Developmental Buffereing as a Mechanism for Stasis: Evidence from the Pulmonate Theba pisana

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DEVELOPMENTAL BUFFERING AS A MECHANISM FOR STASIS:
EVIDENCE FROM THE PULMONATE THEBA PISANA

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Morphological stasis, the absence of significant directional evolution within a species over geologic time, is a phenomenon that now seems generally accepted and in need of an explanation (Lande, 1986; Williamson, 1987). Many proposed mechanisms for stasis and the related phenomenon of geographic species integration (Van Valen, 1982) have been categorized as either selective factors or constraints (Williamson, 1987). As Williamson (1987) points out, some confusion can be avoided in the selection/constraint discussion if one considers that these two types of mechanism are not mutually exclusive and need not oppose each other. Stasis need not result from selection or constraint, but rather from some combination of these factors.

Any process that causes populations to shift toward phenotypic modality through a contraction in variability during a generation may contribute to stasis by repeated action over many generations. Stabilizing selection, one such process that acts by truncating the tails of the phenotypic distribution, has been demonstrated in a variety of organisms (Mayr, 1963 pp. 282–283). Stabilizing selection is typically inferred when the variability of surviving adults is less than the variability of all juveniles, including those that die before adulthood. However, if reduced variability is observed when adults are traced back through ontogeny so that they are compared to what they themselves were like as juveniles, then developmental buffering can be inferred. Here, we show that a contraction in variability, and therefore a shift toward phenotypic modality, occurs within successful subsets of populations of the pulmonate land snail Theba pisana (Müller).

It is stressed that this change in variability is observed when only the individuals that survive to adulthood are considered. All adult snails in this study were collected live, and therefore, no individuals that died before adulthood were considered. Because the observed changes in phenotypic distribution do not involve any mortality, the changes are, by definition, nonselective. It is not argued that selection in general is unimportant in maintaining phenotypic modality in T. pisana. Rather, even within samples that experience no natural mortality, a contraction in variability is observed. This pattern of reduced variability is attributable to developmental homeostasis, which itself may result from stabilizing selection.

MATERIALS AND METHODS

Samples of mature snails were collected live from single demes (Cowie, 1984) between August 1977 and October 1984. Eight samples from Tenby (U.K.) and one from Lesbos (Greek Islands), with an average sample size of 37, were used in this study. Shelled gastropods are ideal organisms for within-cohort morphometric analysis, since the shell is a record of its own growth; i.e., longitudinal studies (Cock, 1966) can be carried out without periodically monitoring live animals. Nevertheless, such studies are limited by the confidence with which one can assign specimens to age classes. The populations of T. pisana from Tenby and Lesbos are known to have determinate growth and a biennial life cycle, breeding only once during a short season (Cowie, 1984). Therefore, the single adult cohort can be readily distinguished by the individuals’ sizes or the numbers of volutions of the shell.

Fixed ontogenetic reference points are needed, because it is crucial to longitudinal analysis that morphological measurements be made at corresponding developmental stages in all members of a population. The junction between the protoconch and teleoconch, which corresponds with hatching in T. pisana, is the first ontogenetic stage considered (Fig. 1). The snails grow roughly three whorls after hatching, so the protoconch and teleoconch together constitute roughly four whorls. The completion of each whorl is considered to mark a subsequent ontogenetic stage (Hickson, 1972).

Radiographs were prepared by mounting specimens with the axis of coiling (estimated by eye), the protoconch-teleoconch junction, and the three subsequent whorl cross sections (i.e., generating curves [Raup, 1966]; separated by integral numbers of volutions) parallel to the plane of the film (Fig. 1). This method of estimating the coiling axis incurs a negligible error of only a few degrees. After enlargement, the radiographs were digitized electronically, and the following parameters were measured or calculated (Fig. 1): 1) shell height (SH), 2) shell width (SW), 3) spire index (SI; Cain, 1977), 4) generating curve height (HT), 5) generating curve width (WD), 6) generating curve shape (S), 7)
Table 1. Results of least-squares linear regressions. Ontogenetic stage is the predictor variable; the variance of the logarithmic transformation is the response variable. \( N = 36 \) for SH, SW, SI, HT, WD, S, and A (nine populations, four ontogenetic stages); \( N = 27 \) for W, T, and OV (nine populations, three ontogenetic stages). Confidence limits are determined empirically by randomization of variance with respect to ontogenetic stage (1,000 trials).

