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The genetic basis of the trade-off between wing morph and fecundity in the sand cricket, *Gryllus firmus* (Orthoptera: Gryllidae): Correlated response in the proportion macropterous when selecting for a decrease in fecundity.

James R. Tucker

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ABSTRACT

The genetic basis of the trade-off between wing morph and fecundity in the sand cricket, *Gryllus firmus* (Orthoptera: Gryllidae): Correlated response in the proportion macropterous when selecting for a decrease in fecundity.

James R. Tucker

Optimal life histories are the result of fitness trade-offs that balance the costs and benefits of particular trait combinations. Trade-offs, represented by the genetic correlations between fitness characters, can constrain evolution by impeding the rate at which traits evolve independently. Wing dimorphisms, in which one morph (micropter) has reduced wings and cannot fly while the other (macropter) possesses fully developed wings and can fly, occur within several major orders of the Insecta (Orthoptera, Hemiptera, Homoptera, Coleoptera). A substantial amount of evidence indicates that a phenotypic trade-off exists between wing morph and fecundity in wing-dimorphic insects. However, to have evolutionary significance trade-offs must be genetically based. A preceding study (Roff, 1994a) conducted on the sand cricket, *Gryllus firmus,* documented a negative correlated response in fecundity to selecting on the proportion macropterous. The present study demonstrates that direct selection for decreased fecundity in *G. firmus* produces a correlated increase in the proportion macropterous. The observed symmetrical correlated response indicates that the genetic constraint acts both ways. From the direct response, the realized heritability of fecundity was estimated to be 0.200 ± 0.0496. The demonstrated correlated response supports the

hypothesis of a genetic basis for the phenotypic trade-off between migratory ability and reproduction commonly observed within wing dimorphic insects. Thus, fecundity is constrained from evolving independently of the proportion macropterous.

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INTRODUCTION

Life history theory predicts that natural selection will maximize the intrinsic rate of increase (r) or the net reproductive rate (R_o) (Isock, 1978; Lande, 1982; Roff, 1992, 1994b; Danks, 1994a). The various morphological, physiological, and behavioral components that determine the age-specific fecundity and mortality schedules of the organism are traded off to produce optimal trait combinations (*ie.* those that maximize fitness). The genetic constraints underlying these character organizations are embodied by the additive genetic variance-covariance matrix (**G**-matrix) (Lande, 1979). In response to directional and stabilizing (or disruptive) selection, the phenotype evolves along a trajectory determined by the **G**-matrix, towards a point of equilibrium (Lande, 1979; Lande and Arnold, 1983).

To be of evolutionary significance, a phenotypic trade-off between separate components of fitness must have a genetic basis (*ie.* be represented by a negative genetic correlation) (Reznick, 1985, 1992; Bell and Koufopanou, 1986; Reznick *et al.* 1986; Loeschcke, 1987; Willis *et al.* 1991; Roff, 1992; Roff and Bradford, 1986). Such genetic correlations arise between traits due to pleiotropy (the property of a gene whereby it affects two or more characters) or because of linkage disequilibrium, the latter being transient in effect (Falconer, 1989). The degree of correlation arising from pleiotropy expresses the extent to which two characters are influenced by the same genes, while the sign of the correlation specifies their relationship with respect to fitness (a positive correlation denotes that the relationship is reinforcing, while a negative correlation indicates an antagonistic association). Traits that are closely associated with fitness (*eg.* life-history traits) are expected to be negatively correlated with other components of fitness because alleles with universally positive effects on fitness are brought to fixation, leaving alleles with positive effects on some fitness traits and negative effects on others to vary (Falconer, 1989). As a result of pleiotropic associations, selection on one trait may produce correlated responses in others so that each trait is prevented from responding independently. In this manner, the course of evolution may be constrained in the short-term, causing characters to evolve in concert (Lande, 1979; Arnold, 1981; Lande and Arnold, 1983; Price and Langen, 1992). In theory, traits which are not perfectly genetically correlated (*ie.* $-1 < r_A < 1$) are not prevented from ultimately achieving their independent optima (Via and Lande, 1985), although the rate at which the traits evolve may be severely retarded.

Natural selection acts on the entire phenotype, rather than on the individual traits that comprise the organism. Because of genetic correlations between characters, selection imposed on a single character not only produces changes in the distribution of that character, but may produce a shift in an entire array of characters (Falconer, 1989). When selection is exclusively imposed on a single trait (X), the response in that trait can be predicted from the following (Falconer, 1989):

$$R_X = h_X{}^2 i_X \sigma_{PX} = h_X{}^2 S_X \qquad \text{eq (1)}$$

If trait X is genetically correlated with a secondary trait (Y), the correlated response is:

$$CR_Y = i_X h_X h_Y r_A \sigma_{PY} \qquad \text{eq (2)}$$

where R_X is the direct response to selection; $h_X{}^2$ is the heritability of trait X under direct selection; i_X is the selection intensity for trait X; σ_{PX} is the phenotypic standard deviation of trait X; S_X is the selection differential for trait X; CR_Y is the correlated response in trait Y; h_i is the square root of the heritability of trait *i*; r_A is the additive genetic correlation between X and Y; and σ_{PY} is the phenotypic standard deviation of trait Y.

An implicit assumption of the former equations is that all other characters are neutral, so that natural selection is not acting on any other correlated characters. In a more realistic scenario, *ie.* when selection is simultaneously acting on both traits, the comprehensive change in either character is the sum of its direct and correlated responses. If the traits are measured in standard deviation units, the responses for either trait are predicted by (Roff, 1997):

$$R_X = \beta_X h_X{}^2 + \beta_Y h_X h_Y r_A \qquad \text{eq (3)}$$

$$R_Y = \beta_Y h_Y{}^2 + \beta_X h_X h_Y r_A \qquad \text{eq (4)}$$

where β_i is the selection gradient for the *i*th trait.

Multivariate formulae written in matrix notation have been established (Lande, 1979) that allow an extension to the prediction of simultaneous phenotypic responses in several characters, thereby permitting a more holistic interpretation of the evolutionary response:

$$\Delta \mathbf{z} = \mathbf{G}\,\beta = \mathbf{G}\,\mathbf{P}^{-1}\mathbf{S} \qquad \text{eq (5)}$$

where $\Delta \mathbf{z}$ is the vector of mean phenotypic response for each of the z_i traits; **G** is the additive genetic variance-covariance matrix; β is the selection gradient vector, $\mathbf{P}^{-1}$ is the inverse of the matrix of phenotypic variances, and **S** is the vector of selection differentials.

From the above, it can be seen that selection imposed on one character indirectly generates changes in other characters that are genetically correlated with it. The existence of negative genetic correlations can therefore be demonstrated by imposing artificial selection on one trait and testing for correlated responses in other traits (Reznick, 1985). Although numerous researchers have demonstrated a genetic basis for trade-offs between components of fitness, these examples are largely concentrated in a few areas of life history constraint. For example, Stearns (1992, pg. 79) asserts that out of 45 conceivable life history trade-offs, "only 5 have received much attention". In addition, many of the existing studies that have demonstrated a genetic basis for trade-offs between life history traits have been conducted on one species, *ie. Drosophila melanogaster* (Diptera: Drosophilidae) investigating the trade-off between early fecundity and longevity (or fecundity late in life) (*eg.* Rose and Charlesworth, 1981; Rose, 1984; Luckinbill *et al.* 1984, 1987; Clare and Luckinbill, 1985; Luckinbill and Clare, 1985; Partridge and Fowler, 1992). Studies of other life history trade-offs are needed, utilising various organisms to evaluate thoroughly the general role of antagonistic pleiotropy in trade-offs.

