

Heritability of body size in a natural population of the Great Tit (*Parus major*) and its relation to age and environmental conditions during growth

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Summary

We have analysed data on weight and tarsus length collected during a long-term study of natural populations of Great Tits to evaluate the relative importance of genetic variation in body size. Some of our data were collected over a 25-year period, and therefore include a relatively large sample of naturally occurring environmental conditions. An overall heritability estimate calculated from the uncorrected mean weights of breeding birds amounts to 0.5. This estimate is unlikely to be influenced by resemblance in environmental conditions between relatives. Heritability estimates based on the size of fledglings vary between zero and the value for adults, depending on the environmental conditions during growth. If the feeding conditions for the nestlings are poor, no resemblance between parents and offspring is observed. Selection against small nestlings acts strongly on the environmental variance. This is concluded from the higher heritability estimates in the same cohorts after survival for at least three months after fledging, compared to measurements on nestlings. Such selection acting differentially on the genetic and environmental components of the phenotypic variance has important consequences for our ability to make predictions of phenotypic change from measured natural selection. Nevertheless, the amount of genetic variation would allow rapid response should selection on adult size occur.

1. Introduction

Body size is interesting from a genetic as well as from an ecological point of view. In many ways it reflects the place of a species in the web of life. It plays a central role in ecological theory. Body size is moulded by natural selection, generated by both abiotic and biotic factors in the environment. Within species, differences in body size are often found between geographical races. In birds, such differences are sometimes related to environmental gradients, such as, for example, in Bergman's rule to temperature (e.g. Snow, 1954). It has been shown that differences in body size between populations can evolve quickly: geographical differences in the House Sparrow (*Passer domesticus*) evolved in the hundred years since their introduction to North America (Johnston, 1973). An explanation in terms of evolution of genetic differences between populations implies the presence of genetic variability within populations.

Only recently has biometrical genetic analysis been

applied to quantitative characters in natural populations. We reported on several characters of ecological importance in the Great Tit *Parus major* (van Noordwijk *et al.* 1980). We found heritabilities of ca. 0.4 for clutch size (van Noordwijk *et al.* 1981a), ca. 0.7 for egg size (van Noordwijk *et al.* 1981b) and ca. 0.3 for date of first egg laying (van Noordwijk *et al.* 1981c). Other studies suggest that a considerable part of the total phenotypic variation for body size is caused by genetic differences (Boag & Grant, 1978; Brooke, 1977; Garnett, 1981; Moss & Watson, 1982; Smith & Zach, 1979). Moreover, Smith & Dhondt (1980) and Dhondt (1982) could exclude environmental factors as a cause of parent-offspring resemblance through cross-fostering experiments.

In all of these studies it was attempted to estimate the heritability for the traits chosen, without further analysis of the interactions between environment and genes. Laboratory studies have shown that the interplay between nutritional and genetic factors in the growth process and its results in adult body size are complex (e.g. in *Drosophila*, Robertson, 1962, 1964, in mice, Falconer, 1973, Parker & Bhatti, 1982,

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Roberts, 1981 and in quail, Marks, 1980, 1981). This is surprising since body size and especially weights have been widely used to measure conditional aspects, or in other words to explain part of the variation in size from variation in environmental conditions (e.g. Askenmo, 1977; van Balen & Cavé, 1970; Clark, 1979). In this paper we report an analysis of data on body size of the Great Tit obtained in a long-term population study initiated by Dr H. N. Kluyver at the Institute for Ecological Research. Before discussing the effect of environmental conditions on the heritability estimates, we will first give an overall estimate of repeatability and heritability for body weight. These estimates are based on all breeding birds for which weight data are available. They are overall estimates because the environmental conditions that are incorporated have been sampled over a period of a quarter-century. Subsequently we will present repeatability and heritability estimates for tarsus length obtained in a normal breeding season. That completely different results are obtained under adverse environmental conditions will be shown next. In most breeding seasons a mixture of the results obtained under good and under poor conditions can be demonstrated. These estimates of heritabilities for single cohorts are important, because most of the selection is likely to occur within cohorts. Finally we will present some data on selection and on correlations with other traits.

2. Methods

(i) *The population study*

Most of the data used in this study were collected for other purposes in the context of the long-term population study of the Great Tit (van Balen, 1967, 1973, 1980; Drent, 1984). The major study area is in the Hoge Veluwe, where the investigations were started in 1955 and are still continuing. Virtually all Great Tits in this area nest in boxes. Throughout the study nestlings were ringed and both parents were caught and identified while feeding the nestlings. This provides the genealogical data for the locally born birds which make up about half (60% in males, 40% in females) the breeding population. There are two major discontinuities in the study, in 1972–3 the area was partly changed after heavy storm damage to the woods, and from 1968 till 1975–6 seed food was provided at 6 or 7 sites throughout the winter. The potential effects of these discontinuities on our estimates are taken up in the discussion.

Weights have been taken in several different ways:

(1) The most important source of weight data in adults is mist-net trapping by day. From 1966 onwards mistnets were operated at six to ten stations one day every week from early July till late March. Data for July, August and April have been disregarded for

reasons explained later. From 1977 onwards tarsus measurements were also made (following Svensson, 1970).

(2) Birds roosting in nestboxes were caught and weighed during regular inspections in autumn and winter. Before 1975 these inspections were held twice during a winter season, in later years they were held monthly. The proportion of boxes occupied is dependent on weather conditions and there is a marked increase in the number of boxes occupied by females towards spring. Older and territorial birds are far more likely to be observed roosting than yearling birds.

(3) In 1975–8 all nestlings were weighed when 14 or 15 days old. Between this age and fledging, some five days later, no systematic changes in weight occur, and several authors refer to these weights as fledging weights. Handling the nestlings closer to fledging involves a serious risk of a prematurely fledged brood. In 1978 tarsus measurements were taken at the same time as the weights. In the period up to 1965 a proportion of the broods have been weighed in connection with growth studies. We have used these data only if measurements at an age of 14 days or older were available and no manipulations of clutch size or brood size were performed.

(4) Weights of breeding birds, taken when caught while feeding their nestlings, have been used only in repeatability estimates.

(ii) *Analysing uncorrected weight data*

Body weight changes continuously. Some of the larger changes follow distinct seasonal and diurnal patterns (e.g. Kluyver, 1952; van Balen, 1967; Haftorn, 1976). Although qualitative patterns are easily detected, quantifying the effects of time of day or time of year for use as a correction factor is difficult and would require the use of detailed environmental (especially meteorological) data. Given the practical impossibilities for working out and testing sophisticated correction functions, we have chosen to use no corrections at all, rather than crude ones. Whereas variation in weight without correction is biologically meaningful, the errors made by over- and under-correcting are hardly so.

