Temporal Flight Patterns in the Mexican Bean Beetle (Coleoptera: Coccinellidae) and their Relation to Weather[1]

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ABSTRACT The flights of adult Mexican bean beetles from experimental plots of lima beans and soybeans were monitored to determine the proximate cues to which beetles respond when initiating flight. Most beetles, including newly eclosed individuals, flew out of the plots within 1 week of their release. Two indices of activity relating to flight frequency and flight intensity varied similarly in response to weather conditions, and indicated that flight was related most strongly to temperature and wind speed. Flight intensity was then modeled as a nonlinear function of these two interacting weather variables. The model accounts for the observed bimodal pattern of daily flight activity.

Adaptations of insects for dealing with spatial and temporal variations in agroecosystem structure have been largely overlooked by applied ecologists in their efforts to model the dynamics of pest populations (Stinner et al. 1982). Foremost among these adaptations is the ability to move or disperse by flight. The influence of movement on population dynamics and distribution is generally recognized in theory (e.g., Den Boer 1968, Gadgil 1971, Hanski 1980). Empirical data on the role of movement in natural populations are lacking, however, and elements of agroecosystem heterogeneity and insect dispersal are rarely incorporated into the design of integrated pest management (IPM) strategies. Stinner et al. (1982) stressed the need for more detailed descriptions of population and individual behaviors in relation to resource structure, and for these interactions to be included in IPM models.

The current study was undertaken as a first step toward understanding the frequency and nature of flight in the Mexican bean beetle (MBB), *Epilachna varivestis* Mulsant, with the ultimate goal of incorporating movement processes into a model of the regional dynamics of this species. In many portions of the eastern United States, the MBB is a predictable spring colonizer of garden beans, *Phaseolus* spp., and occasionally develops large populations on soybeans, *Glycine max* (Thomas), later in the season (Carner et al. 1974). Adults overwinter in ground litter, and the survivors locate and breed in garden beans the following spring (Bernhardt and Shepard 1978). Movements of adults by flight among breeding habitats and overwintering sites are likely to play a significant role in the species' population dynamics (Stinner et al. 1982). Little is known, however, of the flight behaviors and capabilities of the MBB, and the few published accounts are anecdotal (see Auclair [1959] for review).

An initial model of the interfield movement of the MBB has been developed by Dohse (1982), and is particularly sensitive to the probabilities of moving for beetles in various behavioral states. More refined research is required to define the environmental and physiological parameters that affect these probabilities. The objective of the present study was to determine the proximate environmental cues to which beetles respond when initiating flight, because such cues influence the probability that beetles that are "ready" to fly actually take off. The ultimate factors that determine whether or not beetles will be "ready" (i.e., motivated to emigrate) when conditions are appropriate for flight are not addressed here. Our approach was to monitor the flights of MBB adults from experimental field plots and to relate patterns of emigration to the ages of departing beetles, host plant species, time of day, and weather conditions.

Materials and Methods

Description of Experimental Plots

Two field plots were located on a farm in Johnston County, N.C., ca. 23 km southeast of Raleigh. Each plot was 3.7 by 3.7 m, bordered on each side by 1.2 m of bare soil, and located within a 0.2-ha field of sweet corn (var. 'Seneca Chief') which was used as a buffer from other crops grown nearby. The soil was a fertilized, well-drained, coarse, sandy loam. One plot was planted on 6 May 1980 in 10 rows of soybeans (var. 'Davis'), spaced 0.4 m apart. Due to dry conditions during the summer of 1980 and defoliation by rabbits and *Heliothis zea* (Boddie), the soybean plants were poorly developed; by late August they were 0.3 to 0.5 m tall and in development stages R3 to R5 (Fehr et al. 1971). The second plot was planted on 3 June, 1980 in seven rows of lima beans (var. 'Henderson') spaced 0.6 m apart. By late August, the plants were about 0.3 m tall and flowering.

