SOME FACTORS AFFECTING PRESUMED MIGRATORY FLIGHT ACTIVITY OF THE CONVERGENT LADYBEETLE, *HIPPODAMIA CONVERGENS* (COCCINELLIDAE: COLEOPTERA)

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Insect migration is a distinct behavioral, ecological and physiological phenomenon (Dingle, 1972; Kennedy, 1961; Johnson, 1969). Behaviorally, migratory flight can be distinguished from "trivial" or appetitive flight because it is typically prolonged, continuous, undistracted flight which is not arrested by stimuli which would elicit settling behavior during appetitive flight, such as food, an oviposition site, or a mate. Response to such "vegetative" stimuli seems to be inhibited during a migratory flight, although the inhibition ultimately diminishes and settling behavior can again be evoked (Kennedy, 1961).

Ecologically, insect migration may be either an escape in space from unfavorable habitats or an "investment" of a portion of a population in colonizing and exploiting resources in a habitat some distance from the one in which adult emergence of the migrants occurred. Migratory behavior, then, is often displayed by only a portion of a population in response to appropriate environmental cues such as photoperiod, temperature, food quality, population density, and moisture. Migrants are often denizens of temporary or early successional habitats, with very high reproductive potential and great capacity for rapid exploitation of a newly invaded habitat (Johnson, 1969; Dingle, 1972).

Physiologically, migration is usually post-teneral and pre-reproductive, at least in females (Dingle, 1972; Johnson, 1969), and oogenesis or the presence of fully developed ovaries has often been shown to inhibit migratory flight in reproductive females (Rankin, 1974, 1978). Migrants, like insects in adult diapause, typically have undeveloped ovaries and hypertrophied fat bodies, and many of the environmental cues which induce adult diapause elicit migratory behavior where it occurs. There seems to be a hormonal component to migratory behavior in that both juvenile hormone (JH) (Rankin, 1974) and the adipokinetic hormone from the corpus cardiacum (Goldsworthy *et al.*, 1972) have been shown to stimulate migratory behavior in some species. Juvenile hormone has also been shown to cause flight muscle degeneration in a few species (Borden and Slater, 1968; Davis, 1975; Rankin, 1978).

Hippodamia convergens is one of the most widespread of the American coccinellids, occurring throughout the western, central and southern United States. It is an economically important predator of aphid and mite pests on cultivated crops and in fact is commercially available as a natural control agent for such pests. It is highly mobile, however—capable of migrating hundreds of miles under some circumstances (Hagen, 1962), a characteristic which often considerably reduces its effectiveness as a natural pest-control agent. This paper examines some of the

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characteristics of migratory behavior, reproduction, and adult diapause in *H. convergens* as a first step in an investigation of the physiological basis of migration in this species.

MATERIALS AND METHODS

Insect sources and maintenance

Beetles used in these experiments were obtained from several sources:

1. For some experiments adult *Hippodamia convergens* (Guérin-Méneville: Coccinellidae) were purchased from the Bio-Control Company, Auburn, California. Animals obtained from this source were kept in an unilluminated refrigerated chamber at 7° C until needed. One day before an experiment, animals were removed from the low-temperature incubator and placed in small plastic containers in large walk-in environmental chambers in either a 16L : 8D, or a 12L : 12D, 24° C photoperiod regime

2. Some animals, including adults, larvae, and eggs, were collected from the fields and gardens around Austin, Texas. Animals collected from these areas were placed in plastic rearing containers in environmental chambers in either a 16L : 8D, or a 12L : 12D, 24° C regime.

3. For some experiments animals were collected as adults from their mountain-top aggregation sites in the Davis Mountains in western Texas, particularly from the top of Mt. Locke. Such animals were transported back to Austin in insulated containers and placed in plastic rearing containers in environmental chambers either at 7 or 24° C.

4. Some of the ladybeetles were second-generation lab-reared animals, maintained on either a 16L : 8D or a 12L : 12D, 24° C environmental regime.

Beetles were fed either frozen potato aphids, *Macrospihon euphorbia,* or various species of live aphids collected around Austin, Texas. Live aphids were given to the beetles on small sprigs of their host plants, which were placed in the plastic rearing containers.

