

## Maturation of Post-Hibernation Flight Behaviour in the Coccinellid *Coleomegilla maculata* (DeGeer)

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*Summary.* *Coleomegilla maculata* flies from its hibernation sites to breeding areas in the spring. Flight behaviour among the hibernating beetles was studied using the tethered flight technique. It was found that there is a successive maturation of flight behaviour in the spring. This process is mainly controlled by temperature acting over an extended period. From a standstill at 15°C the rate of the maturation process increased as the temperature was raised. Short photoperiods exerted a depressing effect on flight development early in the winter, but later this effect disappears.

### Introduction

Migratory flight behaviour in insects is usually linked to a distinct period in the adult insect's life. This period generally occurs in the young adult after a short maturation period and before reproductive functions develop. By measuring flight time of insects flown on pins or flight mills such a period during which flight behaviour develops has been demonstrated in several species of insects (see Johnson, 1969, 1974; Dingle, 1972).

Many insect species, however, have more than one flight period during their life cycle, for example all the insects that migrate to and from hibernation or estivation sites. Surprisingly little is known about what regulates the rematuration of flight behaviour and the timing of postdiapause flights. An exception is the study by Lewis (1963) on a thrips species.

The coccinellid *Coleomegilla maculata* hibernates in large assemblages in leaf litter in sunexposed wood margins and similar places. In the spring it flies from these sites to fields and forests where it starts feeding. This paper is concerned with the effects of various environmental factors on the maturation of flight behaviour (measured as flight duration of tethered beetles) of *C. maculata* during the spring.

### Material and Methods

The beetles used in the experiments were all collected at the same hibernation site in the leaf litter in a southward facing wood margin adjacent to cultivated fields (corn, *Zea mays* in the previous year) in Iowa City, Iowa, during the spring and fall 1973. Some samples were also taken from nearby dandelion fields after the beetles had dispersed from their hibernation sites. The beetles were immediately brought to the laboratory where they were distributed into plastic boxes 12 × 8.5 × 6 cm covered with nylon mesh, 60–70 beetles in each box. The beetles were provided with some leaf litter and distilled water from a cotton wick.

Before the flight tests the beetles were allowed to acclimate to the conditions of the flight room for at least 1 hr. During all tests the temperature was held at  $25 \pm 0.5^\circ\text{C}$ , the humidity

ranged from 44 to 51% R.H. and the illuminance was approximately 60 ft-c. An applicator stick with a waxed tip was attached to the pronotum of the beetle. It was gently lifted from the substrate and the stick was attached to a stand, the beetle facing a white wall. There was usually a delay of some seconds before the beetles started to fly. If a beetle started to fly within 1 min its flying time was measured using a stop watch. After the flight stopped, the beetle was allowed one more minute to start again etc. Each beetle was allowed to make up to five flights. The total flight time for all the flights was then calculated for each beetle. No additional stimuli for flight (other than loss of tarsal contact) such as blowing or swinging in the air were given to the beetles. Unless otherwise stated, 50 beetles were flight tested in each sample. The beetles were never tested more than once.

### Results

The highest densities of hibernating *C. maculata* occurred where the wood margin was slightly invaginated forming an area sheltered against winds from east, west, and north. The ground was covered with a layer of fallen leaves among some logs and low bushes. The hibernating beetles seemed to prefer areas where the leaf litter had accumulated.

During the winter the beetles were found in dense clusters often consisting of several hundred individuals in the leaf litter, usually in leaves that were folded or curled up. On the first sunny days after the snow had melted (this was one of the earliest bare patches in this area) some beetles could be seen crawling around or sunning themselves on the top leaves. As the spring proceeded, more and more beetles became active on sunny days. However, still in early May when most beetles had flown away from their hibernation sites, some beetles were still found aggregating under leaves (in the moist layer) even during sunny days. A similar description of the successive change in behaviour during the spring is given by Park (1930).

The first flights were observed on April 17 when some beetles made short flights (a couple of decimeters up to some meters). On this same day one beetle was also seen flying away from the hibernation site until lost to sight. Observations in early May showed that the behaviour during the beginning of the dispersal flight is very variable. Some beetles made very short flights of a couple of decimeters only, others flew upwards to a height of about 2 m before they flew away more or less horizontally. Finally, some individuals flew upwards in circles or back and forth until they were above the treetops, where they were carried away by the wind.

Feeding on pollen of spring flowers was observed at the hibernation site, the first observations being made on April 14. However, as few flowers were available at the hibernation site most beetles probably were not able (or willing?) to feed before they dispersed. Some copulations were also observed at the hibernation site, but the mating activity was obviously much higher after the beetles had moved to nearby fields.

