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Sexually differentiated flight responses of the Mexican bean beetle to larval and adult nutrition

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Summary. Flight of male and female Mexican bean beetle adults was examined in laboratory tests. The experimental design made it possible to examine flight behavior not only with respect to different types of hosts (young vs senescent common bean foliage) but also with respect to effects due to their utilization during particular stages of beetle development. The median flight time of males was significantly affected by the adult host, but not by the juvenile host; whereas, the median flight time of females tended to be more affected by the juvenile than by the adult host. These different effects of hosts on the flight times of males and females resulted in sexual dimorphism in flight when the sexes were fed senescent foliage as adults. Although age significantly affected the flight time of both males and females, the reproductive status of females did not affect their flight times. The significance of these results are discussed with respect to the influence of the nutritional complexity of habitats on life history strategies and population dynamics.

Key words: Insect flight – Population dynamics – Insect nutrition – *Epilachna varivestis*

Insect population dynamics are strongly influenced by flight behavior since flight is the principal means of insect dispersal (Andrewartha and Birch 1954). In addition, flight can influence the timing of the onset of reproduction and can thereby affect insect abundance. The oogenesis-flight syndrome of migratory species (Johnson 1969) effectively limits population growth in natal habitats since the peak in flight activity precedes the onset of reproduction. However, whether or not the population dynamics of more sedentary species are influenced by a similar interaction between flight and reproduction is not clearly understood (Davis 1984).

The relationship between insect flight and population dynamics becomes more complex when the potential influence of environmental factors on both flight behavior and reproduction are considered. Initial studies of phytophagous insects indicated that there was an inverse relationship between insect abundance and the diversity of plants within their habitat (Root 1973). Subsequent detailed studies revealed that flight behavior was a causative factor in this relationship since the flight activity of many insects is enhanced when plant diversity is high (see Andow 1986). Although these studies clearly indicate that flight behavior can influence population dynamics in natural populations, they take a somewhat limited view of the environmental factors that insects can encounter in field situations. For example, leaf nitrogen generally decreases when plants set seed and mature (Thimann 1980). Consequently, the nutritional complexity of a habitat can be high even within the low diversity plant stands that result from the cultivation of crops in monocultures. Foliar nitrogen is a key determinant of the growth and reproduction of phytophagous insects (Scriber and Slansky 1981; Slansky 1982). In addition, food quality can influence insect flight behavior (Rankin and Riddiford 1977; Rankin and Rankin 1980). Thus not only the taxonomic but also the nutritional complexity of the habitat may influence the distribution and abundance of insects in natural populations. In light of the potential interaction of environmental factors with both insect flight and reproduction, detailed studies are critical to an understanding of the population dynamics of a particular insect species (Stinner et al. 1982).

We examined the flight behavior of the Mexican bean beetle, *Epilachna varivestis* (Coleoptera: Coccinellidae) in tethered flight assays as an initial step in examining the potential influence of host nutritional quality on the distribution and abundance of the insect. *E. varivestis* is a pest of the common bean *Phaseolus vulgaris* (Leguminosae). Our goal was to examine whether the flight behavior of a phytophagous beetle is influenced by differences in the nutritional quality of a host plant that is commonly cultivated in monocultures.

Materials and methods

Animals for these experiments were reared from eggs produced by females that were collected in North Carolina and that had been maintained in continuous laboratory cultures for ca. 8 generations. At hatch, broods were split into two treatment groups (Fig. 1). One group was fed foliage from pre-bloom (young) *P. vulgaris* (cv. Long Tendergreen) while the other was fed foliage from mature plants (senescent foliage). The protein concentration of young foliage from the cultivar Long Tendergreen is significantly greater than that of senescent foliage (Saks 1987a). At eclosion, adults were randomly assigned to either continue feeding on the same type of foliage they received during larval development or were switched to the alternate host type (Fig. 1). The design resulted in four treatment groups that

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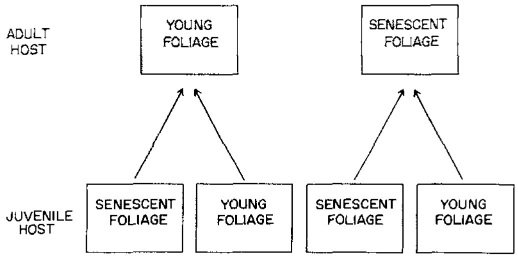

