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Genetic control of the pre-reproductive period in *Autographa gamma* (L.) (Silver Y moth) (Lepidoptera: Noctuidae)

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Adults of the noctuid moth *Autographa gamma* undertake seasonal migrations into areas where they are unable to breed continuously. Individuals migrate into Britain each spring and offspring of these migrants probably return in autumn to over-wintering areas in North Africa and the Middle East, although the existence of these return migrations has been questioned. Insects usually migrate during the adults' pre-reproductive period (PRP). The length of this period is therefore an index of migratory potential because individuals with longer PRPs have more time to express their potential for flight and to travel further. Significant, positive full-sib correlations showed that female offspring with long PRPs came from families where their brothers had correspondingly long PRPs. This suggests that the same genes control the rate of reproductive development in both sexes. There was a rapid response to selection for short and long PRP, with separation of the lines by the second generation of selection. Sib-analysis and parent–offspring regressions showed that the genes with the greatest influence on PRP are X-linked, although there is also an autosomal influence. The significance of X-linkage of genes controlling the PRP is discussed in relation to the migratory strategy of *A. gamma*.

Keywords: adult diapause, *Autographa gamma*, migration, X-linkage.

Introduction

Autographa gamma is a common migratory species which is distributed throughout the holarctic (Balachowsky, 1972). Adults undertake seasonal, northward migrations to areas where they are unable to breed continuously. Individuals migrate into Britain each spring and, after one, two or three generations, descendants of the spring migrants probably return to over-wintering sites in North Africa and the Middle East (Fisher, 1938). The existence of return migrations, however, has been questioned (Rabb & Stinner, 1978; Stinner *et al.*, 1983).

Migration in insects usually takes place during the pre-reproductive period (PRP) of adult life (Johnson, 1969). In migratory noctuid moths, the incidence of prolonged flight greatly decreases with the onset of sexual maturity (Han & Gatehouse, 1993; Colvin & Gatehouse, 1993). The length of the PRP (the time between adult emergence and attainment of sexual maturity) is therefore an index of migratory potential because it determines the interval over which individuals can express their capacity for flight. In some noctuid species there is great variation in the length of the PRP (Turgeon & McNeil, 1983; Han & Gatehouse, 1991a), with individuals with longer PRPs having the potential to travel further.

Factors affecting migratory potential have been shown to be genetically controlled in many insect species. These include flight capacity (Caldwell & Hegmann, 1969; McAnelly, 1985; Parker & Gatehouse, 1985; Palmer & Dingle, 1989) and wing length (Palmer & Dingle, 1986; Dingle & Evans, 1987). Genetic control of the length of the PRP has also been demonstrated (Colvin, 1990; Han & Gatehouse, 1991a; Wilson & Gatehouse, 1992). Many of these characters vary continuously and are therefore under polygenic control, resulting from the action of genes at several loci (Falconer, 1989).

The length of the PRP is strongly influenced by genes on the X chromosome in the noctuid species *Mythimna separata* (Han & Gatehouse, 1991a), *Heliothis armigera* (Colvin, 1990) and *Spodoptera exempta* (Wilson & Gatehouse, 1992). Females are the heterogametic (XY) sex in Lepidoptera and, therefore,

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obtain their single X chromosome from their homogametic (XX) fathers. Females of the above species therefore obtain the majority of genes controlling PRP from their fathers and any resemblance between daughters and mothers is due to autosomal influences and non-genetic maternal effects.

Modelling rates of evolution, Charlesworth *et al.*, (1987) have suggested a number of important consequences of X-linkage of traits, which may have important implications for the control of migration in noctuids (Han & Gatehouse, 1991a). This paper investigates the genetic control of PRP in *A. gamma*, using full-sib correlations, sib-analysis, parent–offspring regressions and selection experiments. Sib-analysis experiments and parent–offspring regressions are used to determine the mode of inheritance of PRP, i.e. whether the major influence is from autosomal or X-linked genes. The implications of X-linkage of genes controlling PRP are discussed for the regulation of migration in this species.

