

Genetic variation and natural selection on blue tit body condition in different environments

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Summary

An increasing amount of evidence indicates that different forms of environmental stress influence the expression of genetic variance in quantitative traits and, consequently, their evolvability. We investigated the causal components of phenotypic variance and natural selection on the body condition index (a trait often related to fitness in wild bird populations) of blue tit (*Parus caeruleus*) nestlings under contrasting environmental conditions. In three different study years, nestlings grown under a poor feeding regime attained lower body condition than their full-sibs grown under a good feeding regime. Genetic influences on condition were large and significant in both feeding regimes, and in all three study years. However, although estimates of additive genetic variance were consistently higher in the poor than in the good environment, heritability estimates for body condition index were very similar in both environments due to higher levels of environmental variance in the poor environment. Evidence for weak genotype \times environment interactions was obtained, but these contributed little to variance in nestling condition. Directional natural selection on fledging condition of nestlings was detected, and there were no indications of year or environmental effects on the form and intensity of selection observed, in a sample of 3659 nestlings over four years. However, selection on fledging condition was very weak (standardized selection gradient, $\beta = 0.027 \pm 0.016$ SE), suggesting that, in the current population, the large additive genetic component to fledging condition is not particularly surprising. The results of these analyses are contrasted with those obtained for other populations and species with similar life-histories.

1. Introduction

There is an increasing awareness of the possibility that those environmental factors that cause selection on given traits may also be influencing the expression of genetic variability in the very same traits (e.g. Larsson, 1993; Hoffmann & Parsons, 1997; Merilä, 1997). Several studies have found that the amount of genetic variation available for selection to act on can be increased under stressful environmental conditions (e.g. Hoffmann & Parsons, 1991; de Moed *et al.*, 1997), suggesting an enhanced opportunity for evolution to occur. However, at the same time, a number of studies have found that heritability estimates of

size-related traits in birds are consistently lower in stressful, as compared with better, environmental conditions (e.g. Merilä, 1997; Larsson *et al.*, 1997). Similar observations are available from a number of other studies (reviewed in Hoffmann & Parsons, 1991), and there is also evidence to indicate that genetic variation may be influenced by stressors in some, but not all, populations of the same species (Noach *et al.*, 1996). Likewise, the expression of genetic variation in different types of traits may respond differently to the same stressors (Srgo & Hoffmann, 1998*a, b*). Hence, although it is obvious that environments and genes interact to cause variation in quantitative trait parameters between different environments, it is not always clear what the proximate causes of changes in heritabilities are. Numerous alternatives exist (e.g. changes in the additive genetic,

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environmental or dominance components of variance), but few studies have provided detailed information to tease these apart. Hence, further studies with different organisms and with different types of traits (e.g. life-history, morphometric, behavioural) are needed to gain better understanding of the details affecting these processes, as well as of the broad patterns of inheritance of quantitative trait variation under different environmental conditions.

Information about possible changes in genetic variance in traits related to fitness is of particular interest since this information may help in assessment of the relative importance of different mechanisms acting to maintain genetic variation in traits under directional selection. In most natural bird populations, estimation of fitness is rather difficult, since natal dispersal rates are usually high and the survival of offspring to their first breeding attempt is very hard to determine accurately. However, several studies of passerine birds have closely monitored the survival of young after leaving the nest, and shown that an individual's survival probability can be predicted relatively well from their body mass or condition (body mass corrected for body size) just before fledging (Perrins, 1965; Garnett, 1981; Nur, 1984; van Noordwijk *et al.*, 1988; Pettifor, 1993; Tinbergen & Boerlijst, 1990; Hochachka & Smith, 1991; Lindén *et al.*, 1992; Verboven & Visser, 1998). Interestingly, although the condition index has been thought to reflect mainly individual variation in nutritional status, recent quantitative genetic studies have demonstrated a significant additive genetic component to individual variation in body condition in the collared flycatcher, *Ficedula albicollis* (Merilä, 1996; Sheldon *et al.*, 1997; B. C. Sheldon & J. Merilä, unpublished data), a species for which evidence for directional selection on condition is particularly strong (Lindén *et al.*, 1992). This finding reinforces the importance of the question as to how genetic variance in a trait subject to directional selection can be maintained (Barton & Turelli, 1989; Stearns, 1992; Lynch & Walsh, 1998). Several alternatives exist, including changes in expression of genetic variance under different environmental conditions, as well as spatially and temporally varying selection pressures (Ellner & Sasaki, 1996; Lynch & Walsh, 1998).

The aims of this study were twofold: first, to estimate genetic variance and heritability of body condition index under different environmental conditions in order to determine whether any response to selection might differ depending on the environment in which the offspring are reared, and second, in an attempt to gauge the extent and form of selection on body condition, to estimate the direct forces of survival selection acting on body condition, using five continuous years of data from a large natural population of blue tit, *Parus caeruleus*.

2. Material and methods

(i) *The study species and population*

The blue tit is a small, cavity-nesting passerine that inhabits mainly mixed deciduous forests in the western Palearctic region (Cramp & Perrins, 1993). It readily accepts nest-boxes as breeding sites and, in our population, lays only one clutch each year. The mean clutch size in genuine first clutches is about 11 eggs (range 4–17 eggs), and incubation is by the female alone. The male feeds the female during incubation, and when the young hatch, both parents feed the nestlings. The nestling period is 16–20 days, and the young reach independence about 2 weeks after fledging. Most of the juveniles presumably disperse far from their natal areas, whereas adult birds are territorial and remain on breeding grounds all year. Annual adult mortality is high, as only about 39% of females ($n = 607$ individual-years) and 51% of males ($n = 442$ individual-years) survive from one breeding season to the next (J. Merilä and R. Przybylo, unpublished data).

