# Is fat fit? — a field study of survival and fatness in the Great Tit, *Parus major* L.

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Three hypotheses are considered regarding the importance of fatness for winter survival in birds. 1) Birds fatter than average survive best (FIF hypothesis). 2) Birds of average fatness do best (AIF hypothesis). 3) Survival is independent of fatness (the null, or NIF, hypothesis). These three hypotheses were tested for the Great Tit in seven winters. Multiple estimates of fatness for the same individual correlated strongly, which indicated that fatness is a sufficiently constant individual measure for this analysis.

In most subsets (winter/age/sex) the null hypothesis (NIF) could not be refuted, which suggests that factors other than fat deposits are more important for winter survival. No support was obtained for the FIF hypothesis in within-winter analyses. The data for first-winter birds agreed with the AIF hypothesis in some winters, indicating that maintenance of high fatness level may be costly (increased predation risk?). The difference in survival between fat and lean birds correlated negatively with winter temperature. This indicates that the optimum fatness varies with winter severity, and fat birds will survive relatively better in the coldest winters. In the Great Tit the average fat level has little value as a measure of fitness. In this species with predictable food resources, behavioural adaptations which ensure daily replenishment of the subcutaneous fat reserves constitute the major adaptation for winter, not winter fattening as such. In species whose winter fattening is more pronounced, a clearer positive relationship probably exists between fatness and winter survival.

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## Introduction

The weight of north temperate passerine birds is usually highest in the winter, and it is natural to conclude that fatness increases an individual's chance of surviving the cold season. Fretwell (1968, 1969a, b) suggested that the visible fat score is a good index of fitness in the non-breeding period. King & Mewaldt (1981) considered that birds fatten to their maximum levels in winter. I will call these suggestions the FIF hypothesis ("fat is fit"). Another view was presented by Helms (1968), Helms & Smythe (1969), Blem (1975, 1976) and Stuebe & Ketterson (1982), who argued that "excessive" fatness can be maladaptive due either to increased predation risk or to the cost of carrying extra weight. I will term this the AIF hypothesis ("averagely fat is fit"). The third, or null hypothesis ("NIF"), will be that there is no difference in survival expectation between birds with different fatness levels.

There is no doubt that fat reserves are beneficial in fasting experiments of short duration (Brenner 1965, Ketterson & King 1977, Stuebe & Ketterson 1982). Baker & Fox (1978) showed experimentally that the survival of the Junco *Junco hyemalis* can be explained (in decreasing order of importance) by dominance, genotype, body weight (= fatness to some extent), etc. In Kikkawa's (1980) laboratory Silvereye flock *Zosterops lateralis,* the most subordinate individual lost weight and the dominant birds gained weight less than the intermediate birds. It may be difficult to extrapolate these results to the field, where birds are faced with more variable environmental challenges and a wider range of choices. I am familiar only with Fretwell's (1968, 1969a) studies of the Junco and the Field Sparrow *Spizella pusilla,* in which survival in the field was examined for some length of time in relation to fatness in passerines.

In this study I tested whether the winter survival of the Great Tit, *Parus major,* varied between fatness categories according to one or another of the above hypotheses. In addition, I studied the relationship between fatness and survival as a function of the severity of the winter.

## Material and methods

The data were collected on the island Ruissalo, Turku, in SW Finland (60°26'N, 22°10'E), in 1971–80. I regarded the birds caught in November–December as the initial population and their survival to March or later was studied in relation to their fat reserves. The birds were classified as surviving (S, caught after the beginning of March) and disappearing (D, not caught after February). It is clear that the D group is heterogeneous and contains birds which died and birds which survived but which I was unable to recapture. To reduce the importance of this bias, I included in the initial population only birds trapped at sites where netting was conducted through the winter (every month), spring and the next winter.

The Great Tits wintering on Ruissalo are very sedentary. In 1970–71, for example, only 17 % of the individuals (n = 910) were observed at more than one feeding site in January–March, although there were 19 feeding sites available, with the minimum distance of c. 400 metres. By November most of the emigration from the island has taken place and there is very little immigration into the island for the winter (Lehikoinen, unpubl.). Another factor increasing the probability of finding surviving birds is that each year hundreds of nest-boxes were inspected on the island and a large fraction of the adult birds were caught.

