# Key-factor analyses of two Finnish hole-nesting passerines: comparisons between species and regions

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Demographic data on the pied flycatcher *Ficedula hypoleuca* (a southern species; 1967–82) and the redstart *Phoenicurus phoenicurus* (a northern species; 1969–82) in northern Finnish Lapland is key-factor analysed. The mortality factors included were: clutch size reduction, hatching failure, nestling mortality and mortality outside the nesting season. The results on the pied flycatcher in the north are compared with a similar analysis performed in southern Finland (Virolainen 1984). In the north the most important mortality factor of both species was mortality outside the nesting season, which seemed to be density-dependent. Mortality during the nesting season was density-independent. In the south and in the north the relative importance of the different mortality factors was remarkably similar in the pied flycatcher, although in the north hatching failure was a relatively more important factor than in the south; in the south polygyny, which is rare in the north, was an important density-dependent regulatory factor. Both in the south and in the north nestling mortality of the pied flycatcher was significantly and positively correlated with mortality outside the nesting season.

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## 1. Introduction

I analyse demographic data of a southern species, the pied flycatcher *Ficedula hypoleuca,* from the northern limit of its range (northern Finnish Lapland) and compare the results with a similar study performed in the central distribution area of the species (southern Finland; Virolainen 1984). From the north I also present demographic data on a northern species, the redstart *Phoenicurus phoenicurus.* Both the pied flycatcher and the redstart are migrants. One aim is to find out the importance of density-dependent and density-independent mortality during and outside the nesting season. Some studies have demonstrated that the mortality of passerines may be density-dependent during the nesting season but density-independent outside the nesting season (Krebs 1970), whereas the opposite has been shown in other studies (Orell & Ojanen 1983a, b, McCleery & Perrins 1985).

This study is mostly based on key-factor analysis (Varley & Gradwell 1960, Podoler & Rogers 1975, Southwood 1978), which allows one to weigh up the significance of each of the various mortality factors, and to distinguish between factors that are crucial in determining the total mortality-rate, factors that are crucial in determining fluctuations in mortality-rate, and factors that are crucial in the regulation of a local population (density dependence).

## 2. Study areas, materials and methods

The data from northern Finnish Lapland (about 69°03′N, 20°50′E) were collected in 1967–1982 (pied flycatcher) and in 1969–1982 (redstart). During these periods the number of nest-boxes suitable for each species was nearly constant (100 boxes for the pied flycatcher, 70 boxes for the redstart). All the nests were in nest-boxes in mountain birch woods about 480–600 m above sea level. The number of pied flycatcher pairs varied annually between 8 and 57 (mean 29±14 pairs, *SD*; *CV*=47 %), the corresponding range for the redstart being 4–20 pairs (mean 10±5 pairs, *CV*=55 %). I have earlier published more details of the study area in northern Lapland, as well as given data on the status and densities of the species (Järvinen 1983). All the figures presented on population numbers (number of nesting pairs, number of eggs laid, number of hatchlings and fledglings) are based on direct counts.

From southern Finland (60°15′N, 24°18′E) Virolainen (1984) has published nesting data for a nest-box population of pied flycatchers. His study period almost coincides with that in northern Lapland (1972–1983). The woods in this area are mainly coniferous with a mixture of deciduous trees. The number of pied flycatcher pairs in the total number of 158 nest-boxes varied annually between 40 and 101 (mean 67±19 pairs, *CV*=28 %). In the north some redstarts, but apparently no pied flycatchers, nested in natural nest sites within the study area (own observations). In the south no cases of nesting in natural cavities were observed (Virolainen 1984). In both areas the age structure of the nesting populations was unknown.

During the study periods the mean daily air temperature in the summer months was 6–8°C higher in southern Finland than in northern Lapland (calculations based on monthly means, ± 1 *SD*):

|  | May | June | July |
|---|---|---|---|
| Southern Finland (*n*=12) | +9.6±1.5 | 14.2±1.7 | 16.3±1.7 |
| Northern Lapland (*n*=16) | +1.2±1.2 | 7.5±2.2 | 10.8±1.6 |

The mean dates (±*SD*) of laying of the first egg in the populations, calculated from the annual means, were as follows:

| Pied flycatcher, N Lapland | 13 June ± 4 days |
|---|---|
| Redstart, N Lapland | 8 June ± 4 days |
| Pied flycatcher, S Finland | 29 May ± 4 days |