We studied a breeding population of blue tits on the southern part of the island of Gotland (about 51° 10' N, 18° 20' E), off the Swedish east coast, during April–June 1992–1997. Our study area consisted of 16 wood lots, which were mostly rich deciduous forest dominated by oak *Quercus robur* and ash *Fraxinus excelsior*, sometimes with a dense understorey of hazel *Corylus avellana*. More details about the study areas and species can be found in Merilä & Wiggins (1995) and Merilä & Fry (1998).

(ii) *The data*

The data for quantitative genetic analyses were collected during regular nest-box inspections in 1992–5 from late April until mid-June when all young had fledged. For each brood the date of clutch initiation, clutch size and hatching date were recorded. To obtain the body condition index, the tarsus length of all 14-day-old young was measured using digital calipers (to an accuracy of 0.1 mm) as detailed in Merilä (1997), and each nestling was weighed to the nearest 0.1 g using a Pesola spring balance. As explained in Merilä & Fry (1998), the tarsus length measurements were very accurate and directly comparable between different study years and between the two observers who took the measurements. The body condition index for quantitative genetic analyses was calculated as the residual from a linear regression of body weight on tarsus length in a pooled sample of nestlings included in the analyses ($b = 1.16$, $SE = 0.02$, $F = 2704.7$, $d.f. = 1,2692$, $P < 0.001$). For selection analyses, the body condition index was calculated separately in each year and the relationship between tarsus length and body mass was highly significant in

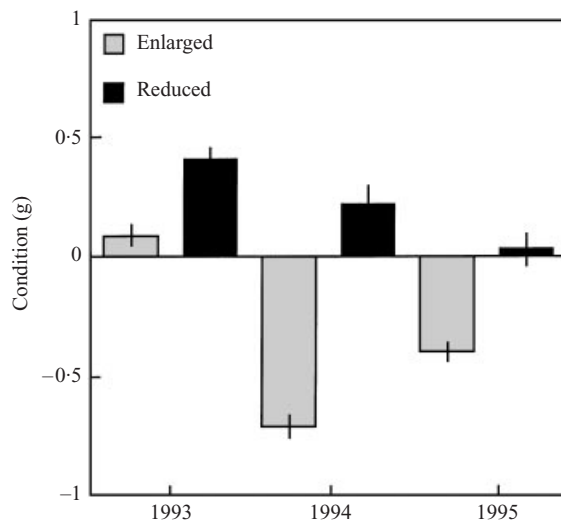


Fig. 1. Mean (\pm SE) body condition of blue tit nestlings grown under different environmental conditions in three different study years. The values are least square means obtained for the experiment \times year interaction from the model presented in Table 2, and hence adjusted for the effects of other factors in the model.

all years ($F \geq 435.30$, $P < 0.00001$). Hence, this index describes the body weight of a given individual as a deviation from predicted body weight for a bird having a given tarsus length. This index, also known as residual mass, is widely used in bird studies and is strongly positively correlated with the size of an individual's subcutaneous fat reserves (Merilä & Svensson, 1995), as well as with survival probability in a number of species of passerine birds (see Section 1).

Family relationships are based on the assumption that all nestlings originally in the same nest-box were full-sibs. Extra-pair paternity is known to occur in this species (two estimates based on large samples in other populations are 7% and 12.5% of nestlings: Krokene *et al.*, 1998; Kempenaers *et al.*, 1997), suggesting that some of the presumed full-sibs might have been maternal half-sibs not related to their putative father. However, even if extra-pair paternity were present at a low frequency, we have no reason to suppose that it would have been anything but randomly distributed with respect to experimental treatment, and should therefore have contributed only to error terms. There are no cases of extra-pair maternity known from this species (Kempenaers *et al.*, 1997; Krokene *et al.*, 1998).

(iii) Cross-fostering and brood size manipulation experiments

To distinguish between genetic and environmental causes of resemblance, we performed reciprocal cross-fostering experiments, creating broods that consisted of approximately equal numbers of nestlings from two different families having the same hatching date and

original clutch size (Merilä & Fry, 1988; their fig. 1). The rationale behind these experiments is that because blue tits, like many other passerine birds, have extensive biparental care after the young hatch, there is a clear possibility of parental effects on traits in the nestlings (but see: e.g. Dhondt, 1982; Merilä, 1997; Merilä & Fry, 1998). To some extent these can be controlled for by cross-fostering young; the possibility of pre-hatching parental effects is discussed below.