Materials and methods

Insect material

Moths were obtained from three sources: over 50 adults were trapped in Bangor, North Wales during the summer and autumn of 1988 and 1989; over 100 adults were collected from Morocco in 1989 and 1990; over 30 adults were collected from Sweden in 1989. Experiments used G_1 offspring from Moroccan and Swedish insects and G_2 and G_3 offspring from British insects. Larvae in all treatments were reared in 500 ml glass 'Kilner' jars with filter paper lids and were provided with an excess of either turnip (*Brassica rapa*), dandelion (*Taraxacum officinale*) or Chinese leaves (*Brassica chinensis*). Cut ends of leaves were placed in vials of water within the jars to retard wilting and any wilting leaves and frass were removed on a daily basis. Larvae were maintained at a density of approximately 80 per jar for the first two instars. Densities were reduced to 15 larvae per jar at the third instar and further reduced to six larvae per jar for the final instar. Once the larvae had pupated and their cuticles hardened (usually 1 day after pupation), they were removed from their silk cocoons. Pupae were sexed according to the position of the genital pore of the last abdominal segment and were placed in individual 50 ml plastic pots, which were checked regularly for newly emerged adults.

Measuring PRP in females

On reaching sexual maturity, females release a sex pheromone to attract males. This 'calling' behaviour can commence at any time throughout the scotophase (Hill, 1991) and can be easily recognized because females fan their wings whilst they extrude their ovipositor from the tip of the abdomen. Single, newly emerged females were transferred to 300-ml clear plastic containers provided with 10 per cent sugar solution. They were observed throughout the scotophase for the onset of calling using a pen-light torch fitted with a red filter (600–1200 nm). PRP was defined as the number of nights from emergence to first call.

Measuring PRP in males

Males respond to calling females by everting their abdominal brushes and clasping the tip of the female's abdomen. They can respond to female sex pheromone throughout the scotophase (Szocs & Toth, 1979). Males were introduced into a netting cage containing at least two calling females and their behaviour was observed. Males were tested at least twice during the scotophase and between test occasions they were kept in incubators away from calling females to prevent the possibility of sensory fatigue to pheromone detection. Females were used only if they had recently started to call because the release of pheromone declines rapidly during a calling bout (Bjostad *et al.*, 1980). Males that mated or attempted to mate, with their brushes everted, were scored as sexually mature. PRP was defined as the number of nights from emergence until the first attempt to mate. Adults were provided with 10 per cent sugar solution from the night of emergence.

Comparison of PRPs between sexes and full-sib correlations

Male and female offspring from Moroccan, British and Swedish insects were reared at 20°C ± 1°C under a photoperiod of 16L:8D. Male and female PRPs were measured as above. For full-sib correlations, at least 10 males and 10 females were reared from each of 10 pairs of Moroccan adults, plus nine British pairs and six Swedish pairs.

Selection for long and short PRPs

Two selection experiments were performed. In the first experiment, a line selected for early reproductive maturity was established from six British females with PRPs of one or two nights. A line selected for late maturity was also established, from 10 British females with PRPs of four nights or longer. These selection criteria were maintained for two generations, with

females being mated to males from their selected line. Selection was carried out solely on the basis of female PRP and the PRPs of males in the parental generations were unknown.

In the second experiment, an early-maturing line was established from 13 Moroccan females with PRPs of one or two nights and a late-maturing line was established from 16 Moroccan females with PRPs of four nights or longer. Selection was again carried out solely on the basis of female PRP but, unlike the previous experiment, early and late-developing families were identified in the parental generation on the basis of female PRPs. Females in the parental generation were then mated to males from these early and late-developing families to establish early and late lines. In both experiments, females were observed for the onset of calling at 16°C ± 1°C under a photoperiod of 12L:12D.

Mode of inheritance of PRP

This was investigated by a sib-analysis experiment and by parent–offspring regressions. In sib-analysis experiments, several males are each mated randomly to several females and the character under study is then measured in the offspring of each mother (Falconer, 1989). If the character is disproportionately affected by genes on the X chromosome, the homogametic (XX) parent will have a large influence on the expression of the trait in its heterogametic (XY) offspring, whereas the XY parent will have little influence on its XY offspring. For autosomally inherited characters, a significant proportion of the phenotypic variance of XY offspring will be attributable to both mothers and fathers.

Sib-analysis. Thirty-three males from 17 families were mated, each to two different females whose PRPs were known. PRPs of mothers and their female offspring were measured at 16°C ± 1°C under a photoperiod of 12L:12D. PRPs of fathers were not known.