An important consideration in deciding to apply no corrections has been that the data were collected in a uniform way. The proportion of data collected by day in mist-net captures and by night in roosting inspections as well as the seasonal distribution of the observational effort have been fairly constant. This reduces the possibility that differences between individuals are merely a consequence of different conditions of observation. There are two periods during the year when weight is more variable than at other times: during the breeding season and during the moulting period. By excluding weight data from these periods, which are relatively scarce anyway, the sta-

bility of the results is improved, i.e. the effect of a few outliers is reduced. The potential pitfall of the effect of different types of measurement conditions will be checked more explicitly in a number of cases.

(iii) *Growth of tarsus*

In 1977 repeated tarsus measurements (after Svensson, 1970) were made on nestlings in a population in the Liesbos near Breda (for a description of this area with broadleaved trees see van Balen 1967, 1973). These measurements, repeated after four days, were made for two or three nestlings per brood. In this year growth turned out to be unusually poor, which made it possible to handle nestlings over 15 days old. Normally this entails some risk of premature fledging.

(iv) *Quantitative genetics*

Only elementary procedures were followed (after Falconer, 1960). The more sophisticated methods of quantitative genetics depend heavily on the control of the environmental variance and the mating structure. While this is possible in the agricultural and laboratory situation for which the methods were developed, there are prohibitive violations of the basic assumptions in our situation.

First we establish the extent of resemblance between relatives. Subsequently we try to discriminate between the two major potential causes for such a resemblance, sharing of genes and sharing of environments. Regression analysis has been used to quantify a resemblance of offspring and parents. The distinction between genetic and environmental causes is based on the different expectations in several comparisons. Further attention to this distinction is given in the discussion.

3. Results

(i) *Repeatability of weight*

The repeatability, which measures the constancy of measurements made on a single individual, can be

regarded as an upper limit to the heritability. Although such a constancy may be caused by non-genetic factors, e.g. lasting effects of conditions during growth, repeatability estimates are valuable, because repeated measurements on individuals are much easier to collect, and are, hence, more numerous in the database. This allows us to partition the data into several subsets and to evaluate the effect of the conditions of measurement.

In Table 1 repeatability estimates for body weight are given for both sexes combined and separately, and for four classes of observational circumstances. The estimates for both sexes combined are given to allow comparison with similar values in the literature and with situations where sexes cannot be distinguished with complete reliability. Combining sexes does, of course, result in a higher repeatability due to the mean difference in weight between sexes. On the other hand, combining the different types of observations results in lower repeatability values, because the systematic differences occur within as well as between individuals.

The repeatability for females during the breeding season is relatively low, especially considering that weights were taken at the same stage during the breeding cycle, about one week after hatching. The repeatability for nestlings is high. A substantial proportion of the repeated measurements on nestlings was made because of their small sizes at the normal age of 15 days. Therefore, the total variance in this group is high, while growth in the two days that usually passed before remeasuring is small. This high repeatability for nestling weights suggests that the exact age at measurement is not very critical.

(ii) *Heritability of weight in breeding birds*

In the Hoge Veluwe population there is no evidence for the existence of a non-breeding part of the population during the breeding season (van Balen, unpubl.) Therefore, all individuals that survive until one year old and that remain in the study area will be included in the group of breeding birds. A heritability

Table 1. *Repeatability of weights for females, males and combined sexes (including individuals of unrecorded sex).*

	Females			Males			Sexes combined		
	<i>N</i>	<i>n</i>	<i>r</i>	<i>N</i>	<i>n</i>	<i>r</i>	<i>N</i>	<i>n</i>	<i>r</i>
Mist-net	1037	4750	0.66	1460	7585	0.66	2539	12440	0.74
Roosting	160	780	0.67	308	1434	0.70	469	2219	0.79
Breeding	96	221	0.52	98	225	0.64	194	446	0.66
Nestlings	—	—	—	—	—	—	494	1090	0.82
Total	1372	6666	0.55	1882	10453	0.56	4058	18945	0.70

N = number of individuals; *n* = number of measurements; *r* = repeatability.

Separate values are given for data from mist-net catches by day, nightly inspections of roosting birds, birds caught while feeding nestlings in the breeding season, nestling weights and all types of weights together. The total also includes individuals for which only one observation from two or more types is available. Data from Hoge Veluwe, 1955–78.

Table 2. *Heritability estimates (with S.E.) of mean body weight. Regressions on single parents and their S.E. have been doubled*

		Mother	Father	Mid-parent
(a)	Daughter	0.63 (0.15) <i>n</i> = 112	0.72 (0.14) <i>n</i> = 137	0.68 (0.10) <i>n</i> = 90
	Son	0.65 (0.13) <i>n</i> = 181	0.59 (0.11) <i>n</i> = 225	0.50 (0.09) <i>n</i> = 146
(b)	Daughter	0.59 (0.13) <i>n</i> = 183	0.48 (0.13) <i>n</i> = 203	0.57 (0.09) <i>n</i> = 156
	Son	0.67 (0.11) <i>n</i> = 284	0.39 (0.10) <i>n</i> = 359	0.46 (0.07) <i>n</i> = 244

In (a) only individuals of which at least three weights were taken outside the breeding and moulting season have been included. In (b) individuals that were only weighed once or twice are also included. Data from Hoge Veluwe, 1955–78

estimate based on breeding birds is the most important overall estimate of the extent of genetic variation. A practical reason is that we have more data per individual for breeding birds, because they are around for a longer time. Furthermore, it may be argued that non-reproducing individuals are unimportant from an evolutionary point of view, except that their absence may provide evidence for selection.

In Table 2(a) heritability estimates are given based on all breeding birds for which at least three measurements are available. By taking the mean of at least three values, some of the extreme effects of observational conditions will be excluded. One expects that including individuals for which only one or two observations are available would result in lower heritability estimates. This is indeed the case (Table 2b). The median number of observations in Table 2b is still 3 to 4, so that some environmental variation is still eliminated.

Comparison of the estimates based on the regression on single parent values with those based on mid-parent values shows that the estimates are consistent with a genetic interpretation and that the phenotypic correlation between parents is negligible. The apparent exception, although not significantly different, is found in the males in Table 2(a), where the heritability from regression on mid-parents is 0.50 which is lower than both 0.65 and 0.59. This discrepancy must be ascribed to the effect of a few aberrant individuals. The effect has largely disappeared in Table 2(b), which includes the data on which Table 2(a) is based.

