

Dependence of winter survival on size in the Great Tit *Parus major*

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An analysis was made of the selective effect of winter mortality on size in the Great Tit in seven winters. Selection differentials were in most winters small. There was a tendency to directional selection for large size in colder winters of the study period. This tendency was statistically significant in adult males, i.e. in the group that shows highest tendency to be sedentary year-round. In females similar trend of selection differentials in relation to the severity of winter was not observed, but a weak tendency towards a positive selection differential was present in first-winter females, on average. The observations can be explained by supposing that dominance system, physiological advantage of large size and total food requirement in relation to size interact. Small Great Tits have behavioural means to escape selection. A known possibility is to disperse for the winter to urban habitats, which are probably more benign. Other possibilities related to feeding behaviour (sites and timing) may well exist.

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Introduction

In seasonal environments birds are subject to seasonally and annually variable selection pressures. Most characteristics must be compromises, which on average predict 'best' performance over animal's lifetime. Within any shorter period in the annual cycle, however, it may be related in some causal way to individual characteristics, like size.

Size is a characteristic, which is believed to have been selected by both environmental selective factors and sexual selection. Ecogeographic trends in size are the rule in many bird species (e.g. Snow 1954) and sexual size dimorphism most widely is explained by competition over mates and/or territory ownership (e.g. Amadon 1949, Widén 1984).

Because annual mortality rates in passerine birds commonly are around 50 % (Perrins & Birkhead 1983), it might be argued that mortality in rather short time periods could depend on some characteristics of the individuals. A plausible hypothesis suggests that overwinter mortality is size dependent. Larger birds may be at an advantage over smaller ones in winter at least for two reasons: (1) large size is advantageous because energy loss is proportionately less from a larger body (e.g. Hamilton 1961, Calder 1974) and (2) large individuals are in many species dominant over small ones (e.g. Fretwell 1969, Garnett 1976, 1981, Baker & Fox 1978, Saitou 1979, Kikkawa 1980a,b, Järvi & Bakken 1984).

Directional selection during winter for large size was observed in male House Sparrows *Passer domesticus* by Johnston and co-workers (Johnston et al. 1972, Johnston & Fleischer 1981, Fleischer & Johnston 1984) in colder than average winters.

Stabilizing selection was suggested by Fretwell (1977) in the Junco *Junco hyemalis* and the Tree Sparrow *Spizella arborea* during winter (original data in Fretwell 1969, 1972). No published work exist for European species in which the possibility of size-dependence in winter survival has been considered.

The suggestion that large size is beneficial in winter is not unequivocal. Because total food intake is greater for large individuals, restrictions of food resources available may counteract the benefits (e.g. Fretwell 1972). On the other hand, relations between size, physiology and available food resources, as modelled e.g. by Fretwell (1972), may be related to dominance. If the size-dominance relationship is strong, the benefit of large size may still be realized in a food-limited situation. Murphy (1981) observed that in the House Sparrow in a mild winter larger males did not survive better, which suggested that optimum body size varies from winter to winter.

I consider in the present paper the relationship between winter disappearance (largely mortality) and size in a Great Tit population in SW-Finland. I show that the effect of winter mortality on the size distribution of birds varies among winters, sexes and age-groups, and that, on average, the net result is stability of size over time.

Material and methods

The present study is based on field work performed on Ruissalo island, Turku, SW-Finland (60° 26' N, 22° 10' E) in 1971–1980 (see Lehikoinen 1986). Because trapping began only in January in 1975–76 I did not analyse survival in this winter. Likewise, data for 1979–80 is neglected, because the period during which survival of individual birds

could be observed was not equivalent to that in earlier winters. The observations during these years are, however, used to yield survival observations of birds from earlier winters.

I caught birds (11 005 net-hours in 1971–80) at feeding sites from October–November to March–May each winter. From 1974 on I measured all the tits as reported in Lehtikoinen (1986). In the first three winters only a proportion of the Great Tits were measured.

