Mortality and reproductive rates in a Finnish population of Dunlin *Calidris alpina*

MARTTI SOIKKELI

Department of Zoology, University of Turku

The population dynamics of the order Charadriiformes is best known within certain species of the suborder Lari, i.e. within those species with relatively dense breeding populations, visible nests, and semi-precocial young, as these breeding habit features make extensive ringing programmes and effective observation possible. Because most species of the suborder Charadrii can be less easily subjected to a thorough and comprehensive population analysis, only a few of the many papers on ringed breeding populations (LAVEN 1940, BERGMAN 1946, JUNGFER 1954, RITTINGHAUS 1956, 1961, BUB 1958, 1962, GROSSKOPF 1958, 1959, 1963, HELDT 1966, HARRIS 1967, and SOIKKELI 1967) are based on an adequate number of individuals under observation and cover a satisfactory span of time to permit an analysis of different population parameters. However, as BOYD (1962) stated at the end of his thorough review of the mortality and fertility of European Charadrii, long-term studies of ringed breeding populations will give the most useful information on the dynamics of wader populations.

This paper is the final report of mortality and reproductive rates in a Dunlin *Calidris alpina* population studied over a period of eight seasons. The dispersal of Dunlin, which, in addition to the mortality and reproductive rates, is the most important variable operating in an avian population, I have treated in another paper (SOIKKELI 1970).

Methods of field study

Field studies were carried out on the coast near Pori, south-western Finland, from 1962 to 1969. The study areas, a main study area of approx. 60 ha and four control areas 1 to 5 kms away, were inhabited during these years by about 60 pairs of Dunlin (race *schinzii*, SOIKKELI 1966). For a further description of the area and population see SOIKKELI (1964, 1967, 1970).

The data to be presented in this paper have been obtained from the birds in the main study area, where 21 to 29 pairs bred annually. In 1962—69, the number of breeding Dunlin trapped and ringed in the main study area amounted to 128. There were 33 to 54 (mean 46) ringed Dunlin present annually. Coloured celluloid leg rings of British manufacture used for individual recognition in the first years of study did not last for more than 2 to 3 years. For this reason I tried to re-ring all birds every second year at least and simultaneously changed the aluminium ring, too, if needed. In later years of study I used more durable coloured rings made of plastic and obtained from Sweden.

The mortality rate of adults (an adult refers here to a bird breeding or which has bred before) is calculated from the non-return rate of individuals with coloured rings as well as on the basis of a few birds found dead in the study area. Each spring I identified returning birds almost daily either with the aid of a telescope or by retrapping birds at feeding grounds or, later in the season, at the nest. There were only a few returning females which were not recognized for the first time in the spring until the start of the breeding. Does the non-return rate of adults equal the mortality rate in the population studied? As shown earlier (SOIKKELI 1970), male Dunlin are faithful to their former breeding territory, and therefore males which are missing may be regarded as dead. Females may occasionally move from the main study area to nearby control areas or farther, or vice versa. Despite quite effective retrapping in the control areas,

Table 1. Mortality rate of adult Dunlin in a Finnish population from 1962—69. (*Täysikasvuisten suosirrien kuolevuus eräässä suomalaisessa populaatiossa 1962—69.)*

Year *Vuosi*	Males *Koiraat*		Females *Naaraat*		Total *Yht.* %
	Alive *Elossa*	Missing next yr *Ei palannut* %	Alive *Elossa*	Missing next yr *Ei palannut* %	
1962-63	19	15.8	14	7.1	12.1
1963-64	19	26.3	21	28.6	27.5
1964-65	22	36.4	24	37.5	37.0
1965-66	25	16.0	24	37.5	26.5
1966-67	26	26.9	25	28.0	27.5
1967-68	26	19.2	28	28.6	24.5
1968-69	23	21.7	27	29.6	26.0
Mean ± SE *Keskim.*	23	23.2±2.8	23	28.1±3.8	25.9±2.8

Note. The date of the first ringing of each bird was used as an initial date for mortality calculations.

too (Soikkeli 1970, Table 1), this source of error affects the non-return rate of females and will be discussed later in this paper.

The percentage of eggs that are actually hatched does not give a true figure for an estimation of hatching rate, as nests are often destroyed before found or a pair may re-nest once or twice unsuccessfully. For this reason I tried to find out the real number of young hatched per number of birds present. This latter figure included a few unpaired adults. Possible bias arising out of this method will also be discussed later.