A value of 0.5 (taken from Table 2b) can be regarded as an overall estimate of heritability for body weight, which is only slightly lower than the comparable repeatability estimate of about 0.55, for both sexes separately.

(iii) *Tarsus length*

Tarsus length is also widely used as a measure for body size in birds. In contrast to weight it does not

change after the completion of growth. Growth of nestling tarsus length was measured in 1977 in Liesbos in the first half of the breeding season. Feeding conditions were poor (see below), yet no growth was found to occur beyond the age of 13 days. The opportunity to measure a fully grown structure on nestlings makes it possible to collect data on parents and offspring in relatively large numbers (see O'Connor, 1977). There were, however, a few problems in measuring tarsus length. These problems were associated with particular birds independent of observer. Still the repeatability is high (Table 3) and no systematic change in tarsus length is found after fledging (Fig. 1).

In 1978 tarsus measurements were made for all nestlings at the Hoge Veluwe. The heritability estimates based on brood-means (Table 4) show a reasonable consistency and a heritability very similar to that for weight in breeding birds.

(iv) *Adverse environmental conditions*

An indication of the effects of environmental conditions on nestling growth and final body size may be obtained from a comparison of the results from Hoge Veluwe, 1978 and those from Liesbos, 1977. Weather conditions were unfavourable in 1977 in Liesbos, especially in the early part of the breeding

Table 3. *Repeatability of tarsus length. The total includes nestling measurements, (data from Hoge Veluwe, 1977–8)*

	<i>N</i>	<i>n</i>	<i>r</i>
Females	278	803	0.80
Males	315	1056	0.77
Total	821	2355	0.85

N = number of individuals; *n* = number of measurements; *r* = repeatability.

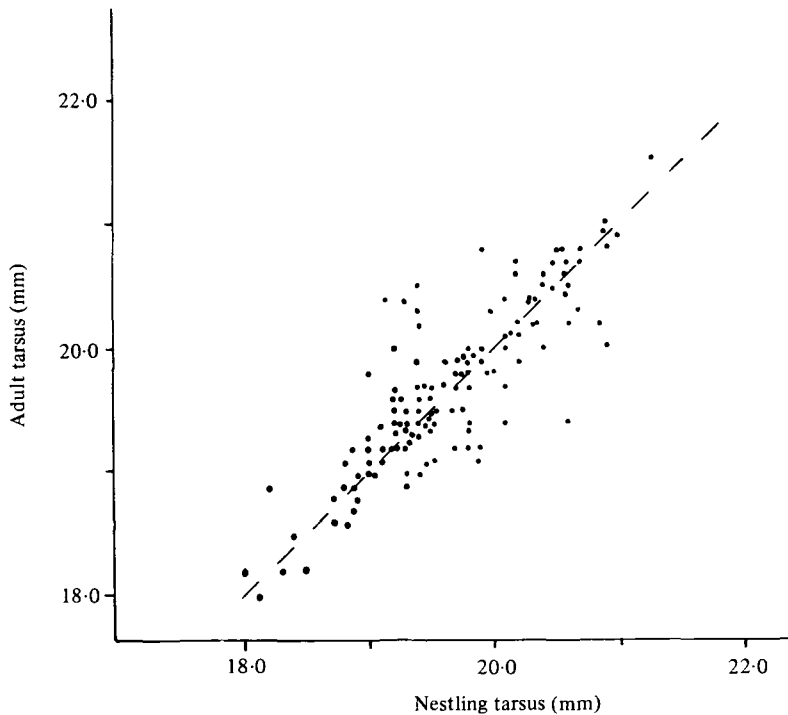


Fig. 1. Tarsus length measured on recapture after at least three months plotted against the measurements of the

same individuals as nestlings. The broken line indicates identical values. Data from Hoge Veluwe, 1978.

season. Poor weather is likely to result in poor feeding conditions, because the development of caterpillars, that form the main food item for the tits, is highly dependent on weather. Normally survival from hatching to fledging is about 95% in first broods; it was much lower in this year (Table 5).

In comparing tarsus length of offspring and their parents it is evident that nestlings are smaller than their parents in broods from the first half of the breeding season and in broods with a nestling mortality of 25% or more (Fig. 2). In the remaining group the offspring and parental means are the same and there is a resemblance between parents and offspring (heritability = 0.51). Nestling mortality is, of course, a very crude yardstick for measuring the quality of feeding conditions, especially with a fairly

small total number of broods. Yet, the conclusion can be drawn that an observed resemblance between parents and offspring is dependent on reasonably good feeding conditions for the nestlings.

(v) Heritability of nestling weight

From 1975 till 1978, nearly all nestlings on the Hoge Veluwe have been weighed when 15 days old. This weight is usually called fledging weight since there is no further systematic change in weight till fledging. In some years fledging weights are similar to adult weights, in other years the mean fledging weight is less than the mean adult weight. Still, we consider fledging weight and adult weight to be a single trait because the repeatabilities including both fledging and adult weights in equal proportions are roughly equal to the repeatability of adult weights only.

Heritability estimates based on regression of brood means on the adult weight of the parents are given in Table 6. These estimates are lower than the estimates for breeding birds (Tables 1 and 2), which may be expected from the presence of a greater amount of environmental variance in the fledging weights. There is, however, a considerable scatter of the points and it is not likely that the environmental variance is normally distributed.

Before attempting to describe patterns in the environmental variance, we may use the data from 1978, when both tarsus and weight were measured, to test whether the assumed presence of patterns in the environmental variance is likely to be real. One may expect that if nestlings remain small due to adverse

Table 4. Regression coefficients (with S.E.) of brood means for tarsus length on mothers, fathers and mid-parent values. The regression coefficients on single parents must be doubled to obtain heritability estimates. Data from Hoge Veluwe, 1978. The number of broods is 59, the correlation between the values of female and male in a pair is -0.00

Regression on	Slope of regression	Mean value
Female parent	0.16 (0.12)	19.62
Male parent	0.32 (0.09)	20.04
Mid-parent	0.52 (0.13)	19.83
Offspring mean	—	19.73

Table 5. Nestling survival from hatching to fledging in Liesbos, 1977

Hatching ...	1-7	8-13	14-17	18-21 May
Number hatching	73	85	119	58
Proportion fledging	0.46	0.72	0.79	0.94

feeding conditions, this would be visible in weight as well as in tarsus length. The size of the parents can be used as a predictor of the genetically programmed size. The difference between parental and offspring size can therefore be used as an index for the condition of the offspring. If there are patterns in the environmental variance, one expects a positive correlation between the index based on tarsus length and the index based on weight. This correlation ($r = 0.55$, $n = 46$, $P < 0.0001$, see Fig. 3) indicates that the deviations of offspring values from the parental values are correlated more strongly than is expected from the phenotypic correlation between weight and tarsus in adults ($r = 0.41$, $n = 173$ in females and $r = 0.34$, $n = 189$ in males) and in nestlings. It is therefore likely that the deviations in weight and in tarsus length are affected by a common cause.