Normal mean temperatures in January and February in Turku are -6.0°C and -6.6°C , respectively. Winter 1971–72 was about normal as to temperature and snow conditions. It was followed by three mild winters (1972–73 to 1974–75). The three last study winters were slightly or considerably colder than normal. Thus the study winters could be grouped into 'severe' (1971–72, 1976–77...1978–79) and 'mild' winters.

For the present analysis I used the birds which were trapped in November–December (= the initial population, Table 1). The purpose of this restriction was to minimize the effect of seasonal movements, which in autumn extend to late October and early November. Hence, survival in the present study is estimated only for that part of the population which stays within its home area year round. In practice, the initial population is completely autochthonous (Lehtikoinen, unpubl.). The future destiny of these individuals was checked from all evidence available (later netting in the non-breeding period, nest-box inspections during breeding, recoveries). A winter survivor was an individual observed alive after March 1. This date was selected because the reorganisation of breeding territories commences in March (in the exceptionally warm spring 1975 even earlier). I did not correct for the annually variable trapping efficiency, because the correction would only concern the levels of indices not the differences in them within any one winter.

Standard wing length. I used wing length as a measure of overall size. It is highly correlated with other size variables in the Great Tit (Lehtikoinen, unpubl.). It was also one of the variables loading significantly on the size axis in House Sparrow analyses by Johnston (e.g. Johnston & Selander 1973). Yet, various objections have been presented about its validity: 1) structure of wing varies independent of size, 2) feathers wear with time, 3) wing length depends on age, 4) wing length depends on sex, 5) interobserver variance may be large and 6) wing length may vary between years. I avoided objections 2 to 5 by treating the sex-age categories separately and standardising the wing length as follows:

$$WI_i = WI_i + b_w \times D + \text{Diff}_{AB}, \text{ where}$$

WI_i = observed wing length of individual i , b_w = rate of primary wear/day in the group concerned, D = days from January 1, and Diff_{AB} = error deviation of observer B_i from author A .

Correction factors for observer deviation were of the order of 0.1 mm in all but one case (0.4 mm) and constant for the working period of each field assistant. Rate of wear was estimated by retrap measurements (Table 2). It depended on age and to a lesser extent on sex during winter months (cf. Van Balen 1967). When several measurements were available through a winter, the mean of WI_i was used. Problems arising from objection 1 are probably minimal, because most of size-independent variation in wing length is linked with sex and age within any one population. Objection 6 is irrelevant in analyses where survival within any one winter is the object of study. When pooling the data over winters I avoided this problem by using z-scores of wing lengths determined by intra-winter wing length distributions instead of wing lengths as such.

The above standardisation procedure makes wing length a valid measure of overall size. When large samples of live birds are collected in harsh conditions and in a limited time it is often impossible to take more than two or three measurements (in addition to measuring wing lengths, I also weighed the birds and determined the visible fat, Lehtikoinen 1986). Because of considerable diurnal and seasonal variation of the energetic component of weight I did not use it as a size measure at all (see also Murphy 1981).

Results

Statistics on the wing lengths of the initial Great Tit populations each winter are given in Table 3. In all cases wing length distributions of the initial winter population were normal (7 winters, 4 sex-age categories) although a slight tendency towards negative skewness (skewed to left) and platykurtosis can be observed in the distributions of these values. The observation of Perrins (1965) as re-evaluated by Garnett (1976, 1981) that larger young Great Tits survive better in their first summer and autumn cannot be verified by checking the normality of the wing length distribution in the early winter population. The slight tendencies towards non-normality may have arisen from size dependent movements as well (see also Källander, 1983, and a study on Ipswich Sparrow *Passerculus sandwichensis* by Ross & McLaren, 1981).

Wing length differences between age groups in each sex are statistically significant in all winters as are sex differences within the age groups. These group differences have been documented a number

Table 1. Efficiency of trapping and the size of the initial winter population by winters.

Winter	Netting sites	Netting hours in XI–XII	N of birds caught in XI–XII
1971–72	14	609	480
1972–73	5	105	194
1973–74	8	192	213
1974–75	5	116	170
1976–77	15	307	561
1977–78	15	239	331
1978–79	10	223	294

Table 2. Rate of wear of the wing tip in the Great Tit by sex and age category. The rate was estimated by regressing the change of wing length between two measuring occasions to time (in days) elapsed between them.