Flight testing procedure

Insects were flight tested using a modified version of the tethered-flight technique of Dingle (1966). Each animal was suspended from its pronotum by a toothpick tipped with melted beeswax and flight was stimulated by moving the animal rapidly through the air in a figure-8 motion five times, or until it began to fly if it started to fly before it was given 5 trials. Flying animals were then placed in front of a low-speed fan and flight activity was timed. All flight tests were performed between $5\frac{1}{2}$ and $9\frac{1}{2}$ hr after lights on because there appears to be a diel periodicity to flight behavior in this species which peaks during that period of the day (Rankin and Rankin, unpublished observations).

Autopsy procedures (determination of weight of female reproductive tract or testes)

Animals were fixed in Heidenhain's susa (Galigher and Kozloff, 1964) for 48 hr. The fixative was then drawn off and the animals were washed repeatedly with 70% ethanol and refrigerated in this solution at least 48 hr before dissection. The entire fixed female reproductive tract was removed, cuticle was carefully teased from the base and the blotted tract was weighed on a Cahn electrobalance, Model M-10. Testes were removed from fixed males and weighed in the same way.
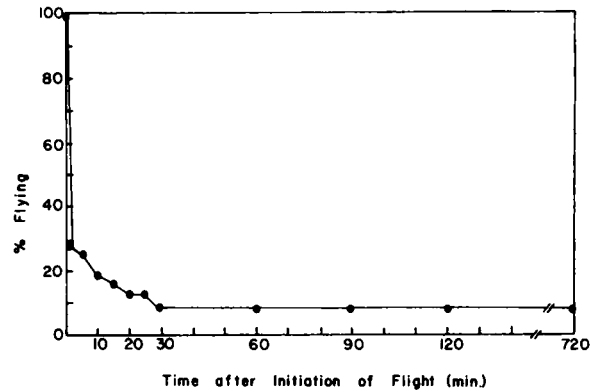
FIGURE 1. Tethered flight activity (up to 12 hr of flight) in a population of *H. convergens* (n = 60). Animals were allowed to fly for 20 hr before they were stopped and removed from the tethers. Those still flying at 12 hr were observed at intervals up to 20 hr and were all flying at each observation. Only flight up to 12 hr was graphed, however, since flight was not monitored continuously after that time.

RESULTS

Tethered flight behavior in laboratory and field populations

Initially we wished to determine whether a tethered flight procedure would provide a useful measurement of migratory behavior in this species. A group of 60 *H. convergens* were flight tested using this technique and the total time up to 20 hr was recorded (beetles were stopped after about 20 hr). As Figure 1 indicates, we observed a sharp drop in flight activity at 1–2 min of flight and a more gradual decline until 15–20 min of flight. Beetles that flew 30 min nearly always continued to fly much longer. The experiment was repeated three times using field-collected animals in December, March, and June. In each case a similar pattern in flight behavior was observed: The timing of short flights was virtually identical to that observed in the first experiment, but the percentage of beetles flying 30 min or more varied at the three times, being 68% in March, 35% in June, and 25% in December. We felt, therefore, that performance of a 30-min flight was a reasonable indication of a migratory response.

In order to determine more directly whether populations of *H. convergens* exhibit a greater tendency to migrate (to display long tethered-flight behavior) at certain times of the year than at others, field-collected beetles were flight tested at intervals throughout the year. Field collections were made from Mt. Locke in the west Texas Davis Mountains and from fields and gardens in and around the University of Texas Brackenridge Field Laboratory in Austin. Animals were flight tested the afternoon of their capture or the following day. Beetles were observed in large aggregations on Mt. Locke from July, 1977, to February, 1978. They began to appear around Austin in late February in 1976 and again in 1977. They were no longer found after June in 1976 and July in 1977.

