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Seasonal and geographical variation in the migratory potential of outbreak populations of the African armyworm moth, *Spodoptera exempta*

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Summary

1. Parker & Gatehouse (1985; Gatehouse 1986) proposed a genetic model to explain variation in the migratory potential of outbreak populations of the African armyworm moth, *Spodoptera exempta* (Walker) (Lepidoptera: Noctuidae). Implicit in this model are predictions regarding the temporal and spatial incidence of migratory phenotypes based on the pattern of rainfall through the season.
2. Migration in female *S. exempta* moths occurs predominantly in immature adults, therefore migratory potential is assumed to correlate with the duration of the pre-reproductive period (PRP). The aim of the present study was to test the predictions of the Parker & Gatehouse model by quantifying PRP variation in moths from 14 outbreak sites in eastern Africa during the 1989–90 and 1990–91 seasons and correlating this with rainfall prevalences.
3. Extensive intra- and inter-population variation in PRP was observed. As predicted by the model, mean PRP was inversely correlated with the prevalence of rainfall at the outbreak site during the month that the moths initiating the outbreaks were migrating: the longest PRPs were exhibited by moths originating from early season outbreaks in regions of low, variable rainfall and the shortest PRPs by moths from areas of high, consistent rainfall. Also as predicted by the model, the mean PRP of moths from outbreaks in Kenya and Tanzania tended to decline through the long rainy season, significantly so for females.
4. Males matured consistently earlier than females.
5. PRP variation cannot be accounted for by any major environmental factor, suggesting that the differences between samples are genetic in origin. This suggestion is strengthened by results from selection and sib-analysis experiments (Wilson & Gatehouse 1992), which demonstrate a substantial additive genetic component to PRP regulation in females, as assumed by the model.

Key-words: armyworm moth, natural selection, migration, *Spodoptera exempta*, habitat heterogeneity.

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Introduction

Larval outbreaks of the African armyworm moth, *Spodoptera exempta* occur throughout eastern, central and southern Africa on graminaceous crops and pasture grasses. The armyworm season generally begins in Tanzania or Kenya in November–December and ends in these countries in June–July, with a peak number of outbreaks in Tanzania during January, and in Kenya during April (Haggis 1986). Usually, there is a seasonal progression of outbreaks associated with movement of the Inter-Tropical Convergence Zone, and hence rainfall, through the region (Rose *et al.* 1987). This progression extends from southern Tanzania southwards to Malawi, Zimbabwe and South Africa and from north-eastern Tanzania and eastern Kenya northwards and westwards to central and western Kenya, Ethiopia, Somalia and the Yemen (Haggis 1986). Evidence that this seasonal pattern of outbreaks is the result of migration of the adult moths has been accumulating for over 50 years (e.g. Hattingh 1941; Faure 1943; Matthee 1952; Brown 1962; Brown & Swaine 1966) but it is only with the deployment of entomological radar and a large-scale mark-and-capture study that it has become incontrovertible (Riley, Reynolds & Farmery 1983; Rose *et al.* 1985, 1987).

The majority of armyworm outbreaks result

when moths flying at night are concentrated, by wind convergence associated with convective storms, into areas suitable for larval development (Pedgley *et al.* 1982, 1989). The probability that an individual moth will be drawn into an outbreak site in this way is a function of the time it remains airborne, as determined by its migratory potential. This, in turn, depends both on its flight capacity (how long it flies each night) and, because migration in this and most other migratory insects occurs predominantly before reproductive maturity is attained (e.g. Kennedy 1961; Rankin, McAnelly & Bodenhamer 1986; Page 1988), on its pre-reproductive period (PRP).

Parker & Gatehouse (1985; Gatehouse 1986) have proposed a genetic model for migration in *S. exempta*, in which fluctuations in the availability of suitable larval habitats generate shifting selection for individuals of differing migratory potential. Their hypothesis can be summarized as follows. During the dry season, armyworm populations in eastern Africa are confined to areas where occasional rainfall supports host-plant growth. These include coastal regions, some highlands, and marshy areas associated with permanent water-courses and lakes (see Fig. 1a; Rose *et al.* 1987). Because meteorological conditions capable of concentrating flying moths do not occur at this time of year, populations remain at low density in the *solitaria* phase and there are no outbreaks (Rose 1979; Rose *et al.* 1987; Gatehouse 1987). *Solitaria* individuals tend to have lower migratory potential than their *gregaria* siblings (see Woodrow, Gatehouse & Davies 1987; K. Wilson, A. Gunn, P. Bower & A.G. Gatehouse, unpublished), but a significant proportion of *solitaria* moths still possess high flight capacity and long PRP. It is these individuals that will tend to be concentrated, during migration, by storms early in the rainy season and so initiate the first outbreaks in areas unsuitable for dry season occupation. If there is heritable variation in flight capacity and PRP, offspring of these founder moths will also have significant migratory potential. Thus, for as long as rainfall remains scattered, and the habitat that is dependent on it patchy, individuals with high migratory potential will dominate outbreak populations. However, where suitable larval habitat is more uniformly distributed, selection will tend to maximize reproductive rate, strongly favouring individuals with short PRP and limited flight capacity. These conditions prevail in areas where rainfall is more consistent and green vegetation more generally available, such as western Kenya throughout the year and elsewhere late in the rainy season (Fig. 1).

The Parker & Gatehouse hypothesis makes the following predictions.

1. At sites that receive infrequent rainfall in the few weeks preceding moth migration (and hence offer widely dispersed larval habitat), outbreaks will tend to comprise insects with high migratory potential, whereas at sites where rainfall (and hence larval habitat) is more extensive, the opposite will be true.

2. Early in the armyworm season (when rainfall, and hence larval habitat, is scattered), outbreaks will tend to comprise moths with high migratory potential, whereas later in the season (after rainfall has become more widespread), outbreak populations will tend to have lower migratory potential.

The present paper tests these predictions by examining PRP variation in *S. exempta* in relation to the seasonal pattern of rainfall. A second paper (Wilson & Gatehouse 1992) utilizes selection and sib-analysis experiments to test the assumption that there is a significant genetic component to PRP variation in this species.

Materials & methods

ORIGIN AND MAINTENANCE OF LARVAE AND PUPAE

Between February and July in 1990 and 1991, samples of late-instar larvae ($n = 9$ samples) or pupae ($n = 5$) were collected from 14 outbreak sites in eastern Africa. Their locations, and key biogeographical data associated with them, are shown in Table 1. Larvae were fed on mats of teff or wheat until pupation and pupae were maintained in well-ventilated plastic jars until 2–3 days before emergence, when they were sexed. Each pupa was then housed in a shallow 500 ml plastic dish lined with filter paper. Netting tops provided for ventilation in the dishes and allowed the observer a clear view of the emerged moth. For seven of the samples, a random subset of pupae was weighed 3–4 h before dusk on the night of emergence (Gunn & Gatehouse 1985) so that the effect of pharate adult weight on PRP could be determined.