For the following estimation of the survival rate up to one year of age only birds hatched and ringed up to 1966 are taken into account, as many young ringed in 1967—68 and which survived may have escaped recognition until 1969, for Dunlin in the population studied usually start breeding when two years old.

Mortality rate of adults

Table 1 gives the mortality rates of adults obtained from the non-return rates of birds in the spring. The mean of different annual rates was 25.9 ± 2.8 %. For 5 years the mortality rate was fairly constant, ranging between 24.5 and 27.5 %, but in 1962—63 it was exceptionally low and in 1964—65 high. A high mortality rate in 1964—65 was evident in some other Dunlin populations, too (Soikkeli 1967, p. 181).

There was a difference of 4.9 in the mean annual mortality rates of the sexes, but the difference is not significant. If real, the difference may be due, at least partly, to a higher dispersal rate among females (Soikkeli 1970) resulting in too high a non-return rate. For the same reason, the mean annual mortality rate of the whole population is very probably lower than 25.9 % and I think that it is justified to round the figure obtained down to 25 %.

After the spring arrival Dunlin fly around and feed in a wide area on the coast before they settle down more permanently in breeding territories. It is therefore quite possible to identify all the birds which have survived over the winter in spring flocks. Returning birds which were seen in the spring flocks but not observed later during or after a breeding season either in the main study area or in the control areas were regarded as dead. As females outnumber males among those birds which returned but soon disappeared, it is conceivable that not all the disappeared females died but some of them may have moved elsewhere.

TABLE 2. Mortality rate of adults in relation to increasing age in a Finnish population of Dunlin. Data excluding the first year of study in parentheses. *(Täysikasvuisten suosirrien kuolevuuden suhde ikään eräässä suomalaisessa populaatiossa. Ilman ensimmäistä tutkimusvuotta lasketut luvut suluissa.)*

Yrs after ringing *V:t reng:n jälkeen*	Present in previous yr *Elossa edell. vuonna*	Birds missing N	*Ei palannut* %
1	124 (91)	32 (27)	26 (30)
2	84 (57)	27 (19)	32 (33)
3	48 (29)	12 (6)	25 (21)
4	32 (19)	7 (3)	22 (16)
5	18 (9)	4 (3)	22 (33)
6 7	15 (1)	3 (1)	20

Table 2 shows the mortality rate as a function of age. In the two first years after ringing the mortality rate seemed, on the average, to be a little higher than later, but the change is not statistically significant. The difference, if genuine, may merely result from a higher dispersal rate of females in younger age classes (see v. HAARTMAN 1949) since a year after the first ringing 34.0 % of the females (n = 53) were missing but only 21.1 % of the males (n = 38). The difference is significant (binomial t-test, $t = 2.63$, $f = \infty$, $P < 0.01$). Birds ringed in the first year of study are excluded in the above comparison as they represent all age classes.

Factors influencing mortality during migration and wintering are unknown with the exception of shooting in France, where three recoveries were made. In the breeding areas I have found the remains of six Dunlin. Three of them had been caught by some predator at the nest and one, a female with an egg in the oviduct, just before laying in the territory. The most severe predators of adult Dunlin during breeding were probably the Merlin *Falco columbarius* and *Mustela* species.

MARTIN-LÖF (1961) found a mean annual mortality rate of 38.9 ± 3.6 % for migrating adult Dunlin (belonging mainly to the nominate race) ringed in Sweden and recovered later and BOYD (1962) a rate of 37.7 ± 3.6 % from combined Scandinavian recoveries of migrating birds. But GROSSKOPF (1964) has shown that mortality rates based on long-distance recoveries are in many cases too high. The mortality rates obtained by MARTIN-LÖF and BOYD are therefore perhaps not real ones. For comparison, HOLMES (1966) found that, in a population of *C. a. pacifica* in northern Alaska, 30 % of males and 28.6 % of females were one-year-olds. As the birds in this population start breeding when one year old according to HOLMES, then the percentages of yearlings equal the annual adult mortality rate if the population remains stable as it was found to do (HOLMES 1966). It also approximates the mortality rate achieved in this paper.

Life expectancy and longevity

The average expectation of life at the beginning of a time period is $100/M - 0.5$ where M is the periodical mortality rate of adults, which is assumed to be constant during a period (LACK 1948, FARNER 1949, 1955). For adult Dunlin, with an annual mortality rate of 25 %, life expectancy is thus $100/25 - 0.5$ or 3.5 years.