Newly arrived animals collected around Austin in March, 1977, showed about 50% long-flight activity. During April and May, times of plentiful aphid supplies and oviposition, long-flight activity was depressed to about 20–30%. By late May and June, long-flight behavior had increased to about 60%. Newly aggregated
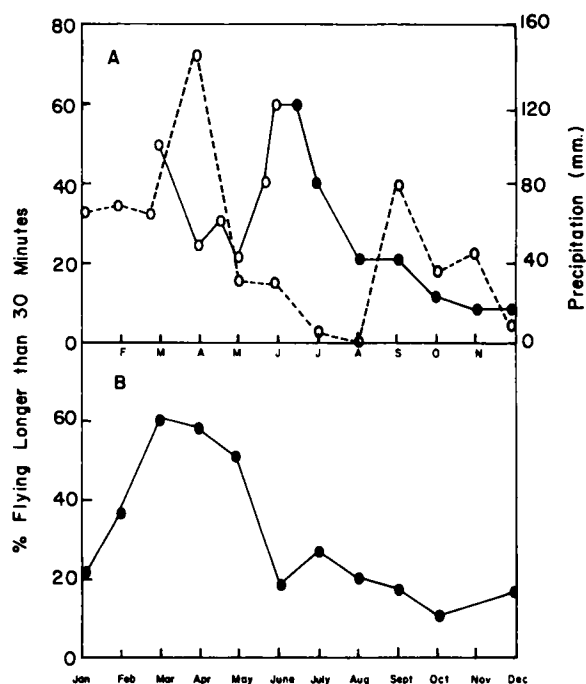
FIGURE 2. A. Flight activity of field collected beetles at monthly intervals from Mar.-Dec., 1977. Open circles, solid line = flight activity of beetles collected in aphid infested fields around Austin, Texas; closed circles, solid line = flight activity of beetles collected on top of Mt. Locke in the Davis Mountains of western Texas; open circles, dashed line = monthly precipitation in the Austin area, Jan.-Dec., 1977. B. Flight activity of California beetles obtained in Nov. and again in June from Bio-Control Co. and held at 7° C until 3 days prior to the flight test. Beetles were tested at monthly intervals, 3 days after being placed in a 16L:8D, 24° C environmental regime.

beetles collected from Mt. Locke in July and August displayed only a 20% migratory population. The proportion of long flights declined through the last collection, which occurred at Mt. Locke in December (See Fig. 2A).

These data suggest a periodic change in willingness to make long flights within the *H. convergens* population. We were interested in investigating this possibility more directly. California beetles which were obtained from Bio-Control in November, 1978, and maintained at 7° C were periodically removed from the low-temperature incubator, held for 3 days at 24° C, 16L:8D, and then flight tested. A significant change in the proportion making long flights was observed over the 11-month testing period (Fig. 2B). Not surprisingly, the pattern of change under these highly artificial conditions was not identical to that observed in the field-collected animals. However, a marked increase in flight activity did occur from February to June. The proportion of animals making a long flight was 20% in January, rose to 30% in February, and increased to nearly 60% during March, April, and May. By the June flight tests the proportion of long flights had again diminished to 20%. The beetles flight tested in June were from a new shipment of beetles. These animals had just been collected as new arrivals at their hibernation sites in California by Bio-Control company.

Another behavioral change in the beetles was observed over the storage period from November to May. When beetles were removed from the low-temperature incubator and placed at 24° C in December they would not feed, even when given live aphids, for 4 days. By February they would begin to feed after 2 days at 24° C and by May they would feed on the first day they were placed at the higher temperature. It would seem that there is a change during the diapause period in threshold of response to both migratory and food stimuli.

Effects of adult age, photoperiod, and food quality on flight behavior

Because migration is often a post-teneral, pre-reproductive phenomenon (Johnson, 1969), we investigated the frequency of long flights in young adult *H. convergens*. Beetles used in this experiment were reared from eggs in either 12L:12D or 16L:8D, 24° C environmental regime. They were isolated after hatching because hatchlings eat nearby eggs and other larvae, and were fed on frozen aphids throughout the larval period. Upon adult emergence, adults in each environmental regime were divided into two groups. One group was maintained on frozen aphids (an adequate but sub-optimal food) while the other was provided with fresh aphids. All beetles were flight tested daily from the first day after adult ecdysis. Animals maintained under either short- or long-day conditions with either frozen or live aphids exhibited a short, 1–2-day teneral period (as assessed by superficial observation of cuticle hardness) and little or no flight activity occurred during that time (Figs. 3A and B). Animals maintained under either photoperiod and fed on frozen aphids showed a high incidence of long-flight be-
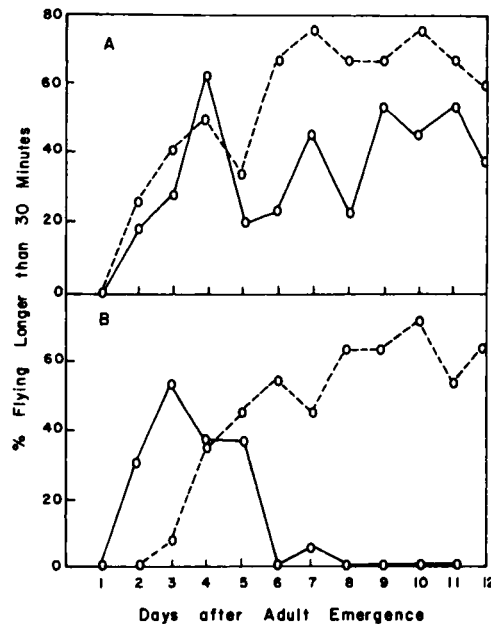