Group	Rate of wear (mm/d)			
	b	s_b	F	n
All	0.0023	0.00030	57.5	2442
Ad males	0.0005	..	0.3	363
Ad females	0.0022	0.00086	6.5	283
Juv males	0.0020	0.00046	19.5	1045
Juv females	0.0038	0.00057	45.6	688

Table 3. Wing length of the Great Tit by winter and sex-age category. In the lower part of the table the results of one-way ANOVA performed in each sex-age category over winters are given together with the results of Student–Newman–Keuls-tests SNK. The latter are given as groups of homogeneous annual means indicated by the last digit of the first year.

Winter	Juv male		Ad male		Juv female		Ad female	
	mean ± sd	n						
71–72	78.3 ± 1.59	63	80.6 ± 1.50	36	75.4 ± 1.20	35	77.2 ± 1.00	22
72–73	78.4 ± 1.46	41	80.9 ± 1.47	28	75.4 ± 2.17	24	78.0 ± 1.01	22
73–74	78.8 ± 1.40	61	80.9 ± 1.40	36	75.4 ± 1.32	53	77.3 ± 1.07	45
74–75	79.0 ± 1.36	60	81.4 ± 1.52	28	75.9 ± 1.09	52	77.2 ± 1.46	29
76–77	78.4 ± 1.33	180	80.9 ± 1.32	152	75.2 ± 1.65	122	77.3 ± 1.38	103
77–78	77.9 ± 1.37	73	80.4 ± 1.36	135	74.8 ± 1.39	55	76.4 ± 1.36	65
78–79	77.9 ± 1.43	130	80.7 ± 1.40	63	75.1 ± 1.38	96	76.5 ± 1.32	41
ANOVA								
F _{winter}	6.67		2.74		2.91		6.94	
P	< 0.001		< 0.05		< 0.01		< 0.001	
SNK	4 3 6 2 1		4 6 3 2 8 1		4 1 2 3		2 6 3 4 1	
(P > 0.05)	2 1 7 8		3 2 8 1 7		1 2 3 6 8 7		1 8 7	

of times (e.g. Kluijver 1939, Van Balen 1967). Wing length varied significantly among winters (ANOVA, Table 3). Variation was mainly due to longer average wing lengths in 1974–75 (Student–Newman–Keuls-test, Table 3).

One-way analyses of variance (ANOVAs) were performed to study whether survivors and non-survivors differed in size. I chose to keep sex-age-categories separate for the reasons given above and because it is not known which of the dominance factors (sex, age, size) reported to be important (e.g. Saitou 1979, Garnett 1976, 1981, Drent 1983) is of higher priority. ANOVAs were made separately for severe and mild winters and pooled over all winters (Table 4). The only case where survival-category affected wing length significantly was in adult males in severe winters. Survivors were larger than non-survivors in this subsample. Variance of wing length was smaller in survivors than non-survivors in all analyses, but in no case was the difference significant (Levene's test, Table 4). There was thus neither a general tendency towards enhanced overwinter survival by larger individuals nor strong indication for stabilizing selection.

I studied the relationship of survival and winter severity more closely by performing both one-way ANOVAs separately for each winter and by calculating correlation coefficients of 'selection differentials' (= difference of the means after and before the selection episode, here the winter, Arnold & Wade, 1984) and winter severity. Survivors were significantly larger in first-winter females in 1976–77, and in adult males and adult females in 1978–79 (Fig. 1). In three mild winters the selection differential varied randomly (survivors larger in 5 out of 12 cases), but in four colder winters there were 12 cases (out of 16) in which the selection differential was positive (Fig. 1). All selection differentials were, however, small. None of the sex-age-category means averaged over winters differed significantly from zero. The average selection differential (over sex-age-categories) was

significantly different from zero (t-test, $P < 0.05$) in 1978–79, but not in other winters. The average selection differentials in cold and mild winters differed at a significance level of $P < 0.1$ (t-test). Because of the large number of tests performed when approaching the problem in an annual basis the risk of accepting an incorrect alternative hypothesis is evident. However, the trend suggesting the benefit of large size in colder winters is evident in the negative correlations between selection differentials and average winter temperature in three of the four sex-age-categories (Fig. 1). That the correlation was statistically significant in adult males in particular, which is the subgroup having highest tendency to be sedentary year-round, is interesting. It raises the question of how much sedentary birds are willing to pay for their habit as an increased risk to die during winter.