Fig. 1. Schematic representation of the experimental design used to examine the flight times of male and female *E. varivestis* as a function of the utilization of young and senescent bean foliage at different times in beetle development

will be referred to by indicating the juvenile and then the adult host (i.e. Y-S signifies the treatment in which animals were fed young foliage in the juvenile stage and senescent foliage in the adult stage). Using this design, it was possible to examine flight behavior not only with respect to different types of hosts, but also with respect to effects due to their utilization during particular stages of beetle development. Sample sizes in the four treatment groups ranged from 26 to 32 pairs of adults. Larvae were reared on caged plants whereas single pairs of adults were fed excised foliage that was placed on moistened filter paper within sealed 16 oz. containers.

Preliminary assays indicated that beetles did not initiate flight until approximately 5 days post-eclosion. Therefore we tested each animal at 5 days post-eclosion and every other day up to and including day 15 post-eclosion. The tethered flight assay of Dingle (1965) and Rankin and Rankin (1980) was modified for *E. varivestis*. Beetles were hung horizontally from a toothpick attached to their dorsal pronotum with Tacky Wax. Flight was initiated by moving the tethered animal through the air in a figure-8 pattern. Each animal was given 5 opportunities to initiate or restart flight during each test period. Once a beetle was flying, it was suspended facing a fan that generated a light breeze. Each animal was allowed a maximum of 120 min of flight. Temperature was 24±2° C and photoperiod was 16L:8D during the rearing and flight testing of animals.

Flight data such as those collected in this experiment have statistical properties similar to those generally associated with survival data. Therefore the data were analyzed using survival statistics (SAS 1985) to calculate the probability that an individual will continue to fly if it has already flown for a certain length of time. Differences between probability curves were determined using the Wilcoxon Rank Test. This test is sensitive to differences in the overall shape of the probability curves and is less sensitive to extremely long flight times than are other methods. The shapes of particular flight curves are indicated within the text and tables by presenting the 25, 50 and 75 percent quantiles for each data set. These values indicate the probability (0.75, 0.50 (median) and 0.25, respectively) that animals in each treatment would fly longer than a given length of time (in minutes). The influence of beetle age, female reproductive status, juvenile and adult hosts, and sex on flight behavior were examined.

Table 1. Quantiles (25%, 50% and 75%) for the flight times (in minutes) of males (M) and females (F) at each age and in each host treatment (see text)

Treatment	Quantile	Sex	Age (days post-eclosion)					
			5	7	9	11	13	15
Y-Y	25%	M	0.0	4.0	6.0	11.0	11.0	9.0
	50%	M	2.5	19.0	18.5	16.5	13.5	16.5
	75%	M	23.0	38.0	42.0	33.0	24.0	21.0
Y-S	25%	M	0.0	0.5	0.0	4.0	8.0	4.0
	50%	M	0.0	6.0	5.0	10.0	16.5	12.0
	75%	M	2.0	25.5	11.0	23.0	23.0	26.0
S-Y	25%	M	0.0	0.0	2.0	9.0	8.0	5.0
	50%	M	0.0	8.5	10.0	19.0	14.0	16.0
	75%	M	10.0	28.5	43.0	36.0	50.0	45.0
S-S	25%	M	0.0	0.0	0.0	0.0	3.0	6.0
	50%	M	0.0	2.0	8.0	6.0	10.0	12.0
	75%	M	13.0	15.0	21.0	18.0	14.0	20.0
Y-Y	25%	F	0.0	3.0	4.0	8.0	10.0	7.0
	50%	F	2.0	23.0	12.5	17.0	21.0	17.0
	75%	F	35.0	74.0	28.0	37.0	46.0	29.0
Y-S	25%	F	0.0	8.0	8.0	13.0	11.0	12.0
	50%	F	4.0	25.0	39.0	25.0	17.0	28.0
	75%	F	42.0	64.0	61.0	50.0	40.0	55.0
S-Y	25%	F	0.0	0.0	0.0	9.0	5.0	6.0
	50%	F	0.0	12.0	11.5	15.0	13.0	12.0
	75%	F	5.0	79.0	28.5	31.0	31.0	20.0
S-S	25%	F	0.0	0.0	0.0	1.0	6.0	6.0
	50%	F	7.0	17.0	14.0	14.0	15.0	15.0
	75%	F	34.0	54.0	39.0	26.0	40.0	32.0

