Quantitative genetic analysis of dispersal in *Epiphyas postvittana*. I. Genetic variation in flight capacity

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The genetic basis for determination of flight capacity in the light brown apple moth, *Epiphyas postvittana* (Walker) (Tortricidae), was investigated by means of heritability estimation, artificial selection and crossbreeding, using samples from two natural populations. The mean heritabilities estimated by offspring–parent regression were 0.559 for offspring on female parents and 0.427 for offspring on male parents. These results were largely consistent with those estimated from paternal half-sibs and with realized heritabilities calculated from selected generations, although the heritability of flight capacity varied, to some extent, with the populations and temperatures to which the individuals were subjected. These estimates indicate the existence of additive genetic variance for flight capacity in the natural populations. The response pattern in the selection experiment indicates that the genetic effect on flight capacity in this species is mainly additive, though the phenotype performance of flights in F_1 progeny from crossbreeding ‘long-fliers’ with ‘short-fliers’ suggests a weak dominance of short-flying genes and a slight maternal effect.

Keywords: *Epiphyas postvittana*, flight capacity, heritability, selection response.

Introduction

The light brown apple moth, *Epiphyas postvittana* (Walker) (Tortricidae), is generally regarded as a sedentary species (Clark, 1970; Danthanarayana, 1983). The flight activity of the moth is mainly reproductively associated (Gu & Danthanarayana, 1990). However, both field observations and laboratory studies have indicated that some individuals of a population are able to make prolonged flights that may contribute to dispersal over long distances under appropriate weather conditions (Danthanarayana, 1976a and unpublished data; Gu & Danthanarayana, 1990), as in other tortricid species, such as *Christoneura fumiferana* (Clem.) (Greenbank *et al.*, 1980) and *Rhyacionia buoliana* (Schif.) (Green, 1962; Green & Pointing, 1962).

Studies with suction traps have shown that the dispersal capacity of *E. postvittana* varies with seasonal changes in environmental conditions, such as temperature and the quality and quantity of food which the larvae receive in the field (Danthanarayana, 1976b). These results have been confirmed by laboratory investigations, with higher temperature at immature stages and water stress of larval food leading to an

increase in flight capacity (H. Gu & W. Danthanarayana, in preparation). Nevertheless, although phenotypic variation in flight capacity is necessary for evolutionary change, it is not sufficient (Barker & Thomas, 1987).

Most studies with other insects have revealed a polygenic effect on flight behaviour (Dingle, 1986; Gatehouse, 1989). Therefore, investigation of the genetic basis for determination of flight capacity of *E. postvittana* moths was carried out by means of quantitative genetic analyses.

Materials and methods

Experimental animals

All moths used in these experiments were derived from larvae and pupae collected from widely spaced host plants in orchards in Canberra and Melbourne. Larvae were reared on an artificial medium (Shorey & Hale, 1965) and cultured in incubators with controlled environmental conditions of temperature, humidity and photoperiod. Pupae were removed from the medium and sexed. Daily checks were made for newly emerged

adults. Moths were maintained within oviposition chambers consisting of corrugated plastic cups (7 cm in diameter and 9 cm in height), and provided with water in glass tubes closed with a cotton bung.

Flight testing

Two-day-old virgin moths were used for all flight tests, using a tethered flight technique, as described previously (Gu & Danthanarayana, 1990). The decision to test 2-day-old moths was based on the age-related oviposition pattern of the species (Gu & Danthanarayana, 1990) and the significant correlations amongst flight capacities at different ages at the early stage of adult life (H. Gu, unpublished observations). Individuals that flew for 15 min or longer were categorized as 'strong-fliers' (Gu & Danthanarayana, 1990).