<table>
<thead>
<tr>
<th>Variable</th>
<th>Regression coefficient</th>
<th>Significance level</th>
</tr>
</thead>
<tbody>
<tr>
<td>SH</td>
<td>-0.000265</td>
<td>-</td>
</tr>
<tr>
<td>SW</td>
<td>-0.000479</td>
<td>( P &lt; 0.05 )</td>
</tr>
<tr>
<td>SI</td>
<td>-0.000476</td>
<td>( P &lt; 0.05 )</td>
</tr>
<tr>
<td>HT</td>
<td>0.000665</td>
<td>( P &lt; 0.01 )</td>
</tr>
<tr>
<td>WD</td>
<td>-0.002178</td>
<td>( P &lt; 0.001 )</td>
</tr>
<tr>
<td>S</td>
<td>-0.002060</td>
<td>( P &lt; 0.01 )</td>
</tr>
<tr>
<td>A</td>
<td>0.000203</td>
<td>-</td>
</tr>
<tr>
<td>W</td>
<td>0.000199</td>
<td>-</td>
</tr>
<tr>
<td>T</td>
<td>0.001181</td>
<td>-</td>
</tr>
<tr>
<td>OV</td>
<td>-0.000159</td>
<td>-</td>
</tr>
</tbody>
</table>

FIG. 1. Axial cross section of *Theba pisana*, showing measurements used in this study. P/T marks the protoconch-teleoconch boundary. X and Y are the Cartesian coordinates of the centroid of the generating curve. In addition, the area (A) of the generating curve is measured. Derived variables are spire index (SI), whorl shape (S), whorl-expansion rate (W), translation rate (T), and whorl overlap (OV). SI is computed as the ratio of SH to SW. S is computed as the ratio of HT to WD. W is computed as the square root of the ratio of \( A_{n-1} \) to \( A_n \), where the subscript refers to the whorl number. T is computed as \( (Y_{n-1} - Y_n)/(X_{n-1} - X_n) \). OV is computed as the ratio of \( H_n \) to \( HT_{n-1} \). SH, SW, SI, HT, WD, S, and A are defined at four ontogenetic stages: W, T, and OV are defined at three ontogenetic stages.

to have artificially high variance. If the scale of measurement is linear, then independent error implies that the sample variance is the sum of the “true” sample variance (\( \sigma^2 \)) and the variance of the measurement error (\( E \)).

A randomly chosen specimen was measured 20 times. The variances (without logarithmic transformation) computed from this replication experiment served as estimates of \( E \) for each respective variable and ontogenetic stage. \( E \) was then subtracted from all sample variances, and the squared coefficient of variation, CV\(^2\), was computed as \( \sigma^2/\text{mean}^2 \). This provides an approximation to the variance of the logarithmic transformation (Lewontin, 1966).

Results

In six of ten variables, there is a negative regression of variance on ontogenetic stage (statistically significant in four cases; Table 1). In the remaining four variables, there is a positive regression (statistically significant in only one case). This suggests that morphological variability, on the whole, decreases intraontogenetically.

With 54 decreases out of 90 \( F \) values (Table 2), the proportion of decreases (0.60) is not statistically discernible from 0.50 at \( P < 0.05 \), but it is discernible at \( P < 0.1 \). Considering only the 18 statistically significant changes in variance, there are 12 decreases at \( P < 0.01 \), three decreases at \( P < 0.05 \), one increase at \( P < 0.01 \) and two increases at \( P < 0.05 \) (two-tailed \( F \) tests). The proportion of significant decreases (0.83) is signifi-
Table 2. $F$ values for each variable in each sample. Underscored numbers indicate increased variance, in which case $F$ is computed as the variance at the final stage divided by the variance at the first stage. Otherwise $F$ is the ratio of the variance at the first stage to the variance at the final stage. Asterisks denote statistical significance. All tests are two-tailed. Sample 7 is from Lesbos, and all others are from Tenby.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Sample (sample size in parentheses)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1 (34)</td>
</tr>
<tr>
<td>SH</td>
<td>1.24</td>
</tr>
<tr>
<td>SW</td>
<td>1.99</td>
</tr>
<tr>
<td>SI</td>
<td>1.66</td>
</tr>
<tr>
<td>HT</td>
<td>1.08</td>
</tr>
<tr>
<td>WD</td>
<td>4.31**</td>
</tr>
<tr>
<td>S</td>
<td>5.72**</td>
</tr>
<tr>
<td>A</td>
<td>1.98</td>
</tr>
<tr>
<td>W</td>
<td>1.21</td>
</tr>
<tr>
<td>T</td>
<td>1.15</td>
</tr>
<tr>
<td>OV</td>
<td>1.49</td>
</tr>
</tbody>
</table>

* $P < 0.05$
** $P < 0.01$.

Significantly different from 0.50 at $P < 0.01$. Furthermore, the mean $F$ value for decreases is 2.10, while it is only 1.55 for increases. Although intraonogenetic reduction in variability does not occur in every parameter in every population of T. pisana, morphological variability is clearly more likely to decrease than to increase.

