Quantitative genetics of the trade-off between fecundity and wing dimorphism in the cricket *Allonemobius socius*

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Considerable evidence indicates that in general there is a phenotypic trade-off between wing dimorphism (a threshold trait) and fecundity in insects. However, the demonstration of a genetic basis to this trade-off has been shown in only one species, *Gryllus firmus*. In this paper we present evidence for another species, the cricket *Allonemobius socius*. There were significant negative phenotypic correlations between wing morph and fecundity during the first two periods following eclosion (0–12 days and 13–16 days) and also cumulative fecundity (i.e. macropterous females laid fewer eggs than micropterous females). Macropterous and micropterous females did not differ in fecundity during the remaining two periods (17–20 days and 21–24 days). Both wing morph and age-specific fecundities had significant heritabilities. There was a significant negative genetic correlation between wing morph and fecundity during the first 12 days after eclosion. The standard errors of the estimates for the remaining periods were too large to permit a meaningful conclusion. Analysis of family mean data indicated that fecundity did not vary in a dichotomous manner with wing morph but was best described as a continuous function of the underlying continuously distributed trait.

Keywords: evolution, genetic correlation, heritability, phenotypic correlation, trade-offs, wing dimorphism.

Introduction

The evolution of lifehistory traits is determined in large measure by trade-offs between traits (Roff, 1992; Stearns, 1992). For such trade-offs to result in evolutionary change they must be manifested at both the phenotypic and genetic levels. In the latter case this implies a negative additive genetic correlation between the traits (Reznick, 1985). Phenotypic trade-offs between fecundity and wing morph in wing-dimorphic insects have been demonstrated in over 20 species of insects; micropterous (= short-winged and incapable of flight) females typically commence egg laying earlier and produce more eggs in total than macropterous (= long-winged and volant) females (Roff, 1986; Roff & Fairbairn, 1991). However, in only one species, the cricket *Gryllus firmus*, has a genetic basis been demonstrated for this trade-off (Roff, 1990, 1994a).

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Wing dimorphism can be understood from a quantitative genetic perspective using the threshold model (Falconer, 1989). According to this model the dimorphism is determined by a continuously distributed underlying trait and a threshold: individuals with a value below the threshold develop into one morph while individuals above the threshold develop into the alternative. The heritability of the dimorphism is then equivalent to the heritability of the underlying trait. Similarly, the genetic correlation between the dimorphism and some other trait (X) is assumed to be equivalent to the genetic correlation between the trait underlying the dimorphism and that of trait X. This model predicts that phenotypically the genetic correlation between wing dimorphism and fecundity is manifested as a negative correlation between the proportion of macropterous individuals within a family and the mean fecundity of that family (Roff, 1994a).

A negative genetic correlation was demonstrated between egg production during the first week after eclosion and wing dimorphism in *G. firmus* both by examining the correlated response of fecundity to

selection for increased and decreased proportion macroptery (Roff, 1990), and by direct estimation using a full-sib pedigree analysis (Roff, 1994a). Prediction of the change in fecundity after 14 generations of selection using the genetic correlation estimated from the full-sib analysis agreed with that observed with an error of less than 5 per cent (Roff, 1994a).

In this paper we present a quantitative genetic analysis, using a full-sib mating design, of the age-schedule of fecundity and wing dimorphism in another species of cricket, *Allonemobius socius*. We address three principal questions. (i) Is there a phenotypic trade-off between fecundity and wing dimorphism? (ii) What are the heritabilities of the two traits? (iii) Is there a statistically significant negative genetic correlation between the two traits?

Materials and methods

Organism and experimental design

Allonemobius socius is a common ground cricket of eastern North America. The stock used in the present experiment originated from approximately 100 adults collected from a moist field near Danville, Virginia (36°40'N, 79°25'W) during late July 1988. Crickets were reared in plastic mouse cages (30 × 17 × 14 cm) and fed lettuce and crushed cat food (Mousseau & Roff, 1989). The field-collected adults were allowed to breed randomly in diapause-averting conditions (30°C, 15L:9D), and their eggs collected and incubated under these conditions until hatched. This second generation was also reared in mass culture, but under fall conditions (25°C, 13L:11D) to ensure production of diapause eggs. Eggs produced by second generation adults were chilled for 3 months at 4°C and then incubated at 28°C until hatching.

