

VARIATION, COVARIATION AND
GENOTYPE-ENVIRONMENT INTERACTION IN THE
LIFE-HISTORY OF NATURAL POPULATIONS OF
TRIBOLIUM CASTANEUM

By
Thomas Anthony McRae

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DECLARATION

I certify that the substance of this thesis has not already been submitted for any degree and is not currently being submitted for any other degree.

I certify that to the best of my knowledge any help received in preparing this thesis, and all sources used, have been acknowledged in this thesis.



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Abstract

A life-history includes “the entire sequence of changes through which an organism passes in its development from conception to death” (Lande 1982b). Life-history traits, as major determinants of fitness, should be subject to the influence of natural selection and undergo evolutionary change. Thus a distinction must be made between genotypic variation in the life-history and environmentally induced phenotypic variation.

In this thesis, two separate but complementary experiments address specific areas concerning life-history evolution in natural populations. The model organism used in these laboratory studies was the ‘rust-red flour beetle’ *Tribolium castaneum* (Herbst), a well known pest of stored grain and cereal products.

In the Nested experiment (Chapter 3), the methods of quantitative genetics were used to give a statistical description of the genetic sources of variation, covariation and genotype-environment interaction for several life-history traits measured on female beetles derived from two geographically distinct natural populations of *T. castaneum*. These results are used to make inferences regarding the potential of populations to respond to natural selection, as well as the past selective regimes experienced by the populations.

Since evolutionary change in response to natural selection requires that phenotypic variation be heritable, as well as that fitness varies according to the phenotype (Endler 1986), heritabilities were estimated for the individual life-history traits within each population. Information about the relationships between the different life-history characters, expressed as genetic correlations, were used to test for the presence of “trade-offs”, and more specifically “reproductive costs”. These genetic correlations also were used to test for “antagonistic pleiotropy” and its potential role in maintaining additive genetic variation within natural populations. In addition, the experiment was conducted under two constant laboratory temperatures (33° and 37°C) to investigate the importance of genotype-environment interaction in the evolution of life-histories. Thus the Nested experiment evaluated the potential

role of genotype-environment interaction in maintaining additive genetic variation, and the stability of the quantitative genetic parameters under different environments. Comparisons between the populations assessed the magnitude of intraspecific genetic variation in life-history traits.

There is abundant additive genetic variation for both reproductive and non-reproductive life-history traits in natural populations of *T. castaneum*. In agreement with Fisher's (1930, 1958) Fundamental Theorem of Natural Selection, the reproductive traits generally displayed lower levels of heritable variation than the non-reproductive traits. Furthermore, although age-specific components of reproduction did show significant and sometimes high heritabilities, the estimates for lifetime reproduction were low and generally not significantly different from zero. These results suggest that, although components of fitness may have significant heritability values, fitness itself need not be heritable.

Because natural selection operates on the whole phenotype rather than on characters in isolation, the additive genetic covariances among life-history characters can substantially influence the rate and direction of evolution. In the Nested experiment, both positive and negative genetic correlations between life-history traits were found, some of which were significantly different from zero.

The finding of negative genetic correlations between early reproductive traits and adult lifespan in both populations suggests that a "reproductive cost" associated with high early reproduction is manifested through a reduction in future survival. However, consistently positive genetic correlations between early and late reproductive traits in the two populations at both laboratory temperatures imply that a cost due to high early reproduction is not manifested through a reduction in later fecundity.

The finding of negative genetic correlations between life-history traits, associated with abundant heritable variation in these traits, also provides empirical evidence to support the role, at least in part, of antagonistic pleiotropy in the maintenance of additive genetic variation.

Although the heritability and genetic correlation estimates for the two natural populations of *T. castaneum* were, in general, compatible across the two laboratory temperatures (33° and 37°C), they were sufficiently different to suggest that the expression of the genetic architecture underlying the life-history of natural populations of this species changes under different environments. Further, even though genotype-environment interaction was not a general phenomenon in the Nested experiment, significant interaction effects from the mixed

model analyses of variance were found for developmental period, body weight, growth rate and lifetime reproduction. This, and the observation that the genetic correlations between character states expressed in different environments were not all unity, indicates that some temperature specific responses had occurred.

