Associations of fecundity with adult size in the cotton stainer bug *Dysdercus fasciatus*

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Components of phenotypic covariance of fecundity with adult size were examined in the bug *Dysdercus fasciatus* in benign and stressful moisture environments. In addition, genetic relationships were explored between the character states in different environments. There was a positive and significant genetic association between fecundity and adult size in a benign environment. By contrast, the observed phenotypic covariability of fecundity with adult size in a stressful environment arose entirely from non-additive genetic plus maternal effects. Genetic correlations between the same character across environments were significantly less than unity for both adult size and fecundity. These results suggest that populations in benign and stressful moisture environments would respond to selection on adult size and fecundity in different ways.

Keywords: adult size, *Dysdercus fasciatus*, fecundity.

Introduction

One objective for the estimation of genetic correlations in life-history studies is to provide an analytical probe with which to examine information on trade-offs and genetic constraints that may influence the rate at which fitness characters evolve (Lande, 1982; Maynard-Smith *et al.*, 1985). If there is pleiotropy between characters and selection is directional on some characters, the response of others will be determined by the genetic correlation between the selected and unselected characters (Falconer, 1981). A pair of characters with high positive correlation will respond to directional selection more rapidly than either character selected separately until the pleiotropic or linked combinations of genes are fixed. The genetic variation that remains will involve genes which have opposite effects on the two characters, so the resulting correlation will be negative due to antagonistic pleiotropy (Falconer, 1977; Lande, 1982; Rose, 1982). Conversely, a genetic constraint is encountered when selection acts to increase simultaneously a set of characters influenced by genes with negatively-correlated effects. An evolutionary increase in one character will produce a correlated decrease in the other so that the characters cannot respond to independent evolution that would lead to their independent optima (Lande, 1982). Such antagonistic pleiotropy may retard the erosion of heritable variation (Falconer, 1977) or in some special cases even main-

tain it at equilibrium (Rose, 1982). In the absence of such pleiotropic effects, selection is expected to eliminate the mutant genetic variability, unless it is maintained by other mechanisms (e.g. Lande, 1975; Hedrick *et al.*, 1976).

However, because environmental stasis is rare, and heritabilities and genetic correlations may vary with environment (Giesel *et al.*, 1982; Service & Rose, 1985), genetic constraints may not be constant or predictable. Characters may genetically uncouple and recouple to allow expansion into environments with different selective parameters.

The concept of genetic correlations can also be applied to gain insight into the phenomenon of phenotypic evolution in a heterogeneous environment via use of Falconer's (1952) idea that a character expressed in two different environments can be regarded as two character states which are genetically correlated, thereby relating genetic correlations to genotype-by-environment interactions. The issue of evolution in a heterogeneous environment is then considered as '... a problem in the evolution of a correlated suite of character states' (Via & Lande, 1987). A high correlation between the character states scored in two different environments implies that the character is influenced by nearly the same genes in the two environments, whereas a low correlation, equivalent to significant genotype-by-environment interactions, indicates that different sets of genes underpin the character states in the different environments (Falconer, 1981).

In a previous paper (Kasule, 1991) I reported a study of quantitative variation in adult size and fecundity in two moisture environments in the cotton stainer bug *Dysdercus fasciatus* Sign. In the present study, genetic relationship is explored: (1) between fecundity and adult size in two moisture environments, and (2) between the same character expressed in two different environments in *Dysdercus fasciatus*. *Dysdercus fasciatus* is a seed predator of Malvales (Pearson, 1958).

Methods

A half-sib, full-sib mating design for estimating quantitative-genetic covariance components of fecundity with adult size in benign and stressful moisture environments was used. The parental generation used was the F_1 offspring of parents collected copulating in the field. Details of rearing and experimental design are given in Kasule (1991).

The data used in this analysis were the same as those used in the previous paper (Kasule, 1991). The components of phenotypic covariance were separated just as the phenotypic variance was partitioned into genetic and environmental components in that paper, and regression and correlation coefficients for the various covariance components were estimated.