Figure 3. Daily flight activity after adult emergence among animals reared under a 12L:12D, 24° C (A) or a 16L:8D, 24° C (B) environmental regime and fed on either frozen aphids (dashed line, n = 11 both A & B) or fresh aphids (solid line, n = 13 both A & B). Differences between frozen and fresh aphid fed groups is significant at the 0.001 level for both A and B.
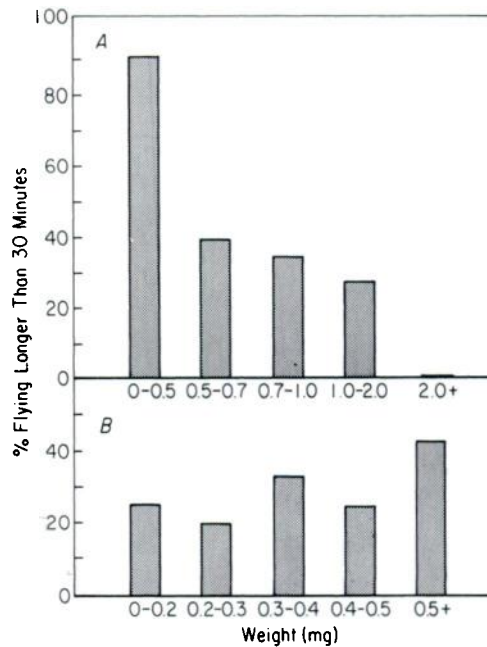
FIGURE 4. Flight activity of female (A) or male (B) *H. convergens* collected in mid-summer (long-day photoperiod) around Austin, Texas with respect to weight of the fixed reproductive tract (females, n = 38) or testes (males, n = 35).

havior by day 4 after emergence. This was maintained throughout the flight-testing period. None of the frozen-aphid-fed females in either photoperiod group displayed oviposition behavior until 21 days after adult emergence.

Animals under either photoperiod regime, and receiving fresh aphids daily, displayed a peak of long flight activity 3–4 days after emergence followed by a decline to much lower levels than that observed in animals maintained on frozen aphids. There appeared to be a photoperiodic response among the live-aphid-fed animals which was not observed in the other groups. Under the long photoperiod regime, long flights were virtually eliminated from the population by 6 days after emergence while under the shorter photoperiod, long flights continued among 20–40% of the population throughout the testing period. Oviposition occurred by day 6 in both groups. Animals fed on live aphid prey were much shorter-lived than those fed on frozen aphids. By 60 days after emergence all of the beetles fed on live aphids were dead while all of the animals fed on frozen aphids that were alive at the end of the testing period (n = 11) were still alive 60 days after emergence.

The relationship between flight activity and reproductive development was examined by flight testing 38 females and 35 males, fixing them in Heidenhain's susa, and weighing the reproductive tract (females) or the testes (males). Beetles were collected from aphid-infested areas around Austin in mid-summer, 1978, and were flight tested immediately after capture. Animals were then fixed and examined to determine reproductive development. Females showed a clear inverse relationship between flight and reproductive development (Fig. 4A) while males showed no correlation between testes weight and flight activity (Fig. 4B).

This experiment was repeated using females collected (as above) in short-day conditions between March 1–15 in Austin, Texas. Flight tests were performed as above (n = 38). The relationship between flight and ovarian development is rather different under short photoperiods. The percent making long flights increases with ovarian weight up to about 1-mg tract weight and then decreases, with some long flight behavior continuing under short photoperiods until the ovary is completely developed (3 mg tract weight) (Fig. 5). The apparent difference in the "oogenesis-flight syndrome" (Johnson, 1969) with photoperiod may have important consequences in the life history strategy of *H. convergens* (see Discussion).

To determine the relationship between reproductive development, photoperiod, and food quality in female *H. convergens*, four groups of 30 females each were removed from the 7° C incubator, placed in either a long-day or a short-day regime and given either frozen or live aphids as food. Every day beginning on the first or second day after the initiation of the experiment, three females from each group were sacrificed, fixed in Heidenhain's susa, and dissected to determine reproductive tract weight. Under either photoperiod regime females fed on live aphids underwent rapid ovarian development which peaked at day 6. Females fed on frozen aphids had reproductive tracts which weighed significantly less than females fed on live prey (Figs. 6A and B).