Parent–offspring regressions. Female offspring were reared from 21 pairs of adults where the PRP of the mother (but not of the father) was known. Male offspring were also reared from 11 of these pairs. PRPs were measured for mothers and for male and female offspring at 20°C ± 1°C under a photoperiod of 16L:8D.

Data analysis

Data were tested for normality and the appropriate parametric or non-parametric analyses were performed. Heritability estimates of PRP and their standard errors were calculated from the slopes of regression lines of offspring upon parents (Falconer, 1989).

Results

Male and female PRPs and full-sib correlations

Median PRPs of Moroccan males and females were three and one nights, respectively (Table 1). This difference is highly significant (Medians test for 266 cases, chi-square = 121.97, 1 d.f., $P < 0.001$). The median PRP of Swedish males was also significantly longer than that of females (Table 1; medians test for 146 cases, chi-square = 27.57, 1 d.f., $P < 0.001$). There was no significant difference between the median PRPs of British male and female moths (Table 1; medians test for 185 cases, chi-square = 2.60, 1 d.f., $P = 0.11$). There was a significant, positive correlation between the mid-PRP value (calculated as the sum of PRPs divided by the sample size) of males and females from the 10 Moroccan families (Spearman rank-order correlation $r_s = 0.602$, $n = 10$, $P = 0.033$) and also for the nine British families ($r_s = 0.814$, $N = 9$, $P = 0.004$), but not for the six Swedish families ($r_s = -0.232$, $N = 6$, $P = 0.329$).

Selection experiments

A rapid response to selection was observed in both experiments. Separation of the lines for British offspring did not occur until the second generation (Fig. 1; Mann–Whitney U-test corrected for ties; G_1 generation, $U = 372.5$, $N = 60$, $P = 0.89$; G_2 generation,

Table 1 PRPs of male and female offspring of *A. gamma* derived from insects collected in Morocco, Britain and Sweden

	Morocco	Britain	Sweden
Female			
Median	1	2	2
Q1–Q3	1–2	2–3	2–2
Range	1–4	1–5	1–4
N	170	153	78
Male			
Median	3	2	3
Q1–Q3	2.25–3	2–3	2–3
Range	2–6	1–4	2–5
N	96	32	68

N = sample size, Q1–Q3 = interquartile distance.

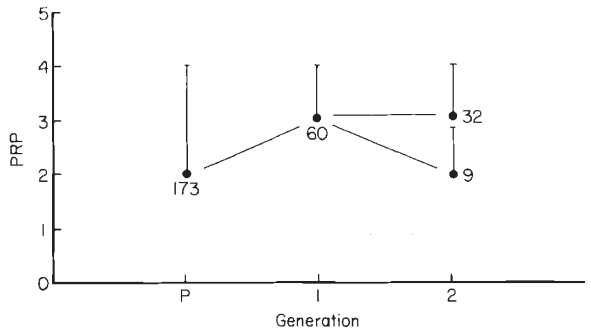

Fig. 1 Selection for early and late reproductive development in British *A. gamma*. There was a significant difference between median PRPs in the two lines by the G_2 generation (Mann–Whitney-test for 41 cases, $U=52$, $P=0.003$; early line, median = 2, Q1–Q3 = 2–3, $N=9$; late line, median = 3, Q1–Q3 = 3–4, $N=32$). Medians and interquartile distances are shown. Numbers by medians give sample sizes.

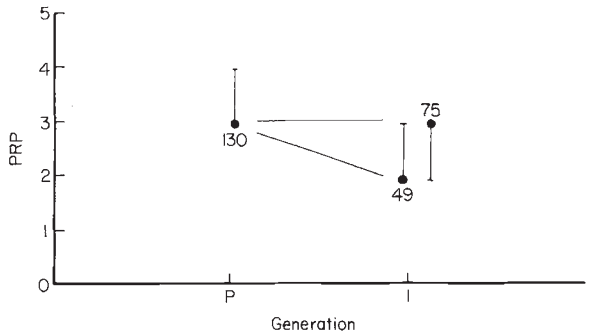

Fig. 2 Selection for early and late reproductive development in Moroccan *A. gamma*. There was a significant difference in the median PRPs of females in the early- and late-developing lines by the first generation (Mann–Whitney U-test for 124 cases, $Z=-2.04$, $P=0.041$; early line, median = 2, Q1–Q3 = 2–3, $N=49$; late line, median = 3, Q1–Q3 = 2–3, $N=75$). Medians and interquartile distances are shown. Numbers by medians give sample sizes.

