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Long-distance flights in Coccinellidae (Coleoptera)

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Trivial flight, foraging, migration, dispersal, diapause, dormancy sites, Richardson's index, air turbulence, *Coccinella septempunctata*, *Coleomegilla maculata*, *Harmonia axyridis*, *Hippodamia convergens*, *Semiadalia undecimnotata*

Abstract. In the period of reproductive activity and foraging for prey coccinellids undertake trivial (appetitive) flights. The irregular long-distance flights of "swarms" of ladybirds originate in hypermobility of starving beetles of the new generation. Two types of regular long-distance flights are related to dormancy: diapausing coccinellids migrate to dormancy sites by directional flight and after dormancy they disperse gradually to breeding sites. There is abundant evidence that most long-distance migrants are hypsotactically attracted to prominent landmarks, at least in the closing part of their migratory flight. None of the methods used to quantify the tendency to migratory flight (duration of tethered flight, incidence of take-offs, wing-spreading response) gave a completely satisfactory result; the first-mentioned technique is the most promising.

When migrating to dormancy sites coccinellids usually have immature ovaries (primary or regressed), and thus conform to Johnson's "oogenesis – flight syndrome". In contrast, during the dispersal flight their ovaries are partly matured. Although there is a general consent about the importance of juvenile hormone for the flight, it is still not clear how the regulation of flight is coordinated with the well established stimulatory role of JH in reproduction. There are indications that an intermediate titre of JH might stimulate both the flight and the early phases of ovarial maturation.

INTRODUCTION

Ladybirds perform several types of flight behaviour: three types of long-distance flight and the so called trivial or appetitive flight undertaken during foraging for prey and ovipositing.

Two types of long-distance flight are associated with dormancy. Coccinellids destined to diapause migrate to their dormancy sites and after the dormancy they disperse to breeding sites. While these two kinds of flight are regular parts of the chain of events representing the lifecycle, the third type of long-distance flight is, according to our view, an irregular phenomenon.

We begin with the third type of flight, which has never been the subject of a systematic study. What follows are assumptions based on observations. We consider this long-distance flight to be an irregular prolongation and intensification of the normal trivial (or appetitive) flight which is produced by overpopulation and the ensuing shortage of prey. In absence of a better, more sophisticated term, we designate it as **"hectic" trivial flight**. We assume that this type of flight is a specific feature of aphidophagous coccinellids. Due to their great fecundity and pronounced numerical response coccinellid females can produce numerous descendants in habitats where aphids are abundant. Before pupation the larvae may then consume practically all prey (or they may even consume the prey earlier and have to resort to cannibalism to complete their development). As there are few or no aphids left for the adults emerging from pupae they are forced by hunger to forage more actively, especially by flight when the summer weather is hot enough. A similar situation may occur over large regions so that the coccinellids form swarms. Eventually they are taken upward by air streams to upper layers of the atmosphere where they are carried passively in the wind. We assume that the huge masses of coccinellids occasionally recorded around lakes or on sea shores result from such flights which originated from hypermobility during foraging. As the absence of aphid prey means not only absence of food but evidently also lowered water intake it is possible that the coccinellids actively move towards larger reservoirs of water. Another plausible explanation of this phenomenon may be that large bodies of water cool down in the evening more slowly than the adjacent land (A.F.G. Dixon, pers. comm.)

MIGRATION TO DORMANCY SITES

There is abundant evidence that the behaviour of migration towards dormancy sites is species-specific, as are the habitats or microhabitats chosen for dormancy. Many species **do not migrate** but remain in the breeding habitat also during dormancy. This is the case in non-entomophagous species *Subcoccinella vigintiquatuorpunctata*, *Micraspis (Tytthaspis) sedecimpunctata* and *Psyllobora (Thea) vigintiduopunctata* (Majerus & Kearns, 1989). In some species, e.g. *Coccinella septempunctata*, only a part of the population migrate to dormancy sites in the mountains, usually the adults that enter diapause early in the season. These adults are larger (Honěk, 1989) and their diapause is deeper (Hodek et al., 1977) than on the plain. Many individuals do not leave the plain and make relatively short flights to nearby forest edges. Some adults remain in their breeding areas and diapause around shrubs on balks or hedges between fields. The study of migration has been limited to those species that make long-distance flights, i.e. *Hippodamia convergens*, *Semiadalia undecimnotata*, *Aiolocaria mirabilis*, *Coleomegilla maculata* and *Harmonia axyridis*, but also *C. septempunctata*.