Migration[1] by flight is an extremely important aspect of the life histories of many insects, allowing persistence in spatially and temporally heterogeneous environments (Southwood, 1962; Johnson, 1969; Harrison, 1980; Dingle, 1985a). Without such a mechanism to buffer the impact of adverse environmental fluctuations, species extinction may be very rapid (Roff, 1974a, 1974b). Although flight capability may confer a substantial fitness advantage by allowing the exploitation of ephemeral habitats, wing loss has independently evolved within several orders of the sub-class Pterygota (winged insects) (Wagner and Liebherr, 1992). Some contemporary orders of the Pterygota exclusively consist of wingless species (*ie.* Grylloblattaria, Mallophaga, Anoplura, Siphonoptera), though in all cases they are derived from an ancestral winged state.

Wing dimorphisms, in which one morph has reduced or absent wings and cannot fly (micropterous) while the other possesses fully developed wings and flight muscles (macropterous), are relatively common within several major orders of the class Insecta (Harrison, 1980; Roff, 1984, 1986a, 1986b, 1994c; Denno *et al.* 1989; Wagner and Liebherr, 1992). The existence of wing dimorphisms found within the insects suggests that the benefits of migration are counter-balanced by some cost in the possession and/ or maintenance of the flight apparatus (Roff, 1984). As the obligate non-migratory morph can be visually differentiated from the long-winged morph with ease, such species make excellent subjects for the analysis of trade-offs between migratory ability and other components of fitness (Roff and Fairbairn, 1991). Wing dimorphic species allow the

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[1] The term migration within the present study is defined as a simple movement between habitats across generations. It is specified in this sense to differentiate it from the random movements associated with foraging or mating within a habitat .

comparison of other life history characters between the two wing morphs without the confounding variation that may arise in inter-specific comparisons.

Phenotypic differences in life history attributes between the two wing morphs have been well documented (see reviews by Harrison, 1980; Roff, 1986a; Denno *et al.* 1989; Roff and Fairbairn, 1991; Rankin and Burchsted, 1992; Zera and Denno, 1997). In general, the micropterous morph reproduces earlier and has a higher early fecundity than the macropterous morph. These consistent phenotypic differences between wing morphs support the hypothesis of phenotypic trade-offs between the ability to fly and other fitness components. A genetic basis for this trade-off has been demonstrated in the cricket *Gryllus firmus* (Orthoptera: Gryllidae) by imposing artificial selection on the incidence of macroptery and observing a negative correlated response in early fecundity (Roff, 1990b, 1994a).

Along with changes in early fecundity, selection for increased and decreased incidence of macroptery in *G. firmus* produced correlated responses in histolysis of flight muscles (auto-digestion of the dorsal longitudinal flight muscles) and flight propensity within macropterous morphs (Fairbairn and Roff, 1990) and in the titre of juvenile hormone esterase[2] in the final nymphal instar (Fairbairn and Yadlowski, 1997). Moreover, a half-sib analysis conducted on *G. firmus* has demonstrated significant genetic

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[2] In *Gryllus,* wing morph is strongly influenced by juvenile hormone titre in the final nymphal instar. While presumptive macropters and micropters do not differ in rates of juvenile hormone synthesis, macropters have an increased level of juvenile hormone degradation via elevated levels of juvenile hormone esterase during the final nymphal instar (Zera *et al.*, 1989; Zera and Tiebel, 1989; Zera and Tobe,1992; Fairbairn and Yadlowski, 1997).

correlations among wing morph proportion, fecundity, and juvenile hormone esterase titre (Roff *et al.* 1997). These genetic correlations connect an assemblage of life history, physiological, behavioural, and morphological characters to the incidence of macroptery in a population. Consequently, individuals from populations with higher incidences of macroptery are expected to exhibit, on average, stronger migratory propensities, retain their wing musculature for a longer period, and possess lower early fecundities when compared with those from populations with lower incidences of macroptery (Fairbairn and Roff, 1990).

A similar situation is found in the milkweed bug, *Oncopeltus fasciatus* (Hemiptera: Lygaeidae), in which traits associated with migratory ability covary and function together in a complex syndrome. Half-sib analysis (Hegmann and Dingle, 1982) and bi-directional selection for wing length accompanied by correlated responses (Palmer and Dingle, 1986) have demonstrated the existence of underlying genetic correlations between several morphological, behavioral, and life-history characters associated with migratory ability in *O. fasciatus*. By means of the two quantitative genetic techniques above, genetic correlations have also been demonstrated between flight capacity and several life-history traits in the brown apple moth, *Epiphyas postvittana* (Lepidoptera: Tortricidae) (Gu and Danthanarayana, 1992). Genetic correlations between characters may commonly account for the concurrent expression of individual traits that together comprise complex characters, such as migratory tendency.

In the present study, the role of antagonistic pleiotropy in trade-offs is examined by imposing artificial selection for decreased early fecundity in a population of *G. firmus* and observing the correlated response in the incidence of macroptery. Roff (1994a) conducted the reciprocal experiment by selecting for a change in the incidence of macroptery, and observed a correlated response in fecundity. A selection experiment conducted by Shiotsugu *et al.* (1997) suggests that a genetic correlation demonstrated by a correlated response to selection on one trait will not necessarily correspond with that obtained from selection on the other trait. Artificial selection for reproduction late in life and crowding tolerance in *D. melanogaster* both produced a correlated response in urea resistance, while section for urea resistance failed to produce a correlated response in either character. Furthermore, both theoretical (Bohren *et al.* 1966; Gromko, 1995; Lascoux, 1997) and empirical evidence (reviewed in Gromko *et al.*, 1991; Gromko, 1995) predict more variance in correlated responses than in direct responses to selection. The purpose of my experiment is to assess the symmetry of the antagonistic pleiotropy underlying the migration/ reproduction trade-off found in *G. firmis*. Based on the previous artificial selection (Roff, 1994a) and half-sib analysis (Roff *et al.* 1997), I expect selection for decreased early fecundity to generate a correlated increase in the incidence of macroptery. Such an experimental result would establish the symmetry of the genetic correlation between fecundity and wing morph in *G. firmus*, support the view that individual components that comprise complex traits (*eg.* migratory tendency) are likely to evolve in concert, and provide further support for the regulation of trade-offs by antagonistic pleiotropy.

MATERIALS AND METHODS.

Experimental population

The sand cricket, *G. firmus,* is a large (approximate adult weight 0.7 grams), ground-dwelling cricket occurring in early successional, sandy habitats of the southeastern United States (Alexander, 1968; Harrison, 1985). The experimental population in this study was derived from a colony founded with approximately 40 individuals (1 : 1 sex ratio), collected from a single location in northern Florida in 1981 (Roff, 1984). The stock population, consisting of approximately 100 - 300 breeding crickets, has been maintained in a laboratory terrarium that is held above 25°C to avert diapause, with *ad libitum* food (crushed Purina © Rabbit Chow) and water (Roff, 1986c).