There are two possible ways of estimating the mean life span or longevity of Dunlin which are starting to breed:

a) As approx. 20 % of Dunlin started breeding when one year old and approx. 80 % when two years old (n = 23 for the main study area), the mean age of first-breeders was 1.8 years. If adult Dunlin have a life expectancy of 3.5 years, then the mean longevity of breeding birds will be 5.3 years.

b) Another way of estimating the mean longevity is from birds of known age. 28 Dunlin were ringed as young and found later breeding in the main study area. Until 1969, 15 of them did not return and the total age of these birds amounted to 43.5 years, assuming that the mortality rate was the same in the first and second halves of a year. In 1969, 13 birds out of 28 were still alive and their total age was then 59 years and their total life expectancy 13 · 3.5 or 45.5 years. The mean longevity of these 28 Dunlin would thus be (43.5 + 59 + 45.5)/28 or 5.3 years. If all the 53 Dunlin of known age found breeding in the main study area and control areas are taken into account, a mean longevity of 6.2 years is obtained using the same method. But the material is not correct, as some birds breeding in the control areas were not recognized the year in which they first bred but only later. Consequently, some birds which died after breeding for the first or second time were not retrapped at all and the mean age of birds trapped for the first time is therefore too high.

Naturally, the mean longevity of young hatched or fledged is much shorter than that of breeding birds.

In 1969, one Dunlin was 13[1] and three were 9 years old at least. Many other birds reached 7 or 8 years of age during the study. They all were first ringed as adults and were assumed then to have been two years old. With an annual mortality rate of 25 %, and if 20 % of birds start breeding at an age of one year and 80 % at an age of two years, it takes approx. 20 years for a year class to disappear from the population.

TABLE 3. Clutch-size at different phases of the laying period in a Finnish population of Dunlin. *(Suosirrin munamäärä munintakauden eri vaiheissa eräässä suomalaisessa populaatiossa.)*

Period *Jakso*	Eggs *Munia*				
	1	2	3	4	$\bar{x}$
24.4.—10.5.	—	—	3	111	4.0
11.5.—20.5.	—	1	2	33	3.9
21.5.—31.5.	—	—	2	24	3.9
1.6.—13.6.	—	3	11	10	3.3
Total *Yht.*	—	4	21	178	3.9

Reproductive rate

Clutch-size

The clutch-sizes at different phases of the laying period are given in Table 3. Only those clutches are included in the material where it was certain that laying was completed. In April and May the clutch-size was usually 4. There were rare cases of smaller clutches of 3 or 2.

These occurred as a result of some external inteference such as disturbance of the female by man just before laying an egg, when snow covered the nest for a short time during laying, the removal of a broken egg by the bird, the removal of an egg from the nest in cases where it had stuck to the belly of the incubating bird, or the activity of egg-predators.

In June, at the end of the laying period the mean clutch-size clearly decreases. I have discussed possible external factors involved in the laying of smaller late clutches in another paper (SOIKKELI 1967, p. 174).

Number of attempts to breed

In general, Dunlin replaced those nests destroyed in May but not those lost in early June or later. Exceptionally, parents laid a substitute clutch even after losing their young when small. This

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[1] In 1970 this oldest known bird returned and was then 14 years old at least.

TABLE 4. Hatching rate in a Finnish population of Dunlin from 1962—69. *(Kuoriutumistulos eräässä suomalaisessa suosirripopulaatiossa 1962—69.)*

Year *Vuosi*	Adults present *Ad. lintuja*	Young hatched *Kuor. poikasia*	Young/adult *Poik./lintu*
1962	38	59	1.55
1963	41	51	1.24
1964	45	68	1.51
1965	47	81	1.72
1966	51	71	1.39
1967	53	48	0.91
1968	48	50*	1.04*
1969	41	34*	0.83*
Total *Yht.*	374	472	1.26

* Approximate figures.

happened twice in 1966. Only in 1967 did I find birds laying three successive clutches when the first two clutches had been destroyed (one direct and two indirect observations). In only one year, furthermore, did Dunlin lay true second clutches. In 1965 three females began to nest a second time with previously unpaired males after successfully incubating the first clutch with other males. The latter then reared the young alone.

Hatching rate

Table 4 gives the hatching rate for adult birds in 1962—69. During these years, 374 adults present hatched 472 young or 1.26 young per adult annually.