A third generation, the parental generation, was raised under the same conditions as the second generation, and the adults from this generation were paired randomly to produce 64 full-sib families for the present experiment. Although estimates of genetical parameters from such a design are potentially inflated by dominance variance (Becker, 1985), space limitations and difficulties with mating prevented us from using the preferred half-sib design. Parental pairs were placed in plastic sandwich boxes and fed carrots and crushed cat food, with a roll of moistened cheesecloth provided for oviposition. Every 4 days the eggs were collected and placed on moistened paper towel in a petri dish, incubated for an additional 10 days, and then trans-

ferred to a 4°C refrigerator for 3 months to break diapause.

After the chilling period the eggs from the parental generation were incubated at 28°C until hatching. Upon hatching, nymphs from each family were placed in one of two environments, 'Early' and 'Late', designed to span the range of conditions experienced during the reproductive season of the first generation of this population, which is bivoltine in its natal site. In the 'Early' environment the photoperiod was set at 15.5L:8.5D for nymphs and 15L:9D for adults, corresponding approximately to photoperiods (including civil twilight; Beck, 1980) at days 195 and 210 (mid-July) at the collection site of the founding population. In the 'Late' environment the conditions were set at 15L:9D for nymphs and 14.5L:9.5D for adults, simulating days 210 and 225 (early August). In all environments a 31:19°C thermoperiod was used on a 12 h cycle, with the increase in temperature set at 1.5 h before lights on. These are average mid-summer temperatures experienced by the crickets at the collection site (Ruffner, 1980).

Newly emerged nymphs were counted out daily from each family into four groups of 40 (two replicates in each environment) and reared in sandwich boxes with carrots and dry cat food as before. Fifty-five families produced sufficient nymphs to make up the four boxes, and nine families yielded sufficient nymphs for two boxes, which were placed in the early environment. The sandwich boxes were cleaned and food changed every 4 days. When final eclosion commenced boxes were checked every 2 days and adults were scored for wing morph and removed. The newly eclosed adults were transferred to their reproductive environment and maintained as singletons for 8 days. This procedure was used to maximize the initial output of eggs for the estimation of change in diapause condition (Bradford, 1991). Previous experiments with the sibling species *A. fasciatus* indicated that few eggs are laid in the first week of adult life (Roff, 1984), and hence it is unlikely that the present design significantly affected the estimation of the age schedule of fecundity.

For each environment 6–8 females were chosen from each family and each provided with two randomly chosen males. The females and their mates were maintained in plastic disposable 100 mL dessert cups, and fed with carrots and dry cat food. A bottle cap filled with moistened sand was provided for oviposition. The bottle caps were changed every 4 days, over a period of 16 days, thereby obtaining four estimates of age-specific fecundity (0–12 days, 13–16 days, 17–20 days, 21–24 days).

Estimation of heritabilities and genetic correlations

A standard assumption of quantitative genetic models is that the traits are normally distributed: estimation of genetic parameters can be made for non-normal distributions but care must be made in their interpretation as prediction of response to selection may be biased (Falconer, 1989). The best transformation for the fecundity data was obtained using the Box-Cox procedure (Sokal & Rohlf, 1981, pp. 423–427). For all periods and for cumulative fecundity Lilliefor's test indicated significant departure from normality. The Box-Cox procedure gave the appropriate values of λ as 0.25 for period 1, 0.5 for periods 2–4, and 0.75 for the total fecundity. In only the last case did the transformation produce a distribution not significantly different from normal ($P = 0.1$; $P < 0.05$ in all other cases). Both the untransformed and transformed data were analysed; both sets of analyses gave the same results and we present here only those for the transformed data. Heritabilities and genetic correlations were estimated using both the raw and the transformed data.

Heritabilities were estimated from the intraclass correlation obtained from a one-way nested ANOVA (Roff, 1994a). In the case of wing morph, the data were scored as 0 (SW = micropterous) and 1 (LW = macropterous) and the heritability so estimated on the 0–1 scale transformed to the underlying scale according to the method of Robertson & Lerner (1949). Because of possible bias arising from non-normality, the significance levels for the heritability estimates were assessed from both the ANOVA results (Becker, 1985) and from the following randomization procedure adapted from Manly (1991, p. 64). Individuals were assigned to families at random and the heritability for the randomized data set computed using a one-way ANOVA (this particular random assignment method was appropriate because the nested ANOVA showed no effects attributable to cage within family). The randomization was repeated 4999 times and the probability level for the observed heritability was estimated as the proportion of times in the 5000 estimates (4999 randomized plus the observed) that the heritability estimated from the randomized data set equalled or exceeded the observed value. The standard error of the heritability was estimated in two ways: first using the delete-one jackknife (Simons & Roff, 1995), and secondly from the probability value, P , obtained from the randomization procedure, assuming that h^2/SE was normally distributed (i.e. $SE = h^2/x$, where x is the value of the abscissa on the normal curve giving a probability of $P/2$).