Sib analysis

A nested experiment was performed on each of the two natural populations from Canberra and Melbourne. One hundred fifth instar larvae and pupae from each population were maintained in a culture room with larvae reared on the artificial medium at a constant temperature of $23 \pm 1^\circ\text{C}$, 60–70 per cent r.h. and a light cycle of L14:D10. Unless otherwise stated, this environment was used throughout. The newly emerged moths in each population were randomly paired in oviposition chambers, and the F_1 generation of each population produced.

Sires and dams for each population were randomly sampled for the virgin F_1 adults; initially 50 sires were each mated with three dams, that is, each male mated with three females while each female mated with only one male, for a total of 150 pairings. Of these 32 and 27 sire groups with three dams per sire were ultimately used for the Canberra and Melbourne population, respectively. The eggs laid during the first 3 days by each dam were collected and incubated.

On the day of hatching, larvae were singly transferred into plastic cups (4 cm in diameter and 3.8 cm high) with 5 g of artificial diet per cup so that the measurements of flight capacity would not be confounded by the density-dependent competition (Danthanarayana *et al.*, 1982). Twenty larvae were randomly sampled from each dam and equally divided into two groups, which were cultured in two controlled environments at temperatures of 23° and $28 \pm 0.5^\circ\text{C}$, a humidity of 60–70 per cent and a light cycle of L14:D10.

Daily checks were made at pupation, to record newly emerged adults. All flight tests were carried out in a room with a temperature of 25°C . Four female

offspring of each dam, where available, were used to provide data of flight capacity.

Within each population and within each environment, an analysis of the data was made as a nested random-effects analysis of variance components model. The phenotypic variance for flight duration is partitioned into observed components attributable to differences between the progeny of different sires, to differences between the progeny of dams mated to the same sire and to differences between individual offspring of the same dam (Falconer, 1981). LSMLMW, a general purpose 'mixed model least-squares' computer program (Harvey, 1970, 1988), was used to estimate the variance components by equating computed mean squares to their expectations and solving the resulting equations. Paternal half-sib and full-sib heritability estimates were calculated within each population at each temperature, according to Becker (1984). Approximate standard errors of the heritability estimates were computed by LSMLMW. A one-tailed *t*-test (Sokal & Rohlf, 1981) was used to determine whether the estimated heritabilities were different from zero. As the means of the data were positively correlated with their variances, a $\log_{10}$ transformation was performed for the data to satisfy the assumptions that pertained to the analysis of variance.

Offspring-parent regression

All moths used in this experiment were obtained from a laboratory stock of insects which were derived from the Melbourne population. The culture had been maintained in the laboratory for five generations when the experiment was started. Larvae were reared in plastic cups (7 cm in diameter and 4.7 cm in height) at a density of 15 per container.

Fifty moths of each sex were flight tested, and the tested moths were paired according to their flight durations, long fliers crossed with long fliers and short fliers with short fliers. Of these moths, 35 pairs produced fertile eggs. Their offspring were reared and flight tested under the same conditions as in the parent generation.

Because the phenotypic variations of flight duration were not equal in the males and the females ($F = 2.33$, $P < 0.025$, 314 males, 268 females), heritability was estimated separately for each sex of offspring and of parents (Falconer, 1981). Heritability estimates were calculated as follows:

(a) by the regressions of the male offspring on the male parent, and of female offspring on the male parent adjusted for the difference in variance, multiplying the regression coefficient by the ratio of phenotypic standard deviations of males to females, and

(b) by the regressions of female offspring on the female parent, and of male offspring on the female parent adjusted for the difference in variance, multiplying the regression coefficient by the ratio of phenotypic standard deviations of females to males.

As the regressions were all of offspring on one parent, the values of the regression coefficient were doubled in order to obtain the correct estimates for the heritability (Falconer, 1981).