Phenotypic, additive genetic, non-additive genetic plus maternal-effect, and residual environmental regressions of fecundity on body size were calculated as the ratio of the appropriate covariance component of fecundity with adult size to the appropriate variance component of adult size. Standard errors were calculated for the phenotypic regressions as per Sokal & Rohlf (1981), but those of the other regressions have not been formulated and are therefore not provided.

The allometric-coefficient method is commonly used to describe the covariance of a life-history character with body size (Peters, 1983). The allometric coefficient b is defined either by a power function of the form

$$L = aW^b$$

or its logarithmic transformation

$$\log L = b \log W + \log a. \quad (1)$$

where L is the life-history character and W is body weight. Thus, with logarithmically transformed data each of the above regressions gives an estimate of b .

Correlations (corresponding to the above regressions) between fecundity and adult size were calculated using the formula (Falconer, 1981)

$$r = \frac{COV_{FW}}{\sqrt{(V_F V_W)}}, \quad (2)$$

where COV_{FW} is the appropriate covariance component of fecundity (F) with adult size (W), and V_F and V_W are the appropriate variance components of fecundity and adult size, respectively. Phenotypic correlations are reported with 95 per cent confidence intervals estimated by the z -transformation (Sokal & Rohlf, 1981). Standard errors for the other correlations are approximated as suggested by Falconer (1981). Correlations are interpretable for effects which had non-zero causal variance components for both fecundity and adult size (see Kasule, 1991).

Genetic correlations between the same character across environments (Falconer, 1952) were calculated via the correlation of family (full-sib) means (Via, 1984).

Results

Correlations between different characters

Figure 1 shows plots of log fecundity versus log adult size, based on the means of paternal half-sib families, to provide an overall view of the nature of the fecundity-adult size relationship observed in this study. Table 1 gives the decomposition of phenotypic allometry and correlation coefficients into their component parts in benign and stressful environments.

Phenotypic regression (Table 1) indicated that fecundity increased significantly ($P < 0.01$) with adult size in benign and stressful environments. The allometric coefficient (Table 1) was significantly greater than zero in benign ($t = 11.78$, d.f. = 310, $P < 0.001$) and stressful ($t = 11.09$, d.f. = 310, $P < 0.001$) environments, and the difference between the slopes in the two environments was not significant ($F = 0.018$, d.f. = 1/620, $P \gg 0.05$).

For siblings in a benign environment, there was a positive and significant genetic association between log fecundity and log adult size. The co-heritability (additive genetic covariance divided by total phenotypic covariance) indicates that 55 per cent of the phenotypic association of fecundity with adult size is attributable to additive genetic effects. The additive genetic correlation was significantly greater than zero, and the genetic regression of log fecundity on log adult size was 2.31.

It is notable that the additive genetic and phenotypic regression results do not correspond in magnitude (Table 1). The genetic allometry coefficient, however, rather than the phenotypic value, defines the evolu-

Fig. 1 Relationship of mean log fecundity (number of eggs) and mean log size (mg) of half-sib families in benign (●) and stressful (○) environments in *Dysdercus fasciatus*. (Regression lines, benign: $\log \text{fecundity} = 1.189 \log \text{adult size} + 0.442$, $r = 0.58$, d.f. = 24, $P < 0.01$; stressful: $\log \text{fecundity} = 0.753 \log \text{adult size} + 0.402$, $r = 0.41$, d.f. = 24, $P < 0.05$.)

tionary trajectory fecundity-adult size would follow during selection.

Non-additive genetic or maternal effects were not important in fecundity-adult size covariability in a benign environment (Table 1). There was, however, a strong residual environment component to fecundity-adult size associations in a benign environment (Table 1). Thus although there was a significant genetic component to fecundity-adult size allometry, a large

amount of the observed covariability of fecundity with adult size in a benign environment is non-heritable and arises from effects unique to individual bugs.

By contrast, the observed phenotypic covariability of fecundity with adult size in a stressful environment arose entirely from non-additive genetic or maternal effect (Table 1).