Figure 1 shows three possible relationships between a continuously distributed trait such as fecundity and a threshold trait such as wing dimorphism. In the first case (Fig. 1a), fecundity is

Fig. 1 Three hypothetical examples of the relationship between a continuously distributed trait such as fecundity and a threshold trait such as wing morph. (a) Fecundity is correlated with the continuously distributed trait underlying the threshold trait, in this case wing dimorphism. (b) Fecundity is correlated with the phenotypic expression of the trait, so that there is a dichotomous fecundity with each morph. (c) Fecundity is correlated both with the underlying trait and the expressed phenotype.

genetically correlated directly with the underlying trait, as described in the Introduction. For such a model the genetic correlation can be estimated using the same ANOVA approach as for two continuously distributed traits (e.g. fecundities at two periods) by scoring wing morph as 0 or 1 (Mercer & Hill, 1984). In the second case (Fig. 1b) fecundity is a function solely of the wing morph, and thus is only indirectly related to the underlying trait (we shall refer to this as the dichotomy model). Figure 1c shows an intermediate case in which there are contributions from both sources. With the exception of the dichotomy model, the fecundity of females of a particular morph varies with the value of the underlying trait. The mean value of the underlying trait, denoted by z , for a particular family is estimated by the probit value of the proportion of macropterous individuals in that family (Roff, 1986, 1994a). If the dichotomy model is correct the mean family fecundity of a particular morph will be uncorrelated with the estimated mean value of the underlying trait. In the other cases the mean family fecundity should decrease with an increase in the value of the underlying trait (i.e. a negative correlation between fecundity and the transformed proportion of macropterous individuals).

Variation in fecundity may result from its correlation with wing form and also from other sources, such as genetic or environmental variation in fecundity that is independent of wing form. Therefore, we analysed the family fecundity in two ways; first, using the actual fecundities, and secondly using fecundity residuals. Finally, for each family we computed the mean residual and the weighted mean value of the underlying trait, $z = (n_1 z_1 + n_2 z_2) / (n_1 + n_2)$, where n_i is the number of fecundity values in environment i .

Results

Preliminary analyses were performed using 'Environment' as a covariate and families nested within cage. No effect of the cage in which the nymphs were reared was found for either fecundity or wing morph, nor for environment on age-specific fecundity. Microptery (SW) was more common in the late environment, as would be expected by the shorter photoperiod (68 per cent vs. 78 per cent, $P = 0.0016$, paired t -test on family means). For the analyses reported below the fecundity data for each family have been combined giving a single sample per family. Where appropriate, analyses involving wing morph were performed separately for each environment, combining cages within environment.

Fig. 2 Age schedules of fecundity in macropterous (LW, dashed line, triangles) and micropterous (SW, solid line, circles) females of *Allonemobius socius*. Dotted envelopes show $\pm$ SE.

Some females died before the end of the experiment. There was no relationship between survival and wing morph, 82.5 per cent (503 of 610) of SW females surviving throughout the experiment compared with 82.8 per cent (226 of 273) of LW females ($\chi^2_1 = 0.01$, $P = 0.91$). The reasons for the deaths are unknown. Preliminary analyses did not suggest that the fecundity of the females that died was less than that of the survivors; however, as we are interested in differences in fecundity alone all further analyses are restricted to those females which survived the entire period.

The phenotypic pattern of fecundity in relation to wing morph

There was a clear difference in the fecundity schedules of SW and LW females (Fig. 2); SW females produced more eggs in periods 1 and 2, but no difference was apparent in period 3. Separate ANOVAs and Mann–Whitney tests for these periods support this conclusion (Table 1; these results remained the same after Bonferroni correction). A marginally significant difference using the Mann–Whitney test was observed for fecundity during period 4 ($P = 0.047$, one-tailed), which does not remain after correcting for experiment-wise error rate; this result although suggestive of a continued difference in fecundity requires further verification. The total fecundity of SW females was highly significantly greater than that of the LW females (Table 1).

