

## THE FLIGHT AND MIGRATION ECOLOGY OF THE RED MILKWEED BEETLE (*TETRAOPES TETRAOPHTHALMUS*)<sup>1</sup>

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**Abstract.** Laboratory experiments showed that female *Tetraopes* beetles possess greater flight capacity than males and that flight capacity is positively correlated with size. Take-off tendency, however, is higher in males and is negatively correlated with size. Both flight capacity and take-off tendency decline with age. Flight capacity is diminished markedly by starving for 48 h, and, in females, was not found to be influenced by oogenesis. The laboratory findings are consistent with field data showing that males move more often within patches (mate-searching flights) while females move more between patches (migration flights). The data suggest that the flight and migration ecology of short-flying sedentary species, like *Tetraopes*, may differ markedly from that of long-flying fugitive species.

**Key words:** *Asclepias syriaca*; dispersal; insect flight; migration; oogenesis; tethered flight; *Tetraopes*.

### INTRODUCTION

In insects, the development of the flight system and migratory behavior is reportedly flexible and under control of the endocrine system, which in turn is cued by the environment (Kennedy 1961, Johnson 1963, 1969). When conditions become, or are about to become, unfavorable for reproduction, energy normally allocated for egg production is used to develop and power the flight system, and the insect disperses (Johnson 1969, Dingle 1972). Following dispersal, egg development resumes. There is no doubt that this describes the flight and dispersal of many insect species (Johnson 1969, Dingle 1972), but does this view represent a general theory of insect dispersal? In order to help assess the generality of this view of insect migration, I investigated the flight ecology of a short-flying and sedentary species, the red milkweed beetle, *Tetraopes tetraophthalmus* Forster (Cerambycidae). (In this paper, the words 'dispersal' and 'migration' are used synonymously and refer to movements between breeding habitats.)

### MATERIALS AND METHODS

#### *The beetle and its host plant*

*T. tetraophthalmus* is a common univoltine beetle that feeds almost exclusively on *Asclepias syriaca*. The adults eat the leaves and flowers of the milkweed, while the fossorial larvae overwinter in the soil and feed on the milkweed roots. Although within-patch flights are common, the adults are not reported to be strong fliers (Chemsak 1963, Eanes et al. 1977). Dispersal in this species consists of flights between patches of its host plant.

#### *Rearing procedures*

Many of the experiments required beetles to be kept in the laboratory for periods of 24 h to 9 wk. Beetles

were housed individually in 1-L containers in the same chamber in which I flight-tested them. I supplied the beetles with fresh milkweed leaves every other day, and every 7–10 d I cleaned the containers.

#### *Measuring ability to disperse*

I tethered animals in still air for a 30 min test period to measure flight capacity (Davis 1980). I recorded the length of each flight during the test period, and except where otherwise noted, all flight times in this paper represent the cumulative flight time. All tethered flight tests were conducted in an environmentally controlled chamber, 28°C, 50% relative humidity.

#### *Measuring tendency to take off*

I measured take-off tendency using a cardboard platform that could be vibrated at a controlled frequency. Beetles were placed one at a time on a round (11 cm diameter) vertical cardboard substrate, which was connected at its center to the face of a loudspeaker by a short (3 cm) cardboard tube (4 cm diameter). The beetle was free to walk around the disk and to take off. If after 1 min the beetle did not take flight, the cardboard substrate was gently vibrated for 15 s using a voltage regulator. Beetles were permitted 30 s following the vibration to take off, and if they did not, they were subjected to a slightly stronger vibration. If necessary, progressively stronger vibrations were applied at 2.5 min and at 3.25 min. I recorded total time to take-off. If after 4 min the beetle had not taken off, it was removed, and the maximum time recorded. All take-off tests were conducted in the same chamber used to measure flight capacity.