Effect of Starvation on Flight

Two groups of males and females (n = 30 each) were removed from the 7° C incubator and placed at 24° C (16L : 8D photoperiod). One group was fed for 7 days on live aphids and then starved, the other was fed for 3 days on live aphids before starvation. Flight tests were administered daily for 10–12 days. When
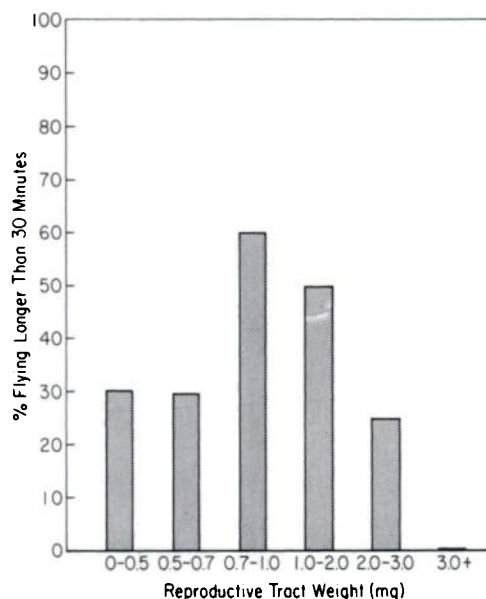

FIGURE 5. Flight activity of female *H. convergens* collected in March (short-day photoperiod) around Austin, Texas with respect to weight of the fixed reproductive tract (n = 38).
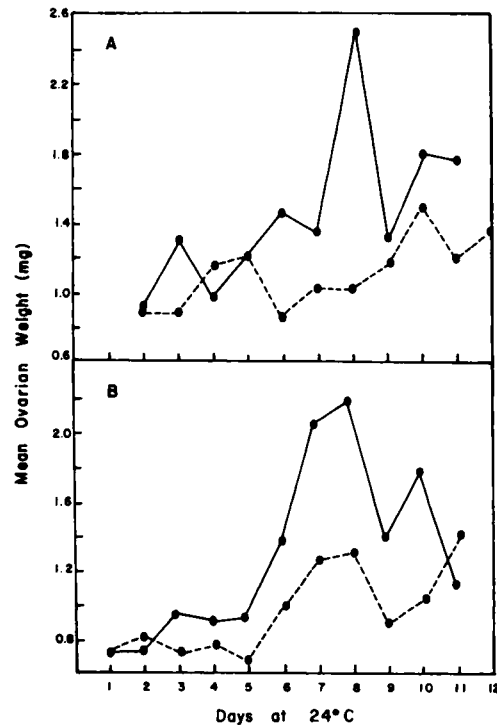
Figure 6. Effect of photoperiod and food quality on ovarian weight of *H. convergens* under either a 12L:12D (A) or 16L:8D (B) environmental regime. Each day three females were sacrificed and the weight of the fixed reproductive tract was determined. Solid circles, broken lines indicate females fed frozen aphids while solid circles, solid lines indi─ate females fed live aphids ($P = 0.025$ for A, $P < 0.001$ for B; Mann Whitney U test).

animals were fed for only 3 days prior to starvation, flight activity was significantly enhanced over that of the fed control group (Fig. 7A). When beetles of either sex were fed for 7 days and then starved, flight activity was not significantly different from that of fed controls at the $P = .05$ level, although it fell near the borderline of significance (Fig. 7B).

Mean ovarian weight of fed controls after 11–12 days was 2.14 mg. Starvation for 5 days after 7 days of food decreased this to a mean of 1.34 mg while females fed for 3 days and starved for 6 days had a mean ovarian weight of 0.69 mg. 33% of the females that were fed for 7 days and then starved oviposited at least once, while none of the females fed for only 3 days prior to starvation laid eggs.

Discussion

In order to investigate the environmental and physiological factors which affect migratory behavior, one must study an insect in which migratory flight can be conveniently assayed in the laboratory and distinguished from "trivial" or appetitive flights. In a group such as the Diptera, in which the animals move about by flying, some ambiguity might exist in interpreting the significance of a long tethered flight. However, since Coleoptera usually move about by walking and fly only occasionally, the tendency to make long continuous flights is likely to indi-

cate the tendency to migrate in this group (Southwood and Johnson, 1957; Southwood, 1962; Dingle, 1965).