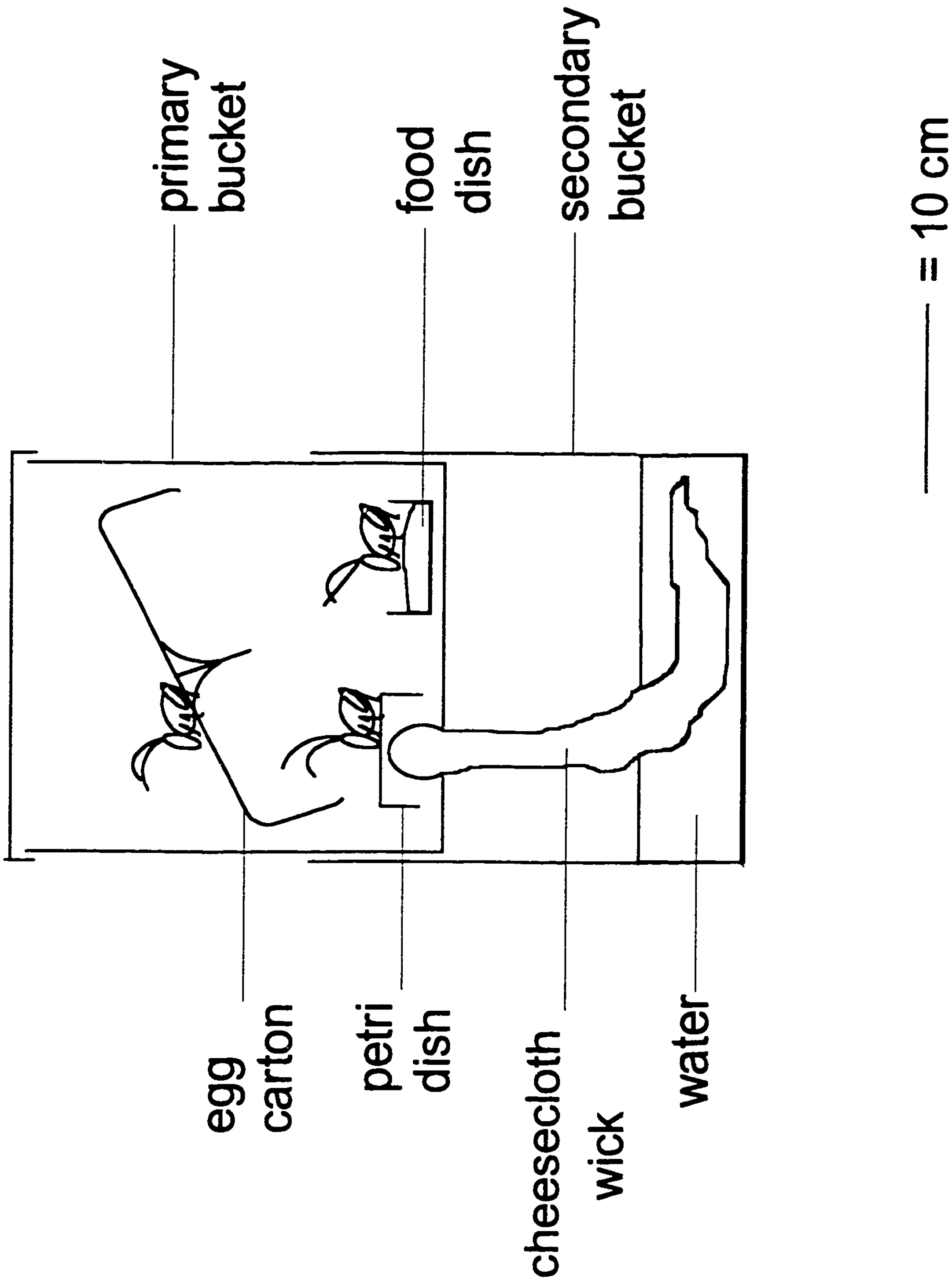
Experimental design

A standard mass selection design (Falconer, 1989) was followed in two experiments, each consisting of a line selected for decreased early fecundity (defined as the number of eggs laid to the seventh day following the initiation of the mating pair) and a control line. To create the selected lines, eggs from the 25 pairs with the lowest phenotypic values in each generation were used to initiate the subsequent populations (25 %, approximate percent selected). Control lines were constructed by selecting eggs from 25 randomly chosen pairs to constitute the following generation. All crickets were reared at a temperature of 28°C with a photoperiod of 15 h light: 9 h dark.

To create the initial population, 25 crickets of each sex were selected haphazardly from the stock population. One male and one female were then placed in each of 25 plastic containers (15.5 cm diameter, 8.5 cm depth) containing a sand-filled cup (6.5 cm diameter, 4 cm depth) for oviposition, a food dish, one sixth of an egg carton (cover to help reduce stress effects, Yadlowski, 1994), and a water vial. After one week the sand from each container was sifted to collect the laid eggs. Each batch of eggs was then spread on cheesecloth and placed on moist filter paper in a petri dish. After hatching, 24 nymphs (of approximately equal ages) from each adult pair were equally distributed among 12 buckets (21 cm diameter, 15.5 cm depth) containing an *ad libitum* food source, half of an egg carton, and a cheesecloth wick that supplied de-chlorinated water via a reservoir held in a second bucket into which the cage was suspended (Fig. 1). Each bucket was thus initiated with two nymphs from each of the 25 families for a total of 50 nymphs per bucket. After approximately three weeks, the water supply was changed to three cotton-plugged, glass vials. Using the same protocol, a second experiment was initiated three weeks after the first.

All buckets were inspected daily for crickets reaching the adult instar, after which the wing morphs were recorded and the new adult crickets were placed individually in containers (15.5 cm diameter, 8.5 cm depth) that held food supplied *ad libitum* (crushed Purina © Rabbit Chow), a sixth of an egg carton and a single water vial, where they were held until they could be placed into mating pairs. Each male was selected at random (without preference for wing morph) and assigned to a female, after which each pair was placed in a container with a sand filled cup. As unmated females produce eggs without ovipositing them (Roff, 1994a), females that could not be paired with a male within two days of eclosion were excluded from the mating population. Three days after the

Figure 1. Double-bucket apparatus used for rearing crickets.


primary bucket
food dish
secondary bucket
egg carton
petri dish
cheesecloth wick
water
= 10 cm

establishment of each mating pair, the sand in the oviposition cup was remoistened to prevent desiccation, and then on the seventh day it was sifted to obtain the accumulated eggs.

The eggs from individuals contributing to the next generation for the control and selected lines were collected from the oviposition cup in the second week following the initiation of the mating pair. To complete development, eggs from each pair were incubated on cheesecloth overlaying a moistened filter paper in a petri dish. On hatching, two nymphs from each of the 25 selected pairs were placed into each of six buckets, set up as previously described, to produce a population of 300 individuals for the subsequent generation. If eggs could not be retrieved from the pair by the second week, the consecutive pair with the next lowest fecundity value was chosen in its place. The codes for the control line mating pairs were shuffled at random, after which the first 25 pairs were chosen to contribute progeny to the next generation. Using the offspring from the parents chosen from the control line, a parallel population was created by the same method as for the selected line. The forementioned protocol was also followed for the second experiment. The mass selection procedure outlined above was carried out through a total of three consecutive generations (base population = generation 0).

Quantitative genetic techniques

I) Calculation of realized heritabity and its standard error

Heritability is defined as the ratio of additive genetic variance to the total phenotypic variance (composed of all genetic and environmental sources of variation), and thus is a major component in the determination of the rate at which a trait can evolve (see equation 1, pg. 3). The realized heritability expresses the response as a proportion of the selection differential, and is estimated from a plot of the generation means against the cumulative selection differential (Falconer, 1989). The cumulative response within each generation is determined by subtracting the generation mean of the control line from that of the selected line. The cumulative selection differential is calculated by summing the deviations of the mean values of the selected parents from their population means over the total number of generations. The slope obtained by regressing the cumulative response on the cumulative selection differential estimates the realized heritability. The linear regression is forced through zero, because the control and selected lines are derived from the same base (Hill, 1972). Because selection was only imposed in one sex in the present experiment, the realized heritability is calculated as twice the estimated slope value.

The standard error of the heritability estimated from the linear regression underestimates its true value, because it does not include the variation arising from genetic drift (Hill, 1972; Falconer, 1989, pg. 211; Roff, 1997). The actual variance in the heritability can be estimated by (Hill, 1972 cited in Roff, 1997):

$$Var(h^2) \approx \frac{6}{t(t+1)(2t+1)} \bullet \left(\frac{S_{cum}}{t}\right)^{-2} \bullet \left(\frac{2t^2+2t+1}{5} Var(drift) + Var(\epsilon)\right) \qquad \text{eq(4)}$$

$$Var(drift) = h^2 V_P\left(\frac{1-h^2}{N} + \frac{1}{L}\right) \qquad \text{eq(5)}$$

$$Var(\epsilon) = V_P\left(\frac{1-h^2}{M} + \frac{h^2}{K}\right) \qquad \text{eq(6)}$$

where $Var(\epsilon)$ is the variance due to measurement error, $Var(drift)$ is the variance due to genetic drift, K and M are the effective number of individuals measured per generation in the control and selected lines respectively, L and N are the effective number of parents used in the control and selected lines respectively calculated by $N = 1/(1/4N_{♂} + 1/4N_{♀})$ and $L = 1/(1/4L_{♂} + 1/4L_{♀})$ where the subscripts refer to males and females, S_{cum} is the cumulative selection differential, t is the number of generations of selection, h^2 is the heritability, and V_P is the phenotypic variance.