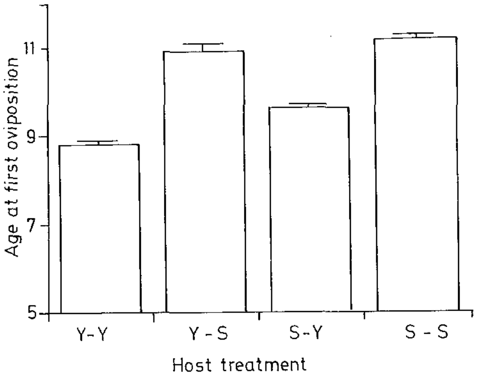

Fig. 2. Mean age (days) at first oviposition ± 95% confidence intervals for females in each treatment

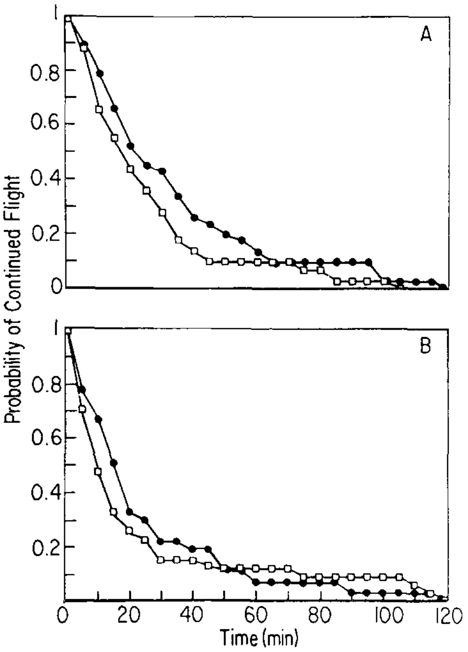

Fig. 3A, B. The probability that a female will continue to fly if she has already flown a given length of time for each treatment. **A** Females fed young foliage in the juvenile stage (□ = Y-Y; ● = Y-S). **B** Females fed senescent foliage in the juvenile stage (□ = S-Y; ● = S-S)

Results

Effect of age

Beetle age significantly affected the flight times of both males ($P<0.0001$) and females ($P<0.0001$) when the data for all treatments were pooled. However, when the effects of age on flight time were analyzed separately for each treatment (Table 1), age significantly affected female flight only when females were given the S-Y treatment ($P<0.007$) whereas male age significantly affected flight in all treatments (Y-Y, $P<0.04$; Y-S, $P<0.0001$; S-Y, $P<0.0005$; S-S, $P<0.01$). The significant effect of age on beetle flight appears to be due to the short flight times of both male and female beetles at 5 days post-eclosion relative to the flight times of beetles at other ages (Table 1). In addition, female flight peaked at approximately 7 days post-eclosion in each of the host treatments (Table 1).

Effect of female reproductive status

Within each age and treatment group, there was no significant difference between the flight times of females that had and had not oviposited. However, when the number of minutes flown in the test period just prior to oviposition was compared to that for the same female in the test period just after oviposition, a slight effect of reproductive status on female flight was revealed for females in the Y-S treatment ($P<0.08$). These females flew slightly longer (quantiles (min): 25% = 18.0, 50% = 46.0, 75% = 61.0) just prior to oviposition than they did just after oviposition (quantiles (min): 25% = 8.0, 50% = 26.0, 75% = 43.0).

The peak in flight activity appears to be influenced more strongly by female age than by her reproductive status. In addition, female flight activity appears to be relatively stable across the four host treatments when the effects of stage-specific host utilization are disregarded (below). In contrast, analysis of variance (ANOVA) revealed that age at first oviposition differed significantly ($F_{[3,113]}=10.23$, $P<0.0001$) among females in the four treatments (Fig. 2).