Our initial tethered-flight experiments indicated that in *H. convergens* the duration of such flight is a reasonable measurement of willingness to migrate. A beetle that flies 30 min is very likely to fly much longer, often for several hours. Only a portion of the population will make long flights under any circumstances but the ratio of fliers to non-fliers changes throughout the year and the life cycle. The times of greatest percentage of long fliers in laboratory flight tests correspond to the times of population movements to and from the aggregation sites in the field. As is true for many insect migrants, long tethered flights tend to occur most frequently among pre-reproductive *H. convergens* females. For all of these reasons we feel justified in assuming that the tendency to make long tethered flights is an indication of willingness to migrate in this species.

The relationship between age and flight activity is affected by both photoperiod and food quality. Long flights are not made at all for the first 24–48 hr after emergence. After 48 hr post-emergence the tendency to make long flights increases rapidly and peaks from 3–5 days after adult ecdysis. Under short photoperiod and/or poor food quality (frozen aphids) long flights continue for some time in the population. Long day length and high quality food result in a sharp decline in
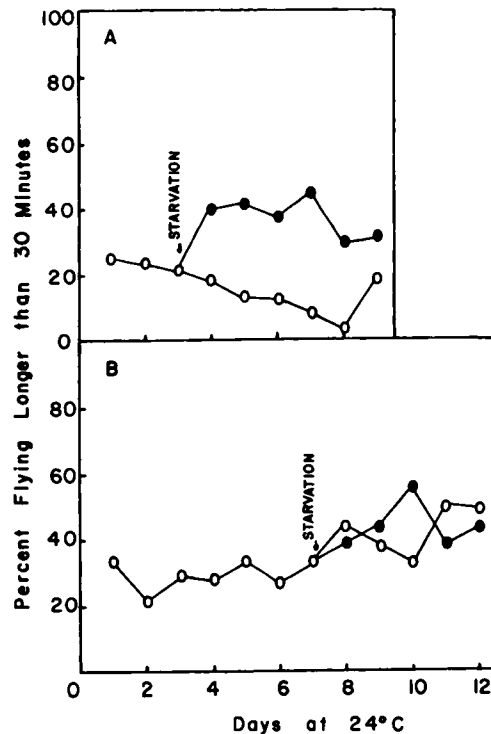

FIGURE 7. Effect of starvation after (A) 3 days of feeding on live aphids or (B) 7 days of feeding on live aphids on flight activity of *H. convergens*. Open circles indicate fed animals, closed circles, starved animals. The difference between the flight performances of starved and control animals is significant at the 0.001 level for A but not significantly different ($P = 0.5$) for B (Mann Whitney U test).

flight after 1 week, by which time oviposition has begun. Photoperiod seems only to influence the duration of the long-flight phase when food quality is optimal. When this is the case, short photoperiod greatly lengthens the period of time in which beetles will make long flights, although the percentage of long fliers in the population is lower when food is optimal than when it is not. When food quality is poor, flight activity is enhanced under either photoperiod regime to quite high levels. Thus the beetles do respond to photoperiod under some conditions, but food quality seems to be the primary cue which triggers migratory behavior. Similarly, ovarian development is dependent upon food quality, photoperiod having little, if any, effect; *H. convergens* can be reproductive under both long- and short-day conditions. This is in agreement with an earlier report by Hagen (1962) and is to be expected from field observations as well: Beetles arrive in the Austin area and begin reproducing in March (short day length) while during the long days of late May, June, and July, beetles may reproduce or migrate depending on prey abundance (Rankin & Rankin, unpublished observations).

Under long days there seems to be a clear oogenesis-flight syndrome (Johnson, 1969) in this species, *i.e.*, ovarian development is inversely correlated with flight activity (Figs. 4A, 5B). While photoperiod does not affect reproduction, it does influence flight activity under some circumstances, as noted earlier. Under short photoperiods, peak flight activity occurs in females with partially developed, rather than completely undeveloped, ovaries. It is interesting to speculate that rising JH titers at the end of the diapause period may be stimulating both flight and ovarian development at this time (Rankin and Rankin, 1980). Furthermore, some flight activity continues in the short-day population until ovarian development is complete (3.0 mg), while it virtually ceases in the long-day animals by the time the reproductive tract has attained 1.5–2.0 mg fixed wet weight (Fig. 5). Thus the "oogenesis-flight syndrome" is less pronounced and flight continues longer in the population under short photoperiods.