In analysing the data I, like Virolainen (1984), have used the method developed by Varley & Gradwell (1960). This method expresses the "killing power" (*k*-value) of mortality factors as: *k*-value = log(initial numbers)–log(survivors). The starting point of the analysis is the maximum potential natality of the populations, i.e. the number of reproducing females multiplied by the maximum mean fecundity per female. In Lapland 6.5 eggs was considered the maximum potential clutch of the pied flycatcher, and 7.3 eggs for the redstart. These figures are constants and their values do not affect the analyses (Virolainen 1984 used 7.0 eggs for the pied flycatcher).

The following mortality factors were calculated (Krebs 1970):

*Clutch size reduction:*
$k1$ = log((potential max. clutch +2)$N$/ (observed clutch +2)$N$). The addition of two is to allow for the presence of adults in the populations.

*Hatching failure*:
$k2$ = log((clutch +2)$N$/(hatchlings +2)$N$).

*Nestling mortality*:
$k3$ = log((hatchlings +2)$N$/ (fledglings +2)$N$).

*Mortality outside the nesting season:*
$k4$ = log((fledglings +2)$N$/(next year's nesting population)).
$k4$ is better called "loss of young and adults between fledging and next spring" because it includes immigration to and emigration from an area. The total generation mortality, $K$, is obtained by summing the individual *k*-values.

## 3. Results

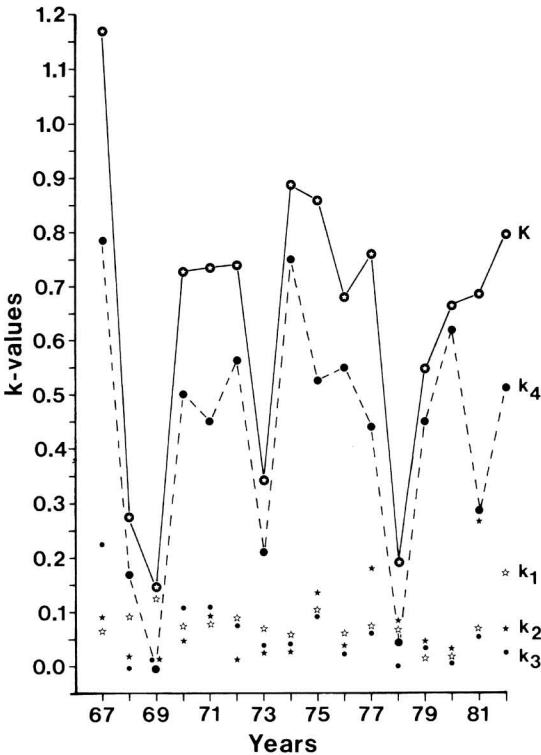In Figs. 1 (pied flycatcher) and 2 (redstart) the different mortality factors (*k*1–*k*4) and the total mor-



Fig. 1. Key factor analysis of population data on the pied flycatcher in northern Lapland in 1967–82. *k*1=clutch size reduction, *k*2=hatching failure, *k*3=nestling mortality, *k*4=mortality outside the nesting season, *K*=total mortality.
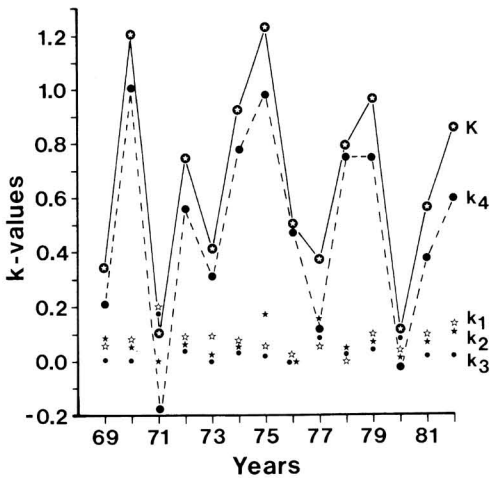


Fig. 2. Key factor analysis of population data on the redstart in northern Lapland in 1969–82. For legend, see Fig. 1.

tality ($K$) are plotted against years in northern Lapland. It is evident that $k4$, mortality outside the nesting season, has the largest submortality and parallels most closely to $K$. The mean $k$-values presented in Tables 1 and 2 also indicate that $k4$ is the most important factor in determining population size in northern Lapland: on average $k4$ comprises 67 % of $K$ in the pied flycatcher and 72 % in the redstart. However, this does not prove that this factor is the most important factor in determining changes in population size, because its effect on the mortality rate may be constant.

