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VARIATION IN FLIGHT DURATION AMONG INDIVIDUAL *TETRAOPES* BEETLES: IMPLICATIONS FOR STUDIES OF INSECT FLIGHT

MARK A. DAVIS

Department of Biology, Dartmouth College, Hanover, New Hampshire 03755 U.S.A.

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Abstract—Milkweed beetles, *Tetraopes tetraopthalmus* (Forster) (Cerambycidae), were flight tested three times weekly throughout their lives. Flight durations peaked early in life and then declined rapidly with age. Significant variation existed (1) between individuals, with some flying for long periods of time, others for only a few seconds, and (2) within individuals, with some flying for long periods on some test days and very briefly or not at all on other days. Long and short fliers were indistinguishable on the basis of size, sex, or lifespan. The data show that studies of insect flight will underestimate the number of long fliers in a population by as much as 50% or more unless individuals are flight tested more than once.

Key Word Index: Insect flight, variation in flight, Coleoptera.

INTRODUCTION

STUDIES on a number of insect species have shown that flight duration varies between individuals (DINGLE, 1965; CALDWELL and HEGMANN, 1969; ROSE, 1972). JOHNSON (1976) pointed out that before considering the causes for individual differences, it would be useful to know how the flight of individuals varies with age. However, studies of flight variation with age usually have been based on average flight durations of many individuals (WILLIAMS *et al.*, 1943; DINGLE, 1965; RYGG, 1966).

This paper presents the results of a study of the red milkweed beetle, *Tetraopes tetraopthalmus* (Forster), in which individuals were flight tested three times weekly throughout their lives.

MATERIALS AND METHODS

Tetraopes is host specific to common milkweed, *Asclepias syriaca*, is univoltine, and is macropterous throughout its range of north central and eastern United States (CHEMSAK, 1963). In New England, the first beetles emerge in late June and populations persist until the middle of August.

On 18 June 1979 12 beetles (7 females and 5 males) were collected from a milkweed patch in Thetford, Vermont. The beetles were housed separately in individual containers in a temperature controlled chamber (28 + 1°C) with a 16 hr light–8 hr dark photoperiod. Beetles were provided with fresh milkweed leaves daily and they were flight tested every Monday, Wednesday, and Friday for the first five weeks, and at least once weekly after that.

The beetles were flight tested in the chamber using a still air tethering technique (DINGLE, 1965). Individual beetles were suspended from an applicator stick with a small bit of adhesive for a period of 30 min. Loss of tarsal contact was sufficient to provoke flight and total cumulative flight time (usually encompassing from 1 to 5 flights) was recorded during the 30 min test period. Body width (at anterior edge of elytra) and weight of each beetle were taken on the day the beetles were collected and at three other times during the season. A Mettler balance was used to weigh the beetles and a hand held micrometer to measure body width.

RESULTS

All individuals lived for at least four weeks following collection, and three individuals lived for more than nine weeks. The mean longevity following collection was 47 days. There is no doubt the lifespans of the beetles were extended under the favourable laboratory conditions. Most *Tetraopes* beetles in the field live for about 3–4 weeks (EDGREN and CALHOUN, 1958; CHEMSAK, 1963). Therefore, in the calculations and discussions that follow, it has been assumed that the normal life span of *Tetraopes* is about four weeks, and except where otherwise noted, only the flight data obtained during the first 28 days following collection have been used. (Since a search of the Thetford milkweed patch on 16 June failed to turn up a single beetle, and since *Tetraopes* has a teneral period of about six days, during which the beetles remain in or near the soil, the 12 individuals were approximately one week old and just post teneral when collected).

When the flight results of all 12 beetles are combined, the data show a peak early in life followed by a fairly rapid decline (Fig. 1). While not universal, this trend has been commonly observed in other insect species (WILLIAMS *et al.*, 1943; DINGLE, 1965; RYGG, 1966). Total flight time during the 30 min test periods ranged from 0 to 29 min. The distribution of flight

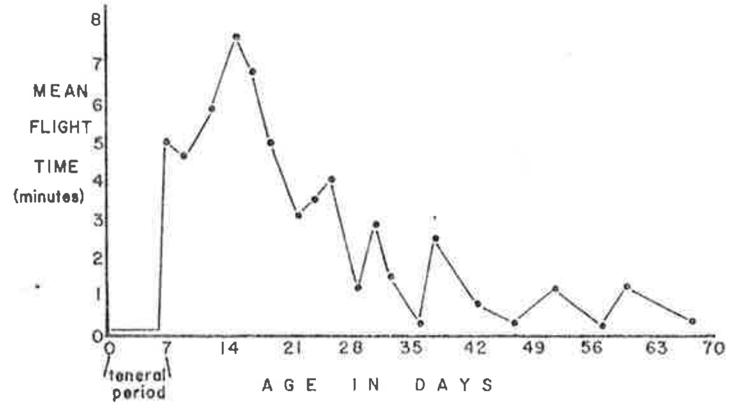

Fig. 1. Change in mean flight duration with age ($n = 12$).

durations for all 12 individuals is skewed toward the short durations. Beetles flew for less than 2 min during 108 or 69% of the 156 test periods.

