Proportion of juveniles as a measure of adult mortality in a breeding population of Great Tits *Parus major* and Blue Tits *P. caeruleus*

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There are many ways of estimating the average annual mortality of a bird species. Most involve ringing of individuals, the two chief methods being long-term population studies of marked birds and large-scale analysis of ringing recoveries. A more simple way is to determine the proportion of first-breeders in a population over several successive years. As the juveniles take the place of the adults dying each year, the percentage of individuals breeding for the first time should tend to equal the mortality of adults. However, the method is applicable only if four conditions hold: (1) the first-breeders can be distinguished from the older ones by certain plumage characters, (2) the breeding adults in the population are site-faithful from year to year, (3) there is no long-term trend in the population, and (4) the study area mainly comprises optimal habitats. The last condition is needed, since in suboptimal habitats the annual number of first-breeders is more dependent upon the prevailing population density than adult mortality, immigration taking place mainly in peak years (cf. Krebs 1971).

The Great Tit and the Blue Tit are suitable species for this method. They breed commonly in nest-boxes, the adults are highly sedentary, and the 1-year-old birds are fairly easy to recognize by the colour of their primary coverts. In my study area in Kirkkonummi, about 30 km west of Helsinki, most boxes are placed in optimal habitats. The number of pairs nesting in them in 1972—82 has varied between 44 and 102 for the Great Tit and between 14 and 41 for the Blue Tit. The 11-year period included both high and low population densities, without any definitive trend, so the average mortality should be close to the true long-term value for these species. Earlier, Snow (1956) has estimated the annual mortality of the Blue Tit in different parts of its range by using the age structure of museum specimens.

Each year, I have tried to capture all the females, usually during incubation. Only a few, from nests destroyed at an early stage, have been missed. The proportion checked for age has thus been high, averaging 92 % for the Great Tit and 93 % for the Blue Tit. Capture of the males, usually during the nestling period, is more time-consuming. Consequently the proportion checked for age was much lower than for the females, averaging 39 % in the Great Tit and 65 % in the Blue Tit.

Table 1 summarizes the results. As indicated by the average annual proportion of juveniles in the nesting population over the 11 years, the mortality of adults was considerably higher in the Blue Tit than in the Great Tit, namely 58.7 % vs. 47.3 % (calculated for each species from the mean of both sexes). This corresponds to expectation, as the reproductive potential of the Blue Tit is also higher than that of the Great Tit. In my area, for instance, their first clutches average 11.32 (N = 249) and 9.19 (N = 704) eggs, respectively, and the difference between the species is still more pronounced at the fledging stage (7.57 vs. 5.11 fledglings per pair). In addition, the proportion of pairs raising a second brood is somewhat higher in the Blue Tit, in contrast to the situation in Central Europe.

Another striking feature of the results is the slightly higher proportion of first-breeders among the females, which implies higher mortality of adult females than adult males. This is noticeable in both species. Although not statistically significant, the difference in mortality between the sexes is most likely real. It is in agreement with an earlier finding that in the winter population of the Great Tit in the same area the sex ratio is about equal among juveniles but significantly skewed towards males among adults (Hildén 1978). Higher annual mortality of females, compared with that of males, has also been found in Holland (Kluyver 1951), England (Bulmer & Perrins 1973, Greenwood et al. 1979) and N Finland (Orell & Ojanen 1979).

The reasons for this difference in mortality between the sexes could be the heavier physiological demands on the female caused by egg-laying, incubation and brooding, and perhaps also her greater susceptibility to predators during the breeding season. Furthermore, the

TABLE 1. Proportion of 1-year-old birds in a nesting population of Great Tits and Blue Tits studied in southern Finland in 1972—82.

Year	*Parus major*				*P. caeruleus*			
	Females		Males		Females		Males	
	No. of birds checked	Percentage yearlings	No. of birds checked	Percentage yearlings	No. of birds checked	Percentage yearlings	No. of birds checked	Percentage yearlings
1972	54	39	28	36	17	65	14	43
1973	86	59	30	63	38	66	19	53
1974	88	45	19	21	11	64	6	67
1975	76	42	26	42	17	59	13	69
1976	86	55	27	30	22	86	19	68
1977	47	32	19	42	17	71	12	33
1978	61	51	35	44	24	58	19	47
1979	69	52	45	53	27	63	20	70
1980	57	60	31	65	40	50	25	60
1981	58	64	9	44	36	61	16	63
1982	41	39	24	29	20	25	17	53
Total	723	49.8	293	44.7	269	60.2	180	57.2

females, being smaller in size, lose a significantly higher percentage of their weight during a winter night than do the males, which could lead to heavier winter mortality among females (Hildén 1977). Indeed, the percentage of females in the population was found to decrease by 2 % during the winter (Hildén 1978).