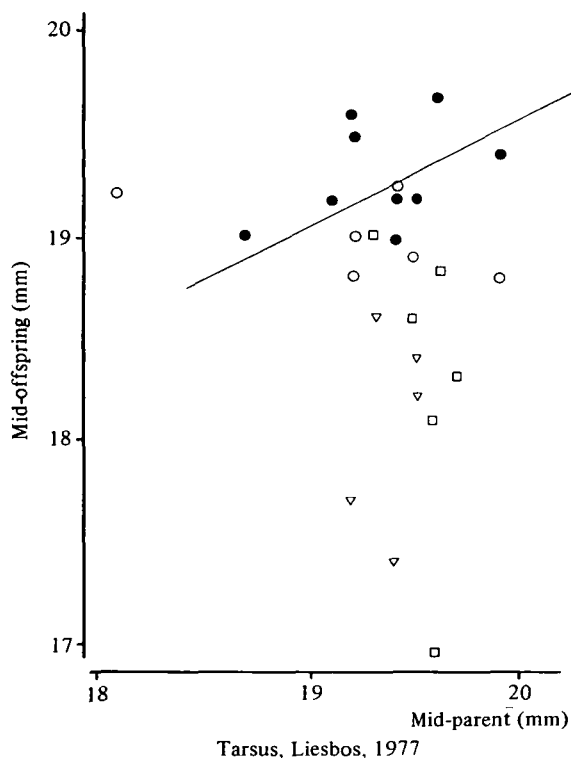


Fig. 2. The brood means of tarsus length in relation to the mid-parent values, hatching date and nestling mortality. Data from Liesbos, 1977, see also Table 6. ●, Hatched after 13 May, nestling mortality $< 25\%$; ○, hatched after 13 May, nestling mortality $\geq 25\%$; ▲, hatched before 13 May, nestling mortality $< 25\%$; □, hatched before 13 May, nestling mortality $\geq 25\%$. The regression equation for the points in the first group is $Y = 0.51X + 9.3$ ($r = 0.36$, $n = 9$).

In all four years, conditions on the Hoge Veluwe were better than in Liesbos 1977, which makes it more difficult to demonstrate the effects of specific environmental circumstances. At present, we are not able to account for the more subtle differences between parent and offspring weight. There is a tendency for the earliest broods to be light, especially in 1976 (see Fig. 4), but also in other years. However, the difference in weight between parents and offspring is no better indicator for condition than the absolute values of offspring weight (Fig. 4b). Compared to the variance in fledging weights, the variance in mid-parent weights is small. At present our conclusion must be that the results are consistent with a hypothesis that parent-offspring resemblance only becomes manifest if sufficient food is available. Conclusive evidence for or against this hypothesis can only come from direct measurements of the availability of food at the level of the individual feeding areas (see discussion).

(vi) Heritability of recapture weights

Many nestlings were recaptured and weighed during their first autumn and winter. The heritability estimates based on the recapture weights (Table 7) are slightly higher than those based on breeding birds (Table 2). This latter result is expected, because the estimates for recovery weights are based on both sexes combined to avoid small sample sizes in 1975 and 1978 (compare the repeatability estimates for separate and combined sexes in Table 1).

Apparently, the environmental variance in weight at recapture is smaller than in nestlings. This could be a consequence of increase in weight after fledging, especially in the lighter fledglings, or it could be a result of selection, i.e. differential local survival after fledging (for a discussion of the effects of emigration on these estimates see van Noordwijk & van Balen, 1988; Drent, 1984). The mean weights of fledglings that were subsequently recaptured (after at least three months), their recapture weights, and the mean weights of nestlings that were not recaptured are given in Table 8 (see also Fig. 5). In all four years, the mean nestling weight of recaptured individuals is higher than that of nestlings that were not recaptured. In at least two years, however, there is also an increase from fledging weight to recapture weight. Except for 1975, when the absolute and relative number of recaptures was smallest, selection seems to be more important than increase in weight after fledging (see Fig. 5). The significantly smaller (phenotypic) variance in the

Table 6. Regression coefficients (with S.E.) of mean nestling weights of broods with at least 5 nestlings on the mothers, the fathers and the mid-parent weights

Year	N broods	Average brood size	r parents	Regression of brood means on		
				Mother	Father	Mid-parent
1975	34	10.2	0.07	0.11 (0.23)	0.27 (0.24)	0.38 (0.28)
1976	68	10.8	0.04	0.65 (0.20)	-0.16 (0.21)	0.47 (0.28)
1977	89	10.0	-0.16	0.27 (0.27)	-0.02 (0.24)	0.26 (0.40)
1978	53	10.0	0.08	0.31 (0.19)	0.07 (0.15)	0.29 (0.22)

The regression coefficients on single parents must be doubled to obtain heritability estimates. Data from the Hoge Veluwe. The correlation between the values of female and male in a pair are also given

weights of nestlings that were recaptured, compared to the variance in weight of the ones that were not recaptured and compared to the variance in the total sample, is in agreement with an interpretation of selection. The difference between fledging and recapture weights is also shown in Fig. 6 for two years with rather different results. In 1975 many individuals gained two grams or more after fledging. Apart from the observation that this concerns mainly light fledglings, we cannot indicate which group of individuals gained much weight. There is a slight sex bias in the recapture rates in that slightly more males are recaptured, but the same results are obtained for both sexes separately. The question arises whether the apparent selection has any effect on the genetic composition of the population with respect to body size, or whether it mainly acts on the condition of the offspring (defined as the difference between genotypic and phenotypic body weight). If the survival of fledglings is classified according to the size of the parents there is no selection, which strongly suggests

that there is no effect on the genetic composition of the population. This question will be addressed further in the discussion.