At the beginning of the study the figure was higher than for later years:

Years	No. of young hatched/adult
1962—66	1.5
1967—69	0.9

The figure may be too high for the first year of study as I possibly missed some unringed birds which failed in attempts to breed early in the season and which did not renest. The same factor may have caused slight error since 1962, too, but not as much as in 1962. The real reasons for the decrease in the hatching rate were principally increased nest-predation:

Years	No. of nests found	% of nests destroyed
1962—66	123	25
1967—69	92	62

The difference is significant (binomial t-test, $t = 5.5$, $f = \infty$, $P < 0.001$). Furthermore, it was clear from the behaviour of the parents, that, in 1967—69, there were many nests which were destroyed during or just after laying and which I did not find at all before predation. I am therefore disposed to estimate that in 1967—69 approx. 70 % of nests were destroyed.

On the other hand, the hatching rate would have been a little higher (0.1 young/adult at least), if breeding had not been disturbed by the investigator (SOIKKELI 1967, p. 185). This error and possible failure to find all breeding birds as mentioned above may offset each other in estimating the hatching rate. The rate of 1.26 young/adult may therefore be considered genuine.

Survival during the first year of life

It is very difficult to get an idea of the mortality rate of young Dunlin after hatching, as young soon leave the nest and then conceal themselves in the grass. After finding some young of a brood, one cannot be sure whether the missing young are dead or alive. If the whole brood is destroyed, which happens not infrequently in the first days after hatching, this fact can be established by

TABLE 5. Age when recovered for the first time and survival up to the age of one year in Dunlin ringed as young in a Finnish population from 1962—66. Calendar year grouping. *(Poikasena rengastettujen suosirrien ikä ensi kertaa löydettäessä ja yksivuotiaaksi eläneiden määrä eräässä suomalaisessa populaatiossa 1962—66. Ryhmittely kalenterivuosittain.)*

Age when first rec. *Ikä 1. kerran kontr.*	Year of ringing *Rengastusvuosi*					Total *Yht.*
	1962	1963	1964	1965	1966	
1	2	5	4	4	1	16
2	3	3	8	18	1	33
3	3	1	2	0	5	11
4	5	1	0	2	.	8
5	0	0	0	.	.	0
6	0	1	.	.	.	1
7	1	.	.	.	.	1
Total rec. *Yht.*	14	11	14	24	7	70
No. ringed *Rengastettu*	78	59	85	138	93	453
Survived 1 year N	29	17	18	33	11	108
Elossa 1-vuotiaana %	37	29	21	24	12	24

the behaviour of the parents. They cease to show signs of alarm and feed together on mud-flats or show courtship behaviour in the breeding territory again. Therefore only a few comments can be made about the survival of broods in different years.

From 1962—65 only 21 % ($n = 76$) of the broods succumbed totally during the two weeks after hatching (SOIKKELI 1967, p. 187), but in 1966 30—35 % ($n = 20$) of the broods were lost as early as five days after hatching and in 1967 50—60 % ($n = 8$) were lost within three days. In 1968—69 brood mortality was not investigated but inferred from the number of broods lost one day after hatching; it was high these years, too. No estimation of fledging success is possible on the basis of the data available.

In 1962—66 altogheter 453 young were ringed soon after hatching. Up to 1969 70 individuals or 15.5 % of them had been recovered, a few of them abroad, some year after hatching (Table 5).

If l_x birds are found for the first time when x years old and if the mean annual survival rate after the age of one year is S, then the number of year-old birds l_1 will be

$$(1) \quad l_1 = l_x \cdot (100/S)^{x-1}$$

Using the figures in the right hand column of Table 5, then if $S = 75$ % (= 100-mortality rate), the number of ringed year-old Dunlin may be calculated as follows:

$$l_1 = 1 \cdot 1.33^6 + 1 \cdot 1.33^5 + 0 \cdot 1.33^4 + 8 \cdot 1.33^3 + 11 \cdot 1.33^2 + 33 \cdot 1.33 + 16 = 108$$

The two bottom lines of Table 5 give the annual numbers and percentages of year-old Dunlin. Annual differences in percentages are significant ($\chi^2 = 12.3$, $f = 4$, $P < 0.025$) and there is a trend for the recovery rate to decrease the younger the year class concerned. This can also be seen in the following:

Yr of ringing	No. ringed	Alive when 1 year old n	Alive when 1 year old %
1962	78	29	37
1962—63	137	46	34
1962—64	222	64	29
1962—65	360	97	27
1962—66	453	108	24

The apparent decrease in the survival rate of later year classes is most probably caused because birds of older year classes are likely to be recovered more frequently than those of younger year classes.