Brood size was simultaneously manipulated by reducing or increasing original clutch size by about one-third to determine how different growth conditions might affect heritability estimates and the causal components of variance. This was accomplished by moving about two-thirds of the young from a 'reduced' brood to an 'enlarged' brood and switching back one-third of the young in the recipient (enlarged) nest to the donor (reduced) nest. Hence, both reduced and enlarged broods consisted of 'foreign' and 'home' young approximately in 1:1 proportion. In these experiments we aimed to affect the growth conditions experienced by nestling blue tits. This outcome relies on parents compensating incompletely for the increase in the size of their family. Although partial compensation is evident from a number of studies of passerine birds, because parents sometimes experience costs of reproduction due to rearing larger broods, that this compensation is usually incomplete is indicated by the majority of such studies revealing a negative relationship between experimentally manipulated brood size and offspring reproductive value (Stearns, 1992, p. 157). All young were banded with individually numbered aluminium rings at the age of 6 days and, until this, foreign young were made identifiable by painning their claws or clipping part of the downy feathers on their head. In 1993, 1994 and 1995, 32, 23 and 29 pairs of broods, respectively, were manipulated, and hence, a total of 168 families were subjected to experimentation. However, to reduce variation due to any differences in the genetic constitution of two experimental groups, only those nests where at least one home and one foreign young survived in both nests of the pair (= dyad) were included in the analyses. Therefore, after excluding all dyads where one nest was lost due to predation, due to death of the whole brood or due to death of all young from one family, 29, 19 and 25 pairs of experimental broods (146 families) were available for analyses in 1993, 1994 and 1995, respectively. The dyads excluded from the genetic analyses were included in the analyses of selection, but since the body condition was quantified at day 14 post-hatch, nestlings that died before this became excluded from all analyses. However, the mortality between hatching and fledging is relatively low (*c.* 10%; Merilä & Fry, 1998) and hence the bias introduced by this is likely to be small. Nevertheless, pre-fledging mortality might have led to

underestimation of the strength of selection on fledging condition.

To check that the transfer itself did not affect the size nestlings attained, we also performed swaps where young were exchanged without changing the original brood size; these nests served as controls to evaluate possible effects of moving. Using the same criteria as for experimental broods, 13 and 6 pairs of control broods were available for analysis in 1993 and 1994, respectively. No control broods were created in 1995. After brood size manipulations, reduced broods contained significantly fewer young both immediately after manipulation (day 2 post-hatch) and at day 14 post-hatch than control broods, while the enlarged broods contained significantly more young than reduced and control broods, except in 1994 when enlarged broods experienced heavy mortality (for details see Merilä & Fry, 1998).

(iv) Full-sib analyses

Three different types of full-sib analysis were used to investigate the relative importance of genetic and environmental factors in determining nestling condition. First, following Merilä & Fry (1998) we performed a mixed-model ANOVA on the data from both offspring environments. In the full model, the main effects were Year and Dyad within Year (both random effects), Experiment (reduced or enlarged broods, a fixed effect), and Box of origin within Dyad and Year (random). We also analysed reduced models for each of the different years to investigate possible among-year heterogeneity in these different effects. Secondly, we performed nested random effects ANOVAs for each offspring environment separately using Box of rearing and Box of origin (nested within Box of rearing) as factors. In this analysis, the Box of origin effect estimates half the additive genetic variance (V_A), plus a quarter of the dominance variance and maternal effects if present. Thirdly, we used the control broods to perform a two-way nested (random effects) ANOVA following Atchley & Rutledge (1980). In this analysis, the terms Box of rearing, Box of origin and their interaction were nested within Dyads.

All full-sib analyses were performed using type III sums-of-squares as obtained from PROC GLM in SAS (SAS Institute, 1989). The variance components for all effects were calculated by equating the observed mean squares with expected mean squares and negative variance components were set to zero, if they occurred. The 'variance' accounted for by experimental environment was also calculated, although the environments were considered to be a fixed effect as a result of their non-random sampling. The estimates based on type III sums-of-squares were usually in good agreement with estimates derived by restricted maximum-likelihood methods.

(v) Across-environment genetic correlations

The genetic correlation across environments quantifies the degree to which expression of a trait in one environment shares a heritable genetic basis with the expression of the same trait in another environment (Falconer & Mackay, 1996). As detailed in Merilä & Fry (1998), there are two ways of estimating across-environment genetic correlation in our experimental design. First, for each year it can be estimated as:

$$r_g = \frac{V_{\text{BOXO, RED+ENL}}}{\sqrt{(V_{\text{BOXO, RED}} \times V_{\text{BOXO, ENL}})}}, \quad (1)$$

where $V_{\text{BOXO, RED+ENL}}$ is the estimated variance component due to Box of origin from the ANOVA with both environments (Tables 2, 3), $V_{\text{BOXO, RED}}$ and $V_{\text{BOXO, ENL}}$ are the estimated variance components from the ANOVA on the single environment (reduced or enlarged broods, respectively) data (Table 4; Fry, 1992). A second estimate for across-environment correlation can be obtained by partitioning the Box of origin \times Experiment interaction from the mixed-model ANOVA (see above) into components attributable to heterogeneity of genetic variance and the lack of genetic correlation between environments (Robertson, 1959, p. 478). Re-arranging Robertson's equation gives

$$r_g = \frac{(V_{\text{BOXO, RED}} + V_{\text{BOXO, ENL}})/2 - V_{\text{BOXO} \times \text{EXP}}}{\sqrt{(V_{\text{BOXO, RED}} \times V_{\text{BOXO, ENL}})}}, \quad (2a)$$

where the numerator includes the average of genetic variances in two environments $[(V_{\text{BOXO, RED}} + V_{\text{BOXO, ENL}})/2]$ and the genotype-environment interaction variance ($V_{\text{BOXO} \times \text{EXP}}$) is estimated by Experiment \times Box of origin interaction in Table 3 or 4. The denominator is the same as in the first method. This equation can also be written as (Robertson, 1959)

$$V_{\text{BOXO} \times \text{EXP}} = 0.5 \times (\sqrt{V_{\text{BOXO, RED}}} - \sqrt{V_{\text{BOXO, ENL}}})^2 + (1 - r_g) \sqrt{(V_{\text{BOXO, RED}} \times V_{\text{BOXO, ENL}})}, \quad (2b)$$

where the first term is the component attributable to difference in the genetic variances and the second term describes the component attributable to cross-environment correlation being less than one (Merilä & Fry, 1998). By solving r_g from (2a) and substituting the variance components into (2b) it is possible to evaluate the relative importance of the two possible causes of genotype-environment interaction by comparing the relative magnitude of these two terms.