The implications of these interactions are that, although performance and therefore selection response in some environments can be accurately predicted from performance in other environments, such a relationship is not general. Not only does this body of empirical evidence reinforce the consensus that estimates of quantitative genetic parameters are specific to the environments under which they are determined, but it also provides evidence in support of the hypothesis that genotype-environment interaction and fluctuating selection pressures in heterogeneous environments play some role in the maintenance of quantitative genetic variation.

There were genetically based differences in life-history traits between the two natural populations of *T. castaneum* sampled from geographically distinct locations. Under uniform laboratory conditions, female beetles from the temperate population had significantly faster rates of development and lower adult body weights than those from the sub-tropical population. Contrasting trends in the heritability and genetic correlation estimates from these two natural populations, although associated with large standard errors, provide further evidence that the genetic architecture underlying the life-history of these populations is different.

Although this evidence suggests that genetically based life-history differences are observable at the population level, not all life-history traits are necessarily differentiated. The lack of significant population differentiation for growth rate, at either laboratory temperature, suggested that the relationship between developmental period and adult body weight may be physiologically constrained within the species. No significant differences between the populations were found for longevity and lifetime reproduction at either laboratory temperature. This lack of differentiation in major fitness components could mean they are highly canalized in this species, or it may simply reflect their high coefficients of variation.

The Clinal experiment (Chapter 4) examined genetic variation in certain early life-history traits (developmental time, adult body weight, growth rate and early fecundity) among 34 geographically distinct populations of *T. castaneum* that were sampled at approximately regular distances along a latitudinal gradient in Eastern Australia. To statistically describe the association between genetic variation and factors associated with geographical

origin, population means for each life-history trait were regressed separately and then simultaneously upon several measures of geographic position and climatological factors. The relationships between the different life-history traits were investigated by intra-locality and inter-locality correlations. Unlike the Nested experiment, members of both sexes were assayed to investigate the importance of genotype-sex interactions. The ecological relevance of temperature effects, expressed as genotype-environment interactions, was assessed by replicating genotypes over five constant laboratory temperatures (21°, 25°, 29°, 33° and 37°C) that are representative of those that the beetles experience in nature.

In the Clinal experiment, significant differences among natural populations of *T. castaneum* were found for developmental period, adult body weight and growth rate in both sexes, and peak fecundity in females, at all five laboratory temperatures. This extensive documentation of life-history variation among populations of *T. castaneum* showed that intraspecific comparisons are valuable and necessary for establishing the importance of life-history adaptation.

One of the most persuasive pieces of evidence that natural selection is acting on the genetic structure of natural populations is the occurrence of latitudinal clines. Significant latitudinal clines were found for developmental rate in males and females at four of the five laboratory temperatures studied, with populations originating from higher latitudes faster developing than those from lower latitudes. Further evidence for latitudinal clines was found at three laboratory temperatures for early fecundity in females, with populations from higher latitudes producing fewer eggs than those from lower latitudes. In contrast, significant latitudinal clines were not found for adult body weight or growth rate at any of the five laboratory temperatures in either sex.

Since life-history traits are synonymous with fitness components, and assuming geographic variation is ordered by natural selection, then strong associations are expected between life-history traits and the measures of environment that influence adaptation. The empirical evidence from the regression analyses implicated temperature, independently of humidity, as being an important selective factor affecting developmental rate in natural populations of *T. castaneum*. However, for body weight and growth rate it was relative humidity and not temperature which was the important climatic variable associated with genetic differentiation in these traits. The multiple regression analyses found both temperature and relative humidity to be important selective factors influencing early fecundity. The implications of these findings are discussed in relation to the genetically based life-history

differences found between the two populations in the Nested experiment.

There were no significant genotype-sex interactions for developmental period, adult body weight or growth rate at any of the five laboratory temperatures studied — the relative performance of the different populations was independent of sex.

However, significant population-temperature interactions indicate that the different populations were adapted to specific thermal regimes. This is further evidence that genotype-environment interaction, in association with fluctuating selection pressures in heterogeneous environments, might be important in the maintenance of genetic variation in natural populations.