II) Preliminary analyses

The selection protocol outlined above was based upon a preliminary feasability analysis in which I used the standard quantitative genetic formulae (eq's 1 and 2) to make predictions for the change per generation in fecundity and the proportion macropterous. I then used these *a priori* predictions for the direct and correlated responses to determine the number of generations and sample sizes required to detect statistically significant direct and correlated responses to selection.

i) Prediction of the direct response

Using the estimates for the heritability of fecundity (estimated value ± SE : 0.073 ± 0.081) obtained from the previous half-sib analysis (Stirling *et al.* 1997, unpublished manuscript), the average phenotypic standard deviation of the base population (212.65 eggs), and assuming an approximate selection intensity of 1.271 (25% proportion selected; Falconer, 1989, Appendix A), it was possible to predict the direct response in fecundity.

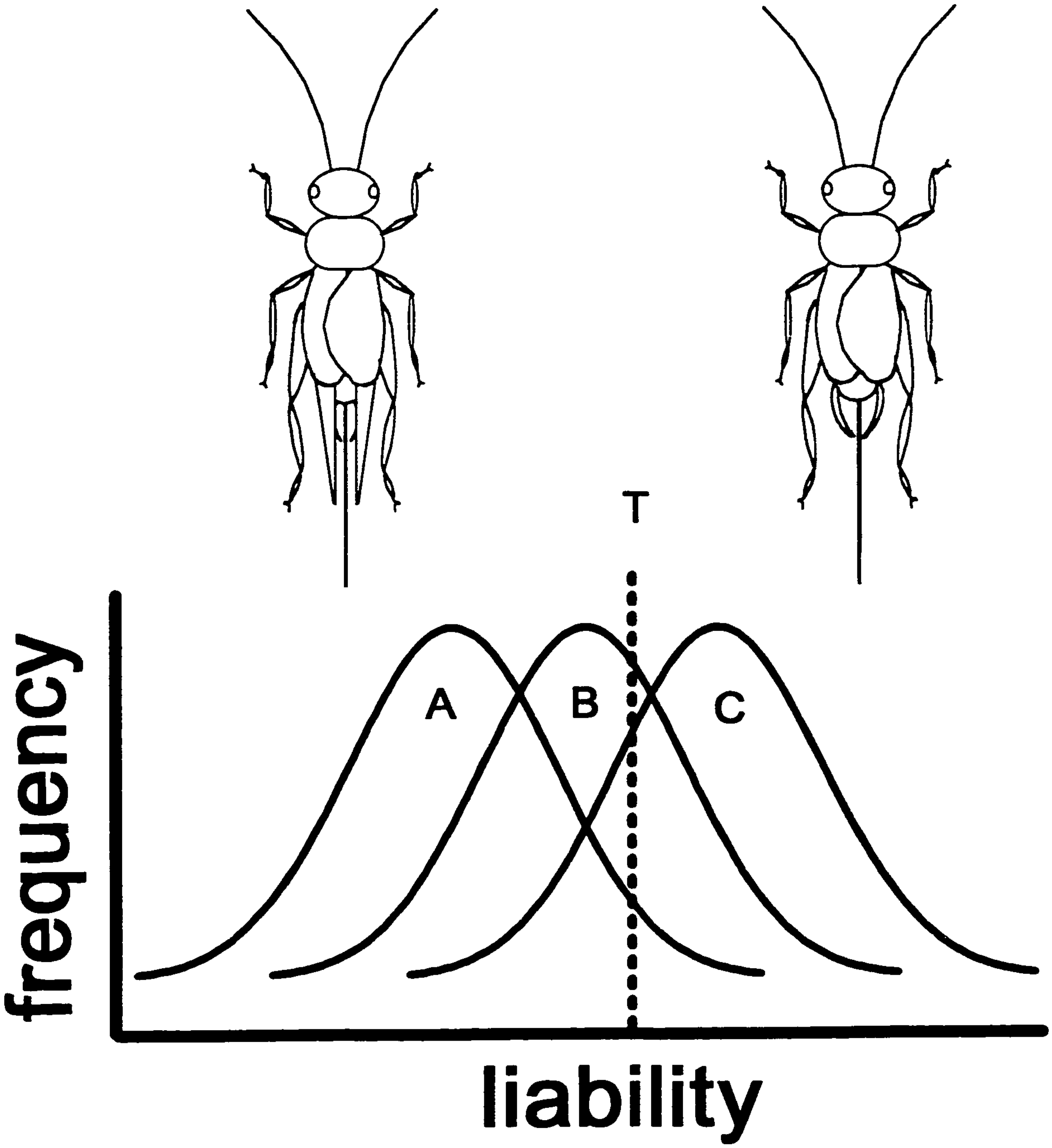
Substitution of the estimated values into equation one and then halving the result (as selection was only imposed in one sex), predicted a response of 9.87 ± 10.95 eggs per generation. After three generations of selection a response of 29.61 ± 32.84 eggs was predicted.

ii) The quantitative genetic threshold model and the prediction of the correlated response

Along with the direct response, artificial selection may produce responses in other characters that are genetically correlated with the primary character. The correlated responses were predicted by employing equation two. The predicted correlated response in wing morph is interpretable in the context of the threshold model of quantitative genetics (Falconer, 1989, Chapter 18). The threshold model assumes that the discontinuous trait (*eg.* wing morph) is regulated by an underlying continuous variable (termed the liability) and its relationship to a specific threshold value (Fig. 2). Individuals above the threshold develop into one morph, while those below it form the alternate morph. The correlated response in the proportion macropterous is predicted in units of the liability (standard deviations): thus the proportion of macropters in the base population is first transformed into a z-score before adding the predicted change. Subsequently this predicted value is transformed back into a proportion, from which the base proportion is subtracted so that a comparison with the realized correlated response can be made.

With estimates of the genetic correlation between fecundity and wing morphology (r_A = -0.85, S.E. = 0.42) obtained from a previous half-sib analysis (Stirling *et al.* 1997), an estimate of heritability for wing morph (0.65 ± 0.080; Roff, 1986c, 1990a), and

Figure 2. The quantitative genetic threshold model. For a dichotomous character (*eg.* wing morph) changes in morph proportion within the population coincide with mean shifts in the liability, with the threshold (T) remaining constant. A, B, and C represent three populations that differ in their morph proportion for the character specified.


T
A
B
C
frequency
liability

assuming the phenotypic standard deviation for the liability to be 1 (by definition of a threshold trait with a [0,1] scale, Roff, 1994a) a prediction of the correlated response was made using equation two. This result was halved, as selection was only imposed in one sex in the current study. The correlated response in wing morph when selecting directly on fecundity was predicted to be 0.118 standard deviation units per generation. It should be noted that this predicted value assumes a genetic correlation of 1 between the sexes for wing morphology (inter-sex genetic correlations for morphological traits are often high, Roff and Fairbairn, 1993; Preziosi, 1997) and that the heritability of fecundity is equal for both sexes. After three generations of selection increases in the proportion macropterous were predicted as 9.9 and 13.4 % for the first and second experiments respectively (see Appendix A).