Periods of food shortage will cause a cessation of ovarian development in young females and elicit long-flight activity in the population. However, once a female has oviposited, starvation probably does not result in an increase in flight behavior (Fig. 7B). A reproductive female, in response to starvation, would apparently lay what eggs she could and then die. Some physiological commitment to reproduction appears to be made by the time of first oviposition. Our observations in this respect are similar to those of Solbreck and Pehrson (1979) who found that in the Lygaeid, *Neacoryphus bicrusis*, pre-reproductive starvation enhances flight activity as it does in *H. convergens*. Cessation of flight in *N. bicrusis* in the presence of ample food is associated with flight muscle histolysis such that post-reproductive starvation does not elicit further flight. Furthermore, as in our short-day animals, an oogenesis-flight syndrome in *N. bicrucis* is observed only during high reproductive activity.

Beetles that begin reproduction soon after emergence are much shorter-lived than those that delay. For example, by 60 days after emergence, all of the short-day females fed on live aphids were dead while most of the short-day females fed on frozen aphids were still alive. One of the latter group had oviposited one egg, but most had not reproduced. It would seem that once the reproductive machinery is fully stimulated, beetles produce eggs rapidly and then die. If this is true, the large population movements to and from aggregation sites are made largely by pre-reproductive animals, and beetles would typically undergo only one period of aestivo-hibernation. The tendency not to migrate after first oviposition may

be less pronounced under short-day conditions or the decision may be made somewhat later. These possibilities are being investigated.

Although several questions concerning the life history of this species remain unanswered, we can surmise a probable sequence of events from our data. Beetles which were newly emerged in June would be exposed to long photoperiods and high temperatures. Summer rainfall conditions, which greatly influence the aphid prey population, are quite variable in Texas. In a wet year, when prey is abundant, these newly emerged beetles would experience a brief period of long flight (2–3 days according to Fig. 3) and then begin reproduction, producing a second generation as they did in 1978 (Rankin and Rankin, unpublished observations). In a dry year, however, such as 1977 (Fig. 2), the aphid prey are very scarce by late June. As Figure 3 indicates, when food quality is poor, the period in which a large percentage of the population makes a long flight is greatly prolonged and the number making long flights is enhanced regardless of photoperiod. Thus shortage of prey would very likely result in the movement of a large portion of the population. Results of flight testing field-collected animals periodically throughout the year support these suggestions. Prevailing winds at this time are such that they would be likely to carry fliers to the west Texas mountains where they subsequently diapause in large aggregations (Crutcher and Halligan, 1967). Initially there may be movement of the beetles around the aggregation area. But as temperatures drop in the fall, activity of any sort diminishes.

In some parts of their range, such as New Mexico and Colorado, beetles have been found under bushes and rocks on mountain tops buried under ice and snow before the spring thaw (M. Rankin, unpublished observations; Douglass, 1930). When such animals are warmed, they will immediately begin to copulate. Similarly, refrigerated animals will quickly begin to mate when they are warmed, even though they will not feed and ovaries are as yet undeveloped. Thus it is likely that female *H. convergens* leave the aggregation sites mated but still reproductively immature. Rising hormone titers may stimulate flight and the onset of reproductive development (Rankin and Riddiford, 1978; Rankin and Rankin, 1980) but the exodus flight is probably made by females unencumbered by large batches of eggs. Feeding on live prey seems to be important in eliciting full ovarian development and according to Figures 3 and 5, long-flight activity would probably continue under the short spring photoperiods, alternating with periods of feeding, until ovarian development was complete. Thus the migrant female would terminate her return flight from the aggregation sites ready to begin immediate reproduction, when her reproductive value is greatest.