ASSESSING THE PRP OF ADULT MOTHS

Adult moths were presented with distilled water ad libitum on a cotton wool wick. In addition, they were fed four drops (*c.* 0·1 ml) of 20% sucrose solution at dawn each day to improve survival to maturity. PRP was defined as the period between the night of emergence (N0) and the night on which sexual responsiveness was demonstrated (see below). To coincide with the known pattern of mating behaviour in *S. exempta* (Khasimuddin 1978; Dewhurst 1984; Page 1988), insects were tested for maturity each night between midnight and 05.30 h local time (1 hour before dawn) from N1 onwards. Observations were made under dim red light (a 15 W bulb plus head torch) and a small fan aided pheromone dispersal.

All females were observed through the latter half of the night and classed as sexually mature on the

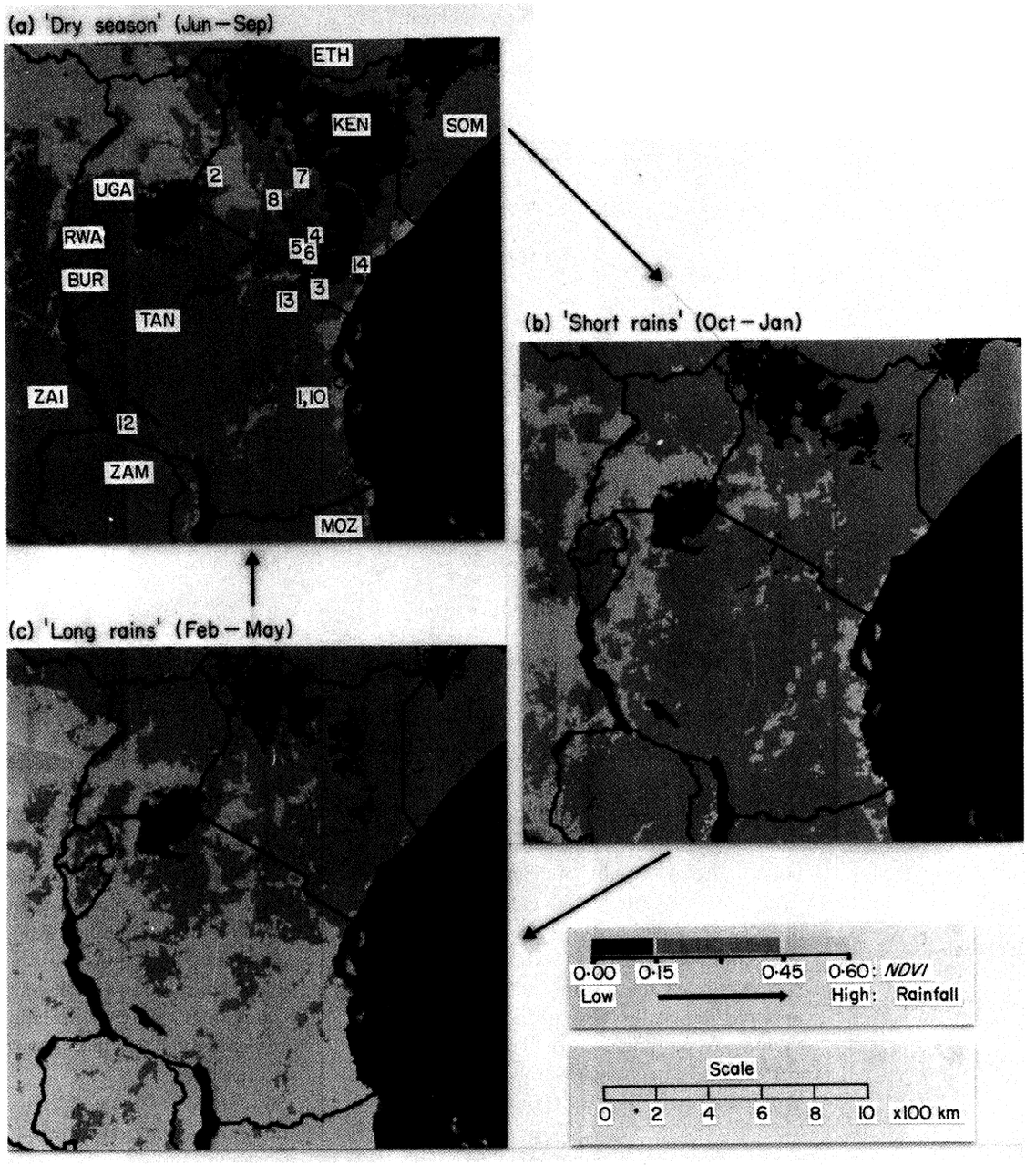

Fig. 1. Variation in rainfall and herbaceous greenness over eastern Africa, as estimated by integrated NDVI images. Each map (a)–(c) represents the maximum value composite NDVI image for the years 1982–88 for 4-month periods, roughly coinciding with the eastern African dry and rainy seasons: (a) 'dry season', June–September; (b) 'short rainy season', October–January; (c) 'long rainy season', February–May. Time-integrated NDVI (Normalized Difference Vegetation Index) is correlated with rainfall and 'herbaceous greenness' in Kenya (Lamprey & de Leeuw 1988). In general, the larger the NDVI, the higher the rainfall and the greener the area. Shadings in the figure are as follows: ■, $0{\cdot}00 \leq \text{NDVI} \leq 0{\cdot}15$, low rainfall/productivity; ▨, $0{\cdot}15 < \text{NDVI} < 0{\cdot}45$, medium rainfall/productivity; □, $0{\cdot}45 \leq \text{NDVI} \leq 0{\cdot}60$, high rainfall/productivity. Dots and numbers refer to the outbreak sites listed in Table 1 (Ndola and Harer are not indicated). The two circles represent Nairobi and Dar es Salaam.

night that they first everted their pheromone gland (see Khasimuddin 1978 for a description of this 'calling' behaviour). However, some females release pheromone and mate successfully before their pheromone gland becomes conspicuous, especially on their first night of maturity (K. Wilson, personal observation). Therefore, all non-calling females were also challenged, for up to 15 min each night, in a small cage ($25 \times 25 \times 25$ cm) with 1–4 mature males. Sometimes, this disturbance or the presence of a mature male induced the female to evert her pheromone gland whilst, on other occasions, calling was not initiated but the female consented to mate with one of the males. As only mature females mate successfully, copulation was taken to indicate that the female was sexually mature. Males were also challenged in a cage, with calling females, and categorized as mature if they everted their brushes.