Stabilizing selection was suggested by non-significant decrease of wing length variance of survivors in

Table 4. One-way ANOVAs of the relationship of wing length to survival (survivors vs. non-survivors) in the Great Tit in the whole data (all) and separately in severe (1971–72, 1976–77, 1977–78, 1978–79) and mild (1972–73, 1973–74, 1974–75) winters. The ANOVAs were made by z-scores of wing lengths calculated for each winter in order to remove year-effects. Levene's test is a test for equal variances in survivors and non-survivors.

Sex	Age	Winter weather	ANOVA		Levene's test (p)	
			F	p		
Male	Ad.	All	1.76	0.185	1,475	0.736
		Severe	4.58	0.033	1,383	0.743
		Mild	1.79	0.186	1,90	0.781
Male	Juv.	All	0.00	0.995	1,584	0.231
		Severe	0.46	0.497	1,422	0.363
		Mild	1.41	0.238	1,160	0.296
Female	Ad.	All	0.21	0.645	1,323	0.300
		Severe	0.33	0.566	1,227	0.705
		Mild	0.00	0.957	1,94	0.161
Female	Juv.	All	1.67	0.196	1,423	0.150
		Severe	0.96	0.327	1,291	0.468
		Mild	0.77	0.383	1,127	0.109

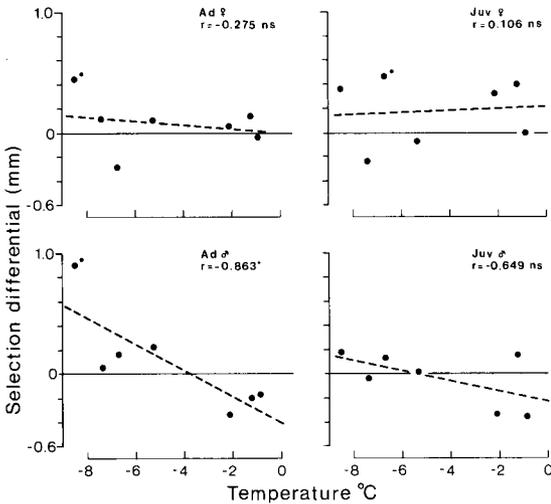


Fig. 1. Selection differentials in relation to average ambient temperature in January–February by sex-age-categories in the Great Tit *Parus major*. Selection differential is the difference between the mean wing length of survivors and that of the initial population. Samples, which differed significantly from 0 when tested singly at $P < 0.05$ and $P < 0.1$ are marked with * and °, respectively.

all sex-age-categories (Table 4). A closer analysis of stabilizing vs. random mortality in respect to wing length can be studied via another approach. I inspected the variability of survival between the size-groups by the following procedure. The wing length distributions of the initial population each winter were divided into quartiles within each sex-age category. Variation in numbers of survivors and disappearers between the quartiles were then compared by the G-test (log-likelihood ratio test, Sokal & Rohlf 1981).

When the data from all winters and sex-age-categories were treated together no significant difference in survival between size-groups was detected. This is not unexpected because winters are far from being alike. When I analysed survival distributions in severe and mild winters separately in different sex-age categories (Fig. 2), significant variability among size groups was present in both adult males and females in severe winters. In adult males the percentage of survivors increased with size category. In adult females highest survival was observed in size group II, i.e. birds just below the median size survived best. None of the survival distributions was clearly of reversed U-shape as expected for stabilizing selection.

Sample sizes for winters 1976–77 and 1977–78 were sufficient to analyse survival in each sex-age category within a single winter. Both winters were colder than average. In adults of both sexes and in both winters the survival rates were heterogeneous

as to size groups (G-test, $P < 0.05$ in males 1976–77, $P < 0.01$ in males 1977–78 and in females in both winters). In young birds of both sexes the survival rates were homogeneous except in juvenile females in 1976–77 ($P < 0.05$). The heterogeneity was only weakly due to a linear size-dependence.