Tables 1 and 2 also give the regression coefficients of individual $k$-values on $K$ (individual $k$-values on the $y$-axis). As pointed out by Podoler & Rogers (1975), if a mortality factor is important in determining population change it will have a regression coefficient close to unity, because its $k$-value will tend to fluctuate parallel to $K$. $k4$ has the largest regression coefficient (0.773 in the pied flycatcher, 1.019 in the redstart), and hence it is the key factor causing population change. In the pied flycatcher hatching failure and nestling mortality have a reasonably high combined regression coefficient on $K$ ($k2 + k3 = 0.236$), but its relative importance is small compared with $k4$.

A standard method of examining the density-dependence of each mortality factor is to plot the $k$-values against the logarithm of the numbers present before the factor acted (Stubbs 1977, Southwood 1978). If the regression is significant, then density-dependence may be suspected. The slope and intercept, as well as the coefficient of determination of this analysis, are presented in Tables 1 and 2. $k4$ seems to be the only factor whose effect is density-dependent (in the pied flycatcher $r^2=24.2$ %, in the redstart $r^2=52.9$ %). It is also possible that nestling mortality, though not significant, plays some role in regulating the pied flycatcher ($r^2=11.0\%$) and the redstart ($r^2=25.1\%$) populations at Kilpisjärvi.

As the variables in the previous test are not independent, density-dependence must be tested further. When the regressions log survivors ($N_{t+1}$) on log summer population ($N_t$) and vice versa were calculated for the pied flycatcher, the slopes did not differ significantly from unity, which indicates that density-dependence is probably absent (Southwood 1978). However, in the pied flycatcher the size of the summer population is of apparent predictive, although not regulative, value since it explained 30 % ($P<0.05$) of the variance of the next summer's nesting population. In the redstart the slopes deviated more than in the pied flycatcher from unity ($P<0.1$), suggesting that density-dependence may be real.

From southern Finland Virolainen (1984) has published results of a key-factor analysis for the pied

Table 1. Summary of key-factor analysis for the pied flycatcher at Kilpisjärvi in 1967–1982. $b$ and $a$ are, respectively, the slope and intercept of the regression of each $k$-factor on the logarithm of the numbers preceding its action; $r^2$ is the coefficient of determination.

| Mortality factor | | Mean | Coefficient of regression on $K$ | Tests of density-dependence | | | |
| --- | --- | --- | --- | --- | --- | --- | --- |
| | | | | $b$ | $a$ | $r^2$ (%) | $P$ |
| Clutch size reduction | $K1$ | 0.078 | −0.006 | −0.031 | 0.149 | 3.4 | NS |
| Hatching failure | $k2$ | 0.073 | 0.079 | 0.005 | 0.062 | 0.0 | NS |
| Nesting mortality | $k3$ | 0.058 | 0.158 | 0.075 | −0.107 | 11.0 | NS |
| Non-breeding mortality | $k4$ | 0.431 | 0.773 | 0.471 | −0.573 | 24.2 | =0.05 |
| Total | $K$ | 0.640 | 1.004 | | | | |

Table 2. Summary of key-factor analysis for the redstart at Kilpisjärvi in 1969–1982. $b$ and $a$ are, respectively, the slope and intercept of the regression of each $k$-factor on the logarithm of the numbers preceding its action; $r^2$ is the coefficient of determination.

| Mortality factor | | Mean | Coefficient of regression on $K$ | Tests of density-dependence | | | |
| --- | --- | --- | --- | --- | --- | --- | --- |
| | | | | $b$ | $a$ | $r^2$ (%) | $P$ |
| Clutch size reduction | $k1$ | 0.072 | −0.009 | 0.041 | −0.004 | 5.7 | NS |
| Hatching failure | $k2$ | 0.065 | 0.049 | 0.054 | −0.032 | 8.9 | NS |
| Nestling mortality | $k3$ | 0.045 | −0.054 | −0.110 | 0.236 | 25.1 | <0.1 |
| Non-breeding mortality | $k4$ | 0.473 | 1.019 | 0.933 | −1.105 | 52.9 | <0.01 |
| Total | $K$ | 0.655 | 1.005 | | | | |

flycatcher. His study period coincides with that in northern Lapland, which allows comparisons of life-tables in very different conditions. The relative importance of different mortality factors is remarkably similar in the south and in the north (Table 3). Hatching failure was less important than nestling failure, these being less important than mortality outside the nesting season. Also the correlation coefficients between $k3$ and $K$ and between $k4$ and $K$ were equally high.