(vi) Selection analyses

To quantify forces of survival selection acting on body condition, we estimated univariate directional and stabilizing selection differentials following the general procedures outlined by Arnold & Wade (1984); see

Table 1. Random-effects nested ANOVAs of condition index in cross-fostered control broods

Source	1993			1994			1993 + 1994			
	d.f.	F	%	d.f.	F	%	d.f.	F	%	
Year	—	—	—	—	—	—	1	3.30†	0.117	9.1
Dyad	12	1.14	0.043	5	1.38	0.085	18	1.19	0.047	6.0
Box of rearing (Dyad)	13	10.52***	0.239	6	5.25*	0.069	19	9.24***	0.233	21.6
Box of origin (Dyad)	13	10.69***	0.243	6	13.03***	0.262	19	11.26***	0.195	27.3
Box of rearing × Box of origin (Dyad)	13	0.72	0.000	6	0.62	0.000	19	0.69	0.000	0.0
Error	205	—	0.343	80	—	0.276	294	—	0.325	36.0
Model	51	7.90***	—	23	6.22***	—	75	7.93***	—	—
n	26/257	—	—	12/104	—	—	38/361	—	—	—

Effects of Box of origin, Box of rearing and their interaction are nested within dyads. Since this is random-effects model, the effects of Box of origin and Box of rearing are tested against the interaction and interaction against error. The effect of Dyad is tested against a complex error term (SAS, 1989). In the combined analysis, all effects are nested within years. Var is the variance component estimate attributable to each of the factors in model (% gives it as a percentage of the total). † $P < 0.10$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Fairbairn & Preziosi (1996) for a more recent example of the reasoning that we follow. In short, an individual was considered as a survivor if it was encountered in the study area as a breeder during the years following its birth. Data concerning recruitment were collected by capturing almost all breeding blue tits in our study population up to the 1997 breeding season, i.e. 2 years after birth for all nestlings considered here; although a small proportion of birds do not recruit until the second year after birth, recruitment delayed beyond this age is rare in our population. Because only a small proportion of nestlings subsequently recruited to the breeding population (see Table 5), we also classified a group of individuals ($n = 75$) re-captured during their first autumn or winter (> 3 months after leaving nest), but not captured as breeding adults, as survivors of a first selection episode. These individuals were re-captured either by two ringing groups in nearby areas, reported to be captured elsewhere, or re-captured by us in sporadic winter visits to the study area. Given the difficulties inherent in assigning relative measures of fitness when fitness has only been measured on a discrete scale (Brodie & Janzen, 1996), we did not attempt analyses assigning this group of birds lower fitness than those that recruited to the breeding population. All other nestlings were considered to be 'non-survivors', although some of these birds might have migrated out of the study area (see Section 4). In all selection analyses each individual was considered to be an independent observation. The dependent variable, survival, was converted into a measure of relative fitness by dividing by the population mean rate of survival (Arnold & Wade, 1984); all independent variables were standardized (zero mean, unit variance) for calculation of standardized selection gradients. Aside from calculating univariate directional and stabilizing selection gradients, we also performed multivariate selection analyses to see whether hatching date and/or nestling condition might have had an independent effect on survival probability. Although selection differentials and gradients were estimated using regression methods, significance testing was carried out with logistic regression in SPSS (SPSS, 1990). We also performed a logistic regression analysis, with backward stepwise elimination of non-significant effects, in which year and experimental effects were included in the model as dummy coded categorical variables. In this analysis, the reference class against which the contrasts for experimental treatment were formed was reduced treatment, and in the case of the year, the reference class was 1995. We also tried alternative reference classes, but the results were qualitatively similar independent of the coding scheme employed (for details of the coding schemes see SPSS, 1990).

In selection analyses, following convention, individuals were the unit of analysis rather than broods.

Although this procedure could be criticized on the grounds of pseudoreplication, we have adopted it for the sake of analytical simplicity. This problem, and further justification for adopting individuals as the unit of analysis, are discussed further in Merilä *et al.* (1997).

Some experimental studies of birds have revealed relationships between fledging condition and fecundity as an adult (e.g. Haywood & Perrins, 1992). We explored the possibility that selection on fledging condition was operating via other components of fitness by investigating the relationship between fledging condition and fecundity (clutch size) in the first year of breeding, for those birds that recruited to the breeding population.