#### *Measuring body size, reproductive state, and frequency and amplitude of wingstroke*

I used the width at the anterior edge of the elytra as a measure of body size. This was highly correlated with elytron length ( $r = 0.93$ , Mason 1964) and with body mass ( $r = 0.93$ ,  $n = 653$ , this study). Width measurements were made using a hand-held micrometer, mass measurements using a Mettler balance (to  $\pm 1$  mg). To

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assess the reproductive condition of females, I removed the ovaries, dried them for 48 h, and weighed them on a Sartorius balance to  $\pm 0.1$  mg. I used a stroboscopic light to measure frequency and amplitude of wingbeat.

#### Glycogen analysis

Glycogen is the main carbohydrate reserve in most insects (Rockstein 1978), and it is known to be an important flight fuel in many species (Weis-Fogh 1952). In addition, it is an important energy source and reserve for the central nervous system and for other basic life-supporting processes, including digestion and absorption (Rockstein 1978). Whether a flight fuel or an energy reserve, or both, the level of stored glycogen should significantly influence the survival of dispersing beetles. I measured glycogen levels using the anthrone reagent (Seifter et al. 1950).

### RESULTS

#### Flight capacity

The full wing stroke of *T. tetraophthalmus* encompassed a  $180^\circ$  arc, wings nearly touching at the top and bottom of the stroke. Comparable stroke amplitudes have been recorded in other Cerambycid beetles (Miller 1966). Frequency of wing beat ranged from 30 to 54 beats/s ( $n = 109$ ), and as in other species (Reed et al. 1942), was negatively correlated with size ( $r = -0.576$ ,  $P < .001$ ).

Most flight occurred during the first 10 min of the test period, and after 20 min flight was infrequent (Fig. 1). Virtually no beetles were in flight after 30 min. Flight times varied from 0 to  $>28$  min. Less than 10% of the beetles flew longer than 10 min. Beetles averaged approximately three flights per 30-min test period; however, this behavior also varied among individuals. While most beetles flew only once or twice, or not at

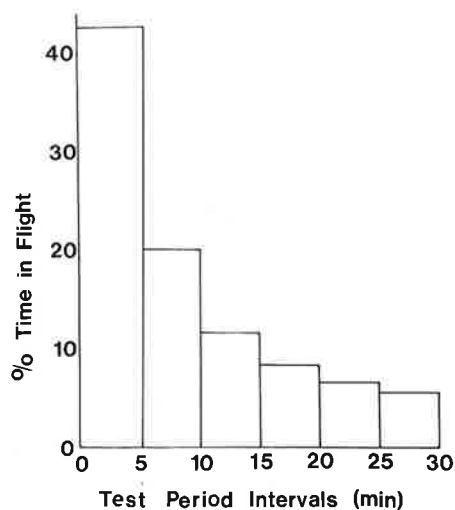


FIG. 1. Percent of the time spent in flight during each of the 5-min intervals of the 30-min test period. Data compiled from the flight logs of 60 beetles.

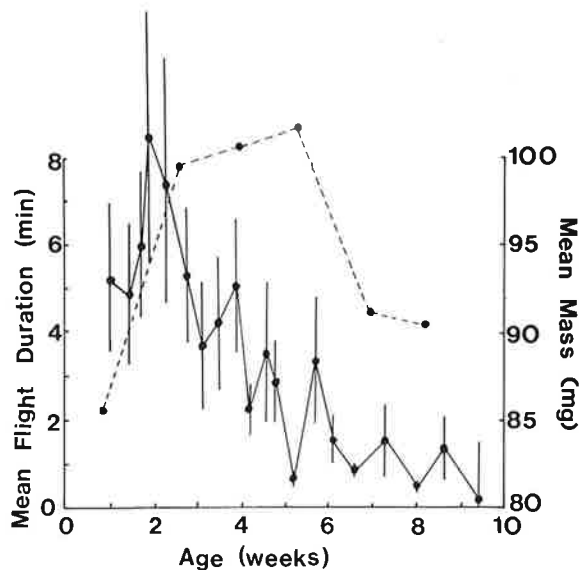


FIG. 2. Change in mean flight duration (—,  $\pm 1$  SE) and mean mass (---) of 12 beetles tested throughout their lives (flight duration data from Davis 1980).

all, a few exhibited more than 20 separate flights. Mean flight capacity peaked early in life, and then declined gradually until death. During the first 10 d, the increase in flight performance was matched by a 12% increase in body mass (Fig. 2).

