuolevuudet ovat varsin samansuuruiset (43—47 %) ja näiden lajien kohdalla pitänevät myös rengastuslöytöihin perustuvien vuosikuolevuuslaskelmien edellytykset (tasainen aikuiskuolevuus, muuttumaton populaatiokoko ja eri ikäisten aikuisten yksilöiden samanlainen löytymistodennäköisyys) parhaiten paikkansa.

Lintujen populaatiodynamiikan selvittelyssä rengastusaineistojen avulla saadaan arvokkaimmat tulokset pesäpoikasten massarengastuksilla, mikä taas on helpointa tavallisimpien lajien kohdalla. Myös selvittelyt löytöjä ilmoittavista ja ilmoittamattomista renkaiden löytäjistä olisivat erittäin tervetulleita.

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