

S38-3 Evolution and expression of genetic variation in nestling traits

Juha MERILÄ¹, Loeske E.B. KRUUK², B.C. SHELDON³

1. Ecological Genetics Research Unit, Dept. of Ecology and Systematics, University of Helsinki, PO Box 65, FIN-00014, Finland; juha.merila@helsinki.fi

2. Institute of Cell, Animal and Population Biology, University of Edinburgh, UK

3. Edward Grey Institute, Dept. of Zoology, University of Oxford, UK

Abstract Environmental conditions experienced during early life are known to impact upon the development of passerine nestlings, as well as on their performance and fitness as adults. Nevertheless, little is yet known about the relative importance of different types of maternal, environmental and genetic effects as proximate determinants of variation in nestling traits, and in particular, how the relative importance of these components is affected by the characteristics of the growth environment. Evidence from a number of studies suggests that the expression of both genetic and maternal effects can be highly environment-dependent, together with their impact upon fitness variation among individuals. Again relatively little is known about how selection acts upon this variation. According to one popular scenario, selection acts mainly on environmental, not genotypic variation. Using data from a long-term study of collared flycatchers (*Ficedula albicollis*) from the Swedish island of Gotland, we demonstrate that: (1) common environmental/parental effects have a strong influence on variation in nestling traits, and (2) different traits are affected differentially by early vs late effects. We further demonstrate that (3) selection acts on genetic, as well as environmental, variation. These results suggest that common environmental/parental effects may be more important sources of variation in nestling traits than previously acknowledged, and that the time-window for these effects differs for different traits. Furthermore, our analyses reinforce the conclusion that selection on environmental deviations cannot alone explain the lack of expected selection responses in heritable nestling traits under directional selection.

Key words Genetic variation, Maternal effects, Environmental effects, Selection, *Ficedula albicollis*

1 Introduction

How do environmental conditions influence individual growth? How does individual variation in growth translate into variation in individual fitness? What are the evolutionary implications of fitness variation stemming from environmentally induced effects on individual growth performance? These all appear to be fairly trivial and unproblematic questions because it is known that: first, poor environmental conditions have a negative impact on individual growth (Gustafsson and Sutherland, 1988; Merilä, 1997); secondly, poor growth performance is often associated with reduced likelihood of survival to adulthood (Alatalo et al., 1990; Lindén et al., 1992); and thirdly, poor growth can translate into other kinds of problems with cascading effects on future performance such as lowered fecundity (Gustafsson and Sutherland, 1988). Furthermore, poor growth performance often leads to lowered heritability of growth related traits in birds (Larsson, 1993; Merilä and Sheldon, 2001), and thereby reduces the efficiency of selection and expected evolutionary response to directional natural selection (Hoffmann and Merilä, 1999).

An idea intimately related to low heritability under poor environmental conditions is 'selection on environmental deviations' (Alatalo et al., 1990). The kernel of this idea is the perception that when environmental variation causes

individual variation in growth, and reduced growth is selected against, then selection will predominantly weed out individuals deviating negatively from the "genetic ideal" (Fig. 1). In other words, selection is considered to be "soft" in the sense that it acts mainly against negative environmental deviations from genotypic (breeding) values (Fig. 1a), rather than "hard" in the sense that it acts mostly on absolute trait values irrespective of the genetic details (Fig. 1b). This argument has been repeatedly evoked as an explanation for the lack of evolution (or expected selection response) in heritable traits under directional selection (Merilä et al., 2001a).

Returning to the opening questions, it is clear that there is now a fairly good understanding of how environmental conditions influence individual growth and how this translates into fitness variation (cf. Stinchcombe et al., 2002). It is not at all clear, however, whether our understanding of the evolutionary implications of environmentally induced variation in individual fitness is adequate (cf. Merilä et al., 2001a). First, evidence for lowered heritability of growth-related traits under poor environmental conditions is somewhat mixed, and although there seems to be a tendency for size-related traits to express less genetic and more environmental variance under such conditions, the evidence is equivocal (Hoffmann and Merilä, 1999; Merilä and Sheldon, 2001). Secondly, although arguments for selection on envi-

ronmental deviations have been made frequently, it is unclear whether this is actually a plausible mechanism in nature: none of the early studies have explicitly tested for selection on environmental deviations. Thirdly, due to the ubiquity and persistence of maternal and common environment effects (Rossiter, 1996; Mousseau and Fox, 1998), it is still unclear how much of the variation attributed to additive genetic effects in the wild can be explained by common environmental and parental effects.