Table 1. Biogeographical data for the 14 outbreak sites

Site (country)*	Grid reference	Altitude (m)	Annual rainfall† TOT (mm)	CVT	FREQ (d)	CVF	Annual RH.‡ 03 (%)	06 (%)	12 (%)	Annual temp.§ range (°C)
1/10. Morogoro (T)	06°51′S, 37°40′E	579	908	85	79	67	90	84	55	18·6–30·0
2. Kisumu (K)	00°28′S, 34°16′E	1149	1323	43	121	30	85	68	47	16·9–29·4
3. Taveta (K)	03°27′S, 37°42′E	770	673	80	68	61	–	74	49	16·6–30·4
4. Machakos (K)	01°58′S, 37°30′E	1573	775	87	73	67	–	79	52	12·7–25·2
5. Kapiti (K)	01°36′S, 37°06′E	1538	548	67	66	56	–	76	46	12·8–26·3
6. Amboseli (K)	02°30′S, 37°00′E	1845	893	99	82	68	–	79	71	10·5–22·5
7. Embu (K)	00°32′S, 37°27′E	1508	1364	85	123	51	91	82	59	13·4–24·0
8. Nairobi (K)	01°27′S, 36°58′E	1798	1049	75	93	60	94	83	50	11·9–23·4
9. Harer (E)	09°20′N, 42°06′E	1855	859	66	–	–	–	–	–	13·8–24·4
11. Ndola (Z)	13°00′S, 28°39′E	1270	1147	119	–	–	–	–	–	12·9–26·9
12. Sumbawanga (T)	07°57′S, 31°36′E	1710	823	103	–	–	–	–	–	11·3–24·4
13. Moshi (T)	03°21′S, 37°20′E	854	856	112	74	69	87	78	49	17·3–29·6
14. Bamba (K)	03°16′S, 40°03′E	30	1096	77	89	61	–	77	74	21·8–28·8

* K, Kenya; T, Tanzania; E, Ethiopia; Z, Zambia.

† Mean annual rainfall (for reference sources see text): TOT, total annual rainfall (mm); CVT, coefficient of variation (CV) in mean monthly rainfall total; FREQ, annual frequency of rainfall (days per year); CVF, CV in monthly frequency of rainfall.

‡ Average annual relative humidity (%): readings taken at 03.00 h (03), 06.00 h (06) and 12.00 h (12).

§ Annual temperature range (°C): mean minimum monthly temperature−mean maximum monthly temperature.

There were no significant correlations between PRP and any of these variables.

Once mature, moths of both sexes were used for testing immature insects.

PRP was also estimated using the change in shape of the patch of black scales around the female's gonopore. These results are reported separately (Wilson, in press) and are in general agreement with those described here.

All samples of moths were tested in a laboratory in Kenya, except those originating from Morogoro (Tanzania) during the 1989–90 season and part of the sample from Sumbawanga (Tanzania 1990–91). The Morogoro-A sample was transported to the UK as pupae and their offspring tested there (Wilson & Gatehouse 1992). Part of the Sumbawanga sample was tested in Kenya, and part in the UK. There was no significant difference between the two PRP distributions for either sex (Mann-Whitney *U*-test: $P > 0{\cdot}05$) and the data were combined for analysis.

CORRELATIONS WITH RAINFALL PREVALENCE

The Parker & Gatehouse model assumes that selection occurs when moths are migrating from the source areas and that the selecting agent is the distribution of habitats suitable for larval survival. It therefore predicts a negative correlation between PRP and rainfall during the period of migration by the parent moths and, because rainfall at other times has little or no effect on the distribution of larval habitats (especially rainfall after moth concentration), little or no correlation with rainfall at other times of the year. Most rainfall data are available as monthly averages, therefore correlations were performed between PRP and rainfall during the calendar month of moth migration (referred to as month 0; see below) and during the two preceding and following months (months −2, −1, +1 and +2). The expectation was that only correlations with rainfall during month 0 would be significant, but significant correlations for other months may result if prevalences during consecutive months are correlated. Therefore, correlations between rainfall during month 0 and during these other months were also performed.

Month 0 was defined as the calendar month in which the moths initiating the focal outbreak were migrating from their source areas and concentrated by meteorological factors. The date of moth concentration was initially estimated (to within 1–2 weeks) by combining information about the age of the insects when the sample was taken (e.g. by larval head capsule measurements or known pupation dates) with likely developmental rates based on average temperature at the outbreak site (see Pedgley *et al.* 1989). When moth concentration appeared to occur during the first week of any given calendar month, month 0 was assigned to the previous month, so as to encompass the beginning of migration. For the eight Kenyan outbreak sites and the Morogoro-A site, daily rainfall data were used to narrow down the night of moth concentration to 1–2 nights. This was possible because convective rainstorms capable of concentrating airborne insects are associated with daily rainfall in excess of 20 mm (Tucker & Pedgley 1983) and these occurred rarely

during these periods. The only site that had more than 1–2 nights with >20 mm rainfall was Embu, which had 3 nights (see below).

Two measures of average rainfall prevalence were readily available: mean monthly rainfall (mm) and frequency of rainfall (days per calendar month with rainfall of greater than 1 mm). Rainfall data pertaining to the actual time of the outbreak, referred to as contemporary data, were available only for the Kenyan outbreak sites and the Morogoro-A site, but long-term monthly averages, termed archive data, were available for most of them (Anon 1975, 1984a,b). For contemporary data, the prevalence of rainfall during the 4 weeks immediately prior to moth concentration was highly correlated with that during the calendar month prior to concentration ($r \geq 0{\cdot}894$, $n = 8$, $P < 0{\cdot}001$). Therefore, for both the contemporary and archive rainfall data, calendar month (rather than 4 week) averages were used so that correlations could be determined not only for contemporary and archive data alone, but also for a combination of the two: contemporary data when these were available, and archive data when they were not. Archive and contemporary rainfall are highly correlated (mean rainfall, $r_s = 0{\cdot}717$, $n = 9$, $P < 0{\cdot}02$; frequency of rainfall, $r_s = 0{\cdot}958$, $n = 8$, $P < 0{\cdot}0001$).