Hagen (1962) distinguishes between **"climatotactic"** (e.g. *C. maculata*) and **"hypsotactic" aggregators** (e.g. *S. undecimnotata*). While for *C. maculata* and *H. convergens* moisture availability is an essential requirement during hibernation (Hagen, 1962), prominent features of the landscape are more important for *S. undecimnotata*, *H. axyridis* and *C. septempunctata*. Therefore, an analogy has been sought between the aggregation of the latter coccinellid species on or near to elevated objects and other phenomena [e.g. the hill-topping habits of ants and other insects (Alcock, 1987), and the flight of *Melolontha* from fields to the feeding sites on trees], where hypsotactic orientation has been suspected (Hodek, 1960; Hagen, 1962).

The two types of long-distance flights associated with dormancy are viewed differently by different authors, which has resulted in a nonuniform classification. Johnson (1969) argues that coccinellids both migrate to and from dormancy sites. We agree, however, with Hagen (1962, 1966) discriminating between the **directional migratory flight** to and **non-directional dispersal flight** from the dormancy sites. This disagreement is not just a semantic one as it concerns the crux of the problem, which is still unresolved: do coccinellids fly toward hibernation sites by a directional flight, or are they brought there more or less passively by wind currents? There is no direct evidence but some circumstantial evidence supporting both these possibilities.

Johnson argues that the direction of both displacements is greatly affected by wind – and is thus not directional. This is opposed by several kinds of observations. In the several hypsotactic aggregators we have evidence that the coccinellids at least partially control their flight when they orient themselves visually to prominent features of the landscape. In the case of those that make lengthy migratory flights (*S. undecimnotata*, *H. axyridis* or *C. septempunctata* partly) these features may be peaks or large rocks or posts on the slopes of hills. For those coccinellids that aggregate within the breeding area, but usually in a different habitat or microhabitat (*C. septempunctata* partly), it may be a forest edge, a balk between fields, a shrub, a tree, or a post in a flat landscape. The same sites are used year after year, if the topography remains the same; but new sites are occupied if the relief is changed by the removal or formation of a prominent object. The creation and removal of triangulation posts, forest fences and huts has provided "unintentional" experiments, which show how the aggregation sites of *S. undecimnotata* can be changed (Hodek, unpubl.). It seems improbable that coccinellids are repeatedly transported passively to the same places.

One of the most recent observations of this kind is by Obata (1986) who noted that the adults of *H. axyridis* flying along a valley turned towards the rocks signalling the dormancy sites. It has also been observed that *S. undecimnotata* landed on a moving person that constituted the most prominent object on the top of a hill (at Raná in northern Bohemia or Kováčov-hills in southern Slovakia), when air currents were too weak to be noticed by the observer (Hodek, unpubl.). In addition, coccinellids have been observed to fly against the wind in the direction of mountain peaks (Mani, 1962). Likewise the field experiments undertaken by Iperti and his collaborators (discussed in detail below) indicate directional flight for about 4 km. Although the labelled adults of *S. undecimnotata* took off from two places in different directions (in the sense of cardinal points), they were found in the same hibernation site on a relatively high mountain (Iperti & Buscarlet, 1972; Iperti & Rolley, 1973).

Honěk (1989) suspected that, in addition to the visual hypsotactic orientation, *C. septempunctata* can by remote perception respond to the overall temperature of the dormancy site.

In contrast, coccinellids have been observed to make use of air currents, especially in mountain valleys. Savoiskaya (1966) reported coccinellids in the Zailiiskii Alatau mountains (Kazakhstan) flying up the valleys to their hibernation sites using the steady breeze that blows up the valley in daytime. According to Hagen's (1962) hypothesis on the migratory flight behaviour of *Hippodamia convergens*, this species is also transported to the region of hibernation sites by air currents.

