Two-stage Selection in which the First Stage Only Reduces the Environmental Variation in Body Size in the Great Tit

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Abstract
Growth data on nestling Great Tits (Parus major) under suboptimal conditions suggest that final size, rather than growth rate, has a genetic component. Furthermore, the time during which growth can take place is limited. If the amount of food has been insufficient to allow the nestling to reach the “programmed” size, the mortality after fledging is much higher. This mortality greatly reduces the phenotypic variation in size (measured either as weight or as tarsus length), but the genetic variation is not affected. This can be demonstrated directly through comparison of the additive genetic variation and the environmental variation between nestlings and recaptured birds, or indirectly through the absence of a relation between parental size and offspring survival. In a second selection phase, the differences in size between survivors and nonsurvivors are also reflected in similar differences between the parents of these birds.

Introduction
In 1909, Johanssen introduced the concepts of genotype and phenotype. The phenotype is the directly observable entity and can be thought of as an integrated whole, in which variation due to genetic or environmental causes cannot be separated. This holistic aspect is an approximation. There are cases in which every biologist will accept that the phenotypic trait under investigation is a complex on which genetic and environmental factors may act differently. One such trait is body weight, which contains an element of condition, i.e., the thickness of fat reserves, as well as an element of size, in the sense of stature. The same is true for many other traits for which a part of the variation was fixed during growth and a part is caused by fluctuations within individuals.

*In cooperation with the Institute for Ecological Research, Heteren, The Netherlands.
In quantitative genetics, one assumes that selection will affect the genetically and environmentally caused components of the phenotypic value in proportion to their contributions to the phenotypic variation. This has been amply corroborated in studies of artificial selection, in which the experimenter or the animal breeder in fact bases his culling decisions on the measured phenotypic value. In connection with natural selection, there are problems, because the environmental variation is both greater and structured. In the example with body weight, selection may be either for stature or for condition, but stature probably has an important genetic component and condition hardly any. In this case, the genetic components of body weight will be affected disproportionately by natural selection.

This paper presents data that demonstrate such a disproportionate effect on the genetic and nongenetic components of body weight in the Great Tit (*Parus major*). There is evidence that the same pattern is found for traits that do not show any within-individual variation apart from measurement error.

**Material and Methods**

The data used in this study come from the population study on Great Tits carried out at the Institute for Ecological Research at Heteren, The Netherlands.

For details about the study area and methods, see van Balen (1980) and Drent (1984). A detailed analysis of the heritability of body-size traits in these populations was given by van Noordwijk *et al.* (in press).

All nestling weights were taken at an age of at least two weeks (these weights are approximately equal to the fledging weights). Recaptures are all birds caught at least once, at least three months after fledging. Recruits are all locally born birds that were found breeding in later years. All adult weights, for parents and for recaptured individuals, are the means of all weights taken on each individual outside the breeding season.

The sex difference in weight causes problems, because this difference is not constant. The best approximation is an adjustment of 0.6 g (plus in females, minus in males) for adults and 0.4 g similarly in nestlings. Calculations were made with and without the correction for sex. Only for the small samples of individuals recruited in the breeding population does the treatment of the sex difference matter, and then mostly for the year 1978, in which the recruited individuals consisted of three relatively heavy females and nine relatively light males. Otherwise, none of the conclusions drawn is sensitive to a sex difference.

**Results**

**Nestling Growth**

For several years, data on the growth of nestlings have been collected by measuring the individual nestlings on days 5, 10, and 15 after hatching. An example of the correlations between the sizes at different ages and the growth, i.e., increase in size, in the intervening periods is given in Table 1. For both weight and tarsus length, strong positive correlations are observed between the sizes at all three ages. However, the big nestlings at age 5 or 10 d will grow
less in the next 5 d than the small nestlings; growth is thus negatively correlated with size. This is found for both absolute growth (g weight and mm tarsus length) and relative growth (e.g., size at day 10 / size at day 15). This can only be interpreted as a slowing down or even stopping of growth when a certain size is reached. It is in agreement with the generally assumed S-shaped growth curve. It is consistent with an individually fixed end point of growth, together with a limited period during which the growth can take place.

Selection

Nearly all nestlings were weighed in the Hoge Veluwe study area from 1975 to 1978. In autumn and winter, weekly mist-net captures were made, as well as monthly roosting inspections, so that a large proportion of the nestlings still alive were recaptured and their weights at recapture recorded. It is not necessary to assume that all individuals not recaptured died. It is assumed, however, that the recaptured birds form a representative sample of all surviving birds.

The nestling weights of the subsequently recaptured individuals are higher than those of all nestlings (Table 2). This difference is marginally significant in 1975 ($P < 0.10$) and significant in the other 3 yr ($P < 0.01$). This is due to a lower survival of light nestlings, as has often been reported (e.g., Perrins 1979). The difference in mean is accompanied by a reduction in the phenotypic variation.

When growing conditions are good, there is little difference between the nestling weight and the subsequent adult weight of the same individual (see 1977 and 1978 in Table 2). I will therefore regard nestling and adult body weight as a single trait, even though in some years (1975, 1976) there can be a considerable increase in weight after fledging.

From parent–offspring regressions based on either nestling weights or recapture weights, the phenotypic variation of the offspring weights can be divided into a (additive) genetic variation and an environmental variation. The heritability and the phenotypic variation are the directly observed quantities. Because the heritability is the proportion of genetic variation in the phenotypic variation, multiplication of the two gives the value of the genetic variation, and subtraction then gives the value of the environmental variation (Table 3).

In all 4 yr, the environmental variation is smaller for the recaptures than for the nestlings. In contrast, the values for the genetic variation are fairly similar for nestlings and for recaptures. On average there is a decrease by two-thirds in environmental variation, and the total decrease in the phenotypic variation is due to the decrease in the environmental component. These data suggest that the apparent selection on nestling weight acted only on the environmental component in the phenotype.

The difference in mean between a selected group and the total group from which the individuals were selected is the selection differential (SD). For example, in 1975 the selection differential for recruits is 0.86 g. With the recaptures as an intermediate group, the selection differential could be broken into two steps, as the recruits are contained in the recaptures. The first step is the selection differential between all nestlings and the recaptured individuals, and the second
Table 1. Correlations between size and growth for nestling Great Tits (data from Vlieland 1982).

<table>
<thead>
<tr>
<th></th>
<th>Weight (g)</th>
<th></th>
<th>Tarsus length</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Day 10</td>
<td>Day 15</td>
<td>Day 10</td>
</tr>
<tr>
<td>Day 5</td>
<td>0.44</td>
<td>0.15</td>
<td>0.52</td>
</tr>
<tr>
<td>Day 10</td>
<td></td>
<td>0.63</td>
<td></td>
</tr>
<tr>
<td>incr. next 5 d</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Weight day 5</td>
<td></td>
<td>-0.28</td>
<td></td>
</tr>
<tr>
<td>day 10</td>
<td>-0.23</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tarsus day 5</td>
<td>-0.70</td>
<td></td>
<td></td>
</tr>
<tr>
<td>day 10</td>
<td>-0.58</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 2. Mean 15-d-old weights of all individual nestlings, those subsequently recaptured, and those subsequently recruited. The weight differences between the groups are given as the selection differentials (SD) (data from Hoge Veluwe).

<table>
<thead>
<tr>
<th>Year</th>
<th>All nestlings</th>
<th>Recaptured nestlings</th>
<th>Recruited nestlings</th>
<th>SD (Stage 1)</th>
<th>SD (Stage 2)</th>
<th>SD (total)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1975</td>
<td>16.38 (n = 614)</td>
<td>16.62 (n = 84)</td>
<td>17.24 (n = 25)</td>
<td>+0.24</td>
<td>+0.62</td>
<td>+0.86</td>
</tr>
<tr>
<td>1976</td>
<td>16.90 (n = 717)</td>
<td>17.58 (n = 206)</td>
<td>17.43 (n = 78)</td>
<td>+0.68</td>
<td>-0.15</td>
<td>+0.53</td>
</tr>
<tr>
<td>1977</td>
<td>17.55 (n = 117)</td>
<td>17.71 (n = 320)</td>
<td>17.77 (n = 40)</td>
<td>+0.16</td>
<td>+0.06</td>
<td>+0.22</td>
</tr>
<tr>
<td>1978</td>
<td>17.06 (n = 658)</td>
<td>17.59 (n = 124)</td>
<td>17.25 (n = 12)</td>
<td>+0.53</td>
<td>(-0.34)</td>
<td>(+0.19)</td>
</tr>
<tr>
<td>mean</td>
<td></td>
<td></td>
<td></td>
<td>0.40</td>
<td>0.18*</td>
<td>0.54*</td>
</tr>
</tbody>
</table>

*With 1978 data omitted owing to small sample size.
Table 3. Estimates of the genetic (Vg) and environmental variation (Ve) for body weights at two different ages of the Great Tit offspring, calculated from the phenotypic variation (Vp) and heritability estimates (h^2).

<table>
<thead>
<tr>
<th>Year</th>
<th>h^2</th>
<th>Vp</th>
<th>Vg</th>
<th>Ve</th>
<th>h^2</th>
<th>Vp</th>
<th>Vg</th>
<th>Ve</th>
</tr>
</thead>
<tbody>
<tr>
<td>1975</td>
<td>0.38</td>
<td>1.84</td>
<td>0.70</td>
<td>1.14</td>
<td>1.01</td>
<td>1.22</td>
<td>1.22</td>
<td>0</td>
</tr>
<tr>
<td>1976</td>
<td>0.47</td>
<td>2.22</td>
<td>1.04</td>
<td>1.18</td>
<td>0.49</td>
<td>1.34</td>
<td>0.66</td>
<td>0.68</td>
</tr>
<tr>
<td>1977</td>
<td>0.26</td>
<td>1.59</td>
<td>0.41</td>
<td>1.18</td>
<td>0.57</td>
<td>1.25</td>
<td>0.71</td>
<td>0.53</td>
</tr>
<tr>
<td>1978</td>
<td>0.29</td>
<td>1.63</td>
<td>0.47</td>
<td>1.16</td>
<td>0.72</td>
<td>1.55</td>
<td>1.11</td>
<td>0.44</td>
</tr>
<tr>
<td>mean</td>
<td>0.35</td>
<td>1.82</td>
<td>0.66</td>
<td>1.16</td>
<td>0.70</td>
<td>1.34</td>
<td>0.92</td>
<td>0.41</td>
</tr>
</tbody>
</table>

Further Analyses
The mean weights of all nestlings vary between years from 16.38 to 17.55 g. The mean nestling weights for recruits vary only between 17.24 and 17.77 g in these 4 yr. This is consistent with the explanation that the differences between nestling weights are due to environmental causes.

The thesis that the genes for body size are not affected by selection can be investigated through the weights of the parents. Inferences about the extent of genetic variation are based on the resemblance between parents and offspring. One of the ways to estimate heritabilities is to select parents and to relate the change in mean in the offspring to the selection differential in the parents. There are no logical reasons why one cannot turn this process around and expect the differences observed in the offspring to be reflected in the parents, insofar as the trait is genetically determined. Using a simple unweighted mean over the years, the selection differential for the recaptures is 0.40 g. With a heritability of 0.35, one expects a difference of 0.14 between the mean weights of all parents and of the parents of the recaptures. (Parental weights are weighted for the number of offspring.) In fact, the difference is much smaller at 0.035 g (Table 4).
Table 4. Selection differentials (SD) based on the winter weights of Great Tit parents of different offspring groups (data from Hoge Veluwe).

<table>
<thead>
<tr>
<th>Year</th>
<th>All parents mean (s.d.)</th>
<th>With recaptured offspring mean (s.d.)</th>
<th>With recruited offspring mean (s.d.)</th>
<th>SD 1</th>
<th>SD 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>1975</td>
<td>17.90 (0.59)</td>
<td>17.90 (0.50)</td>
<td>18.04 (0.53)</td>
<td>0</td>
<td>0.14</td>
</tr>
<tr>
<td>1976</td>
<td>17.98 (0.55)</td>
<td>18.01 (0.52)</td>
<td>17.99 (0.56)</td>
<td>0.03</td>
<td>-0.02</td>
</tr>
<tr>
<td>1977</td>
<td>18.04 (0.55)</td>
<td>18.10 (0.53)</td>
<td>18.17 (0.45)</td>
<td>0.06</td>
<td>0.07</td>
</tr>
<tr>
<td>1978</td>
<td>18.00 (0.56)</td>
<td>18.05 (0.54)</td>
<td>18.18 (0.41)</td>
<td>0.05</td>
<td>(0.13)</td>
</tr>
<tr>
<td>mean</td>
<td></td>
<td></td>
<td></td>
<td>0.035</td>
<td>0.06</td>
</tr>
</tbody>
</table>

In the second selection step—the difference between recaptures and recruits—the fit between apparent selection in offspring and parents is better, especially if one omits the data for 1978 on grounds of the sample being too small. The selection differentials of 0.18 g in the nestling weights and 0.06 g in the parents show exactly the one in three ratio expected from a 0.35 heritability. Moreover, the ordering of the differentials in the 3 yr is the same in parental and offspring values, both values being negative in 1976. For the first step, there is no similar order in offspring and parental values. The fit between parental values and the differential in recapture weights is not so good. A differential of 0.21 g in the offspring with a 0.7 heritability would lead to an expected differential of 0.14 g in the parents, rather than the observed 0.06 g. Still, the figures are closer than for the first step in the selection. Including the data for 1978 would have given a better fit for the recapture data, but a much worse fit for the nestling weights.

In conclusion, the differences in mean parental weights suggest that the genetically determined body weight is not involved in the differences between recaptured and unrecaptured individuals, but the genetic component may well be involved in the second stage of selection, the difference between recaptured and recruited individuals.

Discussion

One can describe the problem as a paradox. Several studies have demonstrated the presence of considerable amounts of genetic variation for body size in natural populations of birds, in fledgling size as well as in adult size. On the other hand, ecologists have normally interpreted differences in fledgling size as entirely environmental and have never run into difficulties using this interpretation. The analysis in this paper shows that the ecologists have been justified: even though genetic variation is present, it does not play a role in the determination of survival.
after fledging. The (naive) interpretation of the quantitative geneticist, that the phenotype is an integrated whole of genetic and environmental effects, cannot be maintained in this case.

One could argue that these results are a consequence of body weight being a poor trait. Two arguments suggest that this is not true and that the patterns are more general. The first is that under controlled environmental conditions, body weight at a standardized age is a perfectly normal trait; many selection experiments for body weight have been undertaken successfully in many species of vertebrates with determinate growth. The problems that were encountered arise from the variation in environmental conditions. A second argument is that data on tarsus length, which does not change at all after an age of 13 d (nestling measurements were made on the 15th d), show the same pattern, although the data are fewer than for weight (H.P. Koelewijn, unpublished data). If one uses the deviation of the offspring from their parental values as a measure of the environmental deviation, the deviations in weight and tarsus are more strongly correlated than weight and tarsus themselves (van Noordwijk et al., in press).

It might seem that part of the problem could be solved by considering the weight of nestlings to be a different trait from adult weight. The relationship could then be studied through (genetic) correlations between traits. This is not practical, because the relationship between nestling weight and adult weight varies strongly from year to year and is likely to be different for the recaptures—in which it can be measured—and for the group that does not survive—in which it cannot. The description as given in this paper in terms of environmental components is simpler and provides more insight into the mechanisms.

Only data for 1975 to 1978 have been used, so that the hypotheses generated from these data can be tested on the data for later years.

The fact that the environmental and genetic components in the variation are treated differently by selection has consequences for our ability to measure selection. It is evident that a simple description of the selection processes in existing terms is inadequate. It is too early to start formulating a vocabulary in which the interactions between processes traditionally studied in either ecology or genetics can be summarized. I trust that with further case studies such a vocabulary will arise.

Acknowledgments

The data on the Hoge Veluwe Great Tits were collected by many people at the Institute for Ecological Research. P.J. Drent coordinated the large-scale measurements of nestling weights. I thank H.P. Koelewijn for stimulating discussions and S.C. Stearns for comments on an earlier version of the manuscript.

References