Table 1 Summary of fecundity data for SW and LW *Allonemobius socius* females by time period

Period	SW		LW		<i>N</i> †	Mann–Whitney	
	$\bar{x}$	SE	$\bar{x}$	SE		χ	<i>P</i>
1	36.0	1.26	17.7	1.51	729	78.0	<0.0005
2	37.0	1.12	29.8	1.77	694	15.9	<0.0005
3	34.1	1.03	33.6	1.76	692	0.37	0.800
4	32.0	1.10	29.0	1.64	699	2.78	0.095
Total	138.4	3.30	110.6	5.00	720	23.4	<0.0005

Results are for the Mann–Whitney tests for the difference in fecundity between wing morphs (ANOVA results are qualitatively identical).

†Total number of SW and LW females. Numbers differ because as a result of a clerical error data from some families are not available.

Table 2 Heritability estimates of egg production in *Allonemobius socius* by time period

Period	Morph	h^2	SE1†	SE2‡	<i>P</i> (ANOVA)	<i>P</i> (RAND)
1	SW	0.22	0.06	0.06	<0.0005	0.0002§
	LW	0.28	0.14	0.10	0.032	0.005
	Combined	0.17	0.05	0.04	<0.0005	0.0002§
2	SW	0.09	0.06	0.04	0.042	0.044
	LW	0.31	0.14	0.08	0.003	0.002
	Combined	0.14	0.05	0.05	<0.0005	0.0002§
3	Combined	0.11	0.05	0.03	0.001	0.001
4	Combined	0.10	0.06	0.03	0.004	0.004
Total	Combined	0.19	0.07	0.05	<0.0005	0.0002§

†Standard error estimated using the jackknife procedure.

‡Standard error estimated based on probability obtained from randomization (see text for details).

§This is an upper estimate as none of the 4999 randomizations produced a heritability estimate greater than that observed (hence, $P \leq 1/5000$).

RAND, randomization procedure.

Family and wing morph effects on fecundity

The above analysis ignores the possibility of differences arising from genetic variation between families. To test for such an effect we used the statistical model

$$\text{Fecundity} = a_0 + a_1 \text{Family} + a_3 \text{Wing morph} + \text{error}$$

where 'Family' and 'Wing morph' are coded as categorical variables and a_0 , a_1 and a_3 are coefficients.

Both 'Family' and 'Wing' effects were highly significant in periods 1 and 2, and for total fecundity ($P < 0.0005$ in all cases), whereas Family was highly significant also in periods 3 and 4 ($P = 0.001$ and 0.002 , respectively). Wing was nonsignificant in period 3 ($P = 0.105$) but significant in period 4 ($P = 0.025$). Thus, as in the previous analysis, SW

females laid more eggs than LW females in periods 1 and 2 and in total, but laid the same number in period 3, with results for period 4 being ambiguous after Bonferroni correction. However, there was also an additional effect from Family at all periods, indicating genetic variation for fecundity.

Heritability of fecundity and wing dimorphism

Heritability estimates for fecundity were made ignoring wing morph, and for periods 1 and 2 they were made for each wing morph separately. With one exception, the probability values given by the ANOVA were very close to those obtained by the randomization procedure (Table 2), demonstrating the robustness of the ANOVA and suggesting that the heritability estimates were not biased by any lack of

normality in the data. As expected from the previous analysis, there was a significant heritability for fecundity at all periods for the combined data, the estimates ranging between 0.10 and 0.17.

Because the proportion of LW differed between the two environments the heritability of wing morph was estimated separately for each environment. In both cases the estimates differed significantly from zero: for the Early environment $h^2 = 0.45$ (SE = 0.07), and for the Late environment $h^2 = 0.59$ (SE = 0.10).

Phenotypic and genetic correlations between fecundity and wing morph

Genetic correlations are notorious for their large standard errors (Klein, 1974; Falconer, 1989) and, therefore, to maximize the sample size we combined the data for the two environments. Because of the difference in proportion of LW between the two environments the estimates of the phenotypic and genetic correlations are to be viewed as estimates for the 'average' environment. As expected from the analyses in sections 1 and 2, there was a significant negative phenotypic correlation between wing morph and fecundity at periods 1 and 2, and overall, but no correlation at periods 3 and 4 (Table 3). Only the genetic correlation for period 1 was significant.

To distinguish between the possible models shown in Fig. 1 we analysed the relationship between mean family fecundities and proportion macropterous. We found no significant relationship using the mean fecundities; however, as noted in Materials and methods variation in fecundity that was independent of wing morph effects could obscure any relationship. To examine this we used residual fecundities. Because of the lack of phenotypic effects found in periods 3 and 4, we analysed the residual fecundities only for the first two periods.