All weights were converted to standard morning weights ($W_m$). The standard morning weight, obtained from a regression model (Lehikoinen 1986a, 1987) gave the probable weight of the bird at the beginning of its daily activity period. The lean weight ($W_l$) of an individual was estimated as its spring morning weight standardised to a 10 h night length (8 April, i.e. the time when birds are leanest), and to zero visible fat score for the size (wing length) of the individual (Lehikoinen 1986a, 1987). The fatness index ($F_i$) used in this paper is:

$$F_i = 100\,(W_m - W_l)\,/\,W_m.$$

$F_i$ gives the minimum estimate of the amount of reserves available for the bird at the start of the daily activity period in winter.

Statistical tests were performed according to Sokal & Rohlf (1981), using self-written BASIC and FORTRAN programs and the BMDP program library (Dixon 1983).

## Results

The fat reserves of a Great Tit vary daily and seasonally. The fatness index is a meaningful individual character only if it is more than just a momentary index of the fat reserves. To check whether this is so, I examined the fatness indices of birds on which repeated determinations were made. Paired estimates of fatness of the same individual were highly significantly correlated throughout the winter (Table 1). The correlation was also significant between winters ($r = 0.403$, $P < 0.05$, $n = 30$). Therefore, the fatness index used here is suitable for grouping birds according to their fatness.

The morning weights and fatness indices in the initial population (Table 2) largely agree with earlier findings: the sex and age categories differ in weight (due to size dimorphism, e.g. Van Balen 1967, Haftorn 1976), but not in fatness (Lehikoinen 1986a). The variation among winters is pronounced, perhaps because the weather conditions in the early winter differed during the study period (cf. Haftorn 1976, Lehikoinen 1980). Because of this variation, I will first examine survival in relation to fatness separately for each winter and sex-age category.

Table 1. Correlations between repeat estimates of fatness indices made in early winter and between estimates made in early winter and January and February, for surviving (S), disappearing (D) and combined (C) birds grouped by sex–age categories. Significance of correlations given as * = P < 0.05, ** = P < 0.01, *** = P < 0.001. Number of observations given in parentheses.

| Sex-age | Nov–Dec vs Jan | | Nov–Dec vs Feb | | Nov vs Dec | |
|---|---|---|---|---|---|---|
| Ad male | | | | | | |
| S | 0.583*** | (46) | 0.368* | (30) | 0.574** | (27) |
| D | 0.283 ns | (33) | 0.576** | (22) | 0.457*** | (34) |
| C | 0.491*** | (79) | 0.448*** | (52) | 0.507*** | (61) |
| Ad female | | | | | | |
| S | 0.580*** | (33) | 0.648*** | (24) | 0.572* | (14) |
| D | 0.433* | (21) | 0.362 ns | (11) | 0.572*** | (38) |
| C | 0.543*** | (54) | 0.551*** | (35) | 0.585*** | (52) |
| Juv male | | | | | | |
| S | 0.457*** | (55) | 0.412* | (32) | 0.597*** | (35) |
| D | 0.281* | (64) | 0.400* | (32) | 0.333** | (72) |
| C | 0.359*** | (119) | 0.407*** | (64) | 0.414*** | (107) |
| Juv female | | | | | | |
| S | 0.657*** | (30) | 0.696* | (11) | 0.450* | (23) |
| D | 0.429* | (35) | 0.651*** | (28) | 0.453*** | (60) |
| C | 0.558*** | (65) | 0.637*** | (39) | 0.453*** | (83) |

Table 2. Winter (November–December) morning weights (g) and estimated fatness (as % of morning weight) in the Great Tit in the study period. Mean ± S.D. and (n).