3. Results

(i) Effects of cross-fostering

Cross-fostering itself did not influence fledging condition of nestling blue tits as the home-grown and cross-fostered full-sibs reared in control broods did not differ in their mean condition index (home-grown [mean \pm SE] 1993: 0.34 ± 0.15 [$n = 26$ families]; 1994: -0.08 ± 0.20 [$n = 12$]; away-grown 1993: 0.39 ± 0.15 [$n = 26$]; 1994: -0.16 ± 0.18 [$n = 12$]; repeated measures ANOVA, Year: $F = 4.85$, $P < 0.05$; repeated measures [home vs away]: $F = 0.01$, $P = 0.94$; interaction: $F = 0.25$, $P = 0.62$). Nested ANOVA applied to control broods revealed that in both 1993 and 1994, as well as in the combined data, both environmental and genetic influences on nestling condition were large and approximately equal (Table 1). The effect of Box of rearing, estimating the environmental contribution to the phenotypic variation, was about 22%, and in the combined analyses the significant effect of year accounted for an additional 9% of the variation (Table 1). The effect of Box of origin, estimating the genetic effects, also accounted for about 27% of variation, corresponding to a heritability of 0.56, 0.67 and 0.42 in 1993, 1994

and in the combined data, respectively. There was no evidence for genotype–environment interactions, as the Box of rearing \times Box of origin interaction terms were not significant in any of the analyses (Table 1).

(ii) Full-sib analyses of experimental broods

A four-factorial mixed-model ANOVA applied to the combined data revealed a significant effect of Box of origin on offspring condition (Table 2). This effect corresponds to a cross-environment heritability of 0.28. Surprisingly, the main effect of the Experiment was not significant in this analysis although, in each of the years, the nestlings raised in enlarged broods were in poorer condition than those raised in reduced broods (Fig. 1). However, the lack of statistical significance of this main effect may result from the significant Experiment \times Year and Dyad \times Experiment interactions, which indicate that the effect of the manipulations influencing offspring condition differed between years and between different dyads, respectively (Table 2). The significant Experiment \times Year interaction was apparently caused by the fact that in 1994, when weather conditions were particularly harsh (Merilä & Fry, 1998), nestlings raised in enlarged broods suffered disproportionately more than those raised in reduced broods (Fig. 1). The main effect of year was not significant, but there was an indication of genotype \times environment interactions, as the variance component attributable to the effect of Experiment \times Box of origin was only marginally non-significant (Table 2).

When the data were analysed for each year separately, the effect of Box of origin was significant in both 1993 and 1995, but not in 1994 (Table 3). However in 1994, which was the harshest year in terms of the weather (and hence feeding) conditions (Merilä & Fry, 1998), there was again an indication of a significant genotype \times environment interaction, as indicated by a marginally non-significant Experiment \times Box of origin interaction (Table 3). In all years, the main effect of Experiment was significant, owing to

Table 2. Mixed-model analysis of variance of condition index in cross-fostered blue tit broods

Source	d.f.	MS	F	Var	%
Year	2	30.93	3.78	0.068	7.6
Dyad (Year)	70	2.92	1.21	0.033	3.7
Experiment	1	75.59	11.62†	0.146	16.4
Box of origin (Year, Dyad)	73	1.40	3.37***	0.128	14.4
Year \times Experiment	2	6.84	5.27**	0.033	3.7
Dyad \times Experiment	70	1.43	3.44***	0.131	14.6
Experiment \times Box of origin (Year, Dyad)	73	0.41	1.25†	0.021	2.4
Error	1076	0.33	—	0.332	37.2
Model	291	2.45	7.37***	0.892	100.0

Var is the variance component calculated from the expected means squares, and % gives it as a percentage of the total.

† $P < 0.10$, ** $P < 0.01$, *** $P < 0.001$.

Table 3. Analysis of variance of nestling body condition for each of the three study years separately

Source	1993			1994			1995		
	d.f.	Var	%	d.f.	Var	%	d.f.	Var	%
Dyad	28	-0.047	0.0	18	0.209*	15.7	24	0.039	5.9
Experiment	1	0.049*	7.4	1	0.426***	31.9	1	0.089***	13.1
Box of origin (Dyad)	29	0.109***	16.4	19	0.085	6.4	25	0.181***	26.8
Experiment × Dyad	28	0.183***	27.5	18	0.073	5.5	24	0.091**	13.3
Experiment × Box of origin (Dyad)	29	0.002	0.4	19	0.091†	6.8	25	-0.002	0.0
Error	484	0.322	48.3	214	0.450	33.7	378	0.674	41.0
V_p	—	0.668	100.0	—	1.337	100.0	—	0.675	100.0
Model	115	$F = 5.90$ ***	—	75	$F = 7.11$ ***	—	99	$F = 6.23$ ***	—
r^2	—	0.58	—	—	0.71	—	—	0.62	—

Var is the variance component due to each factor, obtained by equating observed mean squares with expected ones. % is the variance component expressed as a percentage of the total

† $P < 0.10$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

the fact that nestlings raised in enlarged broods were in poorer condition than those raised in reduced broods (Table 3; Fig. 1). As in the analysis presented above, significant Experiment × Dyad interactions in 1993 and 1995 revealed that there was heterogeneity in the effect of the experiment between the different dyads (Table 3).