The population of *C. maculata* at the hibernation site was sampled by counting all beetles in three 0.25 m<sup>2</sup> squares. The data indicate that the majority of the beetles left their hibernation sites during the latter half of April (Fig. 1A). The slight decrease in numbers prior to this period is probably due to the fact that as the season progressed some beetles walked around during the day, with the result that the hibernacula population became somewhat more dispersed.

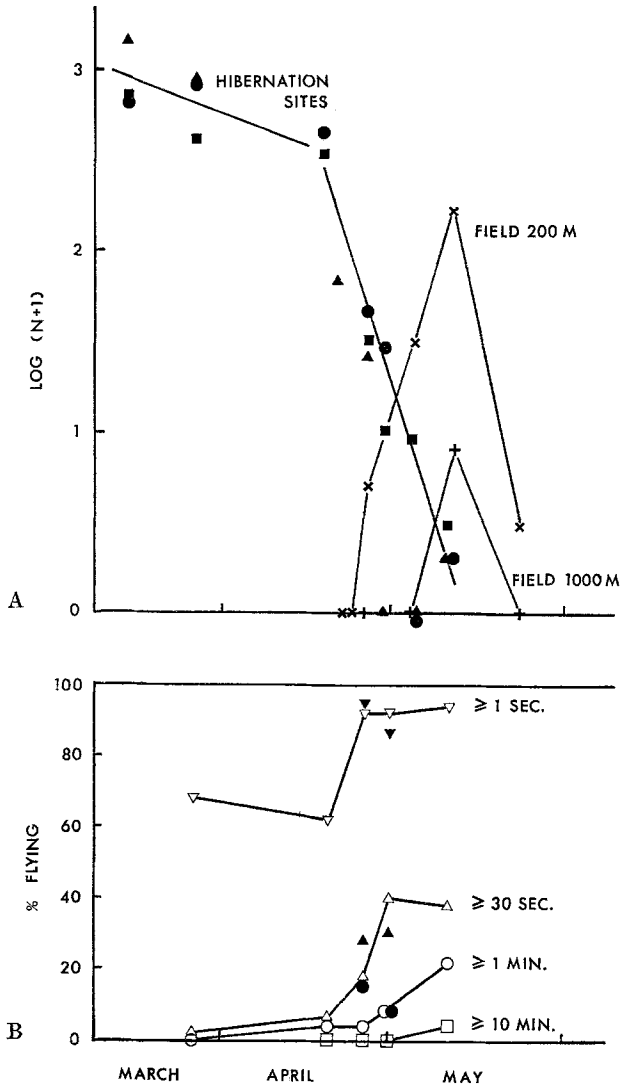


Fig. 1. (A) The number of *C. maculata* in three 0.25 m<sup>2</sup> squares (denoted ●, ■, ▲) at a hibernation site and in two dandelion fields, 200 m (×) and 1000 m (+) south of the hibernation site, during the spring 1973. Each field sample shows the number of beetles found during 20 min of searching. (B) The percentage of *C. maculata* collected on different dates that flew ≥ 1 sec (▽), ≥ 30 sec (△), ≥ 1 min (○), or ≥ 10 min (□). Filled symbols = beetles collected in dandelion fields

The first observations of *C. maculata* away from hibernacula were made on April 26, when several beetles were observed feeding on dandelion (*Taraxacum* spp.) flowers in a field about 200 m south of the closest hibernation site. Censuses of dandelion fields in the surrounding area indicated that the first flights were rather short for most beetles, for not until about 2 weeks later were