The aim of this paper is to describe work that addresses the following three questions. First, is there evidence that the heritabilities measured in earlier studies of wild bird populations could be upwardly biased due to persistent maternal or common environmental effects? Secondly, how much scope is there for parents to influence the performance of their offspring through these effects? Thirdly, is there evidence that selection may be acting on variation in environmental/parental effects, rather than on breeding values per se? The answer to the last question is valuable also because it can shed light on the debate as to why heritable traits under directional selection fail to show the evolutionary responses predicted by quantitative genetic theory (Merilä et al., 2001a).

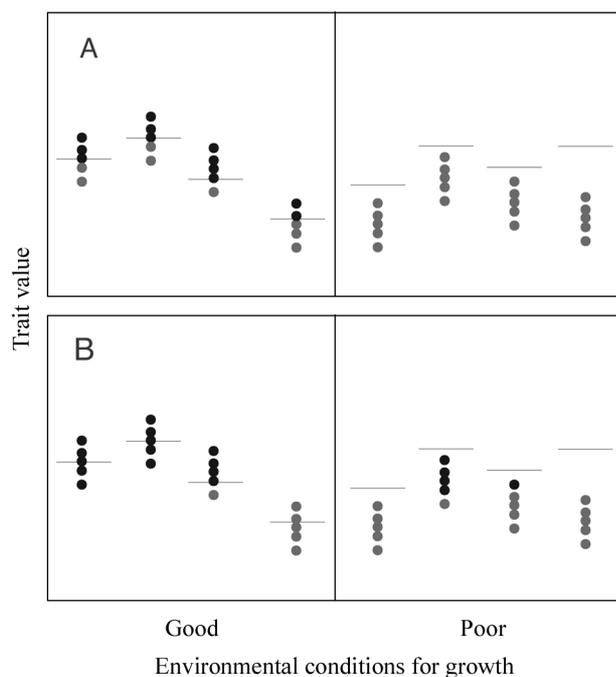


Fig. 1 Schematic illustration of the concepts of (A) “selection on environmental deviations” and (B) “conventional selection” under two different environmental conditions

Environmental conditions are poor vs. good growth conditions, respectively. Each point represents the phenotypic value of an individual, and the horizontal line the expected breeding value for a brood (group of points). The distance and direction between expected breeding value and individual phenotypic value represents the environmental deviation for a given individual. The effect of selection is depicted by red circles: under a given scenario, individuals marked with grey are destined to die (selected against), whereas individuals in black are destined to survive (selected for).

2 Materials and methods

The data for the analyses here derive from a long-term study, between 1980 and 1999, of the collared flycatcher (*Ficedula albicollis*) on the Swedish island of Gotland (Gustafsson, 1989; Merilä, 1997; Kruuk et al., 2001). Every year, nearly all adults and their offspring were captured and banded with individually numbered aluminium rings for their subsequent identification and construction of pedigrees. All banded nestlings were also measured for tarsus length (mm) and body weight (g). Nestling tarsi are full grown at fledging, and can be used as a measure of general body size (Merilä, 1997). Body condition index in nestlings is defined as the mass relative to general body size, as obtained from the linear regression of nestling body weight on tarsus length (Merilä, 1997; Merilä et al., 2001b). Both of these traits are known to be influenced negatively by poor feeding conditions (Merilä, 1996; Merilä, 1997), and to be under positive directional viability selection (Lindén et al., 1992; Merilä et al., 2001b; Kruuk et al., 2001). Yet for one reason or another, they have not shown the phenotypic evolution expected over the study period (Merilä et al., 2001a,c; Kruuk et al., 2001).