| Winter | Ad male | | Juv male | | Ad female | | Juv female | |
|---|---|---|---|---|---|---|---|---|
| A. Morning weights | | | | | | | | |
| 71–72 | 19.9 ± 1.08 | (15) | 20.5 ± 1.16 | (21) | 18.9 ± 1.30 | (2) | 19.7 ± 1.41 | (14) |
| 72–73 | 20.0 ± 0.58 | (13) | 19.6 ± 0.97 | (32) | 18.7 ± 0.66 | (16) | 18.4 ± 1.18 | (27) |
| 73–74 | 20.1 ± 0.93 | (26) | 19.9 ± 1.14 | (41) | 18.9 ± 1.10 | (31) | 18.9 ± 0.96 | (35) |
| 74–75 | 18.9 ± 0.70 | (27) | 18.9 ± 0.79 | (57) | 17.9 ± 0.77 | (29) | 17.8 ± 0.72 | (50) |
| 76–77 | 19.5 ± 0.75 | (150) | 19.3 ± 0.88 | (178) | 18.3 ± 0.82 | (102) | 18.2 ± 0.99 | (115) |
| 77–78 | 19.1 ± 0.88 | (122) | 18.9 ± 0.85 | (67) | 17.8 ± 0.81 | (59) | 17.6 ± 0.88 | (48) |
| 78–79 | 19.3 ± 0.79 | (63) | 19.2 ± 0.80 | (129) | 17.8 ± 0.80 | (41) | 18.0 ± 0.92 | (98) |
| B. Fatness indices | | | | | | | | |
| 71–72 | 8.3 ± 4.57 | (14) | 12.0 ± 4.91 | (20) | 10.3 | (2) | 12.8 ± 5.77 | (14) |
| 72–73 | 8.6 ± 1.61 | (10) | 8.0 ± 4.19 | (32) | 6.9 ± 2.98 | (16) | 7.9 ± 4.77 | (21) |
| 73–74 | 9.3 ± 4.05 | (26) | 9.1 ± 4.91 | (40) | 9.0 ± 5.49 | (31) | 9.5 ± 4.31 | (34) |
| 74–75 | 3.1 ± 3.40 | (27) | 3.8 ± 3.85 | (56) | 4.0 ± 4.10 | (29) | 3.3 ± 3.74 | (50) |
| 76–77 | 6.4 ± 3.50 | (150) | 6.2 ± 4.05 | (178) | 6.4 ± 3.82 | (102) | 6.1 ± 4.76 | (115) |
| 77–78 | 4.8 ± 4.24 | (122) | 4.9 ± 3.78 | (67) | 4.6 ± 3.97 | (58) | 3.6 ± 4.49 | (48) |
| 78–79 | 5.9 ± 3.49 | (63) | 6.6 ± 4.03 | (129) | 4.7 ± 4.09 | (41) | 5.3 ± 4.41 | (96) |

*Is fat fit?*. Fatness showed no constant pattern when tested for each winter over the sex-age and survival categories with a two-way ANOVA (Table 3). In none of the winters did S and D birds in any sex-age category differ in morning reserves in the way predicted by the FIF hypothesis (Fig. 1). In winter 1978–79 survivors had larger morning reserves than non-survivors in first-winter females ($P < 0.05$, Student-Newman-Keuls test), but in view of the large number of paired comparisons, this single statistically significant result may well have arisen by chance.

A logical modification of FIF is that only the leanest birds have lower winter survival. To test this possibility, I divided the 27 initial sex/age groups in each winter into quartiles according to the fatness indices (in 1971–72 there were too few adult females for the analysis). I calculated the proportion of survivors (S birds) in each quartile and tested survival between the quartiles with the G test. There was just one significant interquartile difference: first-winter females in 1976–77 (Table 4). In this case the birds in the lowest fatness quartile had the poorest survival and the second lowest (or lower median) quartile the highest. In the other 26 cases, survival did not vary significantly among quartiles. When the data were divided into two groups — fat and lean birds — around the median value of fatness, there was not a single case supporting the FIF hypothesis (Table 5). In other words, the within-year analyses did not show better survival of fat birds. Consequently, the FIF hypothesis does not explain the variation in survival in the Great Tit.

Table 3. Two-way ANOVAs of the dependence of early winter fatness on sex-age grouping and winter survival. Winters in which the size of the initial sample was less than 100 were omitted.

| Winter (Error df) | Factor | df | F | P |
|---|---|---|---|---|
| 73–74 (154) | Group | 3 | 0.67 | ns |
| | Survival | 1 | 0.11 | ns |
| | Interaction | 3 | 0.75 | ns |
| 74–75 (123) | Group | 3 | 0.09 | ns |
| | Survival | 1 | 0.48 | ns |
| | Interaction | 3 | 0.76 | ns |
| 76–77 (537) | Group | 3 | 0.13 | ns |
| | Survival | 1 | 0.56 | ns |
| | Interaction | 3 | 1.27 | ns |
| 77–78 (287) | Group | 3 | 1.12 | ns |
| | Survival | 1 | 0.01 | ns |
| | Interaction | 3 | 0.38 | ns |
| 78–79 (281) | Group | 3 | 2.71 | <0.05 |
| | Survival | 1 | 0.04 | ns |
| | Interaction | 3 | 2.21 | <0.1 |

*Is the bird with average fatness fit?* To test the AIF hypothesis, I compared the survival of birds belonging to the two central (median ± 25 %) and the two marginal (= leanest and fattest 25 %) fatness quartiles within the 27 subsamples. In two cases the central and marginal groups differed significantly, birds of average fatness surviving better, and there were two more cases in which the probability was $P < 0.1$ (G test, Table 5). In one further case the survival difference was significant (at $P < 0.05$), but in the opposite direction, i.e. birds with marginal fatness survived better. The cases supporting the AIF hypothesis concerned first-winter birds (at $P < 0.05$).