Eight sticky traps were situated around each plot (Fig. 1A). Along each side was a trap (3.0 m long by 1.2 m high) constructed of 0.64-cm-mesh hardware cloth coated lightly with Stikem Special. These lateral traps were suspended by 3.0-m posts of angle iron (3.8 by 3.8 by 0.3 cm) so that they ran parallel to and 0.9 m from the edges of the plot, with their lower edges at the height of the crop canopy. To trap beetles that might have flown directly upward, four additional traps were suspended about 2 m above each plot on frames constructed of angle-iron posts and beams. These overhead traps (Fig. 1B) were composed of clear plastic, stretched in
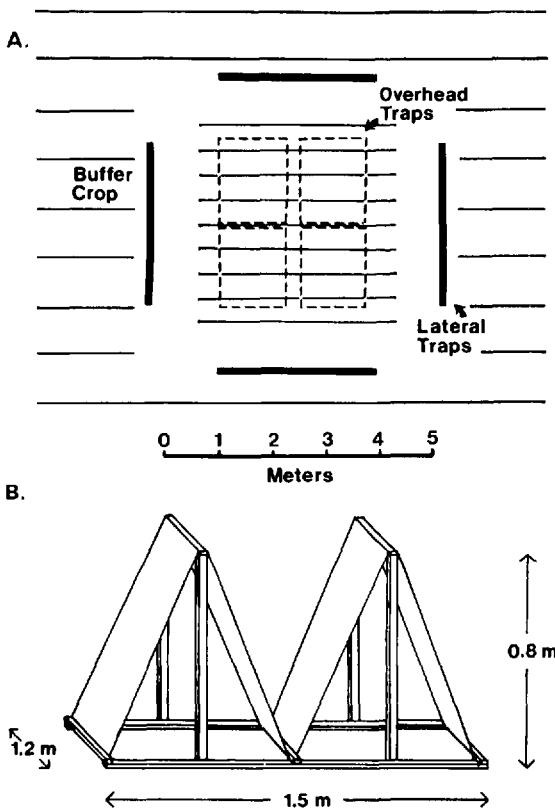
A.

B.

FIG. 1. (A) Schematic representation of the view looking down upon an experimental plot, showing the positions of the lateral and overhead sticky traps. (B) Design of one of the four overhead traps situated above each plot. A sheet of clear plastic (1.2 m wide) is stretched over a wooden frame. For clarity, the three small troughs that serve to catch insects sliding to the bottom of the plastic have been omitted from the diagram.

an inverted "W" shape over a wooden frame, and coated underneath with Stikem Special. Troughs of hardware cloth were suspended beneath both overhead and lateral traps to catch insects that slid off the sticky surfaces. The extent to which sticky traps impeded wind flow across the plots is unknown, but is assumed to be small, since the traps were constructed of a relatively large-mesh hardware cloth to minimize resistance, and were situated so as to leave about 40% of the perimeter completely open to air flow.

Sources of Beetles

Eighty percent of the beetles in this study were obtained from field cultures initiated with adults collected from gardens near West End, N.C. (Moore County) on 5 June and 8 July 1980. These beetles were transferred to North Carolina State University's Central Crops Research Station at Clayton and were confined in field cages on bush beans (var. 'Contender') for oviposition. To minimize egg losses due to predation and cannibalism, clutches were collected, stored in an open-air insectary until hatched, and replaced in the field as cohorts

of 1st-instar larvae. Pupae were collected from this culture and stored in plastic boxes in the insectary. Newly eclosed adults were allowed to harden and feed for 1 day before handling. On the second day, they were sexed, individually marked with color- and position-coded dots of paint on the elytra, and placed in the appropriate field plot beginning 5 August. These beetles will subsequently be referred to as "class 1 beetles." They were not mature enough to fly on the second day, so that they were required to acclimate to plot conditions for at least 1 day before flying. Additional adults of unknown age ("class 2 beetles") were collected from soybean fields in coastal counties, marked, and released in the study plots at times of the day when flights were not observed to occur. Most of these beetles remained in the plots for at least 1 day before flying. Those that were found to be trapped on the first survey subsequent to their release (when on the same day) were excluded from the analysis.

Data Collection and Analysis

Flight was monitored in two ways. (1) Direct observations of beetle activity were recorded by an observer who walked slowly among the rows at 0.5-h intervals during portions of the day selected to encompass the apparent range of beetle activity. Beetles were counted and categorized based on their activity: sedentary (sitting, feeding, mating); preflight (beetles seen attempting to fly or perched high on a plant flexing the wings); or flying (either within or out of the plot). Beetles in the latter two categories were included in the calculation of flight intensity (see below). In all, 243 visual surveys were conducted on 44 days between 4 September and 20 October. (2) Flying beetles were caught in the sticky traps. They were counted and collected, and their marks were recorded, from one to four times daily, the frequency of monitoring increasing with beetle activity. Traps were not always monitored at the same time from 1 day to the next, but surveys were generally limited to the following periods: early morning (at or before 0900 h), late morning (1030 to 1200 h), midafternoon (1430 to 1600 h), and early evening (after 1800 h). Beetles collected from the traps were stored temporarily in vials with paint thinner to remove the sticky coating, and then transferred to alcohol for later dissection to determine reproductive status.