Effect of host treatments

Since beetle age affected flight times (above), the median flight time (i.e. over the 6 flight tests) for each individual was used in analyses that examined the effects of feeding regimens on beetle flight. These analyses revealed that the median flight times of males differed significantly among the four feeding treatments ($P<0.007$) whereas the median flight times of females were only slightly affected by the host treatments ($P<0.08$).

The data were also analyzed to determine whether flight was affected not only by host quality but also by the stage in development at which a beetle was fed a particular type of host. The effect of the juvenile host on the median flight times of each sex was determined in analyses that compared animals that had been fed the same adult host but different juvenile hosts (i.e. first analysis, Y-Y vs S-Y; second analysis, Y-S vs S-S). These analyses revealed that females fed young foliage in the juvenile stage tended to fly longer than those fed senescent foliage in the juvenile stage both when they were fed young foliage in the adult stage ($P<0.15$; quantiles (min): Y-Y 25% = 8.0, 50% = 17.8, 75% = 31.5; S-Y 25% = 4.2, 50% = 10.5, 75% = 24.0) and when they were fed senescent foliage in the adult stage ($P<0.15$; quantiles (min): Y-S 25% = 12.0, 50% = 20.5, 75% = 45.0; S-S 25% = 6.0, 50% = 16.5, 75% = 29.5). The net effect of the juvenile host on female flight times can be seen by comparing the positions of the curves in panel A of Fig. 3 with those in panel B of the same figure. Parallel analyses for males did not reveal a significant effect of the juvenile host on male flight (Fig. 4).

Animals fed young foliage in the juvenile stage weighed significantly more at adult eclosion than those fed senescent foliage (ANOVA; females, $F_{[1,115]}=70.50$, $P<0.0001$; males $F_{[1,115]}=36.89$, $P<0.0001$). Since body weight is sometimes a correlate of flight ability (Dingle et al. 1980; Palmer 1985), the data were analyzed to determine whether the slightly enhanced flight times of females fed young compared to senescent foliage in the juvenile stage were related to the weight they attained when fed these different juvenile hosts. Animals fed young and senescent foliage in the juve-

Table 2. Spearman rank correlation coefficients (r_s) and associated probabilities (p) for the relationship between female weight at eclosion and number of minutes flown at each age (days post-eclosion)

Treatments		Female age					
		5	7	9	11	13	15
Y-Y, S-Y	r_s	0.079	0.088	0.135	0.106	0.127	0.237
(df=60)	p	0.54	0.50	0.30	0.42	0.33	0.07
Y-S, S-S	r_s	0.365	0.285	0.265	0.273	0.205	0.108
(df=54)	p	0.01	0.03	0.05	0.04	0.13	0.44

nile stage but the same host in the adult stage were used for each of the analyses. There was a significant correlation between weight and flight time for females at each age except 13 and 15 days post-eclosion when they were fed senescent foliage in the adult stage. However, there was no significant correlation between these two variables when females were fed young foliage in the adult stage (Table 2). Similar analyses for males only revealed a significant correlation between weight and flight time when males were 5 days old and were fed young foliage in the adult stage ($r=0.248$, $P<0.05$).

The effect of the adult host on flight was examined by comparing the flight times of animals in the Y-Y and Y-S treatments and by comparing the flight times of animals in the S-Y and S-S treatments. Although the effects of the adult host were not significant for females, the analyses revealed that females fed young foliage in the adult stage consistently tended to fly less than those fed senescent foliage both when the juvenile host was young foliage ($P<0.21$; Figure 3A) and when it was senescent foliage ($P<0.31$; Figure 3B). In contrast, the adult host had a large effect on male flight. Males that were fed young foliage in the adult stage flew significantly longer than those fed senescent foliage when the juvenile host was young foliage ($P<0.01$; quantiles (min): Y-Y 25%=9.0, 50%=14.8, 75%=23.5; Y-S 25%=4.5, 50%=7.0, 75%=13.0) as well as when it was senescent foliage ($P<0.04$; quantiles (min): S-Y 25%=5.5, 50%=13.0, 75%=44.0; S-S 25%=0.5, 50%=7.5, 75%=14.0; Fig. 4, compare panels A and B).