(iii) Reduced full-sib analyses of experimental broods

To obtain environment-specific tests of Box of origin and Box of rearing effects, we performed separate ANOVAs for each treatment level and year separately. In almost all years and environments the effect of Box of rearing was significant, indicating significant environmental contribution to nestling condition (Table 4). However, effects of Box of origin were also large and significant in all years and both environments (Table 4). Broad-sense heritability (h^2) estimates ranged between 0.31 and 0.75, but there appeared to be no consistent differences in h^2 estimates between the treatment conditions (Table 4). However, the Nest of origin variance components, and hence genetic variances, were consistently higher in enlarged than in reduced treatments, suggesting that more genetic variance was expressed in poor than in good environmental conditions (Table 4). However, because the environmental components of variance, as indicated by variance components due to Box of rearing, were also usually larger in the enlarged than in reduced broods, the heritabilities for the two environments appeared to be similar (Table 4). However, in the enlarged treatment in 1995, when the effect of Box of rearing was much less than in other years, the genetic component dominated and the heritability of body condition was indicated to be high ($h^2 = 0.75$; Table 4).

(iv) Cross-environment genetic correlations

Cross-environment genetic correlations calculated using (1) gave estimates of 0.95, 0.54, 1.00 and 0.87 for 1993–1995 and combined data, respectively. Using the alternative expression (2a), these estimates were 1.00, 0.48, 1.00 and 0.87, respectively. Hence, estimated in either way, these correlations were high and consistent with each other ($r = 0.995$), suggesting that the phenotypic expression of body condition is largely governed by the same genes in both environments. The only exception to this was the low across-environment genetic correlation in 1994, which was the year in which the experiment had a particularly strong effect on mean nestling condition in enlarged broods (Fig. 1).

Table 4. Causal components of phenotypic variance and broad-sense heritability (h^2) estimates of blue tit condition index from random effects ANOVAs in two experimental environments (reduced vs enlarged broods)

Source	Reduced						Enlarged									
	1993		1994		1995		All		1993		1994		1995		All	
	Var	%	Var	%	Var	%	Var	%	Var	%	Var	%	Var	%	Var	%
Year	—	—	—	—	—	—	0.045*	7.4	—	—	—	—	—	—	0.148***	17.5
Box of rearing	0.057†	13.8	0.229*	32.6	0.254**	38.4	0.160***	26.3	0.234***	32.4	0.376**	34.1	0.010	2.1	0.173***	20.3
Box of origin	0.097***	23.3	0.110*	15.6	0.177***	26.7	0.125***	20.5	0.137***	18.9	0.221***	20.0	0.184***	37.7	0.172***	20.2
Error	0.262	63.9	0.365	51.8	0.231	34.8	0.278	45.7	0.351	48.7	0.507	45.9	0.294	60.2	0.357	42.0
Total	0.417	—	0.705	—	0.662	—	0.6082	—	0.722	—	1.104	—	0.488	—	0.850	—
h^2	0.46	—	0.31	—	0.53	—	0.41	—	0.38	—	0.40	—	0.75	—	0.40	—
n	29/215	—	19/122	—	25/162	—	74/489	—	29/358	—	19/168	—	25/326	—	73/879	—

Var is the variance component calculated from the expected means squares, and % gives it as a percentage of the total. n is the number of families/number of nestlings. † $P < 0.10$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

(v) Selection analyses

Only a small proportion of fledged young recruited to the breeding population in each year (Table 5). Analyses of the characteristics of these nestlings with logistic regression revealed, in the sample as a whole, that there was a weak but statistically significant effect of fledging condition on recruitment ($b = 0.229$, d.f. = 1, Wald = 3.930, $P = 0.042$). No effect of hatching date (Wald = 1.083, d.f. = 1, $P = 0.30$), experiment (Wald = 4.339, d.f. = 2, $P = 0.11$) or the square of either hatching date (Wald = 0.211, d.f. = 1, $P = 0.64$) or fledging condition (Wald = 0.942, d.f. = 1, $P = 0.33$) was found, but there was a significant independent effect of the year on likelihood of recruitment (Wald = 19.757, d.f. = 3, $P = 0.002$; Fig. 2). The selection on fledging condition was very weak, since the standardized selection differential from multivariate analyses of the entire sample of nestlings (i.e. combining years and experimental treatments) was only 0.027 phenotypic standard deviations (Table 6), considerably less than the variation between experimental treatments and years. Selection gradients were not strikingly different in any individual years or experimental treatments (Table 6), and this impression was confirmed by the absence of significant interactions between year or experiment and fledging condition on nestling recruitment (in all cases $P > 0.15$). For individual year and experimental levels, 8 of 10 standardized selection gradients were positive for fledging condition (binomial $P = 0.055$) whereas only 5 of 10 gradients were positive for hatching date ($P = 0.62$). No evidence for directional selection on hatching date (Table 6), or non-linear (i.e. stabilizing or disruptive) selection on hatching date or fledging condition, was found (data not shown).

When nestlings that had been re-captured after fledging (usually in the autumn), but had not recruited to the breeding population, were included in the above analyses, the conclusions above were strengthened. Despite a larger sample size (Table 5), the effect of fledging condition on survival was no longer significant ($\beta = 0.025 \pm 0.019$ SE; $\chi^2 = 1.09$, $P = 0.3$), suggesting that selection occurring some time after fledging (e.g. during the winter) was partly responsible for the effect observed among the recruits.

There was no suggestion that fledging condition was under any selection via fecundity among the birds that recruited to the breeding population, as the relationship between fledging condition and first-time clutch size was far from significant for females ($r = -0.04$, $n = 64$, $P = 0.73$), males ($r = -0.04$, $n = 59$, $P = 0.75$) and both sexes combined ($r = -0.05$, $n = 123$, $P = 0.61$).