We may try to reconcile these contradictory views on the migration to hibernation sites. Although Johnson (1969) may be right when saying that migrants cannot head for a "perceived but far-distant habitat" at the start of their migration flight, they certainly are able to be attracted by optical or other signals when close to dormancy sites. We still wonder, however, why coccinellids should be unable to direct themselves to their dormancy sites, at maximum only about tens of kilometers from their breeding sites, when *Danaus plexippus*, the Monarch Butterfly, can migrate directionally to its hibernation sites in California or Florida, from breeding sites in the area of the Great Lakes, i.e. several thousand kilometers distant!

DISPERSAL FROM DORMANCY SITES

The dispersal flight has been reported as a step-wise process. It is, in fact not a true long-distance flight in the strict sense. We have observed that the beetles fly from the dormancy site only to adjacent fields (Hodek, 1960; Okuda, 1983) and – if aphids are present there – the coccinellids only gradually disperse further. This different flight behaviour need not have a differing endocrinological regulation; the function of the flight muscles will probably be controlled by endocrine glands as in the case of the migration flight to dormancy sites (see the last section). However, on leaving the dormancy site the enormous depletion of reserves would produce hunger which interrupts the dispersal flight into several fractions. Thus the dispersal flight apparently changes gradually into the trivial flight.

METHODS OF STUDY

There are several methods of studying migration. It might seem most appropriate to study the coccinellids directly in the course of their migration. This, however, is the most difficult approach, and has almost never been used. To our knowledge, nobody else has used this method other than Hagen (1962, 1966), who built his classic hypothesis of migration of *H. convergens* partly on flying beetles caught from an airplane. Other researchers have used two alternative ways of study. Either they have tried to measure the flight drive of coccinellids (unfortunately less often before the flight than during dormancy), and/or they have monitored the physiological condition of the beetles, particularly the state of flight muscles and endocrine glands.

The tendency to migrate has been quantified in several ways. Solbreck (1974) and Rankin & Rankin (1980a,b) used **tethered flight** to measure it in *C. maculata* and *H. convergens*, respectively, although details of the method were not identical. While Solbreck (1974) used no stimuli for flight other than loss of tarsal contact, Rankin & Rankin (1980a,b) stimulated the coccinellids to fly by placing them in a slow flow of air. Due to this important difference the absolute values of flight duration cannot be compared. While in *H. convergens* flights longer than 30 minutes were considered to be migratory (Fig. 1), less than 10% of *C. maculata* adults flew ≥ 10 min. in the most suitable period in mid-May, and only aproximately 20% flew ≥ 1 min. Solbreck (1974) considered a 30 sec flight as a good indicator of the development of a capacity for flight.

Tethered beetles in a flight mill have also been used to determine the effect of parasitization by *Perilitus coccinellae* on the flight activity of post-diapause *H. convergens* (Růžička, 1984; Růžička & Hagen, 1985; Růžička & Hagen, 1986). The flight performance of parasitized coccinellids was much poorer, than that of unparasitized beetles (Table 1). The values of 45–50 min recorded for non-parasitized adults, collected before dispersal from hibernation sites in Sierra Nevada, correspond with the above data (Rankin & Rankin, 1980a,b) for migratory flight. This method also enabled the speed of flight to be recorded: it averaged 60–70 m per min (Růžička, 1984).

TABLE 1. Flight duration of unparasitized and parasitized *Hippodamia convergens* collected from mountain aggregations in California during February (Růžička & Hagen, 1985)

Females	Unparasitized		Parasitized		t^a
	n	x̄ (sec) ± SD	n	x̄ (sec) ± SD	
First flight	28	2700 ± 2518	8	1122 ± 1217	1.704
Longest flight	28	3047 ± 2340	8	1152 ± 1187	2.194
Tot. flight time	26	5358 ± 2054	7	3181 ± 2363	1.902

[a] All t values significant at 0.05.