On the average, females were longer fliers than males. Females ( $n = 273$ ) averaged  $3.43 \pm 0.25$  (SE) min, and males ( $n = 306$ ) averaged  $2.24 \pm 0.21$  (SE) min ( $t = 3.99$ ,  $P < .001$ , data log transformed before analysis). Both males and females varied widely in body size. Widths of females ranged from 2.92 to 5.39 mm, while males ranged from 2.78 to 4.75 mm. Although the two distributions largely overlap, females are significantly larger than males on average ( $t = 5.71$ ,  $P < .001$ ). Since there was a significant positive correlation between size and flight time ( $r = 0.122$ ,  $P < .01$ ), I subjected the data to an analysis of covariance to determine whether the greater flight time of females was simply due to their larger size. A difference due to sex did exist ( $F = 7.29$ ,  $P < .01$ ), indicating that, on the average, a female will fly longer than a male of the same size.

To determine how much of the individual variation in flight capacity could be explained by differences in age, size, sex, and day-to-day variation (the latter perhaps due to such factors as time since last meal), I performed a two-factor multiple analysis of covariance on 14 males and 14 females from the same population which were housed and flight tested under identical conditions throughout their adult life. I found that day-to-day variation contributed 27.1% of the total variation, while age, sex, and size contributed only 6.7%, 2.4%, and 0.9%, respectively. Taken together, these factors explain only slightly more than a third of the total variation.

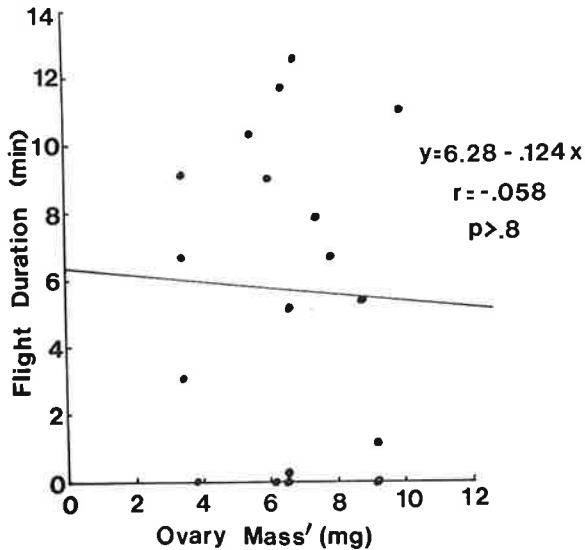


FIG. 3. Tethered flight time shown as a function of statistically adjusted mass (mass') for 18 *Tetraopes* females. Ovary masses were adjusted using a covariance analysis to eliminate the effect of overall body mass. See text.

I found a positive correlation between flight time and mass of the ovaries ( $r = 0.519$ ,  $P < .025$ ). However, when I used a covariance analysis to separate out the effects of body size, which was correlated with both ovary mass ( $r = 0.759$ ,  $P < .001$ ) and flight time ( $r = 0.729$ ,  $P < .001$ ), the correlation between ovary mass and flight time disappeared (Fig. 3). Therefore, flight capacity in females is unaffected by reproductive state.

Beetles kept without food lived for only a few days, and their flight capacity dropped to near zero after only 48 h without food (Fig. 4). I found a significant correlation between total body glycogen and body mass ( $r = 0.39$ ,  $P < .05$ ,  $n = 29$ ). Females possessed more glycogen ( $0.164 \pm 0.018$  mg [SE]  $n = 34$ ) than males ( $0.092 \pm 0.006$  mg,  $n = 24$ ) ( $t = 2.72$ ,  $P < .01$ ).