Table 5. Descriptive statistics of recruitment and survival of blue tit nestlings born in 1992–5

Year of birth	N_n	N_f	R	$R\%$	C	$C\%$
1992	1038	108	44	4.2	65	6.3
1993	1177	122	17	1.4	63	5.3
1994	594	77	24	4.0	32	5.4
1995	850	96	41	4.8	—	—
All	3659	403	126	3.4	160	5.7

N_n , total number of nestlings ringed; N_f , number of families; R , number of nestlings recruiting to breeding population (= survivors); $R\%$, percentage of nestlings recruiting; C , number of nestlings re-captured > 3 months after fledging (therefore also includes some individuals which did not enter the breeding population); $C\%$, as previously but expressed as a percentage of all ringed nestlings.

4. Discussion

(i) General statements

Population genetic models and empirical selection experiments indicate that genetic variance in traits under constant directional selection should be quickly depleted due to fixation of favourable alleles (Kirkpatrick, 1996). Nestling condition is a trait that has been shown to be subject to directional selection in several bird species (Nur, 1984; Pettifor, 1993; van Noordwijk *et al.*, 1988; Tinbergen & Boerlijst, 1990; Hochachka & Smith, 1991; Lindén *et al.*, 1992; Bensch *et al.*, 1996; Verboven & Visser, 1998) and, with the expectation that this would be the case in our study population of blue tits, we performed experimental manipulations and cross-fostering experi-

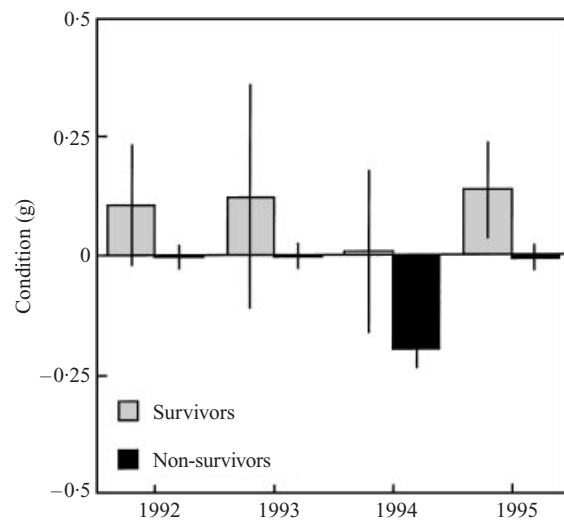


Fig. 2. Mean (\pm SE) body condition index of survivors and non-survivors in four different study years.

ments to determine the contribution of genes to phenotypic variation and to investigate the possibility that genotype–environment interactions might act to maintain genetic variation in populations. We found that genetic effects accounted for about one-quarter of the phenotypic variance, and that there was little evidence for genotype–environment interaction, at least over the range of environments created by our experiments. Selection analyses suggested that such high levels of genetic variation in the absence of genotype–environment interactions are not surprising: this trait is under only very weak selection in this population. Hence, our original expectation (low levels of genetic variation, strong directional selection) was contrary to the pattern that we found in this

Table 6. Standardized selection gradients on nestling fledging condition index and hatching date in the sample of blue tit nestlings over a range of years and experimental conditions

	Year									
	1992		1993		1994		1995		Combined	
	β	SE	β	SE	β	SE	β	SE	β	SE
Reduced										
Condition	—	—	-0.067	0.066	0.102	0.094	0.098	0.079	0.001	0.045
Hatching date	—	—	-0.026	0.066	0.139	0.094	0.072	0.079	0.022	0.045
Control										
Condition	0.034	0.032	0.074	0.043	0.020	0.058	0.034	0.056	0.042*	0.021
Hatching date	0.020	0.032	-0.049	0.043	-0.076	0.058	-0.065	0.056	-0.029	0.021
Enlarged										
Condition	—	—	-0.076	0.050	0.013	0.077	0.039	0.053	-0.020	0.033
Hatching date	—	—	-0.091	0.050	0.122	0.077	0.016	0.053	-0.025	0.033
Combined										
Condition	0.034	0.032	-0.019	0.029	0.041	0.041	0.043	0.034	0.027*	0.016
Hatching date	0.020	0.032	0.050	0.029	-0.001	0.041	-0.010	0.034	-0.019	0.016

The measurement of relative fitness is whether or not a nestling recruited to the breeding population.

* $P < 0.05$.

population (high levels of genetic variation, weak directional selection).

(ii) *Confounding factors*

A shortcoming of our design is that it does not allow us to separate early common environment or maternal effects from additive genetic effects. Since the young were transferred between nests when 2 days old, all maternal effects experienced before this, if persisting to day 14 post-hatch, would be included in our estimate of V_A . Although long-lasting maternal effects are thought to be common in animals (e.g. Rossiter, 1996), there is also evidence to indicate that they may decay quickly with age in passerine birds (e.g. Price & Grant, 1986). For example, Schwabl (1996) demonstrated that maternal testosterone levels in egg yolk of canaries (*Serinus canary*) were positively correlated with nestlings' initial growth performance and begging behaviour but that there were no testosterone-dependent differences in tarsus length or body weight when the nestlings were 2 weeks old. Although we cannot rule out the possibility that maternal effects might have inflated our estimates of heritability, it is worth pointing out that Merilä (1996) used the same design as that used here to estimate heritability of body condition in the collared flycatcher and found a significant nest of origin effect, suggesting a heritable basis for variation in body condition. This result was later confirmed using a maternal half-sib design in which any non-genetic parental effects were strictly excluded, in two different data sets (Sheldon *et al.*, 1997; J. Merilä & B. C. Sheldon, unpublished data).