To analyze the relative contributions of different genetic and environmental factors to nestling tarsus length and condition, two different data sets were used. These were a data set consisting of all nestlings ($n = 17\,769$) that had been reared by their biological parents between 1980 and 1999, and a data set consisting of nestlings cross-fostered two days after hatching during the same period ($n = 5\,567$). These data sets were subjected to “animal model” analyses of variation, which are generalized linear mixed models utilizing pedigree information and allow the partitioning of variance in phenotypic traits into additive genetic effects and other random and fixed effects (Knott et al., 1995; Milner et al., 1999; Merilä et al., 2001a).

These models were also used for BLUP (Best Linear Unbiased Predictor) estimation of the individual breeding values used in the analyses of natural selection on individual breeding values and environmental deviations, respectively. Environmental deviations here were defined as residuals of regressions of phenotypic values on individual breeding values. All animal model analyses were performed using the programs PEST (Groeneveld and Kovacs, 1990; Groeneveld et al., 1992) and VCE (Groeneveld, 1995) running on UNIX-platform. Selection analyses used to estimate linear standardized selection differentials (S) were performed using the methods of Arnold and Wade (1984a,b) with SAS statistical package (SAS Institute, 1996). More details about the data and analyses can be found in Merilä et al. (2001b) and Kruuk et al. (2001).

3 Results and discussion

3.1 Sources of phenotypic variation in nestling traits

“Animal model” analyses of variation in tarsus length and the condition index of non-fostered nestlings revealed

that both traits were significantly heritable (tarsus length: $h^2 = 0.35 \pm 0.021$; condition index: $h^2 = 0.30 \pm 0.023$; Table 1a). After controlling for additive genetic effects, however, large amounts of environmental (*sensu lato*) variation still remained in both traits. This was largely accounted for by a common nest environment effect, and to a minor degree by year and area effects (Table 1a).

The common environment effect could be genuine, due for example to territory quality; but it could also be attributable to parental effects. To explore this, we fitted models where the common environment effect was replaced with maternal and paternal identity effects. The results revealed that the combined effect of the maternal and paternal identities was about the same as the common environment effect for each trait (Table 1b), suggesting that variation captured by the latter in the original models (Table 1a) reflect a genuine common environment effect. For both tarsus and nestling condition traits, however, the maternal identity effect was slightly but significantly larger than the paternal identity effect by ca 5%, suggesting a small maternal effect contribution to both traits (Table 1b).

When the analyses were repeated using data from cross-fostering experiments (Table 2), which allowed fitting the effects of origin and rearing environments together with additive genetic effect, the following intriguing points emerged. First, heritability estimates were lower than those recovered from the analysis of non-fostered nestlings (cf. additive genetic variance in Tables 1a and 2). This suggests that the heritability estimates from non-fostered nestlings may be inflated by unaccounted common environment or parental effects, especially so in the case of tarsus length. Secondly, even after accounting for additive genetic effects, there was a substantial (16.1%) nest of origin effect on tarsus length (Table 2). This further suggests a substantial

Table 1 Sources of variation in nestling condition and tarsus length in collared flycatchers as revealed by “animal model” analyses applied to data (1980–1999) of non-fostered nestlings

Source of variance	Condition	Tarsus
	var% \pm SE	var% \pm SE
a. <i>Nest of rearing</i>		
Additive genetic	29.9 \pm 2.3	35.3 \pm 2.1
Nest of rearing	48.5 \pm 1.4	29.7 \pm 1.4
Year	7.5 \pm 1.7	13.9 \pm 2.6
Area	0.6 \pm 0.4	2.1 \pm 0.7
Residual	13.5	19.0
b. <i>Maternal and paternal identity</i>		
Maternal identity	28.5 \pm 1.1	18.6 \pm 1.0
Paternal identity	23.7 \pm 0.9	12.2 \pm 0.8
N (nests)	3 836	3 844
N (fledglings)	17 717	17 769

Var = variance component as a percentage of total phenotypic variance. N = sample size. Adopted from Merilä et al. (2001b) and Kruuk et al. (2001).

early-life common environment or parental effect on variation in tarsus length. In the case of nestling condition, the nest of origin effect was small (ca 2%), whereas the nest of rearing effect was about twice as large (ca 43%) as the additive genetic effect (22%; Table 2). Hence, in contrast to tarsus length, nestling condition seems to be determined mainly by the environment experienced late in the nestling phase, with little or no influence from the early environment.