Slobodkin (1962) defines reproductive value as "the diminution of future population increase produced by removing a single animal of a given age from a population." It is a measure of sensitivity to natural selection. The time of peak reproductive value, since it represents maximum contribution to future population increase, also indicates that period of the life history at which natural selection exerts its greatest influence (Fisher, 1958). Long flights at this time are likely to have been subjected to strong favorable selection. This may be one reason why there is a high incidence of long-flight behavior in a short-day population even when food is available. Later in the season, when photoperiods are long, the primary cue to migrate is probably food shortage experienced by pre-reproductive adults. Migration at this time precedes a long and somewhat hazardous diapause period. (Our unpublished data indicate that large numbers of beetle carcasses are often found at the aggregation sites in late spring; heavy losses due

to nematode infestations have been observed in both New Mexico and Texas aggregations). This migratory behavior might be expected to have been the result of less strong favorable selection than the post-diapause flight. In addition such hazards during the diapause period may strongly favor immediate reproduction when possible. Indeed, migration prior to diapause is much more facultative. During exceptionally wet and thus aphid-rich years, massive aggregations do not occur (Neuenschwander et al., 1975; Rankin and Rankin, unpublished observations) or aggregations do occur but an actively reproducing population is also maintained in aphid-infested areas.

A similar life history strategy is characteristic of the milkweed bug, *Oncopeltus fasciatus*. Dingle (1965) has shown that migratory behavior in this species is post-teneral and pre-reproductive, long flights being terminated as ovarian development is completed. The propagules arrive at their post-migration habitat at the time of peak reproductive value (Dingle, 1965). Rankin (1974) and Rankin and Riddiford (1977, 1978) have shown that the highly adaptive coordination of flight and reproduction in this species is accomplished via the corpus allatum control of both events. Both reproduction and flight are stimulated by juvenile hormone; lower titers of the hormone or shorter exposure time stimulate flight before reproductive development which ultimately inhibits long flights. We suspect a similar situation exists in *H. convergens*. Juvenile hormone stimulates both long flight and reproduction in this species (Rankin and Rankin, 1980) and the data presented in this paper suggest a similar inhibition of long flight when the ovaries are completely developed.

We have not extensively investigated reproductive development in male *H. convergens* migrants. It is likely, however, that migration in males is not solely pre-reproductive. Reproductive activity was not correlated with the tendency to make a long flight and since males mount females readily during the diapause period if they are warm enough to be mobile, it is likely that males are reproductively mature at least by the time they leave the aggregation sites. Males do seem to share the other aspects of the diapause-migration syndrome, however. They show the same variation in proportion of individuals that will make a long flight in the life cycle, during the year, and in response to poor food quality. Males seem to make a similar commitment not to migrate after about 7 days of optimal food (Fig. 7) and they show the same unwillingness to feed during the diapause period. In short, the only difference between the sexes with respect to these characters seems to be that males are reproductively mature during the migration while females are not. It would, of course, be highly advantageous for mating to occur in the large aggregations before dispersal and this is, indeed, often observed among insect migrants (Johnson, 1969; Caldwell and Rankin, 1974).

In summary we conclude that *Hippodamia convergens* is a fairly typical insect migrant in many ways. Long flights seem to be post-teneral and, in females, primarily pre-reproductive and associated with an adult reproductive diapause. Food quality and photoperiod interact in such a way that a spring migratory flight is very likely under any circumstances while the summer migration is much more facultative. Presumably short fall photoperiods would ultimately induce at least some of the population to migrate at that time if a summer exodus had not occurred

It is interesting to note that Hagen (1962) in an excellent review of coccinellid life histories, supports, on the basis of field observations of California *H. convergens*, many of the conclusions we have drawn from our laboratory studies.

SUMMARY

Hippodamia convergens migrates long distances to and from mountain-top aggregation sites. It undergoes an imaginal diapause associated with a 6–9 month aestivo-hibernation at the aggregation sites. Laboratory tethered-flight tests can be used as an assay for migratory behavior. Beetles that fly 30 min on a tether will nearly always fly much longer.

Long tethered flight is pre-reproductive in females, though apparently not in males. Starvation or poor quality food will greatly enhance migratory behavior. However, the tendency to display migratory behavior is greatly reduced in both sexes after about 7 days of optimum food. Even starvation at that time will not stimulate an increase in long-flight behavior. It would appear that some type of physiological committment to reproduction which excludes or greatly reduces the tendency to migrate is made at that time. Photoperiod has little effect on migratory behavior when food is poor. But under optimal feeding conditions, short photoperiod enhances long flight behavior even among reproductive females.

It would appear that migration to the aestivo-hibernation sites is accomplished primarily by newly emerged (pre-reproductive female) beetles. Strong selection pressure has apparently favored migration away from the aggregation sites in the early spring (short photoperiods) whether or not aphid prey are available, while migration during the summer (long photoperiod) is much more facultative, depending primarily on food abundance.

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