Both in the south and in the north nestling mortality of the pied flycatcher ($k3$) was significantly and positively correlated with mortality outside the nesting season (Table 4).

## 4. Discussion

The view that density-dependent processes are, in general, of secondary importance in the determination of population numbers is most commonly attributed to Andrewartha & Birch (1954). In the present study mortality outside the nesting season was possibly density–dependent. The pied flycatcher and the redstart are summer visitors to Kilpisjärvi, and so it is difficult to say when and where density-dependence occurs. Perhaps during the post-fledging period in late July and August, when the siblings still stay together, the amount of food is limited due to unfavourable weather conditions. An unfavourable nesting season is a stress also for the adults (Hildén et al. 1982, Järvinen 1983), which may reduce their expectation for further life.

Populations change in abundance because of the interactions of many factors, both density-dependent and density-independent. Even though the effects of abiotic environmental factors are accentuated in the north, it is unrealistic to suppose that any population is absolutely free from regulation (density-dependence). However, in the north, egg and nestling mortality due to cold weather may be considerable in some years (Järvinen 1983, Järvinen & Väisänen 1984). Thus, if we wished to predict the production (=abundance) of fledglings, weather would undoubtedly play an important role. In the north hatching failure and nestling mortality contributed clearly to the total mortality in the pied flycatcher, but their effects were density-independent (Table 1). The major components of losses in $k2$ and $k3$ are probably density-independent weather factors. It is suggestive that there is a significant relationship between $k2$ and temperature during the incubation period (an independent measure of the $k$-value; Järvinen 1983).

Table 3. The pied flycatcher in southern (Virolainen 1984) and northern Finland (present study). Correlation and regression coefficients ($b$) between the $k$-values ($y$) and the total $K$ ($x$).

| Mortality factor | $b$ | $r$ | $P$ |
|---|---|---|---|
| S Finland 1972–82 | | | |
| $k1$ | 0.037 | 0.346 | NS |
| $k2$ | 0.008 | 0.142 | NS |
| $k3$ | 0.317 | 0.799 | <0.01 |
| $k4$ | 0.638 | 0.953 | <0.001 |
| $K$ | 1.000 | | |
| N Finland 1967–82 | | | |
| $k1$ | −0.006 | −0.045 | NS |
| $k2$ | 0.079 | 0.308 | NS |
| $k3$ | 0.158 | 0.756 | <0.001 |
| $k4$ | 0.773 | 0.924 | <0.001 |
| $K$ | 1.004 | | |

Table 4. The pied flycatcher in southern (Virolainen 1984) and northern Finland (present study). Correlation between nestling mortality ($k3=x$) and mortality outside the nesting season ($k4=y$). $k4 = bk3 + a$.

| | S Finland 1972–82 | N Finland 1967–82 |
|---|---|---|
| $b$ | 1.030 | 2.353 |
| $a$ | 0.426 | 0.295 |
| $r$ | 0.604 | 0.586 |
| $P$ | <0.05 | <0.05 |

Krebs' (1970) key-factor analysis on a data set for the years 1947–1968 confirmed that clutch size ($k1$) and hatching success ($k2$) of the great tit *Parus major* are density-dependent in England. However, the key-factor, mortality outside the nesting season ($k4$), was apparently not density-dependent. The density-dependent effects of clutch size and hatching success were sufficient enough to regulate the population. However, when using a more recent data set (1964–1983) for the same species and area, McCleery & Perrins (1985) found that $k1$ and $k2$ were apparently density-independent, but $k4$ density-dependent.