The results suggested that the effects of young and senescent foliage on the flight times of adult females were a function of the time in development at which each host was consumed. Young foliage tended to enhance the flight times of adult females when they were fed this host during juvenile development. In contrast, senescent foliage tended to enhance the flight times of adult females when they were fed this host during their adult stage. Therefore, it was of interest to examine the effect of host combinations on female flight times. This was accomplished by comparing the median flight times of females in the Y-S and the S-Y treatments. Females in the Y-S treatment flew significantly longer than those in the S-Y treatment ($P<0.02$). This difference between Y-S and S-Y females clearly indicates that females do not fly in response to the average nutritional quality of their hosts.

Effect of sex

Until approximately 7 days post-eclosion females generally made longer flights than males in each of the four treatment groups (Table 1). Analyses of the effects of sex on the median flight times of animals in each treatment group revealed that females flew significantly longer than males when animals were fed senescent foliage in the adult stage (Y-S, $P<0.0002$; S-S, $P<0.01$; Fig. 5B and D). However, the flight times of males and females did not differ when animals were fed young foliage in the adult stage (Fig. 5A and C). The sexual dimorphism in flight appears to be due to two factors. Analyses of the effects of hosts (above) revealed that feeding on senescent foliage in the adult stage tends to enhance female flight but significantly depresses male flight. This effect, in combination with the increase in female flight that occurs as a consequence of feeding on young foliage in the juvenile stage, appears to account for the significant sexual dimorphism in flight that was revealed for particular host treatments.

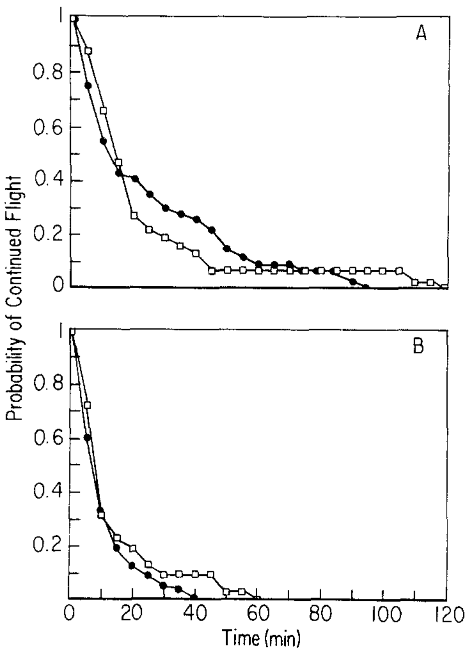

Fig. 4A, B. The probability that a male will continue to fly if he has already flown a given length of time for each treatment. **A** Males fed young foliage in the adult stage (□=Y-Y; ●=S-Y). **B** Males fed senescent foliage in the adult stage (□=Y-S; ●=S-S)

Discussion

Many insect species display an oogenesis-flight syndrome in which flight is greater in post-teneral, pre-reproductive adults than at later stages in adult life (Johnson 1969). Although the syndrome is strictly defined with respect to migratory flights, it is of interest to investigate whether there