(vii) Correlation with other traits

Elsewhere (van Noordwijk *et al.* 1981*a-c*) we have reported heritability estimates for clutch size (0.4), egg

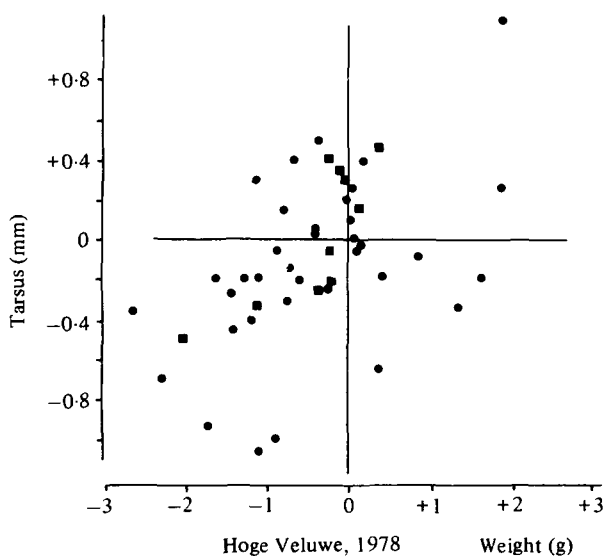


Fig. 3. The difference between mean offspring and mid-parent values for tarsus length plotted against the comparable difference in body weight ($r = 0.55$, $n = 46$, $P < 0.0001$). Data from Hoge Veluwe, 1978. Broods from which at least one nestling was later recorded as a breeding bird are indicated by squares.

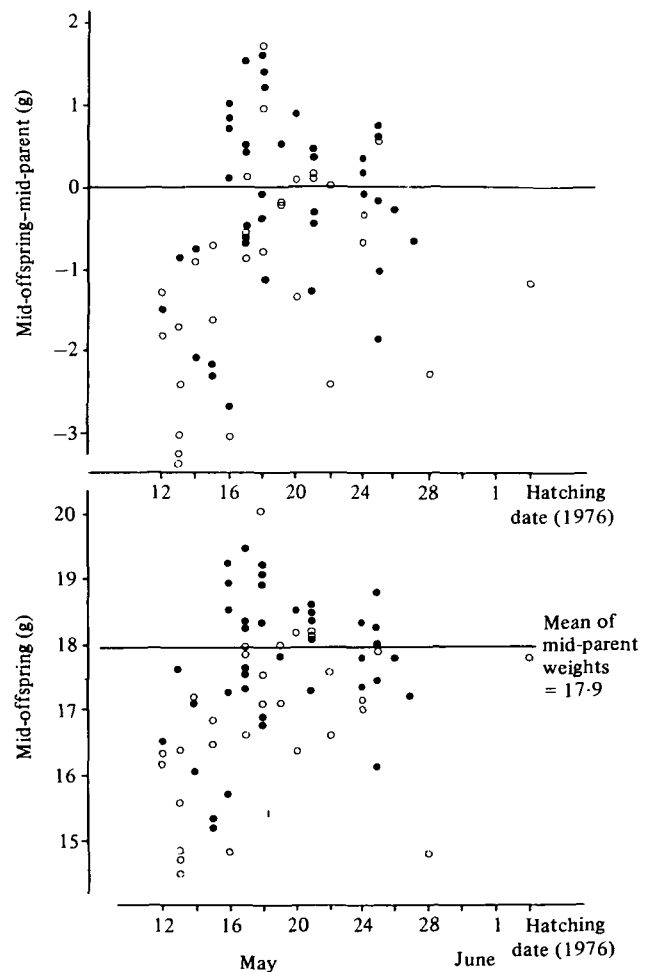


Fig. 4. (a) The difference between offspring and mid-parent weight plotted against the hatching date for first broods from Hoge Veluwe, 1976. (b) The same data expressed as absolute nestling weights. Filled dots indicate broods from which at least one nestling was later recorded as a breeding bird.

Table 7. Regression of offspring body weight, after fledging, on parental body weights

Year	N	r parents	Regression of offspring weights on		
			Mother	Father	Mid-parent
1973	21	0.42	0.77	0.35	1.12
1974	42	0.57	0.37	0.21	0.36
1975	60	-0.19	0.44	0.41	1.01
1976	264	-0.04	0.51	-0.10	0.49
1977	296	-0.09	0.17	0.32	0.57
1978	105	-0.08	0.27	0.36	0.72

The offspring weights were taken at least three months after fledging. Data from Hoge Veluwe for all years with $N > 40$

Table 8. Comparison of means and standard deviation of weights of parents, unrecaptured and recaptured nestlings

Year	Mid-parent weight	Unrecaptured nestlings	Recaptured nestlings	Recapture weights
1975	17.95 (0.35)	16.34 (1.82) $n = 530$	16.62 (1.38) $n = 84$	17.50 (1.06) $n = 84$
1976	17.95 (0.30)	16.63 (2.08) $n = 511$	17.58 (1.50) $n = 206$	18.08 (1.15) $n = 206$
1977	17.99 (0.30)	17.49 (1.56) $n = 797$	17.71 (1.27) $n = 320$	17.73 (1.14) $n = 320$
1978	18.01 (0.31)	17.06 (1.86) $n = 534$	17.59 (1.09) $n = 124$	17.72 (1.24) $n = 124$

size (0.7) and dates of first egg-laying (0.3). It is quite conceivable that some of these traits are correlated with body size. Perrins (1970) and Jones (1973) have reported negative (phenotypic) correlations between female body size and date of first egg-laying in the Great Tit. Moreover, in predicting the effect of selection, the patterns in the phenotypic and genetic correlations between the traits can be important. Particularly, the possibility that selection acts in

opposite directions on the correlated traits has consequences for the interpretation of the results from too simple analyses. In calculating genetic correlations we have encountered a number of problems which will be described separately (van Noordwijk, in preparation); here we only present the phenotypic correlations.

For all females and all males, correlations were calculated between the mean values for weight or

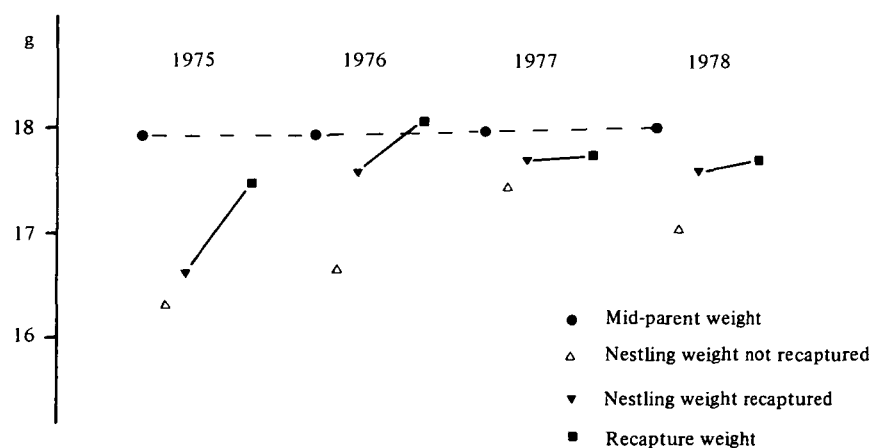


Fig. 5. The difference in weight between nestlings that were, and those that were not, recaptured at least three

months after fledging, together with mid-parent weights and recapture weights. Data from Hoge Veluwe, 1975–8.