Another method for quantifying flight behaviour is to record the incidence of **spontaneous take-offs**. This approach has been used in *Myrrha octodecimguttata* (Pulliainen, 1964) and in *C. septempunctata* (Zaslavsky & Semyanov, 1983; Okuda et al., 1986; Okuda & Hodek, 1989; Honěk, 1990). In comparison with tethered flight this method has an important shortcoming: it simply divides the insects into "fliers" and "non-fliers", and does not measure the performance of the "fliers". Thus we cannot determine whether the flight is migratory or just trivial. Recording take-off produces relative values and is thus suitable for comparing samples from different habitats, of different ages or phases of the life-cycle. The experimental conditions must be identical, as they modify the results in important ways. Honěk (1990) obtained very high values of take-off frequency for *C. septempunctata* at 30°C, when the beetles were stimulated to fly by a weak air current, applied for 10 seconds, at the beginning and in the middle of a 3 minute test period. Under these experimental conditions, 60% of beetles from hibernation sites took off, even in December. When the beetles of the same species and from the same region were not stimulated to take off, and tested at a temperature of 25°C and a lower light intensity (Okuda, 1983; Okuda et al., 1986; Okuda & Hodek, 1989) the frequency of take-offs was much lower and more appropriate to that phase of the life-cycle. After arrival at hibernacula, from late July to mid August, only 10–20% took off. In spring, before dispersal from hibernation, the incidence of take-off ranged from 30 to 70%, while after arrival in the fields it was slightly lower, 20–50%.

An interesting method for monitoring the tendency to migrate (Khrolinsky, 1963) has been used on individuals from several populations of *C. septempunctata* (Semyanov, 1978; Zaslavsky & Semyanov, 1983, 1986). Within 20 min of recovering from a short ether narcosis, the beetles show their urge to fly by opening their elytrae and spreading

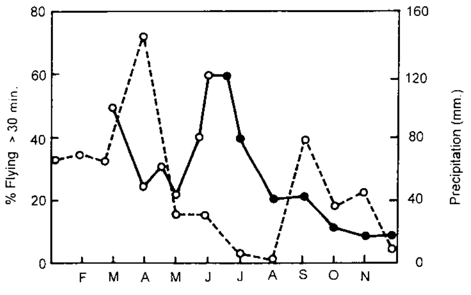

Fig. 1: Flight activity of field collected *Hippodamia convergens*. Solid line: March to June – beetles collected in aphid infested fields around Austin, Texas; July to December – beetles collected on top of Mt. Locke, Davis Mts, W. Texas. Dashed line: precipitation in the Austin area, 1977 (Rankin & Rankin, 1980b).

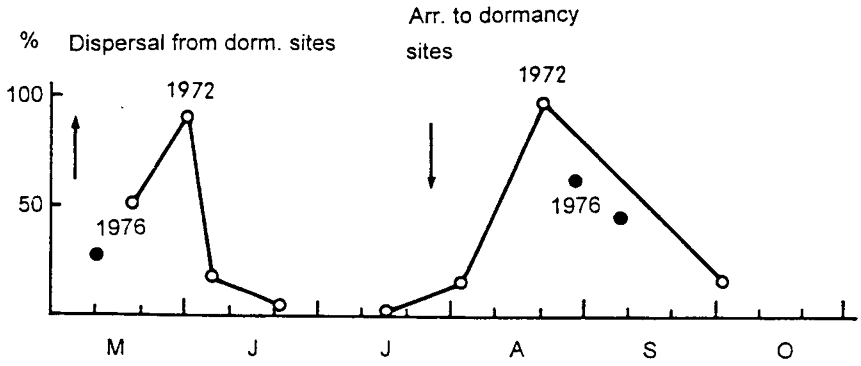

Fig. 2: "Wing spreading response" in the population of beetles of *Coccinella septempunctata* collected around St. Petersburg. The arrows indicate the onset of dispersal from and arrival to dormancy sites. Vertical axis – incidence of response; horizontal axis – months, (Zaslavsky & Semyanov, 1983).

their wings. This urge to fly after a narcosis ("**wing spreading response**", WSR) was used by the authors as an indicator of "**migratory state**, a physiological basis of migration". In beetles from the field in the region of St. Petersburg this response coincided well with the periods of migration from and to estivo-hibernation sites (Fig. 2).