Artificial selection

The selection experiment aimed to demonstrate the response to directional selection for both increased and decreased flight capacity (in terms of flight duration) during the flight test period. The experiment was started with moths of the sixth laboratory generation of the Melbourne population. It consisted of three lines: long-flying, short-flying and randomly selected control. Each line was initiated with 10 families. In later generations, a 'within-family' design (Hartl, 1980) was applied. Fifteen individuals of each sex from each family of the two selected lines and 50 individuals of each sex from the control were flight tested in each generation. Five longest-flying individuals of each sex from each of long-flying families and five shortest-flying individuals of each sex from each of short-flying families were selected as parents for the next generation; meanwhile, 50 unflown individuals of each sex from the control were randomly selected as parents. Larvae were reared in plastic containers (7 cm in diameter and 4.7 cm high) at a density of 15 per container.

Crossbreeding

To further understand the nature of gene effects on flight capacity, a crossbreeding experiment was conducted in the following way: long-flying male $\times$ long-flying female, short-flying male $\times$ long-flying female,

long-flying male $\times$ short-flying female, short-flying male $\times$ short-flying female and control male $\times$ control female. Parental males and females for each of the combinations were randomly selected from under the three lines in generation 9 of selection. All offspring were flight tested under the same conditions.

Results

Sib analysis

Estimates of mean phenotypic values and heritabilities of flight capacity of female moths in the two populations of *E. postvittana* at two temperatures are shown in Table 1.

The mean phenotypic values of flight durations were different in the two populations, with the Canberra population showing longer flight time periods than the Melbourne population at either temperature (ANOVA, $P < 0.01$ at 23°C; $P < 0.05$ at 28°C). In addition, the mean phenotypic values of flight durations in the two populations were larger at 28 than at 23°C.

The full-sib estimates of heritability were larger with smaller standard errors in comparison with the paternal half-sib estimates in all cases. The heritability estimates of flight capacity were all significantly different from zero; but they varied, to some extent, with both the population and temperature to which the individuals were subjected. In terms of heritability estimates, the two populations responded to temperature differentially, with the result that at 23°C the Melbourne population displayed higher heritability than did the Canberra population, and vice versa at 28°C.

Offspring-parent regression

All the regressions of offspring on parents were significant (Table 2), and estimates for heritability and their standard errors are presented in Table 3. The heritabil-

Table 1 Estimated mean phenotypic values and heritabilities ($\pm$ S.E.) of flight duration from full-sibs and paternal half-sibs for two populations of female *E. postvittana* at two temperatures

Population	Temperature (°C)	n	Mean phenotypic values (min)	Heritability	
				Half-sib	Full-sib
Melbourne	23	291	12.78 $\pm$ 2.09	0.489 $\pm$ 0.161**	0.529 $\pm$ 0.082**
	28	289	35.20 $\pm$ 4.87	0.225 $\pm$ 0.128*	0.413 $\pm$ 0.076**
Canberra	23	339	22.89 $\pm$ 2.72	0.400 $\pm$ 0.133**	0.526 $\pm$ 0.070**
	28	335	40.89 $\pm$ 4.13	0.526 $\pm$ 0.148**	0.558 $\pm$ 0.072**

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

Table 2 Regression coefficients of single offspring on the respective single parents ($n = 35$)

Regression	Coefficient (b)	F-value	P
Female offspring on dam	0.315	41.97	< 0.01
Male offspring on dam	0.479	16.64	< 0.01
Female offspring on sire	0.098	9.51	< 0.01
Male offspring on sire	0.233	15.86	< 0.01

Table 3 Heritability estimates ($\pm$ S.E.) for flight capacity from offspring-parent regression with standard errors

Offspring	Parents	
	Male	Female
Male	0.466 $\pm$ 0.020	0.488 $\pm$ 0.019
Female	0.387 $\pm$ 0.021	0.630 $\pm$ 0.016
Mean	0.427 $\pm$ 0.021	0.559 $\pm$ 0.018

ities did not differ significantly according to both the regressions of single sex offspring on the male parent ($F = 3.26$, d.f. = 1, 66, $P < 0.05$) (Sokal & Rohlf, 1981) and the regressions of single sex offspring on the female parent ($F = 0.87$, d.f. = 1, 66, $P < 0.05$). Thus data from the male and female offspring are averaged in Table 3. Similarly, the heritability was not different when male offspring were regressed against the female parent and then they were regressed on the male parent ($F = 2.17$, d.f. = 1, 66, $P < 0.05$). However, the results were significantly different when the female offspring were regressed against the female and male parents ($F = 8.52$, d.f. = 1, 66, $P < 0.01$). The mean heritability was 0.559 for offspring on female parents and 0.427 for offspring on male parents.