CORRELATIONS WITH OTHER ENVIRONMENTAL VARIABLES

The Parker & Gatehouse model assumes that differences between outbreak populations are genetically derived. An alternative explanation is that phenotypic differences are generated by variation in some environmental factor, such as temperature, humidity or diet during development (photoperiod varies little over latitudes at which most of the samples were taken). This possibility was examined by performing correlations between PRP and two potentially important environmental parameters during month +1: temperature (average monthly minimum and maximum) and relative humidity, RH (average monthly RH at 06.00 and 12.00 h GMT). In addition, pharate adult weight (which is related to larval food-plant availability and quality) was also measured. Correlations between month 0 rainfall and month +1 temperature and RH and pharate adult weight were determined in order to ascertain whether any correlations with PRP could be explained by the fact that these variables tend to be correlated with one another (i.e. by the fact that dry areas also tend to be hot, arid and have poor vegetation).

During the 1989–90 season, temperature and humidity readings were made each night at the beginning and end of each adult test period using a Solex meter and, during the following season, continuous readings were made using a 1200 series Squirrel meter/logger. It was therefore possible to determine whether differences between samples were correlated with environmental conditions experienced by the adult moths during testing.

STATISTICAL ANALYSES

PRP was not normally distributed for all samples, therefore differences between samples from different outbreak sites were examined using the (non-parametric) Kruskal-Wallis test, followed by multiple comparisons using the methods outlined by Siegel & Castellan (1988). Relationships between PRP and meteorological variables were determined using non-parametric Spearman rank correlation analyses. These analyses were performed separately for males and females and, for females, also after exclusion of the Embu sample because this was the only one for which a bimodal PRP distribution was observed (with peaks at N2–3 and N6). The bimodal distribution suggests that the sample may comprise individuals from more than one source location (see also Wilson, in press), a hypothesis supported by contemporary meteorological data: during the period of initiation of the Embu outbreak, storms occurred with predominant winds from two disparate areas in the east (two nights) and north (one night).

Results

PRP variation within and between outbreak populations

PRP distributions for the 14 outbreak samples are summarized in Table 2. Mean PRPs of males were shorter than those of females for all samples (Fig. 2), significantly so for seven of the 11 between-sex comparisons (Table 2).

Both sexes exhibited extensive within-sample variation in PRP: for females, PRP ranged between 1 and 13 nights; and, for males, between 1 and 7 nights. However, the 75 percentiles for males rarely extended beyond N2, whereas those for females were frequently N6.

There was also significant variation between samples for both sexes (Kruskal-Wallis test: females: $H = 109{\cdot}4$, df = 13, $P < 0{\cdot}0001$; males: $H = 43{\cdot}9$, df = 11, $P < 0{\cdot}0001$). The median PRPs of females ranged from 1 to 5 nights, whilst those of males were between 1 and 2·5 nights. Across outbreak sites, male and female PRP was not correlated ($r_s = 0{\cdot}270$, $n = 12$, NS; one-tailed probability), even after the Embu sample was excluded ($r_s = 0{\cdot}433$, $n = 11$, $P = 0{\cdot}092$).

Correlations between PRP and prevalence of rainfall

All correlations between PRP and rainfall prevalence during month 0 were negative for both females

Table 2. Variation within and between outbreak populations in the pre-reproductive periods of female and male *S. exempta* moths

Site	Females					Males					Month 0 (year)
	Mean	Med	IQR	Range	*n*	Mean	Med	IQR	Range	*n*	
1. Morogoro-A*	3·00	3^{c-f}	1–4	1–8	28	1·25	1^{a}	1	1–5	24	Dec (89)
2. Kisumu*	2·87	3^{b-e}	2–3	1–9	46	1·39	1^{a-d}	1–2	1–2	70	Feb (90)
3. Taveta*	4·55	4^{ghi}	3–6	2–7	33	1·84	2^{c}	1–2	1–3	37	Feb (90)
4. Machakos*	3·51	3^{dfh}	3–4	1–7	57	1·98	2^{bc}	1–3	1–7	52	Feb (90)
5. Kapiti*	5·25	5^{i}	4–6	2–10	36	1·63	1^{bcd}	1–2	1–4	57	Feb (90)
6. Amboseli	3·36	4^{d-h}	3–4	1–5	14	–	–	–	–	0	Feb (90)
7. Embu	4·13	3^{dfgh}	2–6	1–13	31	1·00	1^{a}	1	1	11	Apr (90)
8. Nairobi	1·46	1^{a}	1–2	1–2	11	–	–	–	–	0	Apr (90)
9. Harer†	1·86	1^{abc}	1–4	1–4	7	1·17	1^{ab}	1	1–2	6	May (90)
10. Morogoro-B†	2·71	2^{bcd}	2–3	1–6	14	1·86	2^{bcd}	1–2	1–3	7	Dec (90)
11. Ndola*	4·86	5^{ghi}	3–6	2–9	14	2·38	$2·5^{c}$	3	1–4	8	Mar (91)
12. Sumbawanga†	2·33	2^{abc}	1–3	1–10	30	2·08	2^{bc}	1–2	1–7	25	Mar (91)
13. Moshi†	1·50	1^{ab}	1–2	1–3	6	1·33	1^{abc}	1–2	1–2	3	Apr (91)
14. Bamba*	3·00	3^{a-g}	2–5	1–6	5	1·43	1^{a-d}	1–2	1–2	7	Apr (91)

Within sexes, samples with shared superscripts above the median values do not differ significantly from each other (Kruskal-Wallis multiple comparisons test; Siegel & Castellan 1988).

Med, median; IQR, inter-quartile range; Range, total range of values; *n*, sample size; Month 0, month during which moths initiating the outbreak were migrating (see Materials & Methods).

Comparisons between the sexes (Mann-Whitney *U*-tests): * significant difference; † non-significant difference; no symbol = comparison not possible.

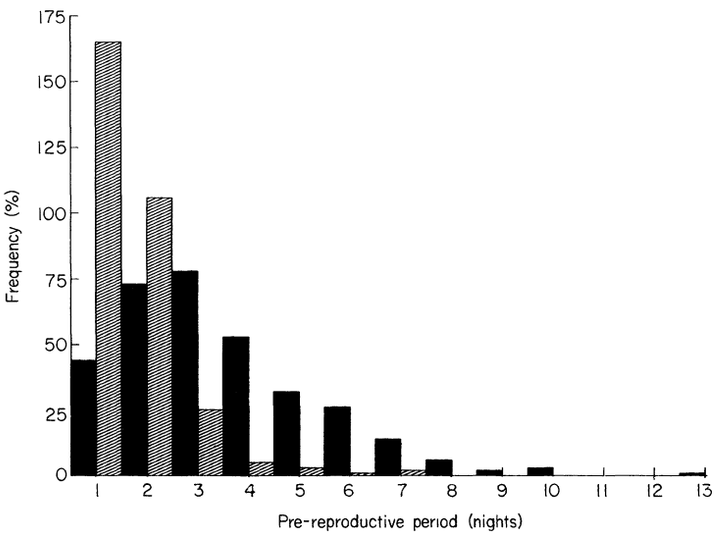

Fig. 2. PRP frequency distributions for females (■) and male (□) *S. exempta* from all outbreak sites combined.