$U=52.0$, $n=41$, $P=0.003$). Separation of the two selected lines for Moroccan offspring occurred in the first generation (Fig. 2; Mann–Whitney *U*-test corrected for ties, $Z=-2.04$, $N=124$, $P=0.041$). In both experiments the insect cultures were lost due to viral disease after relatively few generations.

Sib-analysis experiment

Thirty-three males were mated, each to two females. PRPs were recorded for 95 offspring, from five males which each produced five or more offspring from each female. PRPs of these offspring are shown in Table 2. In all other cases a male's second mating was either infertile or produced offspring which succumbed to disease before pupation. Nested ANOVA revealed a significant between-fathers component of variation ($F=7.09$, 85 and 4 d.f., $P=0.027$) but no significant between-mothers (within-fathers) component of variation ($F=0.58$, 85 and 5 d.f., $P=0.717$). This shows that female PRP is influenced mostly by genes received from their fathers, and hence that there is a substantial influence of genes located on the X-chromosome.

Parent–offspring regressions

Weighted regression analysis revealed a significant, positive regression of mean PRP of sons on maternal PRP ($r^2=0.47$, 10 d.f., $P=0.021$). The regression line is described by the equation:

$$y=1.73\ (\text{S.E.}=0.35)+0.328\ \bar{x}\ (\text{S.E.}=0.117)$$

where y is the mean PRP of sons and x is the maternal PRP. There was also a significant, positive regression of the mean PRP of daughters on maternal PRP ($r^2=0.31$, 20 d.f., $P=0.008$). The regression line is

Table 2 Results of a sib-analysis experiment to investigate the mode of inheritance of PRP in *A. gamma*

	Sire									
	1		2		3		4		5	
Dam	A	B	A	B	A	B	A	B	A	B
PRP	1	1	2	5	3	5	1	5	6	6
F_1										
Mean PRP	1.64	1.57	2.21	2.40	2.17	2.80	2.00	2.27	3.60	4.00
Range	1–4	1–2	2–3	1–4	2–3	2–4	1–5	1–3	3–6	3–6
N	11	7	14	15	6	5	14	11	5	7

N = sample size, PRP = pre-reproductive period.

described by the equation:

$$y = 1.85\,(\text{S.E.} = 0.13) + 0.122\,\bar{x}\,(\text{S.E.} = 0.041)$$

where y is the mean PRP of daughters and x is the maternal PRP. The two regression lines were not significantly different at the 5 per cent level (weighted multiple regression testing the significance of the interaction between male and female offspring, F change = 3.55, 1 and 28 d.f., $P = 0.070$). Narrow-sense heritability estimates (h^2) of PRP, calculated from the slopes of the regression lines (Falconer, 1989), were 0.656 ± 0.234 for sons on mothers and 0.244 ± 0.082 for daughters on mothers.

Discussion

Sex differences in PRP regression

Significant positive correlations between PRPs of male and female siblings, from adults originating from Morocco and Britain (see Results), indicated that female offspring with long PRPs came from families in which their brothers has correspondingly long PRPs. This suggests that the genes regulating the time to onset of calling in females also regulate the length of the PRP in males. These genes can therefore be considered to control the rate of reproductive maturation in both sexes, as has previously been shown for *Heliothis armigera* (Colvin, 1990). In Swedish and Moroccan populations of *A. gamma*, males and females reach sexual maturity asynchronously, as has been shown for other noctuids (Wilson & Gatehouse, 1992), which may be a mechanism to prevent inbreeding with close relatives.

Geographical differences in PRP regulation

Offspring of adults originating in Sweden differed from those of Moroccan and British insects. There was no significant correlation between the PRP of siblings, although these data were based on only six families. However, differences between Swedish insects and those from other areas have also been found in response to photoperiodic cues in insects collected in two successive years (Hill, 1991). This raises the possiblity that the Swedish sample was drawn from a different population from the British and Moroccan insects. Back-tracking techniques, which trace possible flight trajectories from meteorological records, suggest different over-wintering areas for Scandinavian and British populations of *A. gamma* (Mikkola & Salmensuu, 1965; French, 1969; Hurst, 1969; Ryrholm & Kallander, 1987; Lindfors *et al.*, 1989). Although the formation of discrete geographical races would seem unlikely in such a mobile widespread species, different winter breeding areas may well cause some restriction in gene flow.