Response to selection

Bidirectional selection for flight capacity produced substantial divergence from the unselected line (control) in both sexes. The responses of *E. postvittana* moths to selection for increased and decreased flight capacity are shown in Fig. 1. Clearly over 10 generations of selection, the moths responded significantly to selection on flight capacity in both sexes in both positive and negative directions. The mean flight duration in the strong line increased from 5.3 to 84.7 min in females and from 13.4 to 91.9 min in males; in the weak line it decreased from 5.3 to 0.7 min in females and from 13.4 to 1.8 min in males. In contrast, in the

control line the flight duration did not change significantly in both sexes during 10 generations. It is interesting to note that the response of females to selection was more rapid than that of males in both strong and weak lines. Up to generation 8, the mean flight duration of the females increased by nearly 16 times in the strong line and decreased by 7.6 times in the weak line, whereas that of the males increased by 6.9 times in the strong line and decreased by 6.7 times in the weak line.

In addition, bidirectional selection resulted in significant divergence in the proportion of 'strong-fliers' from the control line in both sexes (Fig. 2). In a positive direction, the proportion of 'strong-fliers' increased

Fig. 1 Response to selection on flight capacity in *E. postvittana*. (a) Female, (b) male. (—○—) long-flying, (—●—) control, (—□—) short-flying.

Fig. 2 Percentage of 'strong-fliers' in long-flying (■), control (□) and short-flying (▨) lines in relation to generation of selection.

from 6.9 to 82.4 per cent in females and from 29.1 to 89.5 per cent in males. In a negative direction, the proportion of 'strong-fliers' decreased from 6.9 to 0 per cent in females and from 29.1 to 1.8 per cent in males. In the control, however, the proportion of 'strong-fliers' did not change significantly during the 10 generations under investigation.

In the positive selection, the response in both sexes was relatively slow during the first five or six generations; afterwards it was very rapid, and continued until generation 8 and generation 9 in females and in males, respectively. In the negative selection, the response in both males and females continued gradually until generation 7.

Responses of the moths to selection for flight potential were used to calculate realized heritabilities by using the formula,

$$h^2 = R/S$$

where R = the response to selection, i.e. the difference in the mean phenotypic value between the offspring of the selected parents and the parental generation before selection, S = the selection differential, that is, the mean phenotypic value of the individuals selected as parents

Table 4 Realized heritability (h^2) estimated from the selection experiment

	Male	Female
Upwards	0.220	0.335
Downwards	0.807	0.812
Mean	0.514	0.574

expressed as a deviation from the population mean (Falconer 1981).

The mean values of realized heritabilities, based on the data from the first five generations of selection, are shown in Table 4. The heritabilities for both males and females were much higher in the negative selection than in the positive selection; the mean values of realized heritability in both directions were slightly greater for females than for males. However, when the values for both males and females in the two directions were averaged, the realized heritabilities for both sexes were largely in the range of those estimated with the paternal half-sib correlation and offspring-parent regression.