#### Tendency to take off

Although beetles could take off from any point along the rim of the disk, they generally took off from the upper portion, and the mean incline of the substrate at the point of take-off was  $36.3^\circ \pm 35.6^\circ$  ( $n = 306$ ). The latency period preceding take-off varied greatly among individuals. Some beetles took off in 3 s, and some (15.4%) never took flight. Take-off tendency, like flight capacity, is highest early in life, and declines with age (Fig. 5). Some beetles, however, exhibited high take-off tendencies throughout most of their life, while others always displayed very low tendencies.

Males were quicker to take flight than females. The mean time to take-off for females ( $n = 147$ ), was  $79.9 \pm 5.14$  s (SE), while males ( $n = 159$ ) averaged  $49.9 \pm 4.33$  s ( $t = 5.66$ ,  $P < .001$ , data log transformed before analysis). Twenty-five percent of the males took

flight in  $<20$  s, while only 10.9% of females took off in  $<20$  s ( $t = 5.34$ ,  $P < .001$ , arcsine transform before analysis, Sokal and Rohlf 1969). Only 10.1% of the males never took flight compared to 21.1% of the females ( $t = 2.70$ ,  $P < .01$ ). Size and take-off time are negatively correlated ( $r = -.217$ ,  $P < .001$ ). Nevertheless, a covariance analysis showed that even after size is taken into account, males still exhibit a significantly higher tendency to take off than females ( $F = 16.94$ ,  $P < .001$ ).

#### DISCUSSION

Beetles possess relatively limited powers of dispersal and carry very limited energy reserves. Once a beetle leaves a milkweed patch it will die unless it locates another patch or returns to its original patch within a day or two. If dispersal is risky, remaining in the patch involves comparatively few risks. Milkweed patches are relatively long lived. In marginal habitats or regularly disturbed areas like flood plains, milkweed patches may persist for many decades. In addition, *T. tetraophthalmus* suffers little predation and apparently little parasitism as well (Chemsak 1963). Thus, it has not been necessary for *T. tetraophthalmus* to become a fugitive species in order to survive. Instead, confronting relatively high, if not very high, risks due to mi-

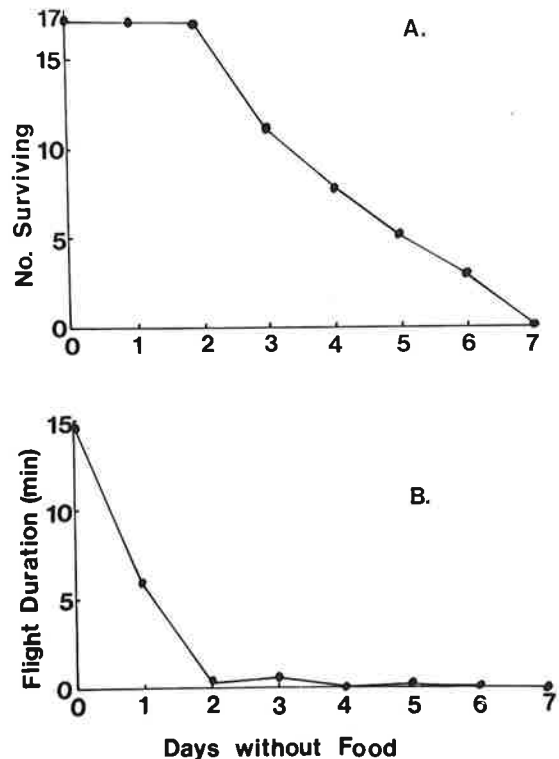


FIG. 4. A. Survivorship of field-captured beetles kept without food. B. Mean dispersal power of the four beetles (of the original 17) that exhibited a long tethered flight ( $>6$  min) shortly after collection (day 0).