Because the numbers of beetles within a plot fluctuated over time, the number of active beetles at any given time was related to the size of the flight-mature population (FMP). The FMP is an estimate of the number of beetles capable of flight in a given plot at a particular time. It is calculated as

$$FMP_x = FMP_{x-1} - F_{x-1} + I_{x-1} \quad (1)$$

where FMP_x refers to the population size at the beginning of the current time interval (i.e., day or survey); FMP_{x-1} is the population size at the beginning of the previous time interval; F_{x-1} is the number of insects flying out of the plot during the previous interval, calculated as the product of the number of beetles trapped

and the inverse of the trap capture efficiency (see below); and I_{n-1} is the increment to FMP during the previous interval. Beetles placed out as new adults were added to the FMP in daily increments after their placement, based on the maturity schedule represented by the early portion of the soybean curve in Fig. 2 (class 1 curve, days 1 to 9; see below). Beetles of unknown age (class 2) were assumed to enter the FMP on the first day (or survey) after their placement. The number of active beetles (observed flying), expressed as a percentage of the FMP, will be referred to as the flight intensity. FMP and flight intensity were calculated only for data from the lima bean plot, since mortality there was low (see below) and estimates of the FMP matched field censuses near the end of the experiment.

Weather Monitoring

Weather variables were monitored continuously throughout the study. Recording thermistors were located within the study plots to measure temperature at the height of the crop canopy. A weather station 12 m from the study plots recorded temperature and relative humidity at heights of 1.4 and 1.0 m above ground, respectively; and wind speed and direction at 2.0 m

above ground. Data on barometric pressure were obtained from a station operated by the Central Crops Research Station, located 5 km away.

Results

Fate of Beetles

By choosing a dry site for the experimental plots and by widely spacing lima bean rows, an attempt was made to create an unfavorable environment for the MBB, which is sensitive to moisture stress (Kitayama et al. 1979, Wilson et al. 1982). The objective was to provide a situation where hosts were available as food for the new adults but where beetles would emigrate as soon as they were capable of flight. Conditions in the soybean plot proved too stressful; nearly 20% of the beetles died before they were able to leave the site, and their carcasses were found among the soybean rows. Conditions in the lima bean plot appear to have suited the objective well; only 3% of the beetles turned up as carcasses. Most adults left the site within a few days of their placement.