Crossbreeding

Table 5 summarizes the mean flight durations and percentage of 'strong-fliers' of all offspring obtained in this experiment. The analysis of variance (based on $\log_{10}$ transformed data) showed significant paternal ($F=88.99$, d.f. = 1, 474, $P<0.001$) and maternal ($F=238.96$, d.f. = 1, 474, $P<0.001$) effects on the flight capacity of offspring, and the significant interaction between paternal and maternal effects ($F=154.73$, d.f. = 1, 474, $P<0.001$), which indicated that there was a remarkably high resemblance in flight capacity between the offspring and parents, long-flying parents producing long-flying offspring, whereas short-flying parents had short-flying progeny, and that the paternal influence varied with the maternal characteristics. Obviously, the flight capacities of offspring produced from crossbreeding 'long-fliers' with 'short-fliers' showed a weak dominance of short-flying genes and a slight maternal effect.

Discussion

Estimates of heritability for a given trait may vary according to different methods of estimation (Falconer, 1981). For this reason, the estimation of heritability for flight capacity of *E. postvittana* was carried out using three methods, i.e. sib analysis, offspring-parent regression and calculation of realized heritabilities from the selection generations.

Table 5 Flight performance (mean $\pm$ S.E.) of F_1 generation ($23 \pm 1^\circ\text{C}$, L14:D10, 60–70 per cent r.h.)

Parental characteristics	Offspring	Sample size (n)	Flight duration (min)	Percentage of 'strong-fliers'
Strong M $\times$ Strong F	Male	91	67.6 ± 6.07	8.02
Weak M $\times$ Strong F	Female	71	59.7 ± 6.43	71.8
Strong M $\times$ Weak F	Male	99	19.7 ± 3.67	28.3
Weak M $\times$ Weak F	Female	57	7.5 ± 1.95	10.5
Strong M $\times$ Control F	Male	38	13.1 ± 2.66	34.2
Weak M $\times$ Control F	Female	31	2.5 ± 0.41	0
Weak M $\times$ Control F	Male	56	1.8 ± 0.26	0
Weak F $\times$ Control F	Female	39	1.3 ± 0.22	0
Control M $\times$ Control F	Male	48	12.9 ± 2.07	25.0
	Female	47	6.3 ± 1.33	14.9

The full-sib estimates were larger with smaller errors than the paternal half-sib estimates for both Canberra and Melbourne populations at two laboratory temperatures (Table 1). However, although they have higher statistical precisions, full-sib estimates may be biased (Falconer, 1981), as they include the components of dominance and maternal effects, which reflect temporary combinations of genes, and also environmental effects common to sibling groups. These effects do not contribute to evolution under natural selection (Møller *et al.*, 1989). In comparison to the full-sib estimates, the estimates from paternal half-sibs are unconfounded with these effects (Falconer, 1981).

The offspring-parent regression was performed as an alternative approach. The significant regressions of offspring on parents (Table 2) indicate a clear tendency for long-flying parents to produce long-flying progeny and vice versa. Mean heritability for flight capacity estimated by this approach was 0.427 from male parents and 0.559 from female parents (Table 3), which was largely confirmed by the estimation of realized heritabilities from selection generations (Table 4). The significantly higher heritability found from female offspring on female parent regression suggests a possible maternal effect on flight capacity in this species. A similar case has been reported for the milkweed bug, *Lygaeus kalmii* Stål (Caldwell & Hegmann, 1969); but in the African armyworm moth, *Spodoptera exempta* (Walker), lower heritabilities were found for

the single sex offspring on female parent regressions in comparison to the single sex offspring on male parent regressions (Parker & Gatehouse, 1985).

In the sense that the estimates from paternal half-sib correlation and the regression of offspring on male parents are the most reliable (Falconer, 1981), the results from these two approaches should be taken as good estimates of heritability for flight capacity of *E. postvittana* moths, which were largely consistent with each other (Tables 1 and 3). These show that the flight capacity in this species has a substantial additive genetic component. The actual values estimated from paternal half-sibs in the two populations, based on data obtained at 23°C and from regressions of offspring on male parents, were comparable to the overall heritability (0.40) obtained for flight duration in *S. exempta* (Parker & Gatehouse, 1985).