($-0·417 \geq r_s \geq -0·843$) and males ($-0·347 \geq r_s \geq -0·786$), regardless of whether the Embu sample was excluded. Moreover, PRP was not correlated with rainfall during any of the 2 months preceding or following month 0, except when rainfall during these periods was correlated with month 0 rainfall (Tables 3–5).

Using archive rainfall data, female PRP was significantly negatively correlated with rainfall during month 0 (Table 3, Fig. 3), especially with the frequency of rainfall after excluding the Embu sample ($r_s = -0·843$, $n = 10$, $P = 0·001$). Male PRP also appeared negatively correlated with rainfall during month 0 but the correlations were not significant (Table 3, Fig. 3).

Negative correlations were also found between female PRP and rainfall prevalence when contemporary rainfall data were used, though they were significant only after the exclusion of the Embu sample ($r_s \leq -0·620$, $n = 8$, $P \leq 0·05$; Table 4, Fig. 4). For males, the correlation coefficients remained highly negative ($r_s \leq -0·551$) but, due to small sample sizes, were significant only for average rainfall during month 0 ($r_s = -0·786$, $n = 7$, $P = 0·018$; Table 4, Fig. 4).

After combining contemporary and archive rain-

Table 3. Spearman rank correlations between pre-reproductive period and archive monthly rainfall during the month of moth migration and the 2 months preceding and following it

	Females Month						Males Month					
Correlation	−2	−1	**0**	+1	+2	*n*	−2	−1	**0**	+1	+2	*n*
Mean1	−0·319 NS	−0·636 *	**−0·642** **	−0·250 NS	+0·237 NS	14	−0·060 NS	−0·326 NS	**−0·347** NS	−0·169 NS	+0·179 NS	12
Mean2	−0·343 NS	−0·621 *	**−0·789** ***	−0·360 NS	+0·277 NS	13						
Corr0	0	++	·	0	−	14	0	++	·	0	−	14
Freq1	+0·242 NS	−0·584 (*)	**−0·662** *	−0·776 **	+0·179 NS	11	−0·202 NS	−0·526 (*)	**−0·477** (*)	−0·109 NS	+0·252 NS	11
Freq2	+0·265 NS	−0·647 *	**−0·843** ***	−0·841 **	+0·228 NS	10						
Corr0	0	+++	·	++	0	11	0	+++	·	++	0	11

Month 0, month of moth migration (see text); months −2 to +2 = 2 months prior to and following month 0.

Mean1, Spearman rank correlation between mean PRP and mean monthly rainfall in months −2 to +2 for all outbreak sites for which there was data; mean2 = as for mean1, except that Embu females are excluded from the analysis (see text for explanation); freq1 = as for mean1, except that mean number of rainy days (>1 mm rain) replaces mean monthly rainfall; freq2 = as for freq1, except that Embu females are excluded from the analysis.

n, number of outbreak sites.

Significance levels for correlations are as follows: NS $P > 0{\cdot}1$; (*) $0{\cdot}05 < P < 0{\cdot}1$; * $P < 0{\cdot}05$; ** $P < 0{\cdot}01$; *** $P < 0{\cdot}001$; The Parker & Gatehouse model predicts negative correlations between PRP and rainfall only for month 0, therefore tests of significance are two-tailed for months −2, −1, +1, +2 and one-tailed for month 0 (month 0 correlations are shown in bold type); corr0 = correlation between rainfall during month 0 and during the month in question (e.g. month −2): 0 = correlation not significant; + (or −) = significantly positive (or negative), $P < 0{\cdot}05$; ++ (or −−) = $P < 0{\cdot}01$, +++ (or −−−) = $P < 0{\cdot}001$. For sources of archive rainfall data, see Materials & Methods.

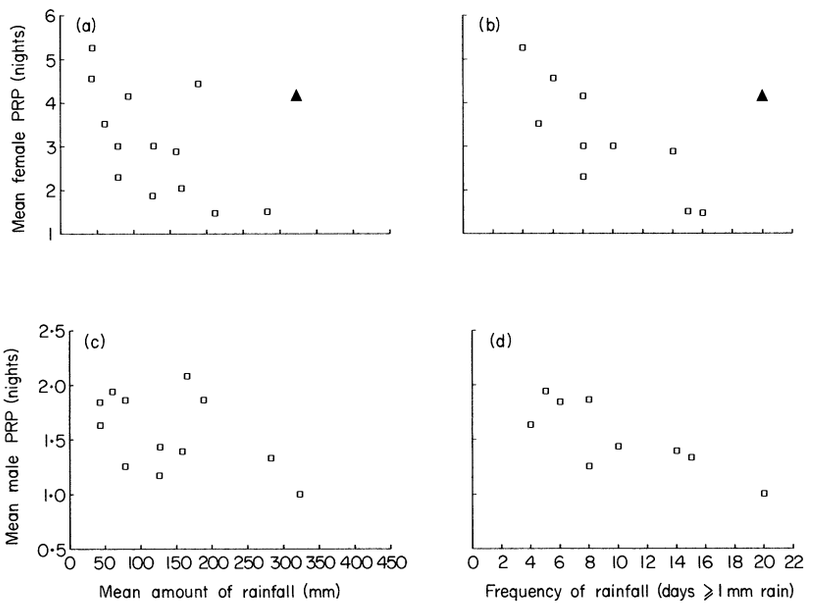

Fig. 3. Correlations between mean PRP and rainfall prevalence during month 0, using archive rainfall data alone. Spearman rank correlation coefficients are given in Table 3. The Embu sample is indicated by ▲. Month 0 is the month that the moths initiating the focal outbreak were migrating.

fall data, the significance of the correlations generally improved slightly, due to increased sample size (Table 5, Fig. 4). The correlation coefficients between PRP and rainfall prevalence were high for both females ($r_s \leq -0{\cdot}491$) and males ($r_s \leq -0{\cdot}559$) and, for average rainfall, were significant for both sexes ($P \leq 0{\cdot}037$), though the correlation with rainfall frequency was significant for females only after the exclusion of the Embu sample ($r_s = -0{\cdot}642$, $n = 10$, $P = 0{\cdot}023$). These results are in general agreement with the Parker & Gatehouse model.