Next I pooled S and D birds over the sex-age categories in each winter. The interquartile variation in survival was significant in winter 1972–73 (pooled G, columns at extreme right, Table 4, Fig. 2) but not in the others. From winter 1976–77 to winter 1978–79, the heterogeneity G value was significant, suggesting that the relation of survival to fatness varied between sex-age categories in these winters (cf. also Fig. 1). When I grouped birds in central and marginal halves instead of analysing them by quartiles, significantly higher survival was found in 1972–73 in the central birds but significantly lower survival in 1978–79 (Table 5). In other winters survival did

Table 4. Results of G tests for goodness of fit with $H_0$: Winter survival is independent of fatness in November–December. The initial population in each winter was divided into four groups at 25 % intervals (lower and upper quartiles and the median).

| Winter | Ad ♂ | Juv ♂ | Ad ♀ | Juv ♀ | Combined over categories Pooled | Heterog. | Total |
|---|---|---|---|---|---|---|---|
| 71–72 | 1.456 | 0.538 | .. | 2.109 | 0.752 | 3.360 | 4.112 |
| 72–73 | 0.115 | 10.298 | 0.355 | 0.811 | 9.183* | 2.396 | 11.579 |
| 73–74 | 0.688 | 5.694 | 1.038 | 0.034 | 1.895 | 5.559 | 7.454 |
| 74–75 | 3.460 | 2.455 | 1.620 | 2.372 | 5.151 | 4.756 | 9.907 |
| 76–77 | 4.479 | 1.093 | 1.401 | 8.958* | 2.425 | 13.506** | 15.931* |
| 77–78 | 2.782 | 2.851 | 2.863 | 5.996 | 2.679 | 11.813** | 14.492* |
| 78–79 | 1.479 | 3.437 | 1.613 | 5.633 | 4.556 | 7.606* | 12.162 |
| Combined over winters | | | | | | | |
| Pooled | 4.652 | 3.201 | 5.420 | 4.051 | 0.607 | 16.717 | 17.324 |
| Heterog. | 6.241 | 12.867* | 1.502 | 21.862** | 26.034*** | 75.030 | |
| Total | 10.893 | 16.068* | 6.922 | 25.913** | 26.641*** | | 75.637 |

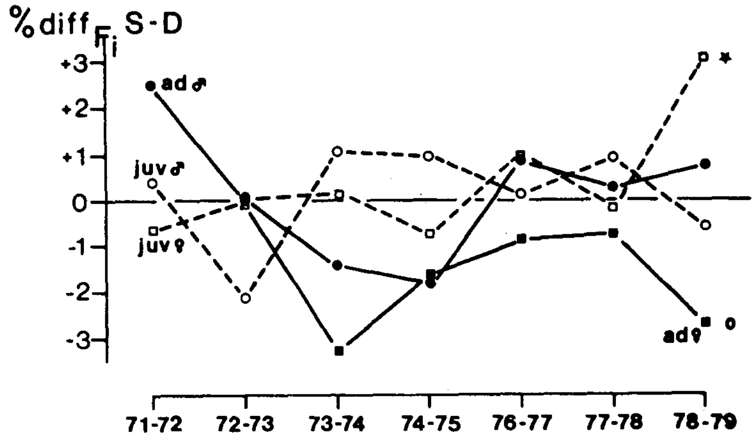


Fig. 1. Differences in percentage morning fatness between surviving and disappearing Great Tits grouped by winters and sex-age. See Table 3 for the results of two-way ANOVAs.

not differ significantly between median and marginal birds. Consequently, the relationship of survival to fatness in early winter varied between years.

Combining the data over winters in each sex-age category by quartiles or by central and marginal fatness groups yielded no significant value for pooled G (Table 4 bottom rows, Fig. 3). In first-winter males and females the heterogeneity G value was significant, while in adults it was not. The heterogeneity may indicate greater susceptibility to environmental constraints in first-winter birds.