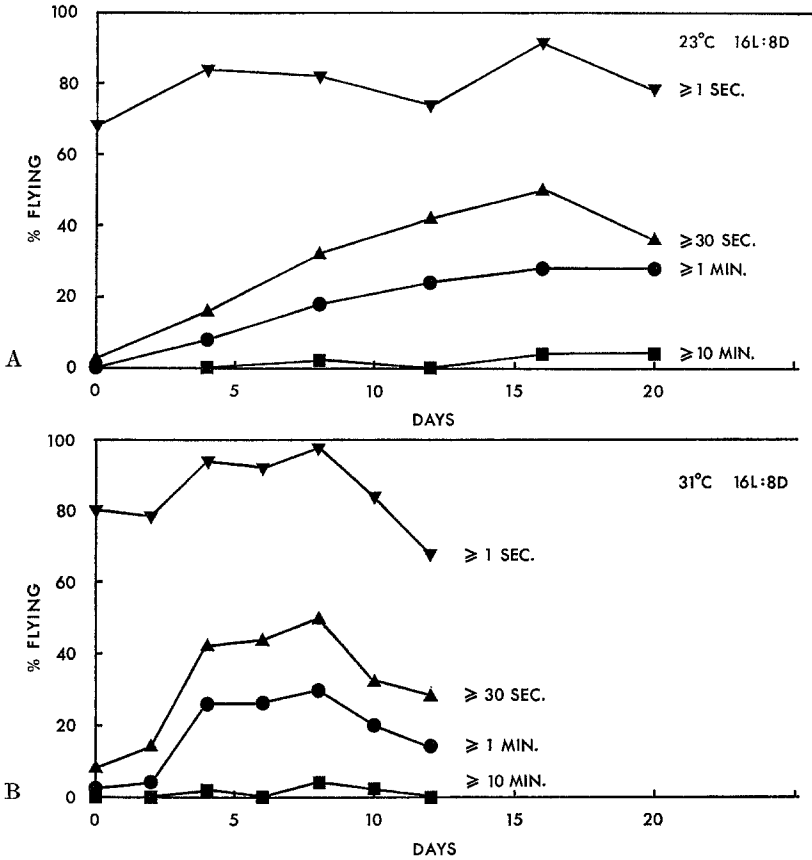


Fig. 2A and B. Flight performance of *C. maculata* using four different criteria for flight. The beetles were collected on March 26, 1973, and then kept for various periods at (A) 23°C and 16L:8D or (B) 31°C and 16L:8D

any beetles observed in similar dandelion fields 1000 m from the presumptive source overwintering populations (Fig. 1A).

Dispersal thus seems to take place stepwise with successive flights during several days or weeks. The decrease in the number of beetles in the last sample from dandelion fields can be explained partly by the decrease in the number of flowering dandelions at that time (thereby causing the beetles to fly to other areas) and partly by the emergence of a hymenopterous parasitoid [*Dinocampus coccinellae* (Schrank)] that caused heavy mortality at this time.

Coinciding with the period that the beetles left their hibernacula (approximately April 20 to May 1) there is a marked change in the flight response of the tethered beetles. This can be seen in Fig. 1B, which shows the flight performance of beetles collected at the hibernation site on different dates during the spring and flight-tested after 2 to 4 hrs in the laboratory. It seems that the beetles successively develop capacity for longer flights. The beetles in the two

samples from dandelion fields show a similar flight performance to those collected at the hibernation site (Fig. 1 B).

When beetles are taken from hibernacula in the spring and transferred to higher temperatures their flight response will successively change (Fig. 2). This maturation process is more easily distinguished using certain criteria for flight than others. Evidently the 30 sec criterion gives the best "resolution" of the development of flight capacity (which can also be seen in Fig. 1 B). Thus this criterion is used in the subsequent experiments. The data are also in accordance with field observations indicating that most flights are of comparatively short duration. The decrease in flight time at 10 and 12 days among the 31°C beetles is probably due to the effect of starvation and thus decreased vitality.

Temperature strongly affects the rate of the flight maturation process. The flight performance of beetles collected at the hibernaculum in March and stored at 5 different temperatures are compared in Fig. 3 A. It is evident that temperatures above 15°C are needed for the flight maturation process to take place at any considerable rate at least. Above this "threshold" (somewhere between 15°C and 19°C) the rate of the maturation process increases, at least up to 31°C—the highest temperature tested.

The rate of the maturation process was expressed in two ways by measuring (1) the time between the collecting day and the day of maximum flight performance and (2) the time from collecting day to 50% of flight maximum was reached. The latter value was graphically estimated by using probability paper. The two values give very similar results. In the interval 19–31°C there seems to be a linear relationship between the temperature and the logarithm for developmental rate (Fig. 3 B).

Under natural conditions the maturation process is fairly extended taking at least one month. It was found that when beetles were collected at the hibernation site on different dates and flight-tested, successively less time was needed for the completion of the maturation process as the season progressed (Fig. 4 A). (The lower maximum values reached in the March sample may be explained by the effect of the longer exposure to starvation among these beetles.) The rate of development gradually becomes faster in late April (Fig. 4 B) as would be expected because of the increasing temperatures during that period. This coincides with the actual spring dispersal flight (*cf.* Fig. 1 A).

In order to test the effect of photoperiodic conditions on the maturation of flight behaviour beetles were collected at the hibernation site on three occasions during the winter and the spring. They were subjected either to long- or short-day conditions and were flight-tested at intervals (Fig. 5). The data indicate that short photoperiods delay the flight maturation process early in the winter, but this effect disappears later. The December data for day 16, 20, and 24 pooled for the two light regimens respectively are significantly different at the 0.001 level ( $X^2 = 34.7$ , *d.f.* = 1).