As expected in the light that heritability is a property not only of a trait but also of a particular population under a certain environmental circumstance (Falconer, 1981), the heritability estimates for flight capacity in *E. postvittana* were, more or less, different both between populations and between environmental temperatures (Table 1). Furthermore, the estimates from the two populations varied with the laboratory temperatures at which they were cultured, although the mean phenotypic values of flight durations in the Canberra population were consistently greater than those in the Melbourne one. These are indicative of possible

genetic differentiation between populations and of possible genotype–environment interaction in the flight capacity of this species.

The high heritability for flight capacity provides a prerequisite for the effective directional selection for increased and decreased flight potential. Artificial selection on flight capacity within the Melbourne population caused significant phenotypic divergence from the control (unselected line) for both selected lines (Figs 1 and 2). Selection for long-flying moths generally resulted in a rapid increase in the mean flight duration as well as in the proportion of ‘strong-fliers’ of the line, although in the initial generations the response was relatively slow; on the other hand, selection for short-flying moths caused a nearly linear decrease in flight capacity. This further demonstrates the genetic effect on flight capacity in this species. In comparison with males, female *E. postvittana* moths showed a faster response to selection in both directions, possibly resulting from the higher heritability from females than from males. A similar relationship between heritability and response to selection has been also shown in *S. exempta* (Parker & Gatehouse, 1985).

That the genetic component plays a major role in the determination of flight capacity in *E. postvittana* is confirmed by the result from the crossbreeding experiment (Table 4). The response pattern of the moths in the selection experiment indicates that the genetic effect on flight capacity in *E. postvittana* is mainly additive, although the phenotypic performance of flight in F_1 offspring from crossbreeding ‘long-fliers’ with ‘short-fliers’ suggests a weak dominance of short-flying genes and a weak maternal effect.

Heritability estimation in laboratory-kept animals may be biased by differences in the amount of additive genetic variance and/or environmental variation between laboratory and natural populations (McClearn, 1967). The heritabilities may be overestimated due to laboratory control of environmental variation, and hence reduction in environmental variance as compared with that in the natural population (Barker & Thomas, 1987). Despite these limitations, the results reported here, which show a non-zero additive genetic variance for flight capacity in the laboratory, at least indicate the existence of such variance in natural *E. postvittana* populations.

The evolutionary significance of dispersal by flight in insects, such as *E. postvittana*, which inhabit changing environments, is undoubted because it enables them to escape from deteriorating habitats and to colonize new ones (Southwood, 1962; Taylor & Taylor, 1983; Harrington & Taylor, 1990). The maintenance of a high degree of variability in flight may be responsible for the maximum utilization of the habitat in such

species (Kennedy, 1961). Previous studies have stressed the importance of environmental factors inducing such variance in *E. postvittana* (Danthanarayana, 1976b; H. Gu & W. Danthanarayana, in preparation). The present study provides the evidence that a substantial proportion of the phenotypic variation of flight performance is attributable to differences in additive genetic values. How genetic variability for dispersal capacity by flight is maintained in natural populations, however, is still speculative. In other insects, the uncertainty of the environments that they inhabit is thought to be a factor that maintains the high additive genetic variance (Dingle *et al.*, 1977; Hoffmann, 1978). According to Van Valen (1971), such variability may result from the interaction of selection within populations with selection between populations; the former selection force is against dispersal caused by the departure of dispersants while the latter is in favour of dispersal as the local populations are initially founded by dispersants. Despite its highly polyphagous habit (Danthanarayana, 1975; Geier & Briese, 1981), the habitats that *E. postvittana* occupy are highly heterogeneous because of the unpredictable fluctuation in ambient temperature and rainfall in natural environments (Danthanarayana, 1983) and the instability of the habitats may have played an important role in the maintenance of high genetic variance for flight capacity in natural populations, although other factors, such as genetic ‘trade-offs’ between flight and fitness-related life-history traits (Gu & Danthanarayana, 1991), cannot be ignored.

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