Are percentages for the first year survival rate genuine? First, there is one source of error which results in too high percentages: some broods may succumb within a few hours after hatching and before the young can be ringed. If these young which died very early could be included in the material, then the survival rate during the first year of life would be a little lower than found. Second, I have assumed that the survival rate during the second year of life is the same as the survival rate of breeding birds, although most yearlings do not breed until two years of age. But, on the basis of the data available here, no correction in the survival rates obtained is possible and the only way to test their reality is to compare them with other population parameters.

Maintenance of population

As the adult mortality rate and the reproductive rate varied annually, it is interesting to see whether these variations were reflected in the size of the breeding population. The numbers of preceding year, and hatching rates in preceding year, and hatching rates in different years of study were as follows:

Year	No. of pairs breeding	Mortality rate %	Hatching rate per adult
1962	24—25	—	1.55
1963	24—27	12.1	1.24
1964	25—26	27.5	1.51
1965	25—26	37.0	1.72
1966	26	26.5	1.39
1967	29	27.5	0.91
1968	25	24.5	1.04*
1969	21	26.0	0.83*

* Approximate figures.

The low adult mortality rate in 1962—63 and the high one in 1964—65 did not affect the size of the population in 1963 and 1965. In 1965 the hatching rate and obviously the fledging rate, too (Table 5), were high. In 1967, on the other hand, the hatching and fledging rates were low. As most Dunlin breed for the first time when two years old, variations in the size of the population in 1967 and 1969, if compared with other years, were probably caused by the hatching and fledging rates two years earlier. In fact, in 1967 I found 15 first-breeders of the year class 1965, 10 of them in the main study area, but in 1969 none of the year class 1967 were found, although similar trapping methods were used (SOIKKELI 1970, Table 1). The numbers of young ringed in 1965 and 1967 correlate in the ratio of 4 to 1.

As stated earlier (SOIKKELI 1970), neither emigration nor immigration play any important part in the studied population, because there are no other breeding grounds in the neighbourhood available to and from which Dunlin can move and because the dispersal rate of first-breeders and adults is relatively low. I have not even observed any abrupt changes in the breeding habitat.

Can the mortality and reproductive rates found above be regarded as satisfactory for the maintenance of the population? The first task is to discover how many first-breeders each adult bird produces per year on the average and how many are needed to keep the population stable. If

l_b = number of first breeders;
h = number of young hatched per adult per year;
s_1 = fraction of ringed young surviving up to the age of one year;
a, b = proportions of birds starting to breed when one year old and two years old, respectively; and
S = survival rate of yearlings and of adults, then

$$(2)\quad l_b = h \cdot s_1 \cdot (a + bS)$$

It was found earlier in this paper that $h = 1.26$, $a = 0.2$, $b = 0.8$, and $S = 0.75$. For different values of s_1, shown on p. 155, the following values for l_b are arrived at:

s_1	l_b
0.24	0.23
0.27	0.26
0.29	0.28
0.34	0.33
0.37	0.36

In a stable population where 0.25 of adults die annually, the fraction of first-breeders l_b should be 0.25. This value for l_b is arrived at if $s_1 = 0.26$. This is within the range of s_1 found from the recoveries of birds ringed as young.

Likewise, in a stable population every bird must produce during its life first-breeders so that l_b equals 1.00. To calculate l_b for the whole life of a bird one must express

$$(3)\quad l_b = L_e \cdot h \cdot s_1 \cdot (a + bS)$$

where L_e is the life expectancy of a bird starting to breed, i.e. 3.5 years for the Dunlin studied. For different values of s_1 (p. 155) we get:

s_1	l_b
0.24	0.81
0.27	0.91
0.29	0.97
0.34	1.14
0.37	1.24

$l_b = 1.00$ is obtained by $s_1 = 0.30$. This, too, is within the range of s_1 calculated from recovered birds.

In spite of the fact that the data concerning population parameters used in this discussion are quite exact, calculations as to the maintenance of the population must be regarded as an approximation of how different factors match each other, as valid data are still lacking. For example, during the study the reproductive rate was not stable nor did it fluctuate randomly but showed a decreasing trend towards the end of the study.

In an earlier paper (SOIKKELI 1967, p. 189—191) I hold an opinion that the population studied showed a reproductive rate exceeding the mortality rate of adults. As the hatching rate during the four last years of study was much less than earlier and as the survival rate s_1 up to the age of one year used in this study was obtained from data during years when the fledging rate was relatively good i.e. 1962—66, in the later years of study the number of offspring surviving until the first breeding l_b will very probably be too low to keep the population stable.