In all, 1,023 and 953 beetles were released in the soybean and lima bean plots, respectively, over a 10-week period from 5 August to 17 October 1980. The fate of the beetles placed in soybeans is uncertain due
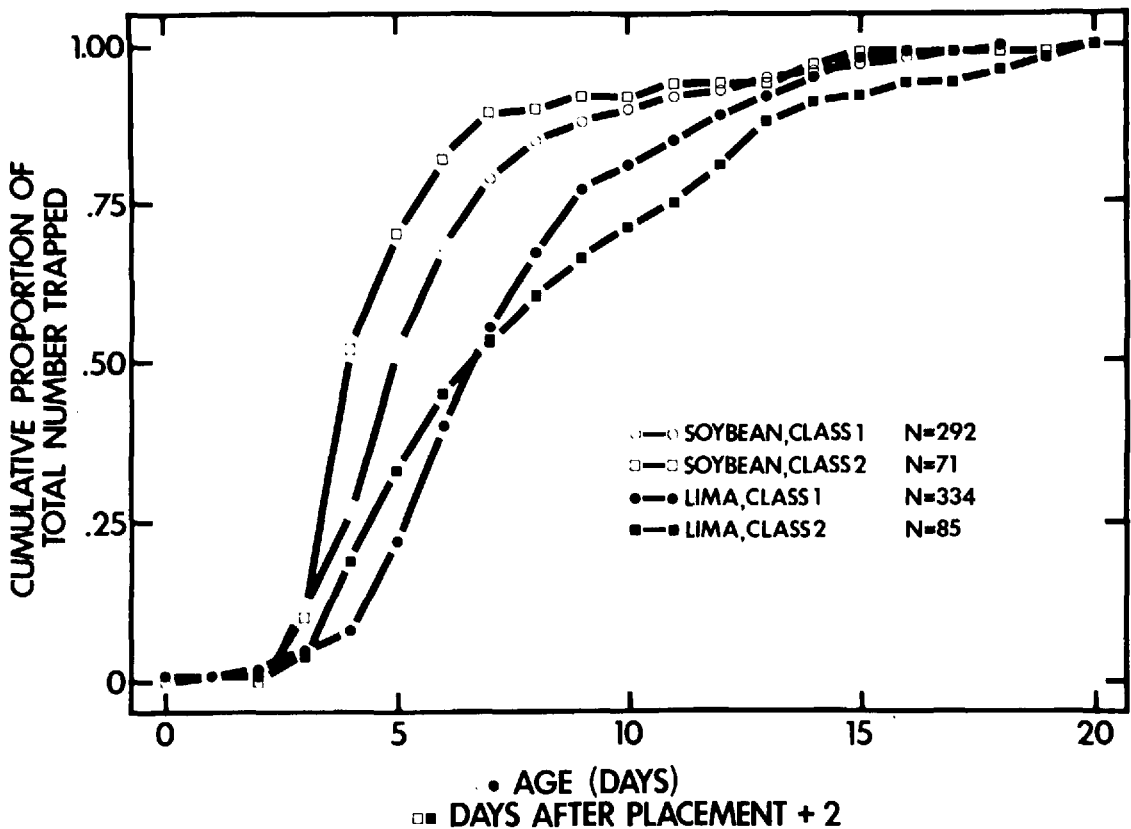

FIG. 2.   Cumulative frequency distributions of the ages of beetles caught in sticky traps (for class 1 beetles) or of the time elapsed since trapped beetles had been placed in the experimental plots (for class 2 beetles). Data for class 2 beetles are initiated on day 2 rather than day 0 for purposes of comparison with class 1 beetles, which are released on day 2 (i.e., at age 2). All data are for beetles placed and trapped during a month of consistently hot, dry weather subsequent to 26 August 1980.

to the high rate of mortality. Of the beetles placed in lima beans, 7.3% remained in the plot at the end of the experiment, and 58.3% were captured in the sticky traps. The remaining beetles that did not turn up as carcasses were assumed to have flown out of the plot and avoided the sticky traps. After these numbers were partitioned by beetle class, the trap capture efficiency (percent of flying beetles caught) was calculated to be about 60% for class 1 beetles and 50% for class 2 beetles.

Very few vertically oriented flights were detected. Only 1% of all beetles trapped in the lima bean plot and 5% of those trapped in the soybean plot were found in the overhead traps. The extent to which light reduction through these traps may have discouraged vertical flights is unknown.

At the latitude of our study area, adult MBBs are likely to be in diapause condition after midSeptember (Pfaender et al. 1981). Where possible, we examined our data visually for evidence that beetles late in the study (i.e., late September and October) behaved differently from those early in the study. No evidence of any differences was observed, and the data we report here are for the two groups combined.

Age at Flight

Most beetles that survived flew out of the experimental plots within 1 week after being released, although the exact shape of the flight-time distributions differed between plots and between beetle classes (Fig. 2). The shapes of the curves in Fig. 2 are determined, in part, by the schedule of maturation in flight capability and in part by behavioral preferences. Flight maturation is likely to be reflected only in the early portions of the curves for class 1 beetles, whereas behavioral preferences are important throughout the curves for all beetles. Both classes of beetles remained longer in the lima bean plot than in the soybean plot (Kolmogorov-Smirnov test, d_{max} = 102 for class 1 and 32 for class 2, $P < 0.01$). In the lima bean plot, the time elapsed before half the population had emigrated was 2 days longer for class 1 beetles, and 3 days longer for class 2 beetles than in the soybean plot. The difference between plots could signify either that beetles took longer to mature on lima beans or that they preferred to remain longer. Since the difference is apparent for class 2 beetles, which are presumed to be flight-mature, the latter alternative seems more likely. Also, in an earlier study (Lockwood et al. 1979), beetles attained reproductive maturity faster on lima beans than on soybeans. Only one of the four groups of beetles (i.e., the combinations of class 1 and class 2 beetles with lima beans and soybeans) exhibited any significant difference in flight distribution between the sexes (lima, class 1; Kolmogorov-Smirnov test, d_{max} = 22, $P < 0.01$), and that difference was slight (flight of males peaked 1 day later than that of females; otherwise, the distributions were similar).