However, in the laboratory WSR occurred in all young beetles, irrespective of diapause-inducing or -preventing photoperiod and the ensuing physiological state. That is, WSR occurred both in active adults and in those beetles in prediapause and/or diapause. This observation could make us suspicious whether the WSR (after ether narcosis) is not a rather general criterion which also encompasses other types of flight. Semyanov (1986) compared the WSR with tethered flight in the same samples of *C. septempunctata* and reported a very similar incidence of "fliers". While Rankin considered only the long flights (> 30 min.) as migratory, Semyanov included also those individuals that "tried to fly". Thus the ambiguity of using WSR as an indicator of **migratory flight** remains.

Regeneration of the flight muscles in *C. septempunctata* (Okuda, 1983; Okuda et al., 1986; Okuda & Hodek, 1989) in October at the hibernation site (seven months before dispersal) is surprising (Fig. 3), and has stimulated us to follow the flight behaviour in detail in the future.

Iperti and colleagues studied migratory behaviour, particularly take-off, by relating the type of take-off to temperature and wind speed and by marking the insects. By **tagging** beetles **with iridium** (stable isotope 191, an element normally absent from the body of coccinellids), it was possible to show that *S. undecimnotata* flies towards dormancy sites prominent in the landscape. Experiments were conducted near Digne (Alpes de Haute Provence, France) from 1972 to 1977, in July or very early August. Adults drank a solution of H_2IrCl_6 before being released at two places, both about 700 m a.s.l., and about 4 km distant from the mountain (St. Michel de Cousson, 1515 m) on the top of which the hibernaculum was situated. Every other day beetles were collected at the dormancy site, killed and irradiated to convert the isotope Ir191 to Ir192 which was then detected by means of gamma-spectroscopy (Iperti & Buscarlet, 1972; Iperti & Rolley, 1973). In some years large numbers of labelled adults were found in the hibernaculum. There were no

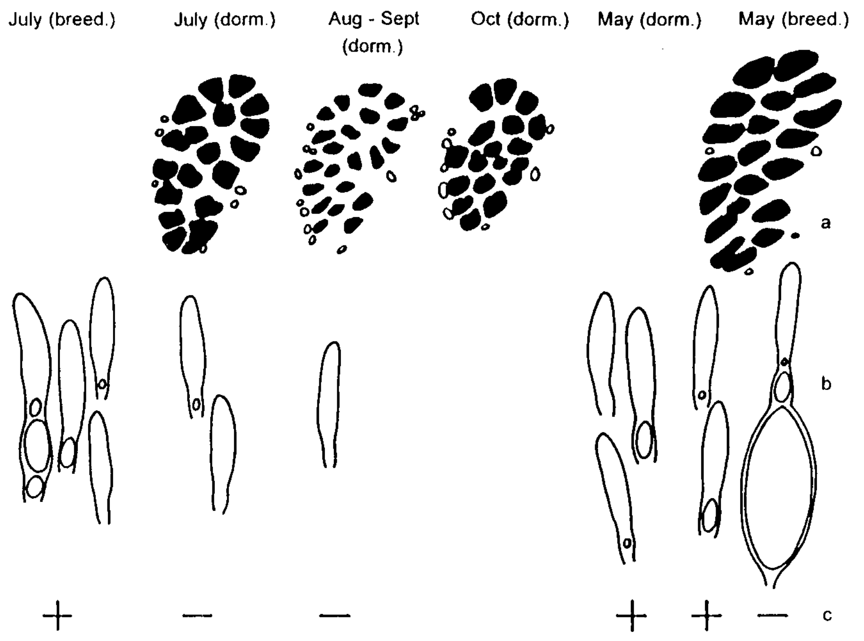

Fig. 3: Schematic representation of the changes in the dorso-longitudinal flight-muscle fibres (a) and ovaries (b) in relation to the change in the flight tendency (c) in *Coccinella septempunctata*. Breed. = breeding sites; dorm. = dormancy sites. Flight tendency relatively high (+), relatively low or absent (–), (Okuda et al., 1986).

significant differences between the sexes (Table 2) but the incidence of beetles that successfully arrived at the dormancy site varied between years. Iperti & Buscarlet (1972) suspected that the direction and speed of wind at high altitudes affected the proportion of beetles arriving at the hibernaculum. The beetles released at Chateauredon (SSW from St. Michel de Cousson) succeeded better than those released at St. Jurson (SWW).