Finally, I combined all subsamples by quartiles. The proportions of survivors were essentially the same in all fatness quartiles (Table 4 bottom-right corner, Fig. 3). Consequently, the present material does not indicate that the fattest birds survived better than leaner ones in the Great Tit. If there is any general dependence of survival on fatness, it approaches the AIF hypothesis and is restricted to birds in their first winter.

*Survival and fatness in relation to winter temperature.* As the relation of survival to fatness varied significantly between winters (heterogeneity G, Table 4) I analysed fatness and survival in relation to the severity of the winter. The survival difference between median and marginal birds ($S_{med}$–$S_{mar}$ in % units) correlated almost significantly with the mean temperature in January–February (Fig. 4). In moderate and mild winters median birds tended to survive better than marginal birds.

The survival difference between fat and lean birds ($S_{fat}$–$S_{lean}$ in % units) correlated significantly with the mean temperature (Fig. 5). The colder the winter, the better did fat birds survive when compared with the lean ones, but in none of the winters was their survival significantly better than in the lean ones.

The long-term average temperatures for January and February in my study area are –6.0°C and –6.6°C, respectively. These correspond to the temperatures at which the survival differences calculated above were zero. Therefore, in normal to warm winters median or leaner than median birds survived better than birds that were fatter than average. The benefit of early-winter fatness increased, however, with increasing severity of the winter.

I performed a similar analysis in the sex-age categories. The correlation of the survival difference between median and marginal birds ($S_{med}$–$S_{mar}$) with winter temperature was positive and statistically significant in first-winter males ($r = +0.872$, $P < 0.05$) and positive also in first-winter females ($r = +0.390$, ns), but close to zero in adults of both sexes. The survival difference between fat and lean birds ($S_{fat}$–$S_{lean}$) showed a statistically significant negative correlation

Table 5. Numbers of G tests supporting the null hypothesis or either of the alternative hypotheses (FIF, AIF) in tests in which the data were divided into two groups (fat vs lean at the median, and median vs marginal birds at lower and upper quartiles). The probability of making type-I error is given in cases in which one or more significant deviations from $H_0$ were observed at $P < 0.05$ and $P < 0.1$.

| | | Supported $H_1$ | | | | Probability of | |
|---|---|---|---|---|---|---|---|
| | | FIF | | AIF | | type I error at | |
| Risk level | | 5 % | 10 % | 5 % | 10 % | 5 % | 10 % |
| Ad male | $H_0$ | 7 | 7 | 7 | 7 | . | . |
| | $H_1$ | 0 | 0 | 0 | 0 | . | . |
| Ad female | $H_0$ | 6 | 6 | 6 | 5 | . | . |
| | $H_1$ | 0 | 0 | 0 | 1[1] | . | 0.469 |
| Juv male | $H_0$ | 7 | 7 | 6 | 5[2] | | |
| | $H_1$ | 0 | 0 | 1[3] | 2[4] | 0.302 | 0.150 |
| Juv female | $H_0$ | 7 | 7 | 6 | 6[5] | | |
| | $H_1$ | 0 | 0 | 1[6] | 1 | 0.302 | 0.522 |

The cases supporting $H_1$ numbered: 1 in 1972–73, 3 in 1972–73, 4 in 1973–74, 6 in 1976–77.
The cases in which the marginal groups survived significantly better than the median birds numbered: 2 in 1978–79, 5 in 1977–78.

Table 6. Change of fatness (mean ± S.E. in grams) from early winter (November–December) to January and February in surviving (S) and disappearing (D) birds grouped by sex-age. Sample sizes in parentheses. Paired comparisons ($P_s$ = tail probability in paired comparisons of surviving birds, $P_d$ = the same for disappearing birds) and ANOVA. $P_{sd}$ gives the probability of the difference between the average changes of surviving and disappearing birds. Winters combined.