Time of Day of Flights

On several days, sticky traps were surveyed at sunset and again shortly after sunrise the following morning to check for nocturnal flight activity. No beetles were found in the early-morning surveys, although considerable flight activity occurred later in the day, indicating that emigration occurs only during daylight hours.

The pattern of diurnal flight is illustrated in Fig. 3A. The data were collected on 17 days during a 1-month period of consistently hot, dry weather starting 26 August, when the temperature usually reached 31°C, with a vapor pressure deficit of 3.3 kPa, by 1500 h. Calculations of hourly trap catches were based upon trap surveys conducted at 3- to 4-h intervals. The total catch at each survey was divided by the number of daylight hours elapsed since the previous survey to obtain hourly rates of catch, which were then averaged. Thus, there is a tendancy for peaks and lulls in flight activity to be somewhat dampened and spread out in the curve. For example, the peak catch between 0700 and 0800 h may be an artifact, since means for the intervals 0700 to 0800 and 0800 to 0900 h are based mostly on the same (28 of 29) observations, i.e., those from surveys conducted at 0900 h. The true morning peak may well have occurred between 0800 and 0900 h. Most flights occurred early in the morning. The numbers of beetles trapped declined more or less steadily throughout the day, reaching a low from 1300 to 1600 h. A second, smaller peak of activity occurred within 2 to 3 h of sunset. The proportions of individuals composing these peaks were similar with regard to age, sex, and reproductive status. This bimodal pattern of flight did not persist later in the study when temperatures moderated and the weather became more variable. On some cool days, a single peak of activity occurred at midday.

Influence of Weather

The diurnal flight patterns described above suggest that flight activity may be limited to those periods of the day when weather conditions are appropriate. We examined this possibilty more closely by plotting each of two indices of flight activity as a function of temperature, wind speed, vapor pressure deficit, and barometric pressure. Since population sizes are seldom known in studies of this sort, the measure of flight activity usually reported is flight frequency, i.e., the proportion of total samples (usually trap catches) collected under a given set of conditions in which one or more flights (insects trapped) occurred (Taylor 1963). Accordingly, the results of our visual surveys are reported as flight frequencies (Fig. 4A). In addition, we report activity as flight intensity, i.e., percentage of the total population (FMP) observed flying or attempting to fly during the visual surveys (Fig. 4B).

The two measures of flight activity indicate a clear relationship between flight and at least two of the four weather variables examined. The relationship with air temperature at 1.4 m is most clear, with activity limited to the range of 20 to 34°C (upper limit estimated by visual extrapolation of the curve in Fig. 4B) and maximum at about 26 to 30°C.[2] Flight also declines with increasing wind speed and ceases completely above speeds of about 2.5 to 3.0 m/sec (5.6 to 6.7 mi/h). No clear
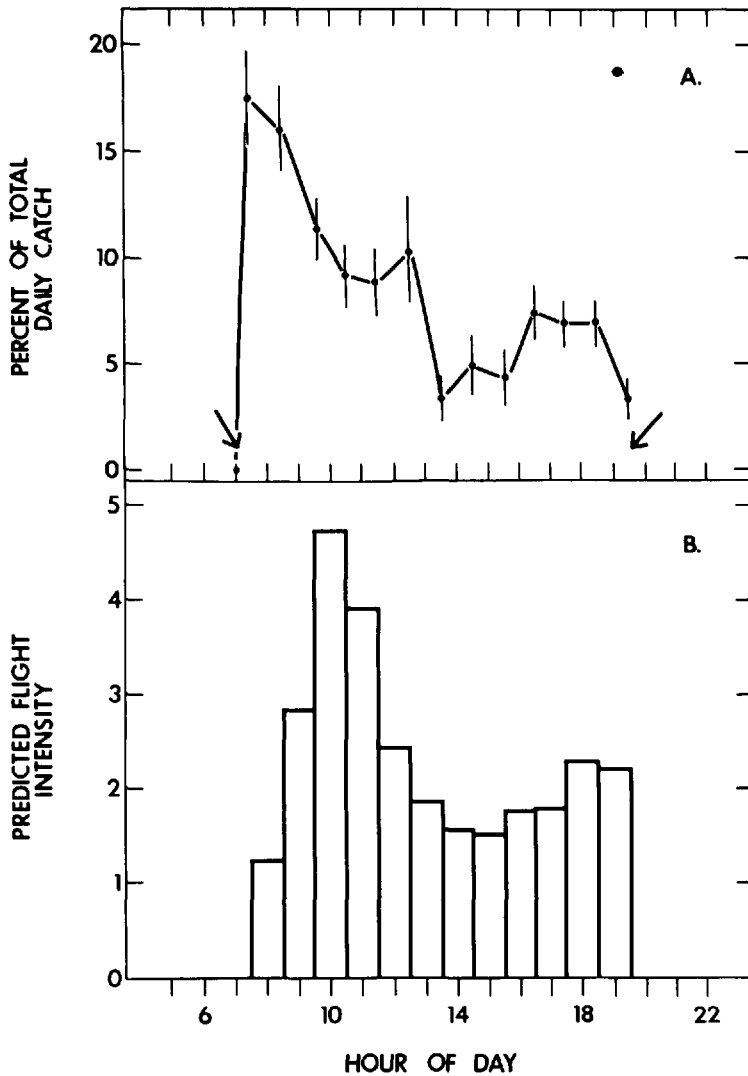
FIG. 3.   (A) Mean number of beetles trapped hourly in sticky traps, expressed as a percentage of the total daily catch. The data from the lima bean and soybean plots are combined; bars represent ± SEs. Arrows indicate sunrise and sunset. (B) Mean predicted FI (FI*) for hourly intervals over the same time period represented by the data in (A). See text for explanation.