RESULTS

Direct Response

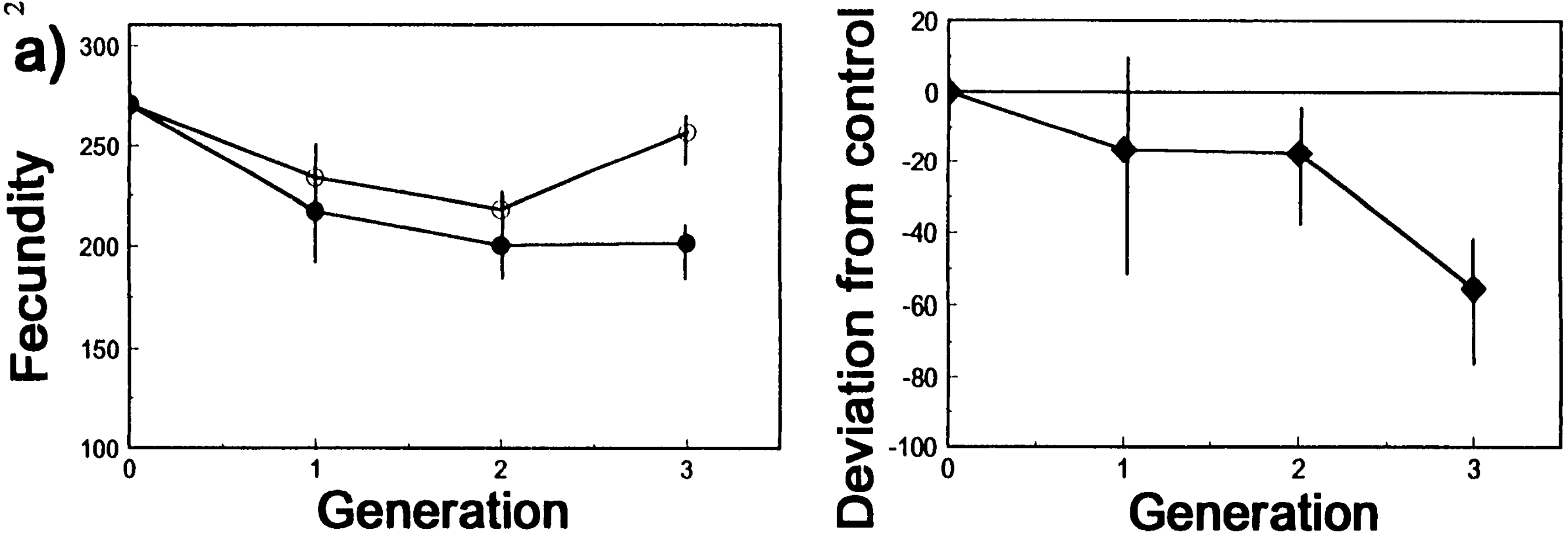
The generation means and standard deviations for fecundity are presented for both experiments in Table 1. Fecundity in the selected lines showed a decrease relative to the controls (Fig. 3), thereby demonstrating the capability of this character to respond to selection. Although the control lines showed some trend for movement away from the initial value throughout the experiment, t-tests indicated that fecundity of the control populations in the final generations did not differ significantly from the initial population base values for either experiment (experiment 1: $t = 0.563$, $df = 234$, $P = 0.563$; experiment 2 : $t = -1.10$, $df = 240$, $P = 0.272$).

A preliminary hierarchial ANOVA with fecundity as the dependent variable, morph as an independent variable, and buckets nested within treatment (selected line vs. control line) demonstrated the absence of any significant "bucket effects" in the final generation for both experiments (experiment 1: $F_{10, 173} = 1.17$, $P = 0.314$; experiment 2: $F_{10, 196} = 1.42$, $P = 0.174$). Consequently buckets were combined within treatments in further statistical analyses. To test for a significant response in fecundity in the final generation, an ANOVA model (Table 2) was constructed with the dependent variable fecundity, and the independent variables morph (long-winged or short-winged) and treatment (selected or control line). As expected, fecundity differed significantly between morphs in both experiments, with micropters laying more eggs in the first week than macropters. Treatments differed significantly in both experiments, confirming the success of the artificial selection imposed on fecundity. A significant interaction term was not present in

Table 1. Generation means and standard deviations for female fecundity (number of eggs laid to the seventh day) in *Gryllus firmus*. LW = long-winged (macropter); SW = short-winged (micropter).

Generation		Selected Line mean (standard dev.)	n	Control Line mean (standard dev.)	n
Experiment 1					
0	Combined	270.8 (216.1)	140	270.8 (216.1)	140
	LW	226.5 (177.2)	26	226.5 (177.2)	26
	SW	280.9 (223.5)	114	280.9 (223.5)	114
1	Combined	217.1 (203.8)	95	233.4 (175.1)	68
	LW	152.1 (210.2)	36	195.8 (142.9)	21
	SW	257.4 (190.6)	58	250.9 (187.1)	45
2	Combined	200.2 (131.2)	121	217.7 (112.0)	94
	LW	140.8 (136.4)	56	169.6 (119.4)	19
	SW	251.4 (102.6)	65	230.3 (107.3)	73
3	Combined	201.4 (122.1)	92	256.8 (121.0)	96
	LW	147.7 (107.7)	32	204.5 (202.8)	17
	SW	230.0 (120.5)	60	268.2 (92.7)	79
Experiment 2					
0	Combined	201.0 (209.2)	142	201.0 (209.2)	142
	LW	106.4 (188.6)	55	106.4 (188.6)	55
	SW	260.9 (200.1)	87	260.9 (200.1)	87
1	Combined	154.5 (148.4)	94	189.1 (155.9)	92
	LW	101.0 (117.2)	53	145.2 (150.9)	32
	SW	223.7 (156.9)	41	214.5 (154.3)	60
2	Combined	164.2 (149.5)	117	236.9 (116.4)	123
	LW	85.1 (120.1)	66	167.9 (128.6)	35
	SW	266.5 (119.0)	51	264.3 (99.4)	88
3	Combined	169.0 (133.8)	110	226.6 (120.2)	100
	LW	127.9 (128.5)	61	195.6 (145.5)	25
	SW	220.1 (123.3)	49	236.9 (109.7)	75

Figure 3.The response to direct selection for decreased early fecundity in *Gryllus firmus* females for the a) first and b) second experiments. Control line (○), selected line (●), selected line corrected for control (◆). Points indicate the mean fecundities (number of eggs laid) to the seventh day after mate pair initiation in both experiments. Vertical lines indicate standard errors.


a)
Fecundity
300
250
200
150
100
0
1
2
3
Generation
Deviation from control
20
0
-20
-40
-60
-80
-100
0
1
2
3
Generation

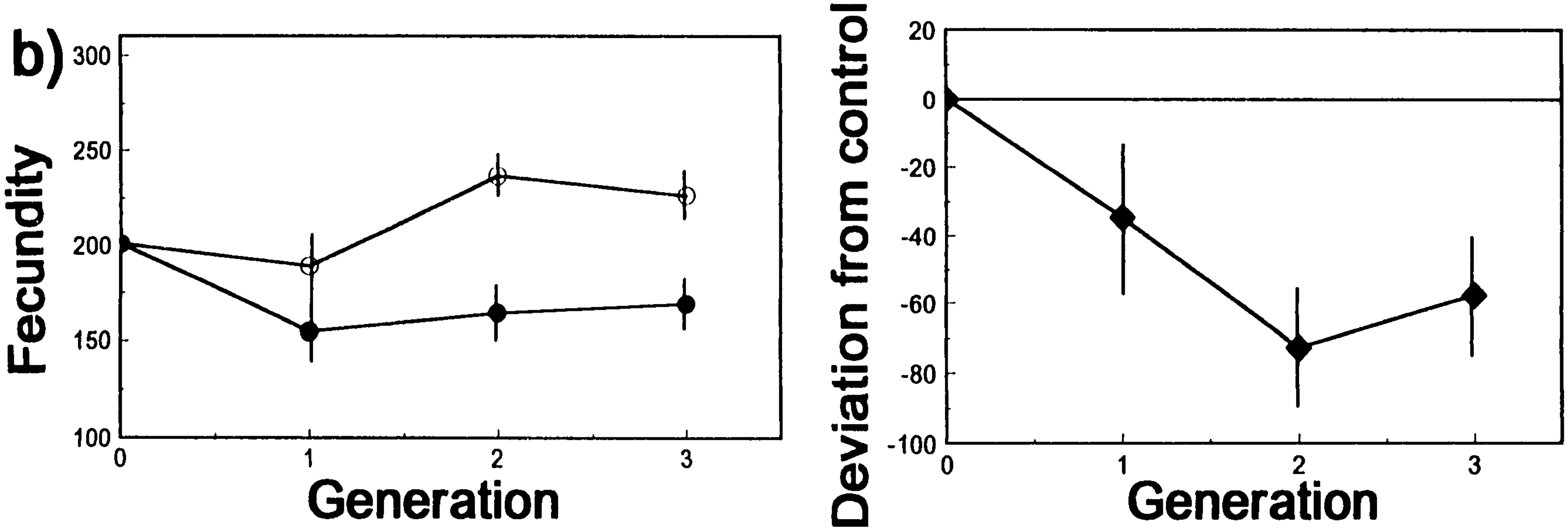

b)
Fecundity
300
250
200
150
100
0
1
2
3
Generation
Deviation from control
20
0
-20
-40
-60
-80
-100
0
1
2
3
Generation

Table 2. ANOVA table for the effects of wing morph and treatment (selected or control) on female fecundity after three generations of selection in *Gryllus firmus*.