There was no density-dependence of hatching failure or nestling mortality in the great tit or in the willow tit *Parus montanus* in the Oulu area in central Finland (65°N), but there was a significant positive correlation between mortality outside the nesting season and population size in the preceding summer (Orell & Ojanen 1983a, b). This suggested density-dependent reduction in the non-breeding population, although in the willow tit the regressions log survivors ($N_{t+1}$) on log summer population ($N_t$), and vice versa, did not verify this relationship (Orell &

Ojanen 1983b). The results obtained by Orell & Ojanen (1983a, b) in the north and Ekman (1984) in the south support the idea of density-dependent regulation in winter; it is important that this relationship seems to exist even at low densities in the north.

However, in the Oulu area density-dependent factors did not influence the reproductive output, in contrast to many studies conducted further south (Orell & Ojanen 1983a, b). The fact that weather, a density-independent factor, has a greater effect than density-dependent factors on the reproductive output in northern areas is in accordance with my earlier results (Järvinen 1983, Järvinen & Väisänen 1984) as well as with those of Orell & Ojanen (1983a, b).

Stubbs (1977) has described the strength and position in the life-cycle of any density-dependent mortality factor as that animal's "population regulation strategy". However, my data can only indicate that in the local populations in northern Lapland, mortality during the nesting season ($k2+k3$) apparently contributes more to the total mortality in the pied flycatcher than in the redstart (Tables 1 and 2). As a southern species which has comparatively recently started to nest in the north, the pied flycatcher suffers from the vicissitudes of cold northern weather (Järvinen 1983). Even though $k4$ seems to be the key factor in the north, and even though its effects may be density-dependent, it must be remembered that it also includes emigration from and immigration to the area. Thus the importance of $k4$ may be too high (emigration) or too low (immigration) in relation to mortality factors during the nesting season.

Due to disturbing external factors the mortality coefficients of the key-factor model may be unable to compensate for changes in density. For example, if spring weather is very cold, less pairs than expected will settle to nest in the north (Järvinen 1983) and their effect on population numbers is seen in the next year's estimate. In general, in the south the pied flycatcher and the redstart populations seem to fluctuate less than in the north (Järvinen 1983). In the redstart the model is also affected by sampling errors caused by the small number of nests in some years. The regression coefficient of $k4$ on summer population was close to unity (0.933, Table 2), which means that it should damp fluctuations. However, the redstart population fluctuated at Kilpisjärvi as much as the pied flycatcher population (see Sect. 2, $t=0.469$, $P> 0.5$) which suggests that in the redstart the obtained density-dependence of $k4$ is too high.

The pied flycatcher seems to be affected by similar factors in southern and northern Finland (Table 3). In both areas nest predation was low (c. 2% and 1% of nests were robbed in the south and north, respectively; Virolainen 1984, Järvinen 1980). In both areas between 2/3 and 3/4 of the total mortality was due to $k4$, and the correlation coefficients between $k3$ and $K$ and $k4$ and $K$ were almost equal (Table 3). Hatching failure in the north was relatively more important than in the south ($b=0.079$ and 0.008, respectively), whereas the reverse was apparently true for the nestling mortality. However, the relatively high nestling mortality in the south was mainly due to polygyny, which was the most important factor influencing nesting success, and it seemed to be an important density-dependent regulatory factor of population size (Virolainen 1984). In the north polygyny is less frequent in the pied flycatcher (Nyholm 1984, own observations) and thus its effects on population size are less important.

Both in the south and in the north nestling mortality of the pied flycatcher correlated positively with mortality outside the nesting season (Table 4). As pointed out by Virolainen (1984), this is probably due to an increase in the immediate postfledging mortality in years with poor nesting success (cold or late summer with undernourished nestlings) rather than to mortality later on in the non-breeding season. The observed lack of density-dependence during the nesting season may partly be due to masking effects of density-independent weather factors (Järvinen 1983, Virolainen 1984). In central Sweden density-dependent effects in the pied flycatcher were most marked in the year with unfavourable weather conditions, probably reducing food availability to nestlings (Alatalo & Lundberg 1984).

Young pied flycatchers nesting for the first time are not site-tenacious (e.g. Järvinen 1983) and they probably disperse widely. Thus all the pied flycatchers nesting in Finland may comprise only one population. Southern and northern pied flycatchers may also winter in the same areas under the same conditions which may contribute to the similarities found in the key-factor analyses. However, there was no significant correlation between the numbers of nesting pairs in the two areas in 1972–83 ($r=0.452$). The lack of a significant correlation was mainly due to years 1979–83; if these years are omitted, the correlation is significant ($r=0.871$, $P\approx0.01$).

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