TABLE 2. Relation between the value of the Richardson's index and the flight behaviour of adults of *Semiadalia undecimnotata* in July, in south-east France, (Iperti et al., 1983)

Richardson's index[a]	Females						Males					
	migratory flight		trivial flight		no flight		migratory flight		trivial flight		no flight	
	n	%	n	%	n	%	n	%	n	%	n	%
(5–9)	136	(58)	50	(21)	48	(21)	64	(62)	28	(27)	11	(11)
(0.1–4)	503	(46)	394	(36)	200	(18)	449	(49)	290	(31)	183	(20)
(0.01–0.09)	538	(45)	359	(25)	290	(25)	429	(52)	237	(29)	155	(19)
(0.001–0.009)	150	(37)	139	(34)	117	(29)	150	(53)	65	(23)	66	(24)
(< 0.001)	25	(30)	31	(33)	27	(37)	19	(28)	23	(33)	27	(39)

[a] R index – 5–9 – high
0.01–0.09 – low
< 0.001 – almost zero

When the beetles (n = 335) were released by Iperti & Medioni (unpubl.) in an arena (70 cm high and 400 cm in diameter) in which view of all terrestrial orientation points was excluded, the initial orientation of the beetles was predominantly towards the west. This experiment was executed in the same region as the above mentioned "non-isolated" releases, i.e. roughly to the west of Mt. Cousson, and could thus be considered as corroboration of the hypsotactic orientation of *S. undecimnotata*. Inside the arena, without the possibility of optical orientation they flew in the opposite direction than in the field. However, Iperti and Medioni rightly warn that they cannot be sure that any non-optical terrestrial cues were excluded.

In the same series of experiments Iperti and his colleagues (Iperti et al., 1983) recorded temperature and wind speed at two heights (0.25 m and 1.25 m) at the moment of take-off. These factors could not be related to take-off if considered separately. Therefore they used Richardson's index of air-turbulence, which gives a measure of the relative influence of mechanical and thermal energy of air. A decrease in the Richardson's index was positively correlated with a decrease in the incidence of coccinellids taking off on a migratory flight (Table 2).

Richardson's index (R_i) can be calculated using the following formula:

$$R_i = \frac{9.81}{273 + \Delta\theta}\Delta z\frac{\Delta\theta}{(\Delta\mu)^2}$$

where: $\Delta\,\theta$ = difference in temperature (°C) at two levels (0.25 m and 1.25 m) above the soil.
$\Delta\,\mu$ = difference in wind speed (m/sec) at two levels (0.25 m and 1.25 m) above the soil.
$\Delta\,z$ = difference in height between 0.25 and 1.25 m: here = 1 m.

When R_i is low, which indicates a strong elevatory lift, take-off is easier for ladybirds, especially for females.

Temporal, physiological and climatic data were combined in variables which were used to develop a predictive model of the initiation of migratory flight in *S. undecimnotata* (Iperti, 1986).

PHYSIOLOGICAL ASPECTS OF FLIGHT

The migratory flight is most probably regulated by the neuroendocrine system. A few studies on hormonal control of flight behaviour point to an important role of juvenile hormone (JH) produced by the corpora allata (CA). Other neuroendocrines implicated in the control of flight behaviour are ecdysone, adipokinetic hormone and octopamine (Rankin, 1985, 1991).

It is not known whether all types of flight are controlled by the same endocrine mechanisms. Stimulation of both flight and oogenesis by the same hormone would maximize an early onset of reproduction after the dispersal flight from dormancy sites. Such a mechanism would be in disagreement with the "oogenesis-flight syndrome" (Johnson, 1969) according to which the ovarian development should be inversely correlated with flight activity. In migration towards a hibernation site there should be a way of stimulating flight without oogenesis.