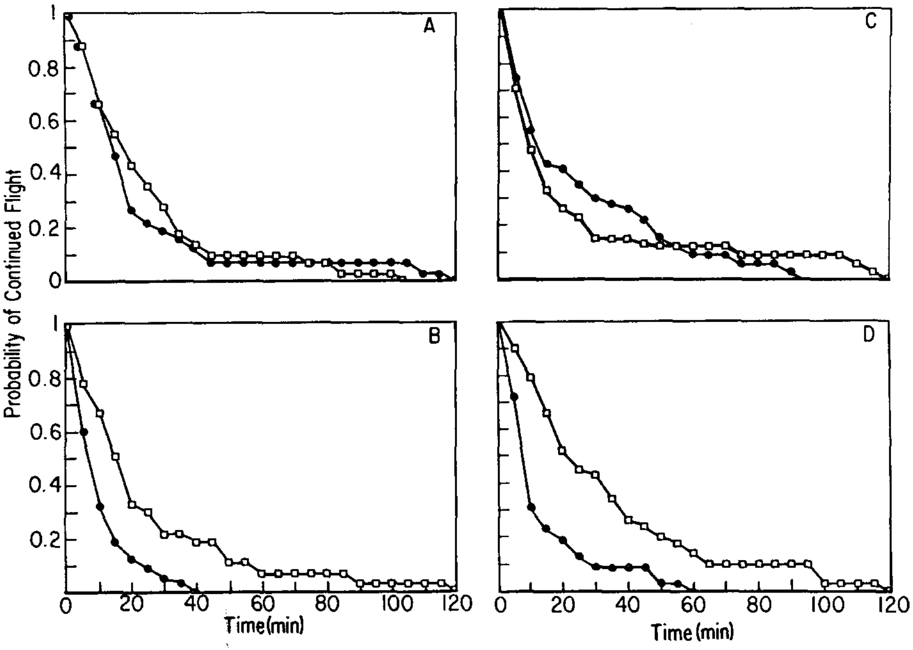

Fig. 5A–D. Sex-specific effects of the treatments **A** Y-Y; **B** Y-S; **C** S-Y; **D** S-S on median flight times (□ = females; ● = males)

is a general interaction between flight and the onset of reproduction in species that disperse but in which a large proportion of the population does not move long distances. Observations of *E. varivestis* in the field suggest that this species is not characterized by a high proportion of long-distance migrants. More than 50 percent of adults that were individually marked, stayed within a field containing patches of young bean plants throughout the greater part of the beetles' life spans (Saks and Stinner, pers. observ.). Thus although individual *E. varivestis* disperse, there is no indication that this is a truly migratory species.

Regardless of host treatment, females tended to make their longest flight at approximately 7 days post-eclosion (Table 1). This laboratory observation seems to reflect movement probabilities in the field since studies of *E. varivestis* showed that emigration from patches of host plants peaked when beetles were approximately this age (Blau and Stinner 1983).

Mean age at first oviposition ranged between approximately 8 and 11 days post-eclosion across the various host treatments (Fig. 2). Thus, superficially, *E. varivestis* appears to display an oogenesis-flight syndrome since peak flight activity (Table 1) tended to precede reproduction. However, several observations suggest that the oogenesis-flight syndrome is not clear-cut in *E. varivestis*. First, although the peak in flight activity was prior to the mean age at first oviposition of females in each of the treatment groups, *E. varivestis* from North Carolina often begin ovipositing by day 6 post-eclosion when hosts are uniformly good throughout development (Saks 1987a). Thus it is possible that some females oviposit prior to taking their longest flight. Second, the presence of eggs in patches of beans in which first generation females developed as larvae suggests that at least some portion of the female population may oviposit prior to moving among adjacent bean fields (Saks 1983). Third, analyses of the flight test data did not reveal the significant decrease in the length of post- compared to pre-oviposition flights that characterizes the oogenesis-flight syndrome (Johnson 1969). Finally, whereas host treatments significantly affected age at first oviposition (Fig. 2) they did not affect the age at which females made their longest flights (Table 1).

A significant decrease in flight activity after the onset of reproduction and a strong influence of reproductive development on flight behavior characterize the oogenesis-flight syndrome. However, neither characteristic was apparent for *E. varivestis*. Rather, it seems that females reach a peak in flight ability and retain the ability to disperse regardless of their reproductive status. The insensitivity of the age at which peak flight activity occurred to both reproductive development and host conditions is interesting in its own right since many other life history traits of *E. varivestis*, including the duration of flight (below), are sensitive to host variation (Saks 1987a; 1987b).

Determinate (bush) bean cultivars are commonly planted throughout the U.S. In some determinate cultivars, such as Long Tendergreen, the young foliage from pre-bloom and flowering plants has a significantly higher protein concentration than does senescent foliage from plants that are setting seed (Saks 1987a). This change in the nutritional quality of bean foliage often occurs within the lifetime of individual beetles (Saks 1983). In addition, the short maturation times of determinate cultivars enable farmers to plant sequentially throughout the growing season. Thus plants in one field can be setting seed and will therefore be low in foliar protein, whereas plants in a neighboring plot or row can be pre-reproductive and thus will have relatively high levels of protein. Consequently, individual *E. varivestis* in North Carolina are likely to feed on young and senescent bean foliage at different times during their development.