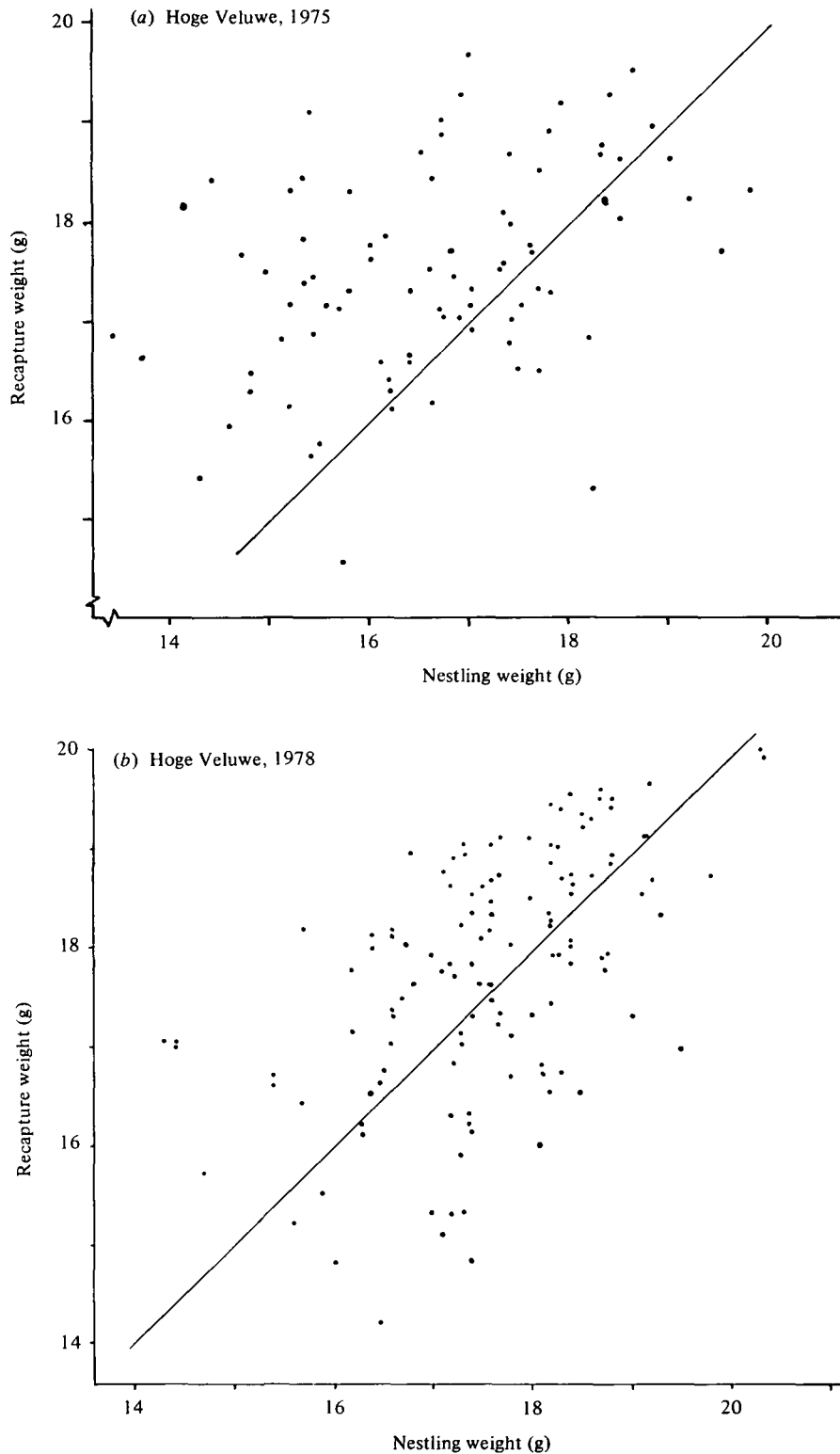


Fig. 6. The relation between individual fledging weight and recapture weight, in (a) 1975 ($r = 0.42$, $n = 84$) and in

(b) 1978 ($r = 0.52$, $n = 124$). The drawn lines indicate identical values.

tarsus length, and the mean values for several reproductive traits of all clutches of which these individuals are known to have been a parent. From a comparison of repeatabilities of males with different partners and females with different partners we know that, in the Great Tit, males have no measurable

influence on the clutch size, egg size or date of laying of their partners (van Noordwijk *et al.* 1981*a-c*). Therefore the correlations between male size and the reproductive traits may serve as a control for correlations arising from combination of data from several years with slightly different mean values.

Table 9. Correlation coefficients between mean adult body weight and 9 reproductive traits

Trait	Female		Male	
	Weight	Tarsus	Weight	Tarsus
(1) Clutch size 1 (absolute)	0.08* <i>n</i> = 707	0.02 <i>n</i> = 201	0.07 <i>n</i> = 794	0.02 <i>n</i> = 210
(2) Clutch size 1 (relative)	0.05 <i>n</i> = 703	-0.00 <i>n</i> = 200	0.05 <i>n</i> = 790	0.01 <i>n</i> = 209
(3) Clutch size 2 (absolute)	0.04 <i>n</i> = 273	0.06 <i>n</i> = 80	0.01 <i>n</i> = 223	-0.07 <i>n</i> = 71
(4) Date of laying 1 (absolute)	-0.02 <i>n</i> = 707	-0.04 <i>n</i> = 201	-0.05 <i>n</i> = 794	0.04 <i>n</i> = 210
(5) Date of laying 1 (relative)	-0.02 <i>n</i> = 707	-0.02 <i>n</i> = 201	0.08* <i>n</i> = 794	0.05 <i>n</i> = 210
(6) Interval 1-2	-0.06 <i>n</i> = 273	-0.16 <i>n</i> = 80	-0.03 <i>n</i> = 223	0.02 <i>n</i> = 71
(7) Frequency 2	0.02 <i>n</i> = 707	0.11 <i>n</i> = 201	0.03 <i>n</i> = 794	-0.04 <i>n</i> = 210
(8) Success 1	0.02 <i>n</i> = 707	-0.12 <i>n</i> = 201	0.06 <i>n</i> = 794	-0.01 <i>n</i> = 210
(9) Success 2 (absolute)	-0.07 <i>n</i> = 273	-0.13 <i>n</i> = 80	-0.02 <i>n</i> = 223	-0.02 <i>n</i> = 71

For each individual the value for the reproductive trait is the mean of all clutches of which the individual is known to have been a parent. Data from Hoge Veluwe, 1955-78. The traits are: (1) absolute clutch size in first clutches, (2) clutch size relative to the mean in that year, (3) absolute clutch size in second clutches, (4) the date on which the first egg in a first clutch was laid, (5) the same date relative to the median first egg date of that year, (6) the interval in days between the first egg dates in first and in second clutches, (7) the frequency of second clutches (defined as the number of years with a second clutch divided by the number of years with a first clutch), (8) the proportion of eggs in first clutches that resulted in fledglings, (9) the same proportion in second clutches. *n* is the number of individuals for which both variables are known.