relationship exists between flight and barometric pressure or vapor pressure deficit, within the observed ranges of these variables.

An initial model for MBB movement developed by Dohse (1982) does not include the effects of climatic variables, although one of the most sensitive parameters in the model is the probability of leaving a given field (a function of flight activity). Since temperature and

wind speed seemed to be most strongly related to MBB flight activity in the present study, a submodel was developed which mimics flight intensity (FI) as a function of these two variables. It appeared that the main effect of temperature was to change the peak FI, designated FI_{max}, observed over all wind speeds. FI_{max} was described as follows:

$$FI_{max} = 10.2 (1 - Z)^{3.39/0.96} \qquad (2)$$

if $18°C <$ temperature $< 35°C$, and

$$FI_{max} = 0 \text{ if temperature} \leq 18°C \text{ or} \geq 35°C \qquad (3)$$

where $Z = | 26.5 -$ temperature $| /8.5$.

(Parameters estimated by Marquardt's algorithm applied to means of the FI over successive 2°C intervals; SAS Institute, Inc. [1979]) For any given temperature, bee-
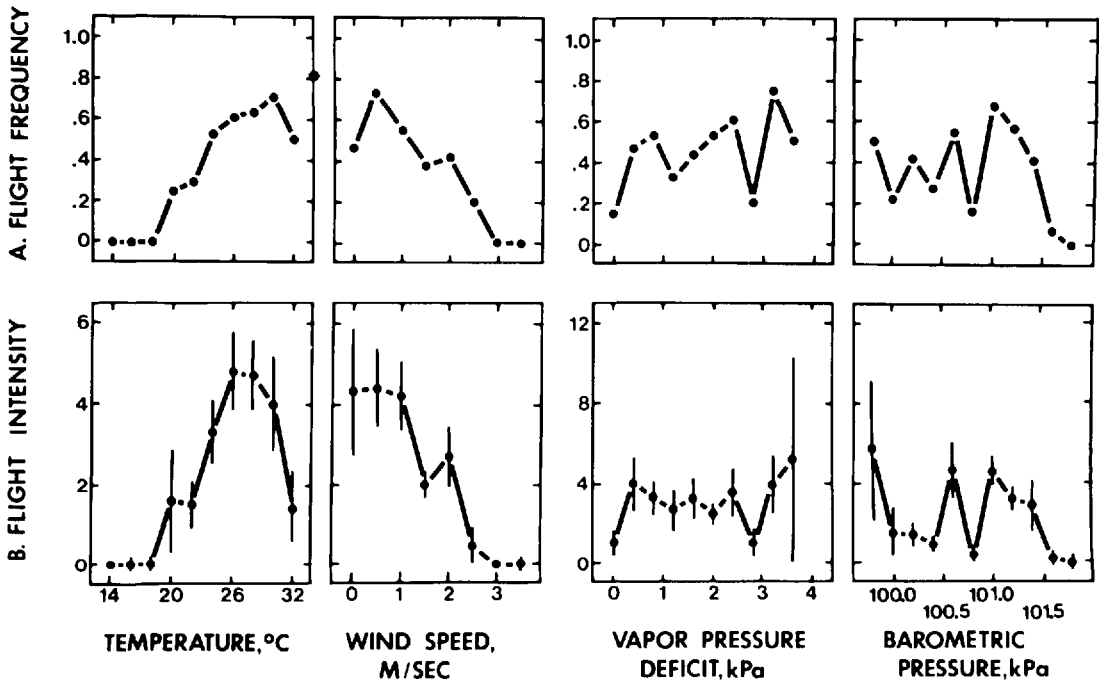
FIG. 4. Two measures of flight activity as a function of temperature, wind speed, vapor pressure deficit, and barometric pressure. Data represent direct observations of beetle activity. Values of weather variables are for hourly intervals, recorded at 1 to 2 m of elevation. (A) Flight frequency is the proportion of total surveys during which at least one flight attempt was observed. (B) Means ± SEs are presented for FI. Absence of SEs indicates a sample size of one.