Correlation between PRP and stage of season

The Parker & Gatehouse model predicts that PRP will decline through the season due to the seasonal

Table 4. Spearman rank correlations between pre-reproductive period and contemporary monthly rainfall during the month of moth migration and the 2 months preceding and following it

	Females Month						Males Month					
	−2	−1	**0**	+1	+2	*n*	−2	−1	**0**	+1	+2	*n*
Mean1	+0·600 (*)	−0·117 NS	**−0·417 NS**	+0·117 NS	+0·483 NS	9	+0·036 NS	−0·536 NS	**−0·786 ***	+0·321 NS	+0·464 NS	7
Mean2	+0·714 *	−0·167 NS	**−0·620 ***	+0·214 NS	+0·810 *	8						
Corr0	−	0	·	0	−	9	−	0	·	0	−	9
Freq1	+0·240 NS	−0·310 NS	**−0·587 (*)**	−0·123 NS	+0·262 NS	8	−0·406 NS	−0·143 NS	**−0·551 NS**	+0·147 NS	+0·029 NS	6
Freq2	+0·414 NS	−0·429 NS	**−0·793 ***	+0·094 NS	+0·536 NS	7						
Corr0	0	+	·	0	0	8	0	+	·	0	0	8

For explanation of symbols see Table 3. Contemporary rainfall data were available only for Kenyan outbreak sites (provided by the Kenya Meteorological Department. Nairobi) and the Morogoro-A site (provided by the Directorate of Meteorology, Arusha).

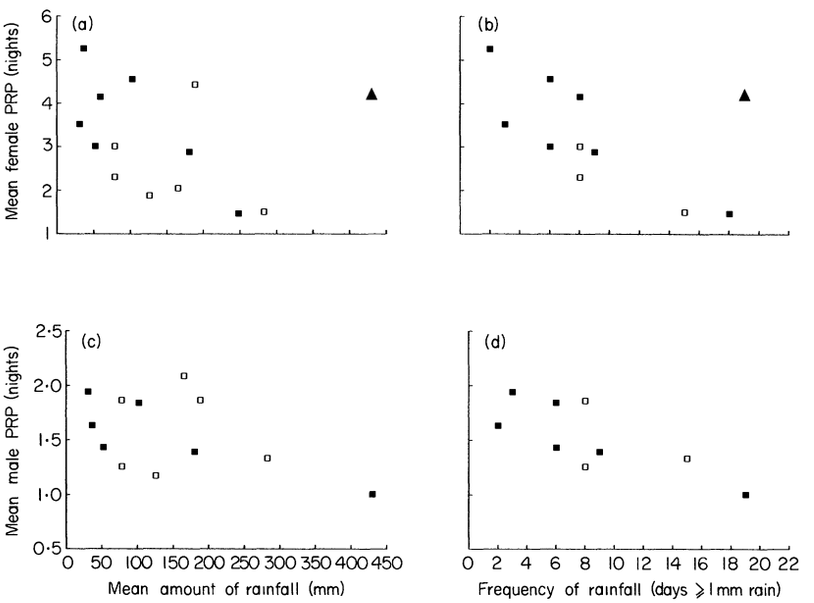

Fig. 4. Correlations between mean PRP and rainfall prevalence during month 0, using contemporary and archive rainfall data combined. Correlation coefficients are given in Tables 4 and 5. ■, contemporary data; □, archive data; and ▲ the (contemporary) Embu sample of females. See legend to Fig. 2 and text for definition of month 0.

increase in rainfall and larval habitat. This prediction was tested using data for outbreaks occurring during the long rainy season in the latitude belt encompassing Kenya and Tanzania (though the same trends are apparent when all the data are used). As predicted, PRP was negatively correlated with calendar month (Fig. 5) significantly so for females ($r_s = -0{\cdot}569$, $n = 10$, $P < 0{\cdot}05$, including Embu; $r_s = -0{\cdot}765$, $n = 9$, $P < 0{\cdot}025$, excluding Embu), but not for males ($r_s = -0{\cdot}535$, $n = 8$, $0{\cdot}05 < P < 0{\cdot}1$).

Correlations between PRP and environmental conditions during larval development

Spearman rank correlations were calculated between PRP and both temperature and RH data for the different localities during month +1 (the month of larval development). None of the correlations between PRP and temperature or RH were significant using contemporary meteorological data alone, or contemporary and archive data combined. However, using archive data, female PRP was significantly negatively correlated with RH at 12.00 h GMT ($r_s = -0{\cdot}619$, $n = 11$, $P = 0{\cdot}042$) and positively correlated with the average daily maximum temperature during month +1, after the Embu sample was excluded ($r_s = 0{\cdot}697$, $n = 13$, $P = 0{\cdot}008$). There was no correlation between male PRP and any of these factors. These results indicate that, amongst females, long PRPs were associated with hot and arid areas. The correlation between PRP and RH

Table 5. Spearman rank correlations between pre-reproductive period and monthly rainfall during the month of moth migration and the 2 months preceding and following it, based on contemporary rainfall data where these were available, and archive data where they were not

	Females Month						Males Month					
	−2	−1	**0**	+1	+2	*n*	−2	−1	**0**	+1	+2	*n*
Mean1	+0·125	−0·392	**−0·491**	+0·244	+0·497	14	−0·007	−0·350	**−0·559**	+0·070	+0·196	12
	NS	NS	*	NS	(*)		NS	NS	*	NS	NS	
Mean2	+0·193	−0·481	**−0·630**	+0·253	+0·680	13						
	NS	(*)	*	NS	*							
Corr0	0	+	·	0	+++	14	0	+	·	0	+++	14
Freq1	+0·240	−0·225	**−0·498**	−0·182	+0·290	11	−0·084	−0·322	**−0·580**	+0·025	+0·209	9
	NS	NS	(*)	NS	NS		NS	NS	(*)	NS	NS	
Freq2	+0·370	−0·308	**−0·642**	−0·084	+0·473	10						
	NS	NS	*	NS	NS							
Corr0	0	++	·	0	0	11	0	++	·	0	0	11

For explanation of symbols see Table 3. For sources of rainfall data see legend to Table 4 and text.