| | S birds | $P_s$ | $P_{sd}$ | D birds | $P_d$ | Anova | df | F | P |
|---|---|---|---|---|---|---|---|---|---|
| To January | | | | | | | | | |
| Ad male | 0.09±0.125 (46) | .467 | .754 | 0.03±0.165 (35) | .868 | Sex-age category | 3 | 2.33 | 0.0740 |
| Ad female | 0.14±0.158 (33) | .363 | .757 | 0.22±0.171 (23) | .213 | Survival | 1 | 0.46 | 0.4960 |
| Juv male | −0.11±0.124 (57) | .363 | .415 | −0.27±0.139 (64) | .058 | Interaction | 3 | 0.21 | 0.8894 |
| Juv female | 0.12±0.172 (30) | .481 | .499 | −0.04±0.165 (36) | .809 | | | | |
| Combined | 0.04±0.070 (166) | .598 | .277 | −0.08±0.081 (158) | .331 | | | | |
| To February | | | | | | | | | |
| Ad male | −0.22±0.152 (30) | .154 | .245 | −0.48±0.154 (22) | .005 | Sex-age category | 3 | 0.13 | 0.9405 |
| Ad female | −0.25±0.146 (24) | .098 | .204 | −0.63±0.293 (12) | .054 | Survival | 1 | 5.29 | 0.0226 |
| Juv male | −0.32±0.154 (35) | .044 | .516 | −0.46±0.150 (32) | .004 | Interaction | 3 | 0.25 | 0.8627 |
| Juv female | −0.12±0.153 (11) | .435 | .144 | −0.52±0.151 (30) | .002 | | | | |
| Combined | −0.25±0.080 (100) | .002 | .030 | −0.51±0.084 (96) | .000 | | | | |

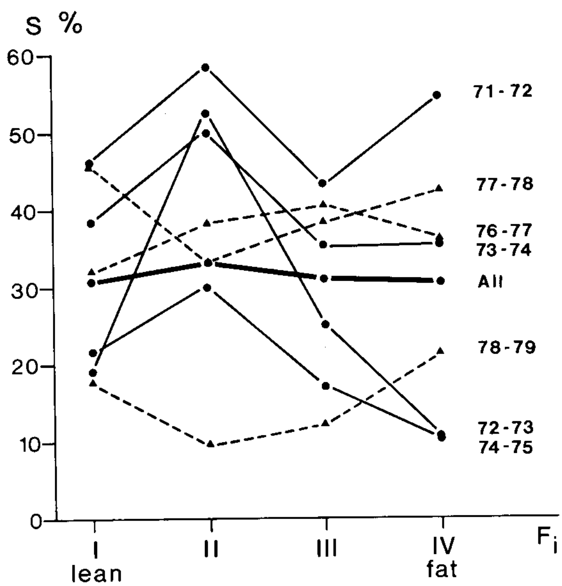


Fig. 2. Survival in relation to fatness quartiles in the data pooled over sex-age categories in different winters. Heavy line = combined data. The results of G tests for variation of survival among fatness groups are given in Table 4.

with temperature in adult males ($r = -0.788$, $P < 0.05$) and a negative correlation in first-winter birds of both sexes. Hence the better survival of median birds in average-to-mild winters seems to concern mainly first-winter birds. Indications that fat birds have higher survival in more severe winters were found in all the sex-age categories except adult females.

*Weight changes in surviving and disappearing birds.* Although fatness is an individual characteristic, which is maintained at the same level relative to other individuals (Table 2), it is also a momentary measure of the condition of the bird and varies with time. Surviving and disappearing birds differed in the way in which fatness changed through the winter. In paired comparisons between the fatness indices of the birds in the early winter period and later months (January and February) the D birds were found to lose more weight than the S birds. The difference was significant up to February (Table 6). Haftorn (1976) suggested that the decreasing trend in the weight of the Great Tit in late winter is due to starvation. This is probably not the whole explanation as the S birds also lost weight from January onwards. The decrease of fatness in late winter in S birds is a normal part of the winter weight cycle, which is regulated by the photoperiod and temperature (Lehikoinen 1986a). Disappearing birds, however, lost weight more. Studies on dominance in the Great Tit and other species (Baker & Fox 1978, Kikkawa 1980, Garnett 1981, Drent 1983) indicate that this difference may result from intraspecific competition.

## Discussion

In most cases the null hypothesis (NIF) that the survival probability of an individual Great Tit is independent of its fatness level in November–December could not be rejected. The FIF hypothesis was not supported in a single case. Therefore, Fretwell's (1969b) suggestion that the visible fat score could be used as a measure of individual fitness in the non-breeding period is invalid for the Great Tit. My results also indicate, in contrast to those of King & Mewaldt (1981), that some other fatness level than "maximal" is optimal for the bird in winter.