Correlation between the same character in different environments

There was no genetic association between adult size in a benign environment and adult size in a stressful environment ($r = 0.103$, confidence intervals (CI) estimated by z -transformation = 0.174 and 0.365, d.f. = 70, $P \geq 0.5$). By contrast, fecundity in a benign environment was genetically correlated with fecundity in a stressful environment ($r = 0.303$, CI = 0.032 and 0.532, d.f. = 70, $P < 0.05$), but the genetic correlation coefficient was significantly less than unity ($t_s = 24.411$, $P < 0.001$).

These results (genetic correlation significantly less than one) are in accord with the significant genotype-by-environment interaction variance estimated in adult size and fecundity (Kasule, 1991).

Discussion

The first thing to say about these results is that they are based on a small sample, only 26 half-sib families. For relatively small samples, estimates of genetic correlations are subject to large sampling errors and are, therefore, seldom precise (Robertson, 1959; Falconer, 1981). For this reason, the results presented (Table 1) should be regarded with caution.

Correlation between different characters

Environmental conditions have been shown to influence genetic relationships between fitness characters in a number of species (Giesel *et al.*, 1982; Via, 1984; Service & Rose, 1985; Pashley, 1988). The results of this study (Table 1) indicate that this is also true for *Dysdercus fasciatus*, subject to sampling error. There was a positive and significant additive genetic correlation between fecundity and adult size in a benign environment. In a stressful environment, the relationship between these two characters was conditioned entirely by non-additive genetic or maternal effects (Table 1). Curiously, however, there was no significant differences in the patterns of phenotypic increase in fecundity with adult size for siblings grown in benign versus stressful environments (Table 1). This result emphasizes, then, that phenotypic correlation

Table 1 Partition of phenotypic covariance of log fecundity and log body size of *Dysdercus fasciatus* in (a) benign and (b) stressful environments. Covariances are given as percentages of the total phenotypic covariance so that the additive genetic covariance is the heritability of the two characters. Numbers in parentheses are the 95 per cent confidence intervals estimated by the z-transformation

	Covariance	Allometry	Correlation
(a) Benign			
Phenotypic	—	0.89 ± 0.075	$0.56 (0.48, 0.63)$
Additive genetic	0.55	2.32	0.8 ± 0.12
Non-additive genetic plus maternal effects	0.0	—	—
Residual environment	0.45	0.78	0.57 ± 0.25
(b) Stressful			
Phenotypic	—	0.88 ± 0.079	$0.53 (0.46, 0.61)$
Additive genetic	0.0	—	—
Non-additive genetic plus maternal effects	1.0	1.19	0.63 ± 0.14
Residual environment	0.0	—	—

‘... need not be a good guide to underlying genetic constraints to, and consequences of, evolution ...’ (Rose & Charlesworth, 1981, p. 179).

A consequence of a positive genetic correlation between fecundity and adult size in a benign environment is that a change in adult size in response to selection would indirectly exert selective pressure on fecundity. On the other hand, most ecologists would subscribe to the view that body size evolves in response to environmental factors such as competition, predation pressure, social interactions and factors of the physical environment that select body size directly, rather than indirectly following selection on fecundity. For *D. fasciatus*, one probable source of direct selection to increase adult size is the spatial distribution of its host plants, the woody Malvales (Derr *et al.*, 1981). Woody Malvales produce large crops of seeds, but the trees are widely spaced. A large body would be advantageous during food deprivation and other stresses associated with migration (Boyce, 1979; Derr *et al.*, 1981).

The absence of genetic correlation (i.e. pleiotropy) between fecundity and adult size in a stressful environment (Table 1) may indicate that genetic constraints imposed on a character are released when individuals grow in that environment. As Via (1984) pointed out, in cases of this kind, selection could act on each character independently moving it to its individual optimum more rapidly in stressful than in benign environments, and in this way shift genotypic combinations that may later form new correlated responses. Populations in benign and stressful environments

should, then, be expected to respond to selection on adult size and fecundity in different ways.