When I combined the data over winters for each sex-age category, linear size-dependence of survival was suggestive in adult males and first-winter females — larger individuals showing higher survival probability. Both distributions were, however, non-significant (G-test, in adult males $p = 0.1615$, in first-winter females: $p = 0.5041$). In adult females and first-winter males, which fall between the former categories as to size, the survival probabilities were intermediate and varied non-linearly between the size-classes (G-test, in adult females $p = 0.0041$, in first-winter males $p = 0.7376$). In first-winter males medium-sized birds tended to survive better than both larger and smaller individuals. In adult females the survival pattern was erratic. Birds in quartile II survived best and those in the third quartile worst. On the whole, when plotted side-by-side against the average wing lengths of the categories, the survival values are ordered nearly linearly (Fig. 3) with the exceptions introduced by adult females and first-winter males. As sample sizes of severe winters were larger than those of mild winters the observed slight size-dependence in combined data is mainly due to them. In general winter survival seems to be rather independent on size. Differences in size-dependence of survival between sex-age categories appear to exist, but they are small and vary between winters (Fig. 1–2).

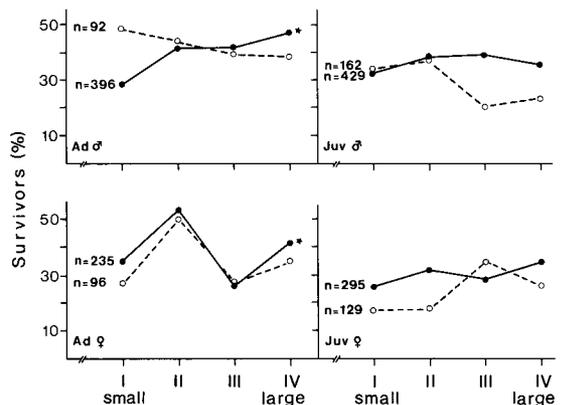


Fig. 2. Percentages of known survivors in relation to size class (I = small, IV = large) in mild (o---o) and severe (o—o) winters by sex-age categories. Significance of variation among size classes is indicated by * ($p < 0.05$) at the right end of the graphs.

Discussion

Johnston and co-workers observed that in the House Sparrow winter survival was size-dependent in males so that larger individuals were at a selective advantage (Johnston et al. 1972, Johnston & Fleischer 1981, Fleischer & Johnston 1984). Females, on the contrary, were subject to stabilizing selection. Rising (1972), Johnston (1976) and Murphy (1981) suggested that the direction of selection varies between winters. This suggestion was reinforced in a recent analysis by Fleischer & Johnston (1984), and, as for the Great Tit, in the present study. Only a few workers have attempted to look at the problem in other species. Fretwell (1977) stated that stabilizing selection was observable in his earlier data on the winter survival of the Junco (1969) and the Tree Sparrow (1972). His results are ambiguous, because in both studies sexes were pooled.

My results for the Great Tit parallel those of Johnston and co-workers. There is a tendency, admittedly a slight one, towards directional selection during some (cold) winters at least. No evidence in favour of stabilizing selection was detected. Rather winter mortality in other winters seemed to be even in all size groups (within any single sex-age category). This suggests that alternative behavioural tactics available for birds of different size even out the advantage of larger size (Fretwell 1972).