The death rates of Great Tits (44 % for males, 52 % for females) obtained in England were based on annual checks of ringed individuals (Bulmer & Perrins 1973). The fact that my results (45 % for males, 50 % for females) are very similar is strong evidence for the reliability of the method of estimating adult mortality from the proportion of first-breeders in breeding populations. Other studies of Great Tits, based either on long-term population studies or on recovery statistics of ringed birds, have yielded mortalities of the same magnitude: 46 % in Switzerland (Plattner & Sutter 1947), 46 % for males and 52 % for females in Holland (Kluyver 1951), 44 % in Finland (Haukioja 1969), 49 % for males and 52 % for females in N Finland (Orell & Ojanen 1979) and 48 % in Denmark (Frederiksen & Larsen 1980).

Our skill in ageing birds, even in the breeding season, by means of slight differences in the colour, shape or wear of certain feathers, has greatly improved in recent years. The simple method of estimating the annual mortality described above could thus be applied to a number of species, both in the field and in museum collections.

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Selostus: **Nuorten lintujen osuus aikuiskuolleisuuden mittana tali- ja sinitiaisen pesimäkannoissa**

Lintujen keskimääräistä vuosikuolevuutta tutkitaan yleensä rengastuksen avulla. Koska nuoret linnut korvaavat vuosittain vanhojen poistuman, on toisena mahdollisuutena selvittää useana peräkkäisenä vuonna ensipesijöiden osuus kannassa. Menetelmän käyttö edellyttää, että ensipesijät ovat tunnistettavissa, että vanhat linnut pysyvät paikkauskollisina ja että kannan suuruus ei muutu tutkimuskauden aikana huomattavasti. Täten on arvioitu aikuisten vuosikuolevuus eräässä tali- ja sinitiaiskannassa Kirkkonummella 1972—82.

Pesivistä naaraista on kontrolloitu keskimäärin yli 90 %, koiraista niiden hankalamman pyydystettävyyden takia vain 39 % (talitiainen) ja 65 % (sinitiainen). Tulosten mukaan (taul. 1) sinitiaisen vuosittainen aikuiskuolleisuus on huomattavasti suurempi kuin talitiaisen (keskimäärin 58.7 ja 47.3 %), vastaten sen suurempaa syntyvyyttä. Kummallakin lajilla naaraiden kuolevuus näyttää olevan hieman korkeampi kuin koiraiden, mikä on todettu myös muualla. Syynä saattaa olla naa-

raiden suurempi rasitus ja alttius vihollisille pesimäaikana sekä niiden pienemmästä koosta aiheutuva heikompi talvenkestävyys.

Rengastusaineistoihin perustuvat tulokset talitiaisen vuosikuolevuudesta Englannissa, Hollannissa, Sveitsissä, Tanskassa ja Suomessa ovat päätyneet hyvin samanlaisiin arvoihin, mikä tukee ensipesijöiden osuuden käyttökelpoisuutta aikuiskuolleisuuden mittana. Menetelmä sopisi epäilemättä moniin lajeihin.

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Constancy of breeding performance of the Pied Flycatcher *Ficedula hypoleuca* in different habitats and nest-boxes in Finnish Lapland

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In this preliminary note we examine the relationship between habitat and the breeding performance of the Pied Flycatcher at the northern limit of the species range. At Kilpisjärvi in NW Finnish Lapland (69°03′N, 20°50′E), a nest-box study has been in progress since 1966 (e.g. Järvinen 1980). There have been about 150 nest-boxes annually, in a variety of habitats in mountain birch woodland. Since the population of hole-nesters is relatively sparse and fluctuates extensively, the same boxes are not occupied each year. Although some boxes have clearly been preferred to others during the 16 study years, only three of them have been occupied by the Pied Flycatcher so often that, for instance, it is possible to calculate nest-box productivity reliably.

The three boxes (nos. 147, 148 and 149) were situated linearly in mountain birch woodland about 150 m apart, and their exposure, altitude, and height above the ground were the same. Number 147 was in an open and relatively unproductive wood with a poorly developed bush layer, whereas numbers 148 and 149 were in closed and relatively productive woods with a thick bush layer. All three boxes were of the same type. In making pair-wise comparisons, only the same years were considered ($N = 9$). Each year different females bred in the boxes, so the results were not influenced by the constancy of the breeding performance of the same female.

The onset of laying was significantly earlier (2 days) in box 147 in an open birch wood than in box 148 in a closed birch wood, while there was no difference between the two boxes situated in the closed birch woods (nos. 148 and 149, Table 1).

At Kilpisjärvi productive and unproductive birch woods form a mosaic with patches of some tens or hundreds of square metres. Since the Pied Flycatcher forages in a wider area than this, it is unlikely that differences in food abundance between the habitats were responsible for the observed difference in the date of laying. It is more probable that the phenological state of the wood plays a role: open and