Correlation between the same character across environments

The low genetic correlations between the same character in different environments (Table 2) should be expected, given the significant effects of genotype-by-environment interaction detected in adult size and fecundity in an earlier study (Kasule, 1991), indicating that the most fit genotypes in a benign environment differ from those in a stressful environment. To gain insight into the potential for different responses in populations in benign and stressful environments to selection in a spatially heterogeneous environment, r^2 was calculated from the genetic correlations between the same character across environments. The r^2 gives an estimate of the amount of genetic variation in the character states (expressed in different environments) which is due to common factors or linkage. These estimates (1 per cent for adult size and 9 per cent for fecundity) suggest that populations should differ in the course of phenotypic evolution of adult size and fecundity, even when they are under similar selective pressures, since different genes would be expressed under different conditions of the environment. This conclusion is essentially identical to the one made above using the change in genetic correlation between fecundity and adult size attendant with the shift in environmental conditions.

Phenotypic plasticity

In addition to indicating the potential for variation in the course of phenotypic evolution among populations in different environments, a low covariance between the same character in different environments reflects a high phenotypic plasticity (Scheiner & Goodnight, 1984). Phenotypic plasticity refers to environmental modification of genotypic expression (Bradshaw, 1965), the importance of which as a buffering mechanism against environmental instabilities has recently received much attention (Gould, 1975; Scheiner & Goodnight, 1984; Schlichting, 1986; Schlichting & Levin, 1986; Stearns & Koella, 1986; Newman, 1988). Gould (1975) suggested that it is probably advantageous for organisms living in heterogeneous environments to possess genes that confer phenetic plasticity, enhancing an organism's ability to contend with environmental perturbations.

The data presented in this paper and in Kasule (1991: significant effects of genotype-by-environment interaction) clearly demonstrate that abundant variability of the sort that would confer plastic response to a change in moisture flux remains segregating for adult size and fecundity in these bugs. *Dysdercus fasciatus* is a colonizing species (Pearson, 1958; Dingle & Arora, 1973; Duviard, 1977; Derr *et al.*, 1981), so individuals are likely to encounter large changes in the physical environments over short periods of time relative to their life-spans, and over short distances when migrating from one site to another. When the environment varies within a period less than an individual's life-span, modification of the phenotype in response to the environment may improve fitness (Schlichting & Levin, 1986).

Conclusion

An earlier study (Kasule, 1991) reported the presence of a sizeable amount of additive genetic variance in adult size and fecundity of *D. fasciatus* in a benign environment. Other workers have also reported considerable genetic variance for the life-history characters of many species (McLaren, 1976; Rose & Charlesworth, 1981; Hegmann & Dingle, 1982; Murphy *et al.*, 1983; Gilbert, 1984; Mousseau & Roff, 1987). Gilbert (1984) envisions that persistent genetic variation in fitness components negates conventional evolutionary theory (e.g. Fisher's fundamental theorem (Fisher, 1930). Falconer (1977), Rose (1982) and Charlesworth (1984), however, pointed out that additive genetic variance could be maintained in life-history characters provided that there is a negative correlation between the characters.

The results of additive genetic correlation analysis revealed positive gene effects on fecundity and adult size (Table 1), but did not explore associations such as developmental rate versus size, developmental rate versus fecundity and juvenile survival versus fecundity which also have obvious effects on fitness and may, indeed, exhibit antagonistic pleiotropy. The results do not allow speculation on the significance of antagonistic pleiotropy in the maintenance of additive genetic variance in adult size and fecundity of *D. fasciatus*.

Fluctuations in environmental conditions also have been proposed to maintain genetic variability in fitness components of some species by genotype-by-environment interaction (Dingle *et al.*, 1977; Giesel *et al.*, 1982; Istock, 1983; Murphy *et al.*, 1983). The data presented in this paper and in Kasule (1991) suggest that the additive genetic variation observed for adult size and fecundity in *Dysdercus fasciatus* may be an example of this.

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