Host nutritional quality influenced flight times in a complex manner. Male and female flight times were differently influenced by young and senescent foliage and by the time in beetle development at which a particular type of host affected subsequent flight. Whereas the juvenile host tended to have the greatest influence on female flight, the adult host had a significant effect on male flight times. Moreover, whereas feeding on senescent foliage in the adult stage tended to enhance female flight, it significantly depressed male flight (Figs. 3, 4). Thus both an individual's sex and its particular feeding history contribute to its flight ability.

The tendency of females to fly longer when they were fed young compared to senescent foliage in the juvenile stage seems to be related, in part, to the higher weight attained by females when fed young compared to senescent foliage. The positive correlation between female weight and flight times when females were fed senescent foliage in the adult stage (Table 2) suggests that juvenile fat body reserves may be used for flight in *E. varivestis*. However, the absence of a correlation between these traits when females were fed young foliage in the adult stage suggests that juvenile fat body reserves may contribute to flight only when individuals are nutritionally stressed in the adult stage.

Two lines of evidence suggest that males differ from females in their utilization of juvenile reserves for flight. First, the juvenile host had no effect on male flight (Fig. 4) although it significantly affected male weight (a trait that should be positively correlated with the quantity of stored juvenile fat body reserves). Second, in contrast to the situation for females, male weight and flight times were not significantly correlated when males were grouped by adult host. A correlation between these two traits for females but not for males may be indicative of a physiological difference that underlies male and female flight behavior. Males and females may differ in the type or quantity of juvenile reserves that can be mobilized for flight or may differ in their ability to mobilize such reserves.

Blau (pers. comm.) collected *E. varivestis* that were emerging from the leaf litter after breaking diapause. He found a significant correlation (Spearman rank correlation $(r_s)=0.243$, $n=73$, $P<0.04$) between the number of flights taken from a stable platform and an animal's flight time. Thus it seems that *E. varivestis* is similar to other species for which flight times are reflective of movement probabilities (Dingle 1965; Rose 1972; Rankin and Rankin 1980; Davis 1981; McAnelly 1985; McAnelly and Rankin 1986). It is therefore reasonable to consider the implications of the data from the tethered flight assays with respect to the population and mating structure of *E. varivestis* in nature. First, since particular types of hosts enhanced female flight, and since females mate repeatedly throughout their lifetimes (Saks, unpublished work), it is likely that there is substantial gene flow among local populations. Second, the significantly longer flight times of females compared to males when animals were fed low nutritional quality foliage throughout development (Fig. 5B) suggest that females may be more likely than are males to emigrate from fields containing this type of foliage. Similarly, females may also leave fields more readily than males when both sexes feed on young foliage during juvenile development but when hosts have begun to mature by the time animals reach adulthood (Fig. 5D). Thus sex ratio is likely to be strongly male biased in fields in which individuals have fed on low quality foliage throughout both the juvenile and the adult stage and in fields in which plants mature during the development of *E. varivestis*. Male-biased sex ratios should strongly influence the magnitude of competition among males for mates and may thereby affect sexual selection in this species (Saks, unpublished work).

The results also have implications with respect to the population dynamics of *E. varivestis* in North Carolina where animals are likely to encounter sequences of hosts similar to those used in this research (Deitz et al. 1976; Saks 1983, 1987a, b). First, the abundance of adults in fields of beans may be due, in part, to the past and present quality of the available bean foliage. Second, the ability of females to fly even after the onset of reproduction suggests that host quality may affect the distribution and local density of beetles in subsequent generations. Thus the population dynamics of *E. varivestis* may be affected not only by the prevalence in the U.S. of bean monocultures (rather than di- or polycultures of beans with other crops), and by other environmental factors (Sweetman 1932; Kitayama et al. 1979; Lockwood et al. 1979; Wilson et al. 1982; Blau and Stinner 1983), but also by the nutritional complexity of the foliage within and among neighboring fields.

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