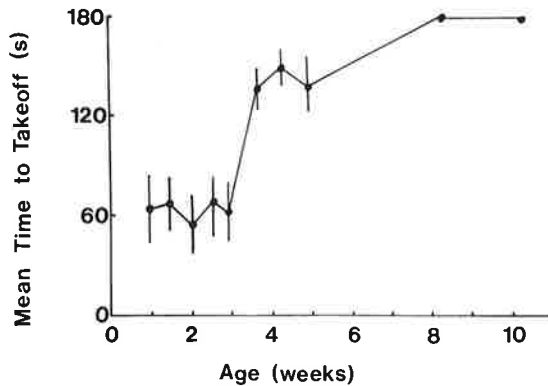


FIG. 5. Mean take-off time for 12 beetles tested throughout their lives. Error bars  $\pm 1$  SE. No beetles took off during the 8th and 10th wk; therefore SE = 0.

gration and a long-lived habitat, the species has evolved a distinctly sedentary mode of life. Beetle populations as close to each other as 400 m have been found to be genetically distinct, indicating little mixing (Eanes et al. 1977).

The tethered flight tests in this study showed that, on the average, females were more vagile than males, young beetles more vagile than old beetles, and large individuals more vagile than small ones. Thus, young, large females possessed the greatest dispersal power. Males, on the other hand, were much more likely to take flight than females. Along with other field data (Davis 1981a, Lathrop 1981, McCauley et al. 1981), these data point to a flight dimorphism in this species that is based on sex. Males are clearly more vagile than females within milkweed patches (Lathrop 1981, McCauley et al. 1981). These short-range flights (usually <20 s) probably represent searches for mates. Flight tests with tethered animals suggest that females might be responsible for most of the long-range dispersal flights, and although field evidence for this hypothesis is scanty, what data exist are supportive. In my 1981a study, 8 of the 10 dispersing beetles collected were female. In 1982, D. E. McCauley (*personal communication*) recorded two dispersal flights of 1 km, and both were by females.

I found no evidence of a trade-off between flight and reproduction, nor of any temporal partitioning of flight and oogenesis during development. Flight data suggest that dispersing females may be gravid, and indeed, when I provided oviposition material to females captured while dispersing (Davis 1981a), two of the eight laid eggs which hatched 10 d later.

Flight capacity in insects is known to have both genetic (Dingle 1968, Caldwell and Hegmann 1969, Rose 1972) and nongenetic (Wellington 1964, 1965, Utida 1970, Johnson 1976) origins. I do not know which is the principal cause for the flight differences in *Tetraopes*. Whether innate or not, however, these flight differences appeared to be intrinsic in the adults. By

this I mean that the flight capacity exhibited by individuals during the 1st 10 d following emergence, whether great or small, generally persisted throughout life. Moreover, these differences were not influenced by oogenesis (in females) or by sexual activity (Davis 1981b), and it is doubtful they were caused by environmental factors, since the beetles were from the same population and were housed and tested under identical conditions.

*Tetraopes* populations thus apparently contain two classes of beetles: those capable of sustained migratory flight, and those that are not. The existence of this flight polymorphism supports a bet-hedging theory of migration in *Tetraopes*. Patches of *A. syriaca* probably seldom persist longer than 20 yr, but during that time they provide everything beetles need to survive and propagate. Under these conditions selection might favor individuals that produce heterogeneous offspring, some of which stay in the patch, and some of which migrate to other patches.

Many of the recent ideas of insect migration are based on the results of studies of fugitive species in which most individuals can or do disperse, often over long distances. Although it is logical to study dispersal where it is most obvious, this approach can reduce the apparent diversity of dispersal syndromes in nature. The evolution of a flexible life history makes sense in fugitive species in which individuals may or may not encounter conditions requiring a long migratory flight. However, it should not be surprising that sedentary species might evolve a very different life history involving a relatively rigid development of the flight system. If the physiological and energetic demands of migration are small, then the insects may easily be able to maintain both the reproductive and flight systems simultaneously, as does *Tetraopes*. Lifespan may also limit the developmental possibilities. In the field, *Tetraopes* beetles live for only about 3 wk (Chemsak 1963). In short-lived species, there simply may not be time to separate reproduction and migration effectively.

Insects clearly exhibit a diversity of migration syndromes, and it is doubtful that any single theory can account for them all. I believe the most fruitful approach will be to contrast the life histories and habitat characteristics of species exhibiting different migration syndromes. The advantage of this approach is that it recognizes the inherent diversity of nature and still permits us to identify the environmental and developmental factors which have shaped the migratory habits of different species.

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