3.2 Selection on environmental vs genetic components of phenotype

Concerning the action of survival selection, analyses of selection over the study period revealed strong and consistent directional selection on the phenotypic values of both tarsus length ($S = 0.18 \pm 0.02$ standard error) and nestling condition ($S = 0.23 \pm 0.02$). Similar analysis of estimated breeding values revealed that selection was acting on breeding values as well (tarsus length: $S = 0.13 \pm 0.02$; condition: $S = 0.14 \pm 0.02$). These analyses suggest that selection is acting not only on environmental deviations, but also on genotypic variation. This conclusion is corroborated by two further lines of evidence. First, comparisons of variance components attributable to additive genetic and environmental effects before and after selection reveal that both are significantly reduced by natural selection (Merilä et al., 2001b; Kruuk et al., 2001). Secondly, analysis of survival selection on offspring deviations from the midparent tarsus length, together with selection on midparent tarsus length, reveal that both midparent values and the offspring deviations from them are subject to selection (Kruuk et al., 2001). Both of these analyses reinforce the conclusion that selection is acting not only on environmental deviations, but also on additive genetic variance.

4 Conclusions and implications

The results above lead to three main conclusions. First, “animal model” analyses of phenotypic variation return lower heritability estimates than traditional midparent-midoffspring regressions, at least for tarsus length ($h^2 =$

Table 2 Sources of variation in nestling condition and tarsus length in collared flycatchers as revealed by “animal model” analyses applied to data (1984–1999) of cross-fostered nestlings

Source of variance	Condition	Tarsus
	var% \pm SE	var% \pm SE
Additive genetic	21.9 \pm 2.9	28.0 \pm 4.4
Nest of rearing	42.8 \pm 2.2	15.2 \pm 2.2
Nest of origin	2.2 \pm 1.3	16.1 \pm 1.3
Year	10.4 \pm 3.0	12.2 \pm 3.2
Area	4.8 \pm 2.3	2.8 \pm 1.5
N (nests)	1 044	1 044
N (nestlings)	5 565	5 567

Var = variance component as a percentage of total phenotypic variance. N = sample size. Adopted from Merilä et al. (2001b) and Kruuk et al. (2001).

0.48, Merilä, 1997; $h^2 = 0.65$, Merilä et al., 1998). This suggests that traditional estimates of heritability in wild animal populations might often be overestimated. Such a difference between the methods can be attributed to the ability of “animal model” analyses, which are based on extensive pedigree information, to remove environmental correlations between relatives more efficiently. The reduction in heritability estimates between the two sets of analyses, non-fostered vs. cross-fostered nestlings, nevertheless suggests that even “animal model” estimates of heritabilities might be to some degree inflated by early common environment or parental effects.

Secondly, the large common environment/parental effects recovered by these analyses suggest ample scope for parental performance to influence the fitness of their offspring. In the case of tarsus length, moreover, the effects of both early and late parental environments (cf. Table 2) seem to be equally important, whereas in the case of the condition index, any effects from the early environment are overwhelmed by late nestling period effects (Table 2). Thus, selection acting on environmental variation, whether due to parental or common environment effects, can in theory act differently on early and late effects of caretaking, depending on the trait concerned.

Thirdly, environmental and parental sources of variation in offspring performance are under directional natural selection, as revealed by selection analyses demonstrating that both genetic and environmental components are under directional selection. The lack of expected response in these traits over time (Merilä et al., 2001c; Kruuk et al., 2001) thus cannot be explained simply as the failure of selection to act on the relevant underlying variation; alternative explanations should be considered. Consideration of further mechanisms, as well as further partitioning of phenotypic variance into its causal components, particularly those attributable to direct and indirect maternal genetic effects (Roff, 1997: 248), remains a challenge for future studies.

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