### Discussion

When quantifying flight behaviour in the laboratory several other measures than flight time of tethered individuals can be used, *e.g.* one can measure the number of spontaneous take-offs. These other methods give measures of different

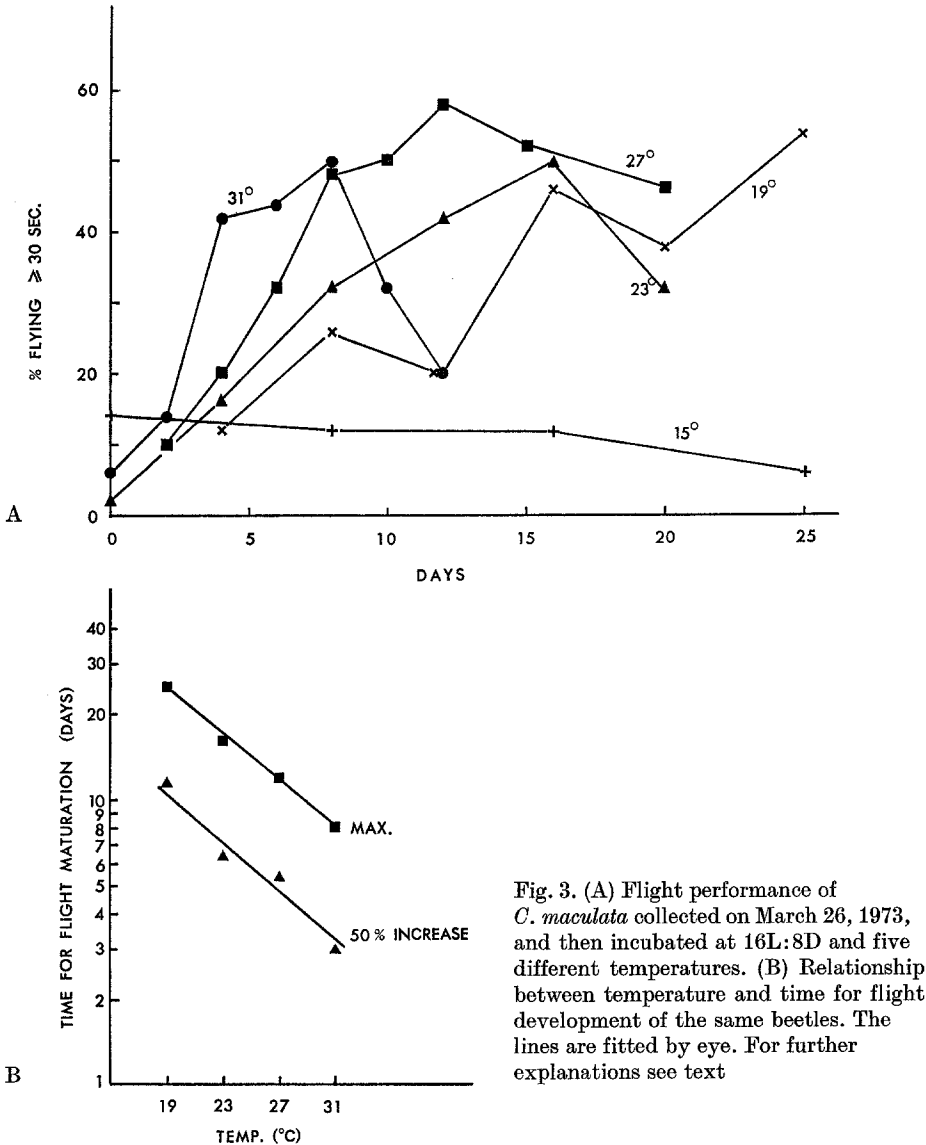


Fig. 3. (A) Flight performance of *C. maculata* collected on March 26, 1973, and then incubated at 16L:8D and five different temperatures. (B) Relationship between temperature and time for flight development of the same beetles. The lines are fitted by eye. For further explanations see text

aspects of flight behaviour. However, it seems reasonable to assume that the different measures are strongly correlated with each other (and with real flight activity) because when an insect is supposed to fly, all behavioural and physiological mechanisms favouring flight ought to be maximized. It is thus believed that the tethered flight technique used in this study gives a measure which is strongly correlated to an overall development of flight capacity and flight willingness. The correlation between the change in behaviour of the tethered beetles and the time for the dispersal flight in the field supports this view (Fig. 1 A and B).