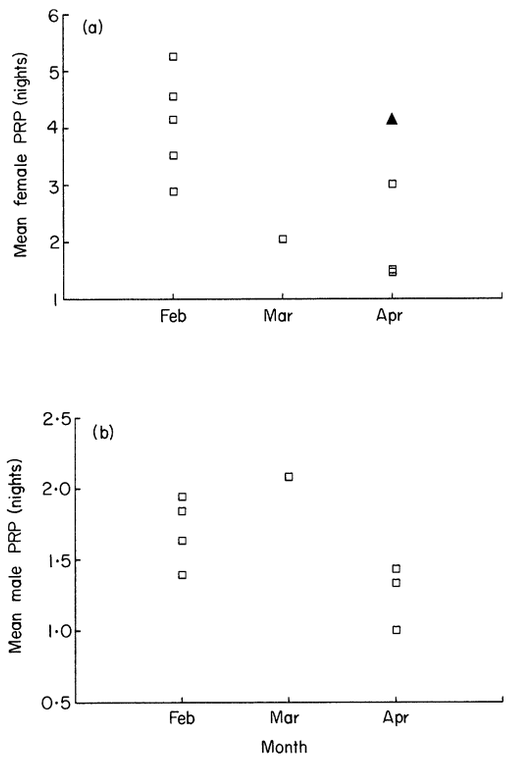

Fig. 5. Correlations between mean PRP and calendar month. Month refers to the calendar month in which the outbreak occurred. Only outbreaks in Kenya and Tanzania during the long rainy season were included in the analyses. (a) females: $r_s = -0{\cdot}569$, $n = 10$, $P < 0{\cdot}05$; excluding Embu, $r_s = -0{\cdot}765$, $n = 9$, $P < 0{\cdot}025$; (b) males: $r_s = -0{\cdot}535$, $n = 8$, $0{\cdot}05 < P < 0{\cdot}1$. For females, the Embu outbreak is indicated by ▲.

reflects the effect of rainfall prevalence on atmospheric water content: RH at 12.00 h GMT in month +1 was positively correlated with mean rainfall ($r_s = 0{\cdot}699$, $n = 11$, $P = 0{\cdot}008$) and frequency of rainfall ($r_s = 0{\cdot}644$, $n = 11$, $P = 0{\cdot}016$) during month 0 in the archive data set. The correlation with average maximum temperature reflects the fact that rainfall tends to be lighter and less frequent in the hotter areas: there are strong negative correlations between maximum temperature during month +1 and mean ($r_s = -0{\cdot}712$, $n = 14$, $P = 0{\cdot}002$) and frequency ($r_s = -0{\cdot}570$, $n = 11$, $P = 0{\cdot}034$) of rainfall during month 0 in the archive data set. In other words, given that rainfall prevalence is the driving force behind inter-population differences in PRP, correlations between PRP, and temperature and humidity are the result of correlations between these two factors and rainfall prevalence.

Across sites, there was no significant correlation between mean pharate adult weight and PRP for either females ($r_s = -0{\cdot}396$, $n = 7$, NS) or males ($r_s = 0{\cdot}036$, $n = 6$, NS). Within sites, only that for Ndola females was significant ($r_s = -0{\cdot}861$, $n = 9$, $P < 0{\cdot}01$), the remaining 12 correlations (six female, six male) were not. In other words, PRP was not markedly influenced by feeding conditions for larvae, as reflected in pharate adult weight.

Correlations between PRP and environmental conditions during adult testing

Night-time temperature ranges during testing in the 1989–90 and 1990–91 seasons were 16·8–21·4 °C and 19·7–24·3 °C, respectively; and the RH ranges were 78–98% and 43–78%, respectively. There were no significant correlations between PRP and either of these factors, except when Embu was excluded from the analysis and the correlation with maximum night-time temperature became significant ($r_s = 0{\cdot}624$, $n = 13$, $P < 0{\cdot}05$). A positive correlation between PRP and temperature is not to be expected (see Hattingh 1941) and is likely to reflect concurrent seasonal declines in PRP and ambient temperature. A better test of the effect of ambient conditions on PRP is to compare the PRP distri-

butions of moths tested simultaneously. If environmental conditions during testing are responsible for differences between samples, then moths from different locations should have similar PRP distributions when tested together (though genotype–environment interactions cannot be excluded). This type of analysis is possible for samples from Kisumu and Taveta (tested 18 March–1 April 1990), Embu and Nairobi (21 May–4 June 1990) and Moshi and Bamba (2–8 May 1991). Of these, Kisumu and Taveta moths differed significantly from each other for both sexes (Kruskal-Wallis multiple comparisons test) and Embu and Nairobi females also differed significantly from each other (there were no males from the Nairobi sample), but the Moshi and Bamba samples did not differ (Table 2). In addition, as stated earlier, part of the Sumbawanga sample was tested in ambient conditions in Nairobi, and part in a constant environment room in Bangor, yet the PRP distributions were not sigificantly different. It seems unlikely, therefore, that temperature or humidity differences during testing contributed to the observed differences between samples.

Discussion

INTER-POPULATION DIFFERENCES IN MIGRATORY POTENTIAL

Several studies have demonstrated significant differences in migratory potential between populations of tropical or subtropical insects (e.g. Dingle *et al.* 1980; McAnelly 1985; Han & Gatehouse 1991; Hill & Gatehouse 1992). The explanation for the observed differences often appears to be genetic partitioning mediated by migration: genes for long PRP and/or extensive flight capacity are carried seasonally by migrant individuals to high latitudes, whilst those for short PRPs and limited flight remain nearer the equator (e.g. the large milkweed bug *Oncopeltus fasciatus*, Dingle *et al.* 1980; the Oriental armyworm moth *Mythimna separata*; Han & Gatehouse 1991; the silver Y moth *Autographa gamma*; Hill & Gatehouse 1992). Similarly, the relatively low migratory potential of island populations, relative to those on the mainland, can be attributed to the loss of genes coding for high migratory potential with emigrants that fail to return (e.g. *O. fasciatus*, Dingle *et al.* 1980).

The only previous study to suggest that variation in habitat heterogeneity may select for individuals differing in migratory potential is that by McAnelly (1985). She observed significant (genetic) variation in the tethered-flight performance of the polyphagous grasshopper *Melanoplus sanguinipes* from three populations in North America. The percentage of migrants in each population appears to be related to variation in the availability of suitable habitat. For example, in Colorado, which is more or less uniformly green throughout the summer, only 5% of grasshoppers were migrants; whereas in Arizona, where the long and arid dry season is ended by scattered rains, at least 28% of insects exhibited migratory behaviour. The highest percentage of migrant individuals (58%) was at a site in New Mexico that had only recently been reseeded with grasses and colonized by *M. sanguinipes* (McAnelly 1985). It is unlikely that these differences can be explained by genetic partitioning because the three sites differed in latitude by as little as 4° (latitude range = 34–38 °N), and the least migratory population (Colorado) was also the most northerly.