tles did not fly at 0 m/sec or above 3 m/sec, and FI between these wind speeds resembled a skewed sine curve. (Note that Fig. 4B lacks the resolution to show the drop in activity when wind speed = 0.) Therefore, the predicted FI, designated FI*, was described by:

$$FI^* = \frac{FI_{max}}{2} \{sin \{2\pi w^{1.64} - \pi/2\} + 1\} \quad (4)$$

if 0 < wind < 3 m/sec, and

$$FI^* = 0 \text{ if wind } = 0 \text{ or wind } \geq 3 \text{ m/sec} \quad (5)$$

where w = (3 − wind)/3. The power parameter for w (i.e., 1.64) was estimated by linear transformation and standard regression analysis of means of FI over successive 0.5-m/sec intervals of wind speed (df = 13, F = 33.18, P < 0.0001, r² = 0.7344).

The variance in observed flight activity that remained unaccounted for by expressions 4 and 5 above (expressed as deviations of observed from predicted values) was examined for any influence of solar radiation, atmospheric pressure, or vapor pressure deficit. No clear relationship existed between the residual variance and radiation or atmospheric pressure, but all else being equal, flight activity decreased at vapor pressure deficits above 1.8 kPa (Fig. 5). Therefore, when vapor pressure deficits exceeded this value, an expected deviation (calculated from the regression in Fig. 5) was added to the value of FI* from expression (4) (negative values of FI* were set to 0).
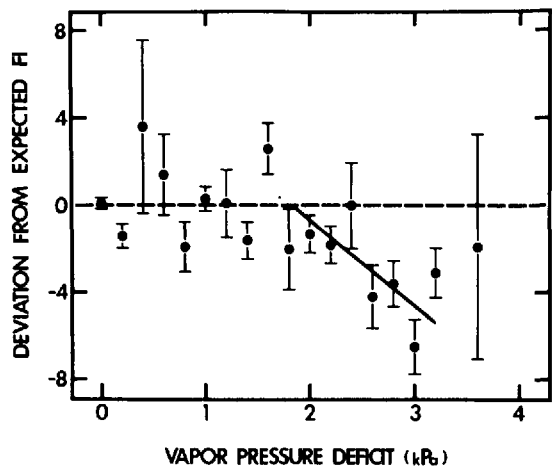

FIG. 5. Residual variation (unaccounted for by expressions 4 and 5) as a function of vapor pressure deficit (VPD). The dashed line is where the deviation from expected FI is zero. Linear regression equation for 1.8 ≤ VPD < 3.2 is: deviation = −3.95 (VPD) + 7.281 (df = 86, F = 14.00, P = 0.0003, r² = 0.14). The data point at VPD = 3.6 is the mean of two widely divergent observations, and it was excluded from the regression analysis.