Genetic regulation of PRP

Sib-analysis and parent–offspring regressions revealed that the genes with the greatest influence on the length of the PRP are located on the X-chromosome (see Results). Low heritability estimates (0.244 ± 0.082) were obtained from regressions of mean PRP of daughters on those of their mothers (see Results), as is generally the case with X-linked characters when the trait is measured in the heterogametic sex (Falconer, 1989). The significant regression of mean PRP of daughters on the PRPs of their mothers indicates autosomal influences, although this may also be due to non-genetic maternal effects. The genetic control of PRP has been shown to be strongly influenced by X-linked genes in other noctuids (Colvin, 1990; Wilson & Gatehouse, 1992), with autosomal influences on the inheritance of female PRP also being apparent in *Mythimna separata* (Han & Gatehouse, 1991a).

Differences in the rate of response to selection between the two experiments (Figs 1 and 2) can be explained by X-linkage of genes and by differences in the procedures for establishing late and early-maturing lines. In the first selection experiment (Fig. 1), females in the parental generation were mated to males whose PRP was unknown. Early and late-maturing genes that were selected in parental females would have been carried by G_1 males and would not, therefore, be expressed in females until the G_2 generation. In the second selection experiment (Fig. 2), early and late-maturing females were mated assortatively with males from early and late-maturing families. Therefore, most males that were mated to late-maturing females would themselves have carried genes coding for late maturity, which would be inherited by, and expressed in, G_1 females.

Both the selection and the sib analysis experiments were carried out under short (12L:12D) photoperiods and at low temperatures. Under these environmental conditions, individuals extend their PRPs (Hill, 1991). By carrying out selection under these conditions it is therefore not possible to distinguish whether it is the length of PRP that is being selected or sensitivity to environmental cues. In either case, the major influence on the expression of the character under selection was from X-linked genes.

Implications of X-linkage for migration

Adults of *A. gamma* and other noctuid species make regular seasonal migrations into areas where they are

unable to maintain permanent populations and the existence of return migrations to over-wintering sites has been questioned (Rabb & Stinner, 1978; Stinner *et al.*, 1983; but see Walker, 1980). There is, however, some evidence for southward return movement in autumn in *A. gamma* (Fisher, 1938) and also in other noctuids (Spitzer, 1972; Lingren *et al.*, 1979). Furthermore, mark-and-capture experiments have provided unequivocal evidence of return migration over 800 km by *M. separata* in China (Li *et al.*, 1964). Han & Gatehouse (1991a) suggested that X-linkage of genes regulating PRP may have been an essential pre-adaptation for the stability of migratory cycles in *Mythimna separata*, providing the potential for return migrations. They argued that X-linkage will minimize the frequencies of inappropriate alleles in populations at different latitudes because females (XY) will not carry genes for early-calling into northern regions. In *A. gamma*, X-linkage of genes controlling PRP will ensure that most insects at any latitude will have the genetic constitution to return to southerly latitudes where continuous breeding is possible. Charlesworth *et al.*, (1987) demonstrated that X-linked characters have a decreased rate of fixation in response to directional selection compared with autosomally inherited characters. This may be important for *A. gamma* because fixation of PRP alleles must be avoided with the seasonally changing selection pressures experienced by migrants (Han & Gatehouse, 1991a).

Variation in PRP in over-wintering populations will result in differential migration because individuals with longer PRPs will have potential to travel further and reach higher latitudes (termed genetic partitioning by Han & Gatehouse, 1991a). There is some evidence for PRPs increasing with latitude in *A. gamma* because samples of insects from Britain and Germany (50–53°N) have longer median PRPs than samples of insects collected in Morocco at 34°N (Hill, 1991). Environmental factors also influence PRP in noctuids (Han & Gatehouse, 1991b) and, in *A. gamma*, PRPs are longer in decreasing and short photoperiods and at low temperatures (Hill & Gatehouse, in press). The ability to respond to environmental cues that signal impending habitat deterioration, in conjunction with genes coding for later maturity, will further facilitate southward return migrations by individuals at high latitudes.

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