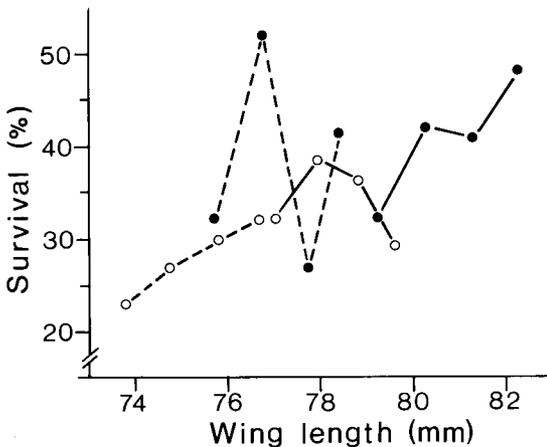


Fig. 3. Percentages of known survivors in relation to sex, age and wing length class in the combined data. Wing length classes defined separately for each sex-age category are plotted on a common x-axis at the mean wing lengths of the size class. Symbols used: adult males (●—●), first-winter males (○—○), adult females (●—●) and first-winter females (○—○). Note that the x-axis is not directly equivalent to the size axis because of the dependence of wing length on age.

The present analysis differs from that of Johnston's in some respects. Johnston used killed birds and thus removed his "prior-to-selection" sample from the population. This leaves one unaware of how autumn sampling might have affected the population parameters and individual overwinter survival probabilities. Another drawback in comparing two removal samples is that selection differentials remain more open to the effects of dispersal and sampling error variance. Live-trapping, as performed in this study, is of use as a check that the differences observed are not caused by removal trapping, although some practical complications are added. E.g. the present approach did not reach the accuracy level of Johnston, because I could use only one size measure and univariate methods. On the whole, the two approaches are complementary and both are needed.

Fleischer & Johnston (1984) discussed the mechanisms causing size-dependence in overwinter survival. Their conclusion was that a combination of physiological, behavioural and ecological pressures causes the observed changes. Direct observations of the importance of most of the suggested factors is lacking. I will discuss some of their suggestions further. Several studies of the role of dominance indicate that acquiring a high rank position depends partially on size. Evidence for this is extensive both in the Great Tit (Garnett 1976, 1981, Saitou 1979, Ulfstrand et al. 1981, Drent 1983, Järvi & Bakken 1984) and other passerines (Cink 1978, Baker & Fox 1978, Kikkawa 1980a,b). In addition to size several other correlates of high dominance are known or speculated to exist, both morphological and other, e.g. prior acquaintance or ownership of a particular site (site-related dominance), status signalled by morphological signs, fat score, age, sex and others. Because dominance depends on many simultaneous factors and previous events, it is hardly unexpected that no simple linear relation exists between survival expectation and size.

Reality of the physiological advantage of size has been criticised by e.g. Scholander (1955) in the context of explaining ecogeographic rules. According to him, intraspecific size differences are too small to be of importance. Mayr (1956), Hamilton (1961) and Murphy (1985) among others, regarded physiology as one plausible cause behind the clinal size trend known as Bergmann's rule. Yet, within the temperature range in my study area no additional effect of size on overnight weight loss was detectable after sexual size dimorphism was taken into account (Lehikoinen 1986). That is why directional selection for large size is not accounted for by physiological advantage alone.

I agree with Fleischer & Johnston (1984) that the effects of physiology, dominance and behavioural means of avoiding competitive effects are interrelated. The advantage of larger size can materialize only in that part of the population, which is relatively

free of intra- and interspecific competition for the limited food resources available in winter, i.e. the dominant individuals (see also Murphy 1985). Small subordinate individuals then, will have higher survival probability than large subordinates because of the reduced total energy requirement. This hypothesis may account for Johnston's observations of the House Sparrow and my own of the Great Tit.

The model for the evolution of optimum size in sparrows presented by Fretwell (1972) was based purely on physiological allometric functions (see also Calder 1974 for a technical comment). Therefore his approach is only a partial one. Observations of the House Sparrow (works of Johnston and others) and of the Great Tit favour the opinion that there is no single constant optimum size, but the optimum size will vary depending on environmental variability and relationships between individuals within the population.

The initial populations of adult and first-winter birds differ in one important respect. The older birds have been tested for their ability to survive over the winter at least once while first-winter birds have undergone the same test only via their parents. Therefore one might expect correlation of survival and size to be stronger in young birds (Lehtikoinen 1980). The sparrow studies referred to above cannot elucidate this subject, because the age-groups were inseparable in the spring samples. Average selection differentials in the first-winter birds did not differ from those of adults in both sexes in the Great Tit. Therefore one may deduce that all winter "tests" faced by earlier generations have already resulted in efficient selection towards an adapted mean size and variance. Even young birds will therefore not suffer from other than random mortality (or frequency-dependent selection) in respect to size during the winter unless the winter conditions deviate extremely from what has been experienced by previous generations.