Summary

This paper deals with the mortality and reproductive rates of an individually marked *Calidris alpina schinzii* population in southern Finland.

The mean annual mortality rate of males was 23.2±2.8 % and that of females 28.1±3.8 %.The real difference in the mortality rates between sexes was probably not so great as found since some females which have been regarded as dead may have moved to other places. For the whole population, a mean annual mortality rate of 25 % was estimated. The mortality rate did not show any clear tendency to decrease in relation to the increasing age of birds.

Approx 20 % of first-breeders were one year old and the others two years old. Breeding birds had a mean life expectancy of 3.5 years and lived 5.3 years on the average. The oldest bird known in the population was 14, and the turnover of an age class was found to be 20 years.

The mean clutch-size was 3.9. In three cases birds were found laying three successive clutches, when the first two clutches had been destroyed, and in three cases females laid a true second clutch with another male. Adult birds present hatched 1.26 young per bird annually. Out of 453 young ringed as young, 15.5 % were recovered in later years and a mean survival rate 26—30 % during the first year of life after hatching was estimated.

The size of the population remained quite stable during the eight years of study except for small variations brought about by changes in the reproductive rate. The adult mortality rate and the reproductive rate were found to be satisfactory for the maintenance of the population, although in the last years of study the mortality rate very probably exceeded the reproductive rate.

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Selostus: **Suosirrin kuolevuudesta ja syntyvyydestä eräässä suomalaisessa populaatiossa.**

Tutkimus suoritettiin Porin rannikolla vuosina 1962—69 yksilöllisesti merkityillä linnuilla.

Koska suosirrit, erityisesti koiraat, ovat pesimäpaikkauskollisia, pesivien lintujen vuosikuolevuus voidaan laskea palaamatta jääneiden ja tutkimusalueella kuolleiden lintujen perusteella (taulukko 1). Koiraiden ja naaraiden välillä ei kuolevuudessa ole tilastollisesti merkitsevää eroa. Jotkin naarat ovat mahdollisesti siirtyneet muualle, joten todellinen kuolevuus lienee naarailla ja samalla koko populaatiossa havaittua hiukan pienempi. Havaittu kuolevuuden vähäinen pieneneminen iän karttuessa (taulukko 2) ei ole tilastollisesti merkitsevä.

Pesivillä suosirreillä on keskimäärin 3.5 v. elinaikaa jäljellä. Koska n. 20 % linnuista pesi ensi kerran 1-vuotiaana ja muut 2-vuotiaana, pesimään ryhtyvien lintujen keskimääräinen ikä on 1.8 v. ja elinaika 1.8+3.5 eli 5.3 v. Samaan elinaikaan päädytään käyttämällä laskussa poikasena rengastettujen, myöhemmin pesivänä tavattujen lintujen todettua elinaikaa (jo kuolleet) ja jäljellä olevaa elinikään (vielä elävät).

Munamäärä oli munintakauden alussa keskim. 4.0 ja lopussa 3.3 (taulukko 3). Yleensä suosirrit munivat uusintapesueen tuhoutuneen tilalle, ellei tuhoutuminen tapahtunut munintakauden lopussa. Kuoriutumistulos laskettiin poikasten määränä pesivien lintujen määrää kohti (taulukko 4). Viitenä ensimmäisenä vuonna poikasia kuoriutui keskim. 1.5 pesivää lintua kohti, mutta myöhemmin vain 0.9. Ero johtuu ennen muuta pesärosvojen toiminnan lisääntymisestä.

Yksivuotiaaksi eläneiden poikasten määrä on laskettu poikasena rengastettujen, myöhempinä vuosina kontrolloitujen lintujen perusteella (taulukko 5). Koska nuorimpien vuosiluokkien linnuilla on ollut pienempi mahdollisuus tulla kontrolloiduiksi, todettu 1-vuotiaaksi säilyneiden osuus, 24 %, on todennäköisesti liian pieni. Vertaamalla kaikkia kannan kokoon vaikuttavia tekijöitä todetaan, että kannan ollessa tasapainossa poikasista 26—30 %:n tulisi elää 1-vuotiaaksi.

Pesivän kannan koossa ei ole tapahtunut suuria muutoksia. Pienet heilahtelut vuosina 1967 ja 1969 (s. 7, oik. palsta) on selitettävissä kaksi vuotta aikaisemmin todettujen lisääntymistulosten vaihtelujen avulla.

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Address of the author: Department of Zoology, University of Turku, Turku 2.