The suspected function of JH in the regulation of flight activity was studied in *Hippodamia convergens* by application of JH mimics (JHM). Repeated treatments with JHM induced a sustained increase in flight activity in females collected at the beginning of diapause (in summer) from hibernation sites in California. These females responded to JHM application by only a moderate increase in the weight of their gonads (Rankin & Rankin, 1980a). It was assumed that an additional factor, probably from the brain, is necessary for ovarian maturation in conjunction with JH (Rankin, 1991). A possible absence of this factor in early diapause evidently does not prevent the stimulatory effect of JHM on flight activity.

The "oogenesis-flight syndrome" hypothesis is supported by the inverse relationship between ovarian weight and flight activity in females of *H. convergens* collected on the plain in mid-summer before migration to hibernation sites. Males showed no correlation between weight of testes and flight activity (Rankin & Rankin, 1980 b).

After the completion of diapause, application of JHM stimulated flight behaviour in both sexes and ovarian maturation. The maturation of ovaries was suspected as the cause of the decline in flight activity of females on day 8, as it did not occur in males (Rankin & Rankin, 1980a). The flight activity of both males and females was inhibited by precocene II, and reappeared in these precocene-treated beetles after application of JHM (Rankin & Rankin, 1980a). Because precocene II is known to destroy the corpora allata (Bowers, 1981; Staal, 1986), these results confirm the stimulatory effect of JH on flight activity.

In contrast to pre-migratory females collected in mid-summer, a negative correlation between ovarian weight and flight activity was not found in females collected in March, shortly after dispersal from the dormancy sites; females with moderately developed ovaries had the highest flight activity (Rankin & Rankin, 1980 b).

This difference may indicate that a relatively low JH titre does not stimulate ovarian maturation in young females in early, (i.e. deep) diapause, but it is high enough to keep the flight muscles in an active condition and stimulate the migration to dormancy sites. In post-dormant females, a high JH titre stimulates both ovarian maturation and dispersal flight. Alternatively, migration to dormancy sites may be stimulated by JH at a time when their ovaries are not sensitive to stimulation by JH, due to, for example the absence of a brain factor.

Starvation stimulates flight in several insect species (*Oncopeltus fasciatus* – Rankin & Riddiford, 1977; *Leptinotarsa decemlineata* – Caprio & Grafius, 1990). Rankin & Rankin compared the effect of less suitable food (frozen aphids) with good food (fresh aphids) (Fig. 4). Females reared on live aphids from the egg stage under either long day or short day conditions show high incidence of flight behaviour when 4 days old. In both photoperiods, oviposition occurred by day 6. The incidence of long flights sharply decreased to zero after the first oviposition under long days but was maintained at intermediate level under short days. When the beetles were reared on suboptimal prey (frozen aphids), flight activity of females was maintained in similar high proportions under both photoperiods while reproduction was inhibited for at least 3 weeks (Rankin & Rankin, 1980b). Thus, in females starvation (or poor nutrition in this case) may favour long-distance flights by inhibiting ovarian maturation. The effect of food on flight activity of males has not yet been studied.

In a previous paper, Rankin & Riddiford (1977) concluded that an intermediate activity of the CA, which was below the threshold for ovarian development, stimulated flight activity in starving *O. fasciatus*. However, in *H. convergens* flight activity was stimulated by relatively high doses of JHM (10 μg) and the subsequent decrease in flight activity seemed