(* = 0.05 > *P* > 0.01.)

The correlation coefficients (Table 9) are surprisingly low. For all practical purposes body size can be considered to be phenotypically independent of these reproductive traits. There is, however a significant correlation ($r = 0.26$, $n = 186$, $P < 0.01$) between female body weight and egg volume (Fig. 7), but not between tarsus length and egg volume ($r = 0.08$, $n = 191$, n.s.). Our egg measurements were made during three years only (1977-9) and there are some systematic differences in mean egg volume between three years (van Noordwijk *et al.* 1981*b*, and in preparation). Therefore this correlation, although in accordance with general results in poultry, should be interpreted with some caution. The complications arising from a correlation between female body weight and egg volume and the weight of the individual hatching from this egg are discussed in van Noordwijk (1987 and in preparation). In general the effect of egg size on fledging weight is negligible (unpubl. results), as has been reported for several other species (e.g. Ankney, 1980; Bryant, 1978; Murton *et al.* 1974). This is in agreement with the absence of a maternal effect on fledging weight or tarsus length.

4. Discussion

(i) Assortative mating

It is essential to evaluate the possibility that parent-offspring resemblance is not genetic, but is instead a result of a similarity in environmental conditions. In this respect the absence of a correlation between the phenotypes of the parents is very important. Throughout their breeding life most Great Tits remain in the same part of the study area. During autumn and winter, when most of our measurements were made, male and female usually roost in small overlapping areas which extend slightly beyond the territory in the breeding season (Kluyver, 1950). Therefore, if body weights of adults reflect the environmental conditions experienced shortly before the measurement takes place, one expects a positive correlation between the weights of male and female partners, because they share the same environment. If, alternatively, the body weights of adults reflect the environmental conditions experienced during growth, a parent-offspring resemblance will only result if the juvenile environments (i.e. the conditions experienced

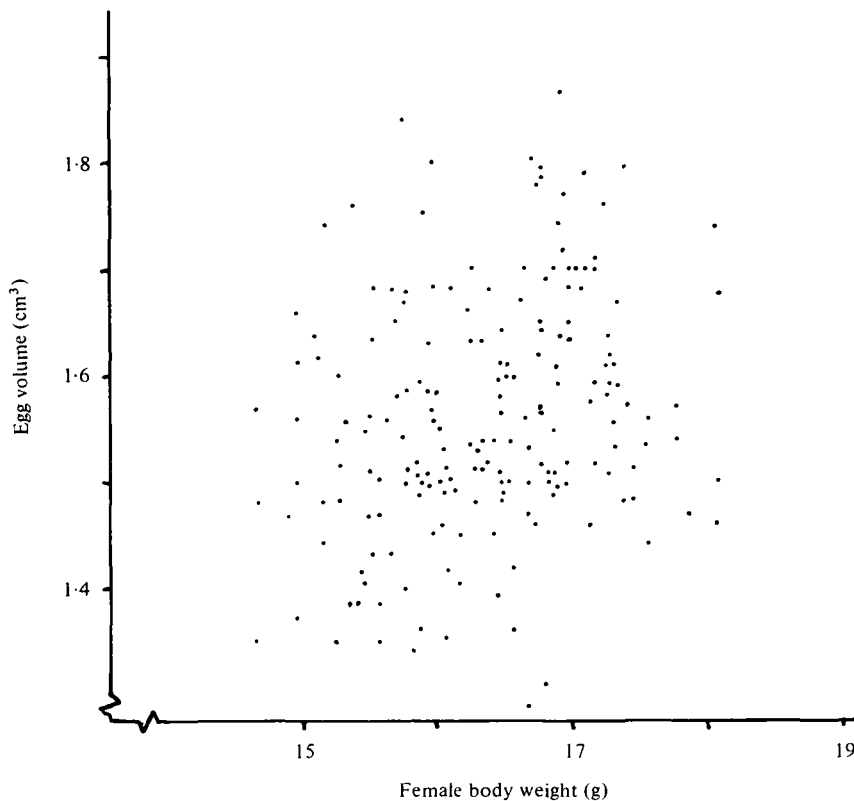


Fig. 7. The relation between female weight and mean egg volume in first clutches ($r = 0.26$, $n = 186$). Data from Hoge Veluwe, 1977–9.

during growth in the nest) of both the parents are correlated with the juvenile environments of their offspring. Hence, one would expect a correlation between the phenotypes of the parents if offspring resemble both parents and if the similarity of environments is an important cause of the parent-offspring resemblance. In our data there are no significant positive or negative correlations between the phenotypic values of the parents.

The absence of a phenotypic correlation between the female and male parent also indicates that the effect of winter feeding on the mean weight does not play a large role in the resemblance between offspring and parents in our data. Such an effect is not unlikely, because our data are derived from a series of years with, and a series of years without, winter feeding. Furthermore, it is also likely that the distribution of feeding stations over the study area has an effect on the body weight of individuals. It seems that the effect of feeding on the distribution of weights is negligible. This could mean that the effect of winter feeding on body weight is small, but it is more likely that there are several effects that largely compensate each other, so that no overall effect remains. Especially the positive effect of winter feeding on the survival of older birds (see van Balen, 1980) may come about through a better survival of lighter birds. In this manner it is possible that the overall distribution of weights does not change, apart from an increase in

number of birds, even though there is an effect of winter feeding on the weight of each individual bird.

(ii) *Environmental conditions during growth*

Our data suggest that about half of the phenotypic variance for body size in Great Tits at breeding age has a genetic basis. The relative importance of genetic variation in the body size of nestlings and fledglings depends strongly on the environmental conditions during growth. This suggests that the finding of high heritabilities for fledgling size is not necessarily in contradiction with the results of other studies in which variation in body size was interpreted exclusively as variation in condition and in which relationships between size and environmental factors were demonstrated (e.g. van Balen, 1973; Perrins, 1965). This is because environmental variance is especially important when the phenotypic variance is large, and hence easily correlated with environmental factors.