The part of the tit population which remains in my study area for the whole winter is approximately a half to three quarters of the total autumn population in the natal/breeding area (Lehtikoinen, unpubl.). Much has taken place before November (see also Perrins 1979, Garnett 1981) with respect to the composition of the initial winter population. Therefore the selection differentials observed do not concern the whole population. Territoriality during autumn probably leads to a non-breeding organisation of the population in which dominant birds tend to remain within their territories, and the rest disperse (e.g. Drent 1983). There is some equivocal evidence that the dispersing birds are on average smaller than the stationary ones (Lehtikoinen, unpubl.). Dispersing birds may live in more benign environments, because they move to urban areas where food is not as limiting a resource (but predation may be higher) as in the breeding forests. The selection differentials in the

two parts of the population need not be the same either in direction or magnitude. So, subordinate small Great Tits have the opportunity to "escape" selection for size by leaving their natal area for the time of severe stringencies. For the House Sparrow such seasonal refuges are not available. Because of this difference, effects of selection may be more apparent in the House Sparrow. Other means of avoiding selection caused by dominance and competition may well exist e.g. as to the temporal and spatial pattern of feeding.

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Selostus: Talitiaisen talvikuolevuuden riippuvuus koosta.

Marras-joulukuussa rengastettujen (taul. 1) talitiaisten elossa säilymistä seuraavaan maaliskuuhun asti tutkittiin seitsemän talvikautena Turun Ruissalossa. Elossasäilyvyyden riippuvuutta koosta tutkittiin käyttämällä koon mitana standardoitua siiven pituutta. Se saatiin poistamalla siivenkärkien kulumisesta (taul. 2) ja eri mittaajista johtuvat systemaattiset virheet. Vuosien välisen vaihtelun vaikutus poistettiin käyttämällä kunkin vuoden sisällä laskettuja normoituja arvoja. Kokoon perustuva valikoiva kuolevuus osoittautui yleisesti ottaen vähäiseksi, sillä elossa säilyneiden yksilöiden siiven pituus ei yleensä eronnut merkitsevästi lähtöpopulaation arvosta. Suuren koon valintaetu näyttää riippuvan talven ankaruudesta koirailta, sillä sekä vanhoilla että nuorilla koirilla siiven pituuden keskiarvon muutos korreloi negatiivisesti talvilämpötilaan (vanhoilla tilastollisesti merkitsevästi, kuva 1). Naarailta ei tätä suhdetta ollut havaittavissa. Jaettaessa kunkin vuoden aineisto yhtä suuriin siivenpituusluokkiin (kokoluokkiin) ilmeni, että varsinkin kylmimpinä talvina pienimmän neljänneksen elossasäilyvyys oli alhaisempi.

Tulokset voidaan ymmärtää siten, että kokoon kohdistuva valinta on suuren koon tuottaman edun, siitä aiheutuvan suuremman ravinnon kokonaistarpeen sekä koon ja populaation sisäisten dominanssisuhteiden yhteisvaikutuksen tulosta. Havaitut suuntaukset ovat samankaltaisia kuin ai-noalla tämän kysymyksen suhteen perusteellisemmin tutkitulla lajilla, varpusella (sukupuolten välinen ero, suhde talven ankaruuteen, valinnan lievyys). Toisin kuin varpusilla, kokonsa ja dominanssiasemansa suhteen heikossa asemassa olevilla talitiaisyksilöillä on mahdollisuus siirtyä jo ennen talven tuloa ympäristöihin, joissa talven yli selviäminen onnistuu varmemmin. Tähän karstiksi tulemisen välttämismahdollisuuteen perustuen selittynevät sukupuoli- ja ikäryhmien väliset erot tuloksissa, sillä talitiaiskoiraat, erityisesti vanhat, ovat haluttomimpia jättämään reviirinsä syksyllä.

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