Source	SS	df	MS	F	P	P*
Experiment 1						
Morph	178355.88	1	178355.88	12.9	<0.0001	0.0008
Treatment	75436.66	1	75436.66	5.44	0.021	0.0092
Morph x Treatment	2873.06	1	2873.06	0.21	0.649	0.3821
Error	2536450.00	183	13860.38			
Experiment 2						
Morph	197809.94	1	197809.94	13.07	<0.0001	0.0001
Treat	79184.68	1	79184.68	5.23	0.023	0.0478
Morph x Treatment	28759.66	1	28759.66	1.90	0.170	0.1616
Error	3118573.02	206	15138.70			

P* Generated through Manly's randomization program (Manly, 1997) either experiment, indicating that the artificial selection had a similar effect on fecundity within both wing morphs.

As fecundity exhibited a non-normal distribution that could not be normalized with any transformation, the previous results were further tested with a randomization procedure (Manly, 1997). Fecundities were shuffled at random with respect to treatment and morph after which F statistics were calculated using the general linear model, the whole process being repeated 9999 times. The probability of obtaining the F statistic by chance alone was estimated as (n+1)/10000 where n is the number of times the F statistic exceeded or equalled that of the unrandomized data set. The probabilities generated by the randomization test yielded the same statistical conclusions as the previous parametric analysis (Table 2).

Realized heritabilities and their standard errors were calculated by the methods given in Hill (1972, cited by Roff, 1997) and are presented in Table 3. Mean fecundities of the individuals contributing to each subsequent generation for selected or control lines are listed in Appendix B. Firstly, I conducted separate linear regressions of cumulative response on cumulative selection differential for each experiment. Secondly, I combined the data from the two experiments and performed a single regression . For the combined regression I used the statistical model:

$$\text{Response} = a_0 + a_1 \text{ Selection differential} + a_2 \text{ Experiment x Selection differential} + \text{error}$$

where Response = the cumulative response, Selection differential = the cumulative selection differential, Experiment = a categorical variable coding for experiment, a_0 is a constant set to zero, and a_1 and a_2 are coefficients. Although the regressions from the

Table 3. Realized heritabilities (h^2) and their standard errors (S.E.) for female fecundity in *Gryllus firmus*.

Experiment	S[a]	b_{RS}[b]	P-value[c]	h^2	S.E.	S.E.[d]
1	-210.62	0.070	0.0465	0.141	0.0409	0.0314
2	-164.92	0.151	0.0413	0.302	0.0628	0.0632
Combined estimate	-187.78	0.100	0.007	0.200	0.0496	0.0454

[a] the mean selection differential per generation; [b] the slope from the regression of cumulative response on cumulative selection differential; [c]significance of the regression coefficient; [d] standard errors calculated as twice the standard error of the regression coefficient (standard errors calculated in this manner are presented in comparison with those calculated by the method detailed by Hill (1972, cited by Roff, 1997). The similarity between standard errors obtained by the different methods suggests a low degree of genetic drift).

separate experiments are both forced through the origin and hence both possess the common constant of zero, they may differ in their slope values. This difference would be indicated by a significant interaction term in the combined model (*ie.* $a_2 \neq 0$). However, the interaction term was non-significant (t = 2.392, df = 1, P = 0.0750), and so was excluded and the combined slope was estimated from:

$$\text{Response} = a_0 + a_1 \text{ Selection differential} + \text{error}$$

With a_0 again set to zero, the estimated slope from the regression of cumulative response on cumulative selection differential is presented in Table 3. The heritabilities and their standard errors can also be estimated from the mean of several replicate regressions of response on cumulative selection differential (Falconer, 1989, p. 210). The estimate and standard error of the heritability from the combined regression (0.200 ± 0.0496 eggs, calculated using the method in Hill, 1972) is very similar to the value obtained directly from the average of the two separate regressions (0.221 ± 0.0806 eggs).

Correlated Response

Figure 4 depicts the cumulative correlated response in the mean proportion of macropters, shown with the sexes separate for the two experiments. For each generation, the mean proportions of macropterous individuals per bucket for both selected and control lines are listed with their standard deviations in Table 4. The mean proportion of macropterous individuals increased rapidly in both experiments when contrasted with their corresponding controls. A significant change in the total proportion of macropters in the control line in the final generation from the base value only was detected within the second

Figure 4. The correlated response in the mean proportion of macropterous *Gryllus firmus* for the a) first and b) second experiments as a result of direct selection for decreased early female fecundity. Points indicate the mean proportion of macropters per bucket. Control line females (○), selected line females (●), control line males (□), selected line males (■), selected line females corrected for control (◆), selected line males corrected for control (◇).