Another potentially problematic factor, shared with most studies that have not used NC II or diallele type breeding designs (e.g. Kearsley & Pooni, 1996), is that effects of dominance variance cannot be identified and, if present, have been included in our estimates of V_A . In fitness-related traits, strong directional selection is expected to drive some alleles to fixation, with the consequence that additive genetic variance is reduced and the relative importance of the dominance component increased (Fisher, 1958; Lynch, 1994). Indeed, in a recent comparison of the relative magnitudes of dominance and additive contributions to various traits, Crnokrak & Roff (1995) found that the dominance component in fitness-related traits was usually substantial, as predicted by Fisher's (1958) theory. However, as fledging condition in nestling blue tits is apparently under only very weak directional selection, there is no reason to suspect that an increased dominance component of variance will have substantially inflated our estimates of additive genetic variance.

The selection analyses are sensitive to the assumption that dispersal distance (presumably negatively related to recapture probability) is unrelated to

the independent variables for which selection is calculated. We assessed the validity of this assumption by calculating the distance between the nest box in which an individual was born and that in which it bred in its first breeding year, and constructing ANCOVA models. These analyses revealed a significant effect of fledging condition on dispersal distance, together with a significant effect of sex (R. Przybylo & J. Merilä, unpublished data). The effect of fledging condition on dispersal distance was negative, so that birds that fledged in poorer condition dispersed further. This will have the effect of leading us to overestimate the strength of selection on fledging condition, so that the true strength of selection on fledging condition is probably even less than we have estimated in this study. However, it should also be noted that as some mortality occurs before fledging, this might act to decrease the estimated strength of selection.

(iii) *Genetic variation under different environmental conditions*

Several studies have found that heritability estimates for quantitative traits vary with environmental conditions (e.g. Blum, 1988; Hoffmann & Parsons, 1991; Ebert *et al.*, 1993). In studies of birds, heritabilities of morphological traits have generally been lower when estimated under poor than under good feeding conditions (Larsson, 1993; Merilä, 1997; Larsson *et al.*, 1997), but fewer data have been available for other types of traits. In this study, heritability estimates for body condition index were moderate to high, and there were no consistent differences between the two experimental treatments in their magnitudes. Nevertheless, a tendency for genetic variance in body condition to be higher in the poor environment than in the good environment was observed, but this was accompanied by increased environmental variance. Consequently, the increased expression of genetic variance was offset by increased environmental variance and so there is little reason to expect that responses to selection in body size would differ between different environments. This interpretation is also supported by the fact that the cross-environment genetic correlations were usually very high, suggesting that largely the same genes govern the expression of variation in body condition in different environments.

(iv) *Selection on offspring condition*

That there should be positive directional selection on nestling fledging condition is often assumed in studies of passerine birds. Indeed, such selection has been demonstrated in a number of species with rather similar breeding ecology to that of the blue tit (e.g. great tit: Tinbergen & Boerlijst, 1990; Verboven & Visser, 1998), and even in another population of the

blue tit (Nur, 1984), although in the latter case selection was on body weight and the possibility of a confounding effect of hatching date, or indeed of body size, was not excluded. In this study we found that although fledging condition was subject to directional selection, selection was rather weak, and it is only due to the rather large sample size that statistical significance is achieved.

The strength of selection observed in this study is only about 5% of the mean strength of selection observed in a large sample of studies of natural selection in natural populations (Endler, 1986). Further, the estimated strength of selection on fledging condition for blue tits in this population is considerably less than on the same trait in nestling great tits and collared flycatchers breeding in the same woodlands (Lindén *et al.*, 1992). Data in Lindén *et al.* (1992; their tables 1 and 2) suggest that the directional selection gradient (β) on fledging condition in great tits is 0.135 and in collared flycatchers 0.219 (mean weighted by sample size in each year), 4.6 and 7.6 times that in this sample of blue tits, and our estimates of selection on fledging condition in blue tits are, if anything, overestimates. What could explain these differences? In the case of the comparison with the collared flycatcher, Lindén *et al.* (1992) have suggested that the stronger selection on fledging condition in flycatchers than in great tit nestlings reflects the greater importance in non-migrating tits of leaving the nest early to obtain an autumn territory rather than attaining a high fledging weight. This is not suggested as an explanation for reduced selection on fledging condition in blue tits, since we found no indication of selection on hatching date in this population. At present, we are unable to explain the differences between our study of blue tits and those of other species.

(v) Conclusions

In conclusion, the results of this study show that body condition in fledging blue tits is moderately to highly heritable, and that there is little evidence that phenotypic variation in body condition is governed by different genes under different environmental conditions. The relatively high heritabilities are surprising in the light of the fact that nestling condition is a trait thought to be under strong directional selection in most passerine species (Alatalo *et al.*, 1990; Hochachka & Smith, 1991; Lindén *et al.*, 1992; Thessing & Ekman, 1994), but consistent with the relatively weak selection intensities documented in this study.

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