We predict a negative correlation between the residual fecundity and the value on the underlying scale (z , Fig. 1). For the first period there was a highly significant negative correlation ($r = -0.34$, $n = 63$, $P = 0.015$), but not for the second ($r = 0.009$, $n = 63$, $P = 0.944$). We tested the dichotomy model (Fig. 1b) by computing the family mean correlation within morph, using residuals estimated independently for each morph. If the dichotomy hypothesis is correct there should be no correlation between family mean fecundity and family mean z . Because we obtained a significant correlation previously only with period 1, we tested only this period. There was a significant negative correlation using the SW females ($r = -0.29$, $n = 61$, $P = 0.025$), and

a negative but nonsignificant correlation using the LW females ($r = -0.14$, $n = 51$, $P = 0.347$). The lack of significance in the LW females may be a consequence of the considerably smaller sample size (mean family sizes are 3.6 and 7.1, for LW and SW, respectively). The significant negative correlation in SW females leads us to reject the dichotomy hypothesis, but the data are insufficient to distinguish between the other two possibilities (Figs 1a, c).

Discussion

The most important finding of the present research is that the phenotypic trade-off between wing morph and fecundity in *A. socius* has a genetic basis, i.e. there was a negative genetic correlation between wing morph and fecundity during the first 12 days after eclosion. Although there were highly significant phenotypic correlations between wing morph and fecundity during the second period, and between wing morph and cumulative fecundity, the genetic correlations were not significant (Table 3). However, the standard errors of these correlations are so large that the statistical tests have little power to differentiate biologically significant correlations from biologically insignificant correlations. Further experiments are required to resolve this issue.

A negative genetic correlation between wing morph and early fecundity has previously been demonstrated in another cricket *Gryllus firmus* (Roff, 1990, 1994a); these, plus the present results, suggest that such correlations may generally underlie the phenotypic trade-offs observed in wing dimorphic insects (Roff, 1986, Roff & Fairbairn, 1991). Consequently, the evolution of wing dimorphism will be modulated by the fecundity costs associated with macroptery (for a theoretical treatment of this see Roff, 1994b).

Analysis of mean residual family values indicates that variation in fecundity is functionally related to the underlying continuously distributed trait, and not simply to the dichotomous phenotype (Fig. 1b).

Table 3 Phenotypic and genetic correlations between wing morph and fecundity for each of four time periods in *Allonemobius socius*

Fecundity	r_P (SE)	r_G (SE)
Period 1	-0.30 (0.04)	-0.53 (0.15)
Period 2	-0.13 (0.04)	-0.07 (0.27)
Period 3	-0.009 (0.04)	0.35 (0.26)
Period 4	-0.06 (0.05)	0.17 (0.26)
Total	-0.18 (0.04)	-0.05 (0.22)

Because of the relatively small sample size associated with the LW females, it is not possible to distinguish between the two other models displayed in Fig. 1. For *G. firmus* the data suggest that the fecundity of the LW females varies markedly with the value of the underlying trait, whereas the fecundity of the SW females varies little (i.e. the situation displayed in the lower panel of Fig. 1: Roff, 1994a). This scenario makes sense from a biological perspective: fecundity in LW females is expected to be reduced while there is 'competition' between the flight muscles and the gonads, but no such competition is expected in the SW females which lack functional muscles (Mole & Zera, 1993, 1994; Zera *et al.*, 1994). This hypothesis is reinforced by the observation that fecundity increases with histolysis of the flight muscles (Roff, 1989), and that there is a highly significant positive genetic correlation between flight muscle histolysis and fecundity in *G. firmus* (Roff, 1994a). The present data cannot confirm this hypothesis; indeed the observed regression slope between the fecundity residuals and z within the SW females is larger in magnitude (-0.145) than that in the LW females (-0.075), though the two slopes are not statistically different.

Theoretical analysis of the evolution of wing dimorphism has shown that the dimorphism will be maintained in an environment that is spatially and temporally heterogeneous, making migration of part of the population necessary (Roff, 1994b). Similar arguments can also be advanced for the maintenance of another dimorphism, paedomorphosis in salamanders (Roff, 1996). Fundamental to these arguments is the assumption that the trade-off between lifehistory components and morphology is genetically based. We have demonstrated that such a condition is satisfied for *A. socius*. Further analyses are required to examine the generality of this phenomenon not only with respect to wing dimorphism but also for other dimorphisms, for which no genetic analyses have been performed.

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