When the effect of vapor pressure deficit is included, the submodel accounts for a large proportion (60%) of the variance in FI means (Fig. 6). Note, however, that
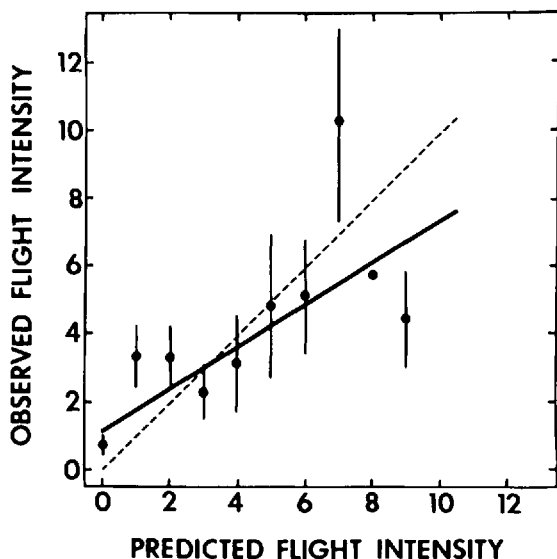
FIG. 6.   Relationship between observed mean FI, calculated over one-unit intervals (FI), and predicted values (FI*) based on weather conditions. Dashed line is where $\overline{FI} = FI^*$. Regression line (weighted by sample size) is $\overline{FI} = 0.61\ FI^* + 1.19$ (df = 9, F = 12.25, $P < 0.01$, $r^2 = 0.60$).

(1) the submodel tends to underestimate flight activity slightly at low predicted values and overestimate slightly at high predicted values, and (2) the large SEs indicate that there is a wide degree of scatter in the original data. This scatter is also evident in the data of Fig. 4. At least two factors seem likely to contribute to the variability in flight. The first is experimental error in visually sampling insect activity and especially in estimating the size of the FMP used in calculating the flight intensity. Second, there may be high variability within the insect population itself in response to varying density or weather conditions. For example, some inconsistency in response might be expected if flight behavior is modified by the rate or direction of change of weather variables. In spite of the variability in the data, the predictions of the submodel appear to provide realistic estimates of general population trends. For example, the diurnal pattern of flight as represented by sticky-trap catches (Fig. 3A) is reproduced quite well when the mean expected flight intensity (based on weather records) is plotted on an hourly basis (Fig. 3B).

Discussion

In many beetles, the initiation or maintenance of flight appears to be limited by ambient weather conditions, including temperature, wind, relative humidity, and solar radiation (Taylor 1963, Perttunen and Boman 1964, B.-O. Landin 1968, J. Landin 1968, Landin and Stark 1973, Koskela 1979, Solbreck and Gyldberg 1979). We found that flight in the MBB varied in a predictable manner (at the population level) with weather conditions, particularly in response to levels of temperature and wind speed (Fig. 4). The observed lower temperature threshold for flight probably reflects the minimum

heat requirement for such vigorous activity. Before taking off, the beetles may spend several minutes or more perched high on the host plant, flexing the wings and presumably basking in the sunlight. In contrast, at temperatures above those at which flight normally occurs, beetles rarely appear on the upper surfaces of the host plant. They remain sedentary on the leaf undersurfaces, apparently seeking shelter from the effects of high temperature and vapor pressure deficit, to which they are known to be sensitive (Kitayama et al. 1979, Lockwood et al. 1979). The direct effect of wind speed is apparent when beetles are observed attempting to fly under breezy conditions (>2 to 3 m/sec). Such individuals climb to the highest point in the surrounding vegetation, then face into the wind and usually wait for a momentary lull before attempting to fly. The elytra must be elevated and the hind wings unfolded for this to occur, and by the time flight is initiated, the beetles are frequently blown to the ground by a renewed gust of wind.

Any speculation about the evolutionary processes responsible for limiting the activity of the MBB to the observed range of weather conditions is beyond the scope of this paper. However, one consequence of the beetles' behavior may be an enhanced ability to cope with short-term and seasonal fluctuations in weather. Lewis and Taylor (1965) and Koskela (1979) have noted how the bimodal flight patterns of some insect species become unimodal as weather conditions change in late summer and fall. The activity range of the MBB is such that it has ample opportunity to fly both on cool days during the spring and fall (at midday) and in the heat of midsummer (early and late in the day).

The response of flight frequency to weather conditions matches quite closely the shape of the flight intensity response (Fig. 4). This relationship, which has not been investigated previously, suggests that the flight frequency data available for other species could be used to predict the numbers of individuals of those species dispersing under various conditions, given estimates of population size and maximum flight intensity (i.e., under optimal conditions).

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