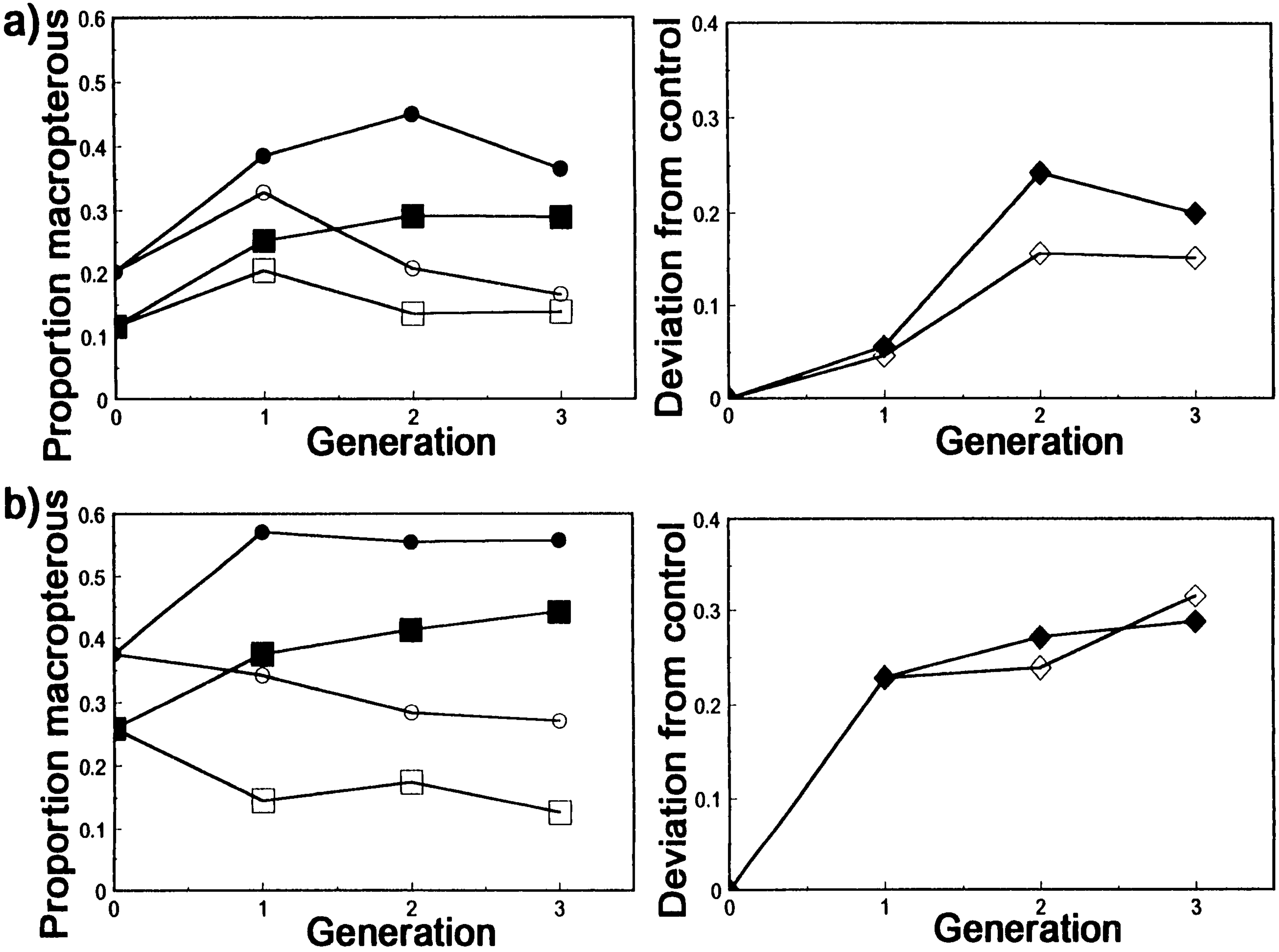

a)
Proportion macropterous
0
0.1
0.2
0.3
0.4
0.5
0.6
0
1
2
3
Generation
Deviation from control
0
0.1
0.2
0.3
0.4
0
1
2
3
Generation
b)
Proportion macropterous
0
0.1
0.2
0.3
0.4
0.5
0.6
0
1
2
3
Generation
Deviation from control
0
0.1
0.2
0.3
0.4
0
1
2
3
Generation

Table 4. Generation means and standard deviations for the mean proportion of macropters per bucket in *Gryllus firmus*.

		♂		♀	
Gen	**n**	**Selected (Std. dev)**	**Control (Std. dev)**	**Selected (Std. dev)**	**Control (Std. dev)**
Experiment 1					
0	12	0.116 (0.092)	0.116 (0.092)	0.202 (0.113)	0.202 (0.113)
1	6	0.252 (0.106)	0.204 (0.087)	0.386 (0.134)	0.329 (0.177)
2	6	0.292 (0.110)	0.136 (0.056)	0.450 (0.143)	0.208 (0.063)
3	6	0.290 (0.092)	0.139 (0.042)	0.366 (0.143)	0.166 (0.055)
Experiment 2					
0	12	0.259 (0.100)	0.259 (0.100)	0.375 (0.136)	0.375 (0.136)
1	6	0.375 (0.100)	0.146 (0.066)	0.571 (0.142)	0.342 (0.115)
2	6	0.413 (0.154)	0.174 (0.059)	0.555 (0.099)	0.284 (0.059)
3	6	0.442 (0.129)	0.126 (0.084)	0.558 (0.120)	0.270 (0.142)

experiment (generation 0 vs. generation 3; experiment 1: t = 0.200, df = 16, P = 0.847; experiment 2: t = 3.44, df = 16, P = 0.003), indicating an effect of genetic drift and/ or sampling error within that experiment.

To assess the statistical significance of the correlated responses in wing morphology, an ANOVA model (Table 5) was constructed with the proportion of macropters per bucket as the dependent variable and treatment (selected or control line) as an independent variable. Sex was included as a factor because a stronger correlated response was expected in females than in males, as selection was directly imposed on females. The effect of treatment was highly significant in both experiments demonstrating that the direct selection placed on fecundity produced a correlated response in the proportion of macropters. The interaction term between treatment and sex was non-significant indicating that selection on female fecundity produced a similar increase in the proportion of macropterous individuals within both sexes. The data were further analysed using the randomization procedure (Manly, 1997) as previously described, with the proportion of macropters shuffled with respect to treatment and sex. The randomization analysis gave the same statistical conclusions as the parametric analysis (Table 5).

Table 5. ANOVA table for the effects of treatment (selected or control) and sex on the proportion of macropterous *Gryllus firmus* after three generations of selection.

Source	**SS**	**df**	**MS**	**F**	**P**	**P***
Experiment 1						
Treatment	0.18	1	0.18	21.81	<0.0001	0.0001
Sex	0.02	1	0.02	1.87	0.187	0.133
Treatment x Sex	0.00	1	0.00	0.43	0.521	0.431
Error	0.17	20	0.01			
Experiment 2						
Treatment	0.55	1	0.55	37.48	<0.0001	0.0001
Sex	0.10	1	0.10	6.99	0.016	0.016
Treatment x Sex	0.00	1	0.00	0.08	0.774	0.772
Error	0.29	20	0.01			

P* generated through Manly's randomization program (Manly, 1997)

DISCUSSION

Both experiments showed a direct response to selection for decreased early fecundity, indicating the presence of additive genetic variance for this character. Additive genetic variance for major components of fitness is expected to be low (Fisher, 1958) because directional selection consistently acts upon these characters, driving many alleles to fixation. The realized heritability estimate of fecundity within the current study (0.200 ± 0.0496) is typical of life history characters ($\bar{x}$= 0.262, Mousseau and Roff, 1987, Table. 2). This study and those reviewed by Mousseau and Roff (1987) document that moderate amounts of heritable variation may persist for such characters. Rose (1982, 1985) has suggested that antagonistic pleiotropic associations between separate components of fitness may have a considerable influence on the preservation of additive genetic variance. If antagonism between fitness components is to contribute towards the maintenance of polymorphisms, dominance variance is required to be approximately half as large as the additive genetic variance for the traits (see Curtsinger *et al.* 1994). This is not entirely unrealistic for life history traits, which do generally possess a large dominance component (for wild outbred species: $\bar{x}$ = 0.544 ± 0.072 {dominance variance / additive variance + dominance variance}, Table 1a, Crnokrak and Roff, 1995).

Although a statistical difference was not evident, the realized heritability estimate of fecundity in the current study was larger in magnitude than that obtained from the half-sib analysis conducted on the stock population (Stirling *et al.* 1997). This difference was unexpected because heritability estimates from half-sib analyses are typically higher than those derived through selection experiments, due to the erosion of the additive genetic variance over the course of selection (ensuing from the fixation of alleles) (Falconer, 1989). In the half-sib analysis (Stirling *et al.* 1997) a 1 μl haemolymph sample was extracted from each cricket for use in a hormone assay, and the consequential stress may have increased the environmental variance in fecundity (Fairbairn, personal communication). Any supplementary environmental variance would inflate the total phenotypic variance, thereby depleting the heritability estimate. A previous estimate of the heritability for total fecundity in the first week (defined by the number of eggs laid plus an estimate of the number of eggs remaining in the ovaries) from a full-sib analysis (0.65, S.E. = 0.16, Roff, 1994a) suggests that the heritability of fecundity is higher than estimated by Stirling *et al.* (1997). Hence, values predicted for the direct and correlated responses (pg. 15 and 19) may have underestimated the realized responses (Fig. 3 and 4) because the heritability for fecundity may indeed be higher than the value obtained by Stirling *et al.* (1997).