The present study demonstrates that significant differences in migratory potential between outbreak populations of *S. exempta* are also a consequence of variation in the degree of temporal and spatial heterogeneity of larval habitats. Moths from outbreaks in regions of high and consistent rainfall, where habitats are typically uniformly green during the period of moth migration (e.g. Nairobi in April), tended to mature rapidly whilst those from regions that receive low, infrequent rainfall, and offer patchily distributed habitats (e.g. Taveta, Machakos and Kapiti in February), tended to mature much later. Moreover, average PRP (of females, at least) tended to decline through the season, as predicted by the genetic model.

Correlations between PRP and rainfall prevalence during the month of migration were uniformly negative, for both sexes, despite the crudity of the measure of habitat heterogeneity. The correlations were most significant using archive, as opposed to contemporary, data. This may be a consequence of the way in which the two data sets reflect rainfall prevalence. Contemporary rainfall data were taken from the nearest meteorological station to the outbreak site (often some distance from it) and so reflect prevalence at a specific location rather than over the area through which the moths were migrating. Archive data, on the other hand, reflect the average pattern of rainfall and may be more representative of the area as a whole.

The generally higher correlations with frequency of rainfall, as opposed to mean rainfall, may indicate that the selecting agent producing these trends is not the spatial pattern of larval habitats but the temporal and spatial pattern of the process that generates them, i.e. rainstorms. In other words, the correlation between PRP and rainfall could be explained if moth migration is halted or delayed by convective rainstorms and individuals with the shortest PRPs begin reproducing at the site first. This proposal incorporates the same principles as the Parker & Gatehouse model and differs from it only in depending more on the frequency of rainfall *during* moth migration rather than immediately prior to it. It should be viewed as complementary to

the original model and there is no way to assess their relative importance.

RELATIVE IMPORTANCE OF GENETIC AND ENVIRONMENTAL FACTORS

Although selection and sib-analysis experiments indicate that female PRP has a significant heritable component (Wilson & Gatehouse 1992), it still could be argued that differences between samples were primarily a consequence of environmental conditions experienced by the larvae or pupae at the different outbreak sites. However, analysis of the relationship between PRP and two key environmental variables provides little support for this view: the only significant correlations (those between female PRP and long-term average maximum temperature and RH at 12·00h GMT during month +1) can be explained by correlations between these variables and rainfall prevalence during month 0.

Variation in PRP could also be due to differences in environmental conditions experienced by the adult moths. However, temperature and humidity had no consistent effect on the rate of maturation in either sex. A third factor is the diet of the adult moths. There is some evidence that female *S. exempta* moths fed sucrose solution begin oviposition later than those fed distilled water (Gunn & Gatehouse 1987) though the delay is small (rarely exceeding 1 day). In the present study, there seems little possibility that differential sucrose uptake by moths in the different samples could have contributed to inter-population differences in PRP.

SEX DIFFERENCE IN PRP

A striking feature of the present study is the difference in PRP between the sexes: female *S. exempta* generally started calling between N2 and N5, whereas over 75% of males in most samples were already mature by the end of N2. Only in the corn earworm moth *Heliothis zea* has it been shown that males mature earlier than females (Lingren *et al.* 1988). In other species of migratory noctuid, either females mature before males (e.g. *Autographa gamma*; Hill & Gatehouse 1992), or there is no difference between the sexes (*Helicoverpa armigera*; Colvin 1990).

Gatehouse (1987) has suggested that for much of the season, when *S. exempta* is invading areas that are inhospitable during the dry season and therefore unoccupied early in the rains, moths are probably constrained to mate, after migration, with others from the same source. If males mature substantially earlier than females but reach the same destination after migration, then they must continue migratory flight after they have become sexually mature. This suggests that most males probably embark on migratory flights with females early in the night (Rose & Dewhurst 1979; Riley, Reynolds & Farmery 1983), but mature males descend in the latter half of the night and mate with any mature females they encounter. Some support for this conclusion comes from field observations at an outbreak site in Kenya in which the sex ratio became increasingly male-biased through the night, presumably due to the arrival of males from elsewhere (W.W. Page, unpublished data). This result clearly has important consequences for the interpretation of pheromone-trap data for this species.

NATURAL SELECTION AND PRP

Endler (1986) describes three conditions for natural selection to act on a given trait: (i) there must be variation in the trait; (ii) there must be differences in the fitness of individuals with different trait values; and (iii) the trait must be heritable. We have demonstrated that there is significant variation in PRP between outbreak populations (Table 2) and that this trait has a heritable component (Wilson & Gatehouse 1992), but the relationship between PRP and fitness in the field is more difficult to demonstrate. However, it is generally accepted that, in the absence of advantages due to migrating out of an unfavourable area, early reproduction will be associated with greater fitness (Southwood 1977; Gatehouse 1987). This is illustrated in *S. exempta* by the fact that, in laboratory cultures, fecundity is negatively correlated with pre-oviposition period and PRP quickly collapses to $\leq$N2 unless steps are taken to prevent it (K. Wilson, A. Gunn, P. Bower & A.G. Gatehouse, unpublished).

Pre-reproductive period in *S. exempta* therefore satisfies all of the conditions necessary for natural selection to operate and the seasonal pattern of rainfall in eastern Africa, by acting as a natural perturbation to field populations (see method VI, Endler 1986), provides a mechanism for obtaining direct evidence for natural selection in the field. This evidence is strengthened by the fact that the relationship between PRP and rainfall prevalence was predicted a priori (Parker & Gatehouse 1985; Gatehouse 1986), based on arguments about the putative relationship between the trait and fitness and how this relationship changes through the season (see method IX, Endler 1986).

The genetic model for the determination of migratory potential in *S. exempta* provides implicit support for the regional control strategy against this pest in eastern Africa, which proposes focusing control effort against early season outbreaks in eastern Kenya and Tanzania (Rose *et al.* 1987). The model, together with other evidence (Pedgley *et al.* 1989), suggests that moths from these outbreaks are most likely to initiate subsequent infestations by virtue of their high migratory potential. Moreover, it provides a biological mechanism to explain the empirical association between poor early season

rainfall and subsequent severe armyworm infestation (Tucker 1984).

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