One may expect that the dependence of the heritability estimate on the environmental conditions would affect the outcome of cross-fostering experiments. Such experiments can eliminate the possibility that a resemblance between offspring and parental size is e.g. a consequence of variation in feeding capacities of the parents, correlated with parental size. In fact, cross-fostering experiments that have been

carried out in natural populations have led to opposite conclusions. Smith & Dhondt (1980) working with Song Sparrows (*Melospiza melodia*) and Dhondt (1982) working with Blue Tits (*Parus caeruleus*) found no effect of the foster parents, while there were significant regressions of tarsus length on the biological parents. Ricklefs & Peters (1981) working with Starlings (*Sturnus vulgaris*) came to the conclusion that there was little evidence for genetic variation in parameters of growth curves, among which the asymptotic weight is similar to fledging weight. Part of the difference in conclusion may be due to a different experimental design. They compared foster-sibs and true sibs rather than resemblance to parents. We would like to suggest, however, that the opposite conclusions are likely to have been caused by a difference in environmental conditions, which should then have been good in the Song Sparrow and the Blue Tit experiment and poor in the Starling experiment. There is some circumstantial evidence to support this suggestion. In the Song Sparrow experiment the mean nestling weight was average (Smith, 1981 and pers. comm.), while in the Starling experiments there was a considerable increase in nestling weights, whenever broods were experimentally reduced (R. E. Ricklefs, pers. comm.). Tinbergen (1981) has demonstrated a very strong relationship between food-availability and the effect of brood size on nestling mortality and nestling weight in the Starling.

We suggest that if we had carried out cross-fostering experiments in Liesbos in 1977, our results would have been very similar to those of Ricklefs & Peters (1981), while the same experiment would lead to different conclusions under better environmental conditions. This hypothesis can be tested by carrying out cross-fostering and simultaneous manipulation of brood size to affect the amount of food that is available per nestling. Initial results are suggestive, but not yet conclusive (Schoemaker unpubl.; van Noordwijk, 1984).

(iii) *Theoretical considerations*

Our interpretation of the heritability for body weight being higher in the recaptured birds than in the nestlings was that the elimination of weak birds had not affected the genetic variance, but reduced the environmental variance. Calculations using the slope of the regression and the observed phenotypic variance confirm that the genetic variance is the same for both nestlings and survivors, but that a considerable reduction has occurred in the environmental variance (van Noordwijk, 1982). The difference in slope of regression is due to an increase in the covariance between parents and offspring. This increase in covariance, with a simultaneous decrease in the variance of the offspring, implies, however, that there is an interaction between the parental values and the

absence of part of the environmental component in the offspring values included in the set of survivors. This contradicts the absence of selection relative to the parental phenotype. This apparent contradiction is still unsolved.

(iv) *Contribution of parental genes*

There seems to be a flaw in the conclusions that we have drawn from our data with respect to the inheritance of body size variation. In three out of four years the regression of nestling weights on the male parents is low (Tables 6 and 7). We can argue that this is due to a small number of males (born in 1975) that are phenotypically much smaller than genotypically. The occurrence of a few offspring that are much larger than their parents in both tarsus and weight (Fig. 3) lends support to this interpretation.

However, if there are a number of individuals in which conditions during growth apparently have a lasting effect on the adult phenotype we would expect that the repeatability was higher than the heritability. In fact, we find a value of 0.55 for the repeatability and 0.57 for the heritability in females (values taken from Tables 1 and 2*b*) while the values for males are 0.56 and 0.46 respectively. Therefore, the quantitative importance of lasting effects of conditions during growth over the population as a whole must be small. This is in accordance with our supposition that only a small number of males with a large discrepancy between phenotype and genotype is involved. It is also in agreement with our interpretation that the difference between heritability estimates based on nestling weights and recapture weights is largely due to selection. This selection is, of course, different from the type of selection carried out in artificial selection experiments. Instead of a single value above which all individuals survive and below which they are culled, there is a gradual increase in survival with phenotypic value. The difference in survival probability between the extremes of the distribution may be tenfold (see e.g. Garnett, 1981; Perrins, 1965). So, if 40 out of 100 heavy fledglings survive, 4 out of 100 light ones will also survive. Such a low number of aberrant individuals can easily upset the results of the regression analysis in the kind of data we are working with.

(v) *Selection*

Our results confirm that there is a positive correlation between fledging weight and subsequent survival (e.g. Perrins, 1965). The increase in heritability when data for recaptured birds are compared to those for nestlings suggests that the observed selection is mainly a matter of weeding out of individuals in poor condition rather than a selection acting on small size *per se*. We have no evidence for the presence of selection on body size that might have an effect on the genetic composition of the population. In fact, the

mid-parent weights for 1975–8 are remarkably constant, even considering that there is a 50% overlap in the breeding population in subsequent years, which dampens fluctuations.

The change of heritability values with age and our interpretation that differential survival is mainly due to the environmental component in the phenotypic variance, re-emphasizes the necessity of comparing similar stages in the life-cycle in measuring natural selection as an agent capable of changing the genetic composition of the population. Strictly speaking this criterion is not met in comparing survivors and non-survivors in a snow storm (Grant, 1972; Johnston *et al.* 1972; O'Donald, 1973) or autumn and spring samples (Johnston & Fleischer, 1981) in House Sparrows (*Passer domesticus*), which are considered classical examples of natural selection for a quantitative trait. A separate analysis of yearling and older birds within both sexes would largely remedy this difficulty.

It is often possible to look for specific patterns that are likely to occur if selection acts on phenotypic size, but unlikely if mainly aspects of condition are involved. The dramatic change in sex ratio favouring the larger sex observed by Boag & Grant (1981) that accompanied the selection for large individuals within each sex, would not be expected if condition rather than size was selected upon. Likewise, the gradualness of the change in body size of Great Tits observed by Dhondt *et al.* (1979) and the fact that there is no correlation between body size and population density in adults strongly suggest that a change in genetic composition as a result of natural selection on phenotypic size is involved.

(vi) Conclusions

All heritability estimates are valid only for the population and the conditions for which they were calculated. Fortunately, however, we can regard some populations and sets of environmental conditions as representative for many others. We believe that our data come from a relatively large sample of environmental conditions. Although the heritability estimates from data in single years are rather variable, the overall estimate is fairly stable. The next step should be a more detailed study in which the environmental factors are measured on a fine scale, together with a genetic analysis. This may allow us not only to look at reaction norms, but also to use sets of conditional heritability estimates, depending on environmental conditions during growth, for predictive purposes. Given such conditional heritability estimates, one should be able to predict future evolution for different scenarios of future environmental conditions.

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