The production of a negative correlated response in the proportion macropterous by means of the directional selection for decreased early fecundity establishes that at least some genes contributing to the variation in fecundity have antagonistic pleiotropic effects on wing morphology. This is the most important finding of the present research, as the demonstrated negative genetic correlation confirms the genetic foundation for the trade-off between migratory ability and reproduction. Furthermore, the genetic basis for the trade-off between fecundity and wing morphology is demonstrated to function symmetrically, so that direct selection imposed on either character produces a correlated response in the other. As a result of the existing antagonistic pleiotropy, short-term evolutionary changes in one character can only be modulated through a decrease in the other. A negative genetic correlation has previously been demonstrated between wing morph and early fecundity in the crickets *G. firmus* (Roff, 1990b, 1994a, Roff *et al.* 1997) and *Allonemobius socius* (Roff and Bradford, 1996). These and the current study imply that genetic correlations may generally underlie the phenotypic trade-off between migration and reproduction commonly observed in wing dimorphic insects.

Quantitative genetic theory predicts that functionally and developmentally related traits will be relatively highly correlated and evolve together in a coordinated manner (Lande, 1979, 1980a, 1984; 1986; Cheverud, 1982, 1984, 1995, 1996). Organismal designs that integrate functionally and developmentally related characters are selectively favoured over those in which such characters are controlled independently. Once genetic correlations between the separate components of fitness have been formed by the local selective pressures, it becomes extremely difficult to follow different evolutionary trajectories (Fairbairn, 1994; Fairbairn and Yadlowski, 1997). Migration determines the time and place of breeding, consequentially migratory and reproductive characters are connected in a functional relationship (Dingle, 1988, 1991). Johnson (1969) deems the "oogenesis-flight" syndrome (the antagonistic development in insect ontogeny of the flight apparatus, ovaries, and the ancillary systems such as the fat-body) to be such an important and distinctive attribute of the Insecta, that it be recognized as a definitive character of the class. In response to the common functional and developmental demands imposed on the production of migratory and reproductive characters, these characters have been integrated into a co-adapted complex known as the migratory syndrome (Dingle, 1985b).

Given the central role of migration in many insect life histories, it is not surprising that the various traits that contribute towards migratory tendency do not vary independently (Fairbairn and Roff, 1990). Because of the genetic correlations existing between several traits, selection for migratory tendency within a population may shift an entire developmental profile so that along with the delay in reproduction, there are concurrent increases in wing muscle retention and flight behaviour (Fairbairn and Roff, 1990; Fairbairn, 1994). Such coordinated responses of several characters to a given selection pressure may commonly be mediated through an underlying physiological mechanism, such as variation in hormonal titre (Roff, 1986a; Roff and Fairbairn, 1991; Fairbairn, 1994; Finch and Rose, 1995).

Roff (1986a) and Fairbairn (1994) have detailed a model for the expression of wing dimorphisms in insects, based on the threshold model of quantitative genetics (Fig. 2) (Falconer, 1989, Chapter 18). Evidence from studies that demonstrate the common contribution of juvenile hormone to the expression of several traits associated with the migratory syndrome (Nijhout, 1994; reviewed in Fairbairn, 1994) and genetic analyses that connect the mean juvenile hormone esterase titre to the incidence of macroptery and fecundity (Fairbairn and Yadlowski, 1997; Roff *et al.* 1997) indicate that juvenile hormone is a least a partial regulator of the migratory syndrome in *G. firmus*. An implicit assumption of the model proposed by Roff (1986a) and Fairbairn (1994) is that the suite of traits associated with each morph is not fixed. The symmetrical function of the genetic correlation between wing morph and fecundity demonstrated within the current study supports this model.

The trade-off between migratory ability and early fecundity in wing dimorphic insects is interpretable with reference to the ecological context in which these organisms live. In a substantial analysis of the occurrence of insect flight loss with respect to habitat type, Roff (1990c) concluded that decreased environmental heterogeneity favours the evolution of flightlessness. The environments which wing dimorphic insects commonly inhabit are spatially and temporally heterogeneous in nature, so that local habitats may be stable for a number of years during which the micropterous morph may be favoured because of the advantage procured from its elevated early fecundity. Long term persistence of insect populations within a fluctuating environment largely depends on their capability to respond to the degradation of environmental quality through the rapid production of emigrants. In wing dimorphic insects, the incidence of macroptery is negatively associated with habitat persistance (Vepsäläinen, 1978; Denno and Grissell, 1979; Denno *et al.* 1991; Denno *et al.* 1996; Dingle, 1985a; Roff, 1990c). In such capricious environments a balance is struck between migratory and reproductive abilities, as the relative value of each attribute is contingent upon the state of the environment. Given that resources in the environment are ultimately limited, the negative genetic correlation between fecundity and wing morph may have ensued from the distinctive selective forces competing within the population.

Genetic correlations demonstrated through a selection experiment provide a means to demonstrate the causal relationships between the separate components of fitness. Although selection experiments provide a promising method for the measurement of trade-offs, it is important to acknowledge the limitations of this technique. Firstly, the trade-off between migratory ability and reproduction is more pronounced for early fecundity. At 28 °C (15 hL: 9 hD) the difference between the wing morphs for total lifetime fecundity is less, because the m_x curves actually cross over (Roff, 1990b). Secondly, the genetic correlations only consider the internal trade-offs, while components external to the individual (*eg*. predators, inter-specific competitors, diseases, etc.) that also contribute to the phenotypic trade-off may also be of substantial importance (Reznick, 1985). Thirdly, the trade-off can only be interpreted within the context of the experimental conditions (*ie*. temperature, photoperiod, density, etc.). This condition is conventional to all artificial selection experiments (Stearns, 1992), but by choosing experimental settings similar to those the organism may actually find in nature such analyses become more realistic. Within *G. firmus,* the expression of wing morph is known to be phenotypically plastic with respect to temperature and photoperiod (Roff, 1986c). Field studies conducted on *G. firmus* have also reported seasonal variation in the proportion macropterous (Veazey *et al.* 1976). To evaluate this genetic trade-off thoroughly, further studies are needed to determine if the cost to fecundity is realized under multiple environmental conditions (*ie*. test for any genotype-environmental interactions).

Given a restricted quantity of resources, allocation of nutrients to one function will inevitably decrease those available for another. Life history theory assumes that energy is ultimately limiting, so that it must be budgeted amongst the various functions in an organism (Gadgil and Bossert, 1970). As it is impossible to maximize all of the temporal and energetic functions simultaneously, trade-offs are forced among the different components of the organism (Danks, 1994b). In this way, variation in the phenotypic values a trait may hold is restricted by the costs incurred in other traits. Trade-offs occurring at the genetic level establish constraints on the evolutionary process, as they govern which potential directions of change are possible. The current study demonstrates a negative correlated response in the proportion of macropterous *G. firmus* to the selection imposed on fecundity, thereby confirming the symmetrical function of the genetic correlation. This result, in conjunction with preceding genetic analyses (Roff, 1994a; Roff *et al.* 1997), supports the hypothesis that the migratory/ reproductive trade-off found in *G. firmus* is attributable to an underlying negative genetic correlation between the characters. Antagonistic pleiotropic associations between the separate components of fitness may generally underlie life history trade-offs, and thus may represent a significant constraint on the process of evolution.

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APPENDIX A

Sample calculation for the predicted correlated response

eg) experiment 1

$$CR_Y = i_X h_X h_Y r_A \sigma_{PY} / 2$$
$$= 1.271 \sqrt{0.073}\sqrt{0.65}\,(-0.85)(1) / 2$$
$$= -0.118 \text{ standard deviations}$$

initial proportion macropterous = 0.153 (converted to a z-score = -1.0237)

initial value - 3(predicted correlated response) = value at the end of generation three
-1.0237 - 3(-0.118) = -0.6697 (converted into a percent = 25.2 %)

25.2 % (predicted percentage by generation three) - 15.3 % (initial percentage) = 9.9 %

APPENDIX B

Mean fecundities of *Gryllus firmus* parents chosen for each generation of the control and selected lines

Experiment 1

Generation	selected line	n	control line	n
0	19.76	25	307.16	25
1	13.88	25	218.56	25
2	22.56	25	206.68	25
3	54.92	25	234.32	25

Experiment 2

Generation	selected line	n	control line	n
0	1.20	25	236.96	25
1	17.40	25	153.48	25
2	6.36	25	228.52	25
3	8.36	25	241.04	25