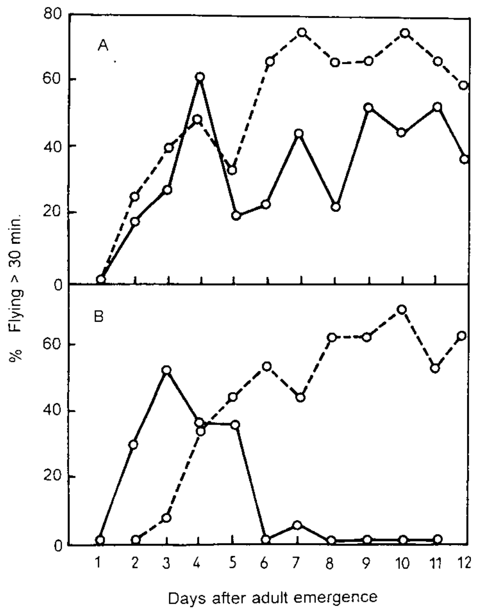

Fig. 4: Flight activity of adults of *Hippodamia convergens* reared at 24°C and under 12L:12D (A) or 16L:8D (B) and fed frozen (dashed line) or fresh aphids (solid line), (Rankin & Rankin, 1980b).

to be associated with ovarian maturation (Rankin & Rankin, 1980a). Evidently the regulation of flight activity cannot be attributed to one factor, i.e. different titres of JH.

In *Semiadalia undecimnotata* and *Coccinella septempunctata*, flight activity has been studied in relation to the size of flight muscles, size of the CA and ovarian development. Flight activity during the summer migration to dormancy sites and spring dispersal was much higher in the long distance migrant, *S. undecimnotata* than in *C. septempunctata* which often hibernates close to breeding sites. Decrease in flight activity after arrival at dormancy sites was followed by a partial autolysis of the flight muscles in both species (Okuda & Hodek, 1989). In *C. septempunctata*, the flight muscles began to regenerate in autumn, long before the spring dispersal flight (Fig. 3). As the basal metabolic rate of the flight muscles is rather high their untimely premature regeneration seems to be maladaptive. It might be explained, however, in terms of the bivoltine cycle of this species in warmer climates, which includes an autumnal return to breeding sites. Decrease in the flight tendency after dispersal to the breeding sites was not followed by flight muscle autolysis (Okuda et al., 1986).

In pre-diapause, ovaries developed up to the vitellogenic stage in most females of *S. undecimnotata*, and some females of *C. septempunctata*. The oocytes began to be resorbed prior to or after arrival at dormancy sites. The incidence of flight activity decreased to zero on completion of oosorption (Okuda & Hodek, 1989). A similar decrease in flight activity in relation to resorption of vitellogenic oocytes was observed in pre-diapause *C. septempunctata* reared under two contrasting laboratory photoperiods (Okuda et al., 1986). A high incidence of flight activity in post-diapause beetles coincided with the onset of vitellogenesis, which started before the beetles left dormancy sites. The flight activity of beetles at breeding sites dropped to near zero when chorionated eggs were present in their ovary.

Changes in volume of the CA were partially correlated with changes in size of the ovaries (Okuda et al., 1986; Okuda & Hodek, 1989). The relatively high flight activity coincided with an intermediate size of the CA. However, there is no conclusive evidence that there is a causal relationship between the titre of JH and flight activity. Also the above findings on the relation between reproductive and flight activity in *C. septempunctata* and *S. undecimnotata* are ambiguous. Thus in all three species (*H. convergens* and the two mentioned above) the physiological regulation of flight activity still awaits elucidation.

CONCLUSIONS

Although the long-distance flights of coccinellids have prompted much more research activity than the similar behaviour shown by other aphidophagous insects, there remains a rather incomplete understanding of the phenomenon.

Some aspects of the migratory behaviour have been at least partly elucidated, such as the effect of some environmental cues on the induction of diapause and migration to dormancy sites, and the termination of diapause and dispersal. There is, however, little understanding of the effect of feeding and reserves on flight activity. We suspect that intermediate titres of juvenile hormone stimulate flight. Meteorological prerequisites for take-off have been determined by multi-year records for at least one species, *S. undecimnotata.* The cycle of degeneration and regeneration of flight muscles is known, although there is still no satisfactory explanation of why the muscles regenerate in October, 7 months before the beetles disperse from dormancy sites.

In our view the greatest unsolved methodological problem is how to discriminate safely between the different types of flight behaviour in the laboratory. It seems that none of the three methods in current use give unambiguous results.

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