These mean trends notwithstanding, significant variation in flight performances exists between individuals (Fig. 2) [Kruskal–Wallis coefficient $H = 49.8$, 11 d.f., $P < 0.001$ (SOKAL and ROHLF, 1969)]. The data show that there are two distinct types of beetles: those that exhibit a propensity for sustained flight sometime during their life, and those that never fly for more than a minute or two. The weights, widths and life-spans of the four longest fliers (Nos. 1, 7, 9, 11) and the four shortest fliers (Nos. 4, 6, 10, 12) were compared using a Mann–Whitney U test and were found to be not significantly different, $P > 0.1$. The same test was applied to males and females and again no difference in flight performance was found, $P > 0.05$.

The 12 beetles were flight tested 13 times each during the first 28 days, and a Spearman correlation coefficient (SOKAL and ROHLF, 1969) was obtained by using all pairs of sequential flight durations ($r = 0.4960$, $P < 0.001$). Although there is a significant positive correlation between the length of time a beetle flew one day and the length of time the same beetle flew two days later, the correlation is a weak one. One of the most striking results of this study is this weak correlation, indicating significant day to day variation in flight performances (Fig. 3). Eight of

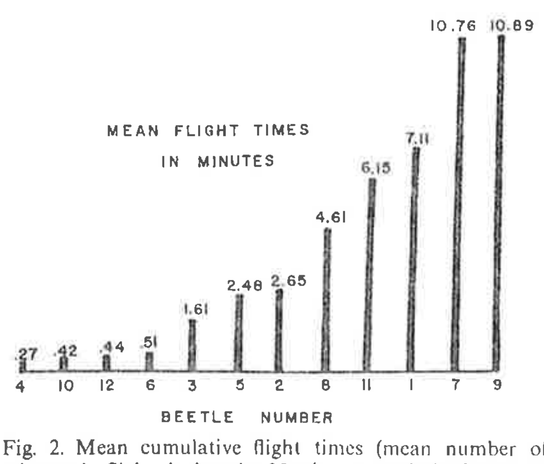

Fig. 2. Mean cumulative flight times (mean number of minutes in flight during the 30 min test periods) for all 12 beetles.

the 12 beetles exhibited a cumulative flight time greater than six minutes during at least one of the 13 test periods. However, not one of these individuals exhibited long flights on every test day. For example, beetles 1, 7, and 9, which usually flew for extended periods, occasionally were very reluctant to fly on some test days and exhibited only short flight durations. Then, just as suddenly, they would resume their long flights one or two test days later (Fig. 3).

DISCUSSION

It is significant that the patterns of flight variation obtained for *Tetraopes* are remarkably similar to those patterns obtained for other species (DINGLE, 1966; ROSE, 1972), despite the fact that the species possess very different migratory habits. *Oncopeltus fasciatus* (Heteroptera: Lygaeidae) is a migratory bug which recolonizes its habitats in the northern USA each spring (DINGLE, 1966). *Tetraopes* overwinters in the soil beneath its host plant and migration consists only of local flights between milkweed patches. *Cicadulina* spp. (Homoptera: Cidadellidae) consist of long and short body morphs, corresponding to short and long fliers, which vary in abundance during the season (ROSE, 1972). Even though the mean flight durations varied by more than an order of magnitude (e.g. *Tetraopes* and *Oncopeltus*), the three species share the following flight patterns in common: (1) Most flights are for a relatively brief duration; (2) Some individuals never fly for an extended period; (3) Individuals that do fly for an extended period on some test days, fly only briefly on other days. Thus, significant variation exists between and within individuals of all three species.

While a flight continuum definitely exists in *Tetraopes*, the data indicate that samples must be tested on several occasions to identify all the long fliers. This daily variation in flight duration represents a major source of experimental error in insect flight studies and has not been previously indicated.