Acceptance of the null hypothesis in a strict sense would mean that individual fatness is of little or no adaptive value for overwintering, or that the individual fatness level is less important than other causes of disappearance (= mortality) in winter. There are other individual characteristics which may affect survival (size, Lehikoinen 1986b, behavioural traits, see below) and also causes of death, such as pathogens and predation, which are potentially unrelated to individual characteristics (but see below).

The relation of fatness to survival differed between the age and sex classes of the Great Tit. In adult Great Tits, the NIF hypothesis could not be rejected in a single case. Adults may be buffered against mortality linked with the fatness level, the buffer effect probably being produced by the dominance organisation in wintering groups of Great Tits, and by the acquaintance of adults with feeding opportunities within the home range. According to Saitou (1979) and Drent (1983), adults are always dominant over first-winter birds in winter flocks. Therefore, they need not maintain a high fat level in environments where the availability of food is sufficiently predictable. Alternatively, acceptance of the null hypothesis (NIF) indicates prior selection for fatness in adults. The causes of winter mortality in adult tits may be largely random.

In first-winter birds stabilising selection for fatness was observed in some winters, which supported the AIF hypothesis. The mechanism underlying the difference observed between adult and first-winter Great Tits could be that suggested by Helms (1968) and others, and reformulated below:

(1) The higher the fat level that the bird attempts to maintain,

(2) the larger will be the proportion of the daylight period during which it is feeding and

(3) at the same time vulnerable to predators.

(4) With a relatively reliable feeding location and especially if dominant, the bird may reduce its overall feeding time during the winter by not fattening excessively.

(5) First-winter birds have to use more time to achieve the same fatness level as older birds and

(6) also to carry the possible costs of suboptimal feeding times (De Laet 1985) and sites (Ekman et al. 1981, Ekman & Askenmo 1984).

Stuebe & Ketterson (1982) suggested that the cost of locomotion may be higher for fatter birds. Earlier, Blem (1975) argued that wing loading may set an upper limit to fat reserves. This drawback to fatness is unlikely to be important in the Great Tit, because the weight increases only moderately (5–7 % in average).

The correlations between the survival differences among fatness groups and the severity of the winter (Figs 4 and 5) indicated that optimum fatness varied with the environmental conditions. Higher than average fatness is important only in winters colder than average. In normal to warm winters survival is independent of fatness or, in first-winter birds, may be stabilising. In adults survival was independent of fatness in all conditions studied. The survival difference between fat and lean birds correlated negatively with the winter temperature in adult males, but not in adult females. This may indicate that territorial adult males do not use richer feeding stations outside the territory as readily as adult females. They perhaps tolerate some degree of trade-off between the expected benefit (during breeding) of their territory oc-

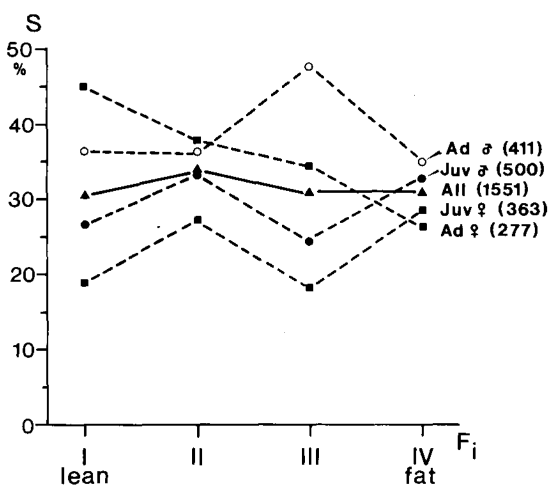


Fig. 3. Survival in relation to fatness quartiles in the data pooled over winters in different sex-age categories. Heavy line = combined data. The results of G tests for variation of survival among fatness groups are given in Table 4.

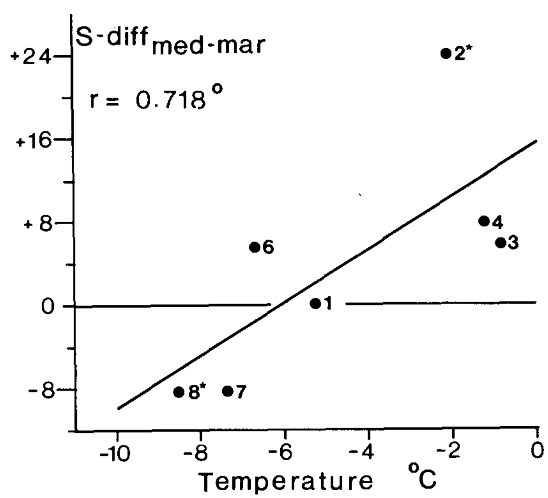


Fig. 4. The correlation of the survival difference between the median and marginal birds ($S\text{-diff}_{med\text{-}mar}$) with winter temperature (January–February).

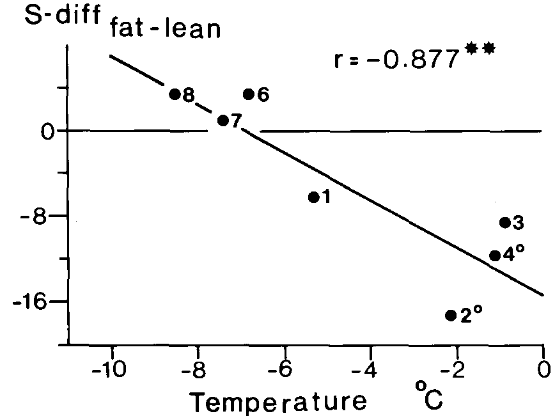


Fig. 5. The correlation of the survival difference between the fat and lean birds (S-diff$_{fat-lean}$) with winter temperature (January–February).

cupancy and winter survival. This interpretation is consistent with the order in which the sex-age categories leave their home range: first-winter birds, adult females and adult males (Lehikoinen, unpubl.).

The importance of winter fattening depends on the predictability of sources of daily food and varies between species (Lehikoinen 1986a). In some species survival is linearly related to fat deposits. In the Great Tit the reserves remaining after a night's roosting are small and the diurnal weight gain rate is adjusted seasonally to match the overnight loss rate. This variation of the daily weight cycle is more important to winter survival than winter fattening (Lehikoinen 1986a, 1987). Accordingly, behavioural adaptations which increase the likelihood of finding food daily are the primary adaptations for winter survival in the Great Tit, and in other species whose morning fat reserves are too low to allow survival without food for a further 24 hours (Lehikoinen 1986a). The species studied by Fretwell (1968, 1969a) belong to a group exploiting temporarily unavailable food resources and therefore carrying high subcutaneous fat reserves (Lehikoinen 1986a). A positive relationship could be expected between their fatness level and survival, and was in fact observed by Fretwell.

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Selostus: **Onko lihavalla talitiaisella talvella helppoa?**

Tässä tutkimuksessa tarkastellaan talvilihomisen merkitystä talvesta selviämisen kannalta. Tutkimus on tehty Turun Ruissalossa vuosina 1971–80. Aikaisempiin tutkimuksiin perustuen voidaan laatia kolme vaihtoehtoista hypoteesia: 1) lihavat menestyvät (FIF), 2) keskilihavat menestyvät (AIF) ja 3) lihavuus ei aiheuta (havaittavassa mitassa) yksilöiden välistä vaihtelua talvikuolevuuteen (NIF). Kun aineisto analysoitiin osaryhmissä, talvet ja sukupuoli-ikäluokat erikseen, ei yleensä voitu hylätä nollahypoteesia (NIF). Keskilihavien menestystä (AIF) osoittavia tuloksia saatiin parina talvena nuorten lintujen ryhmässä kun lihavien menestyksen puolesta todistavia tuloksia ei saatu lainkaan. Testien tulokset on esitetty taulukoissa 4 ja 5. Lihavuus ei ole kuitenkaan kokonaan vailla merkitystä mitä osoittaa se, että lihavat yksilöt selvisivät sitä paremmin mitä ankarampi talvi oli (Kuva 5).

Tulokset osoittavat, että yksi ominaisuus ei anna riittävää pohjaa ennustaa pitkän aikavälin yksilökohtaista elossa säilymistä. Käyttäytymissopeutumien joustavuus peittää todennäköisesti alleen yksinkertaiset suorat suhteet rakenteen ja seurausten välillä. Tässä tutkimuksessa käytetty lihavuus on lisäksi ominaisuus, johon lintu itse voi vaikuttaa ruokailuintensiteettiään muuttamalla. Se, että oletettavasti dominantit yksilöt lihovat talvella vain keskimääräisesti viittaa siihen, että ylenmääräinen lihavuus ei kannata. Lisäksi tulokset tukevat sitä ajatusta että talveen sopeuttavat käyttäytymismekanismit ovat keskeisempiä kuin rakennepiirteet sinänsä.

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