$F$ values (not presented here) based on the corrected CVs indicate that all statistically significant changes in variance within populations still hold. This demonstrates that intraonogenetic reduction in variability is not an artifact of constant measurement error.

Discussion

This study demonstrates a significant, nonselective component to within-generation increases in the frequency of morphologically intermediate individuals. However, the results give no reason to doubt the well documented force of stabilizing selection. The observed, nonselective reduction in variability may be explained by the action of homeostatic development. The same pattern has been demonstrated in mice by Chai (1957), who also attributed it to developmental homeostasis.

It has been suggested that that stabilizing selection is the principal, if not the sole, cause of stasis (Charlesworth et al., 1982). One difficulty with this suggestion has been an inability to explain why environmental change fails to cause selection pressures of sufficient intensity to force directional evolution (Williamson, 1987).

Stabilizing selection, in addition to reducing phenotypic variability within a single generation, should lead to an increase in the frequency of genotypes that allow buffered development (Schmalhausen, 1949; Mayr, 1963). This suggests that stabilizing selection may indeed be an important factor in maintaining stasis but that stabilizing selection need not continue to act relentlessly over geologic time. Williamson and Foote (1984) found that developmental buffering was active during stasis in the prosobranch Melanoides tuberculata but was ineffective during a speciation event. Buffering, however, was restored within a geologically brief time after the event. This suggests the general possibility that the establishment of species-specific homeostatic mechanisms may occur in the early history of a species, conceivably as a result of intense stabilizing selection. Thus, both selection and constraint may be important factors in the common pattern of morphological stasis, the recognition of which continues to stimulate paleontologists and evolutionary biologists.

Acknowledgments

This work was supported in part by a National Science Foundation Graduate Fellowship to M.F. We thank P. G. Williamson, W. Allmon, K. Boss, B. Charlesworth, J. S. Jones, and D. Raup for their help during the development of this project. W. Allmon, G. Boyajian, M. LaBarbera, M. Listokin, D. Miller, D. Raup, and an anonymous reviewer read the manuscript and made many useful suggestions.

Literature Cited


POPSULATION DIFFERENTIATION AND THE TRANSMISSION OF DENSITY EFFECTS BETWEEN GENERATIONS

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The ability of interdemic selection to bring about a rapid response to selection in experimental situations has become firmly established by a number of experimental studies (Wade, 1977, 1982; Craig, 1980, 1982; Wade and McCauley, 1980; Goodnight, 1985). In these studies, the observed responses have been attributed entirely to genetic changes occurring as a result of selection. The possibility exists, however, that a portion of the observed responses to selection could be due to nongenetic factors that are passed between generations and thus contribute to the response to selection. Such an effect could be analogous to maternal effects at the individual level that tend to increase the resemblance between mothers and offspring. Cheverud (1984) has shown that maternal effects of this type can contribute to a response to individual selection. The study reported here investigated the possibility that nongenetic factors at the population level can affect the response to interdemic selection.

McCauley and Wade (1980) investigated the effects of initial adult numbers on the total number of offspring produced by a population. They found that there was a positive relationship between founding numbers and the number of offspring produced; however, this effect could not account for the observed divergence between the populations they were studying. Their study investigated the effects of the number and density of parents on offspring number but did not examine the effects of parental rearing density on the number of offspring produced. It is the effect of parental rearing density on population size that is the subject of the present note.

In Tribolium populations of the type used in this and many other studies of interdemic selection, density effects are a likely cause of nongenetic correlations between generations. High-density populations produce smaller adults, and the flour medium of these populations becomes heavily conditioned, even to the extent of becoming dark brown and heavily caked. Low-density populations, on the other hand, tend to produce larger adults, and the flour remains light in color and loose. It is possible that these environmental differences could affect the population density in subsequent generations. For example, in Drosophila, adult body weight is strongly negatively correlated with larval rearing density, and adult body weight is highly correlated with the fecundity of females, with large females having a greater fecundity than small females. This leads to a negative correlation between larval density and the number of eggs subsequently laid by the adults (Sang, 1950; Robertson, 1957; Prout and McChesney, 1985). Because of these correlations, in Drosophila grown using a discrete generation culture system, the adult density in one generation is negatively correlated with the adult density in the subsequent generation (Prout and McChesney, 1985). In Drosophila this cross-generational environmental correlation is negative; however, both positive and negative cross generational correlations in productivity are possible (Prout and McChesney, 1985). If these cross-generational environmental effects are present and of large magnitude, they could contribute to the response to interdemic selection and, thus, affect the interpretation of previous studies of interdemic selection.

MATERIALS AND METHODS

The experimental design (Fig. 1) consisted of two major phases. These phases, which are described be-