In this study, eight of the 12 beetles flew longer than six minutes at least once during their life. However, on any test day, not more than five individuals exhibited these long flights, and on some days, only one or two individuals flew for extended periods. To be more specific, on the average there was a 36%

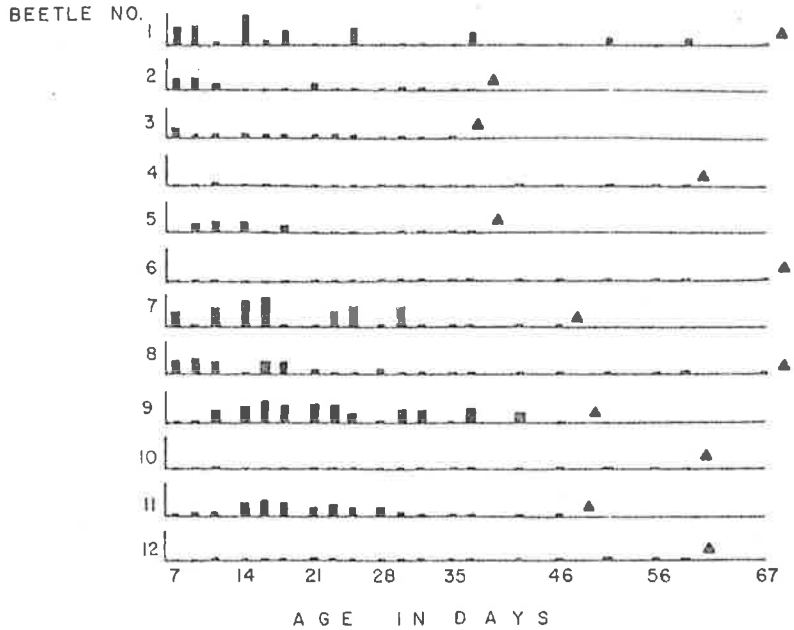

Fig. 3. Daily variation in flight duration for individual beetles. (The y axis extends from 0 to 30 min for all 12 beetles.) ▲ Indicates the death of a beetle.

chance that a particular long flying individual would exhibit a long flight (>6 minutes) on a given test day. Given a probability of long flight, the proportion of long fliers actually identified as long fliers increases with the number of test days (n) according to the function $1 - (1 - p)^n$. If $p = 0.36$, the sample must be tested on seven different occasions to be sure that no more than 5% of the long fliers have gone undetected. However, the number of test days can be reduced by testing the insects during the peak flight period. In this study, $p = 0.52$ during days 7–19, meaning that only four test days would be required to identify 95% of the long fliers at this time. Thus, studies will almost certainly underestimate the number of long fliers in a population, perhaps by as much as 50% or more, if individuals are flight tested only once (Dingle, 1965; Caldwell and Hegmann, 1969).

When insects have been flight tested, the resulting flight distributions have been sharply skewed, with most flights being relatively brief (Dingle, 1965; Caldwell and Hegmann, 1969; Rose, 1972). However, the skew in insect flight distributions will be significantly reduced if individuals are flight tested more than once, and the mean flight value is plotted. In fact, if instead of the mean, the longest flight duration for each individual is plotted, the skew could disappear altogether. In this study, longest flights less than 5 min were exhibited by four individuals, between 5 and 10 min by two individuals, between 10 and 15 min by three individuals, and greater than 15 min by three individuals. The actual migratory potential of a population is probably best characterized by using the latter procedure, since an insect need only be capable of migrating during a short period of its life to be a migrant.

The significance of the experimental error introduced by this day to day variation in flight duration is clear, however the physiological basis for this sporadic variation is more difficult to explain. At least 48 hr transpired between all flight tests and it is doubtful that beetles require more time to recover from a 20 min flight, i.e. No. 9 flew for more than 10 min on six consecutive test days.

A constellation of factors are known to influence flight duration. Flight requires the presence of certain key enzymes (Brosemer, 1965; de Kort, 1969). Muscles are known to histolyze in many insects (Johnson, 1976). Certain hormones have been shown to significantly influence flight durations (Wajc and Pener, 1971; Rankin, 1974). Insects use a variety of flight fuels, carbohydrates (Weis-Fogh, 1952; Karuhize, 1972; Bedford, 1977), lipids (Weis-Fogh, 1952; Karuhize, 1972) and amino acids (Bursell, 1963; Brouwers and de Kort, 1979), and the absence or very low levels of these substances will prevent flight.

However, while muscle histolysis, and levels of enzymes, hormones, and fuel vary significantly throughout the life of most insects, the change is usually a developmental one. And although flight ability is known to fluctuate widely during the lifetimes of some insects, e.g. due to histolysis followed by regeneration of the flight muscles (Reid, 1962; Stegwee, 1964; de Kort, 1969), these fluctuations require too much time and cannot account for the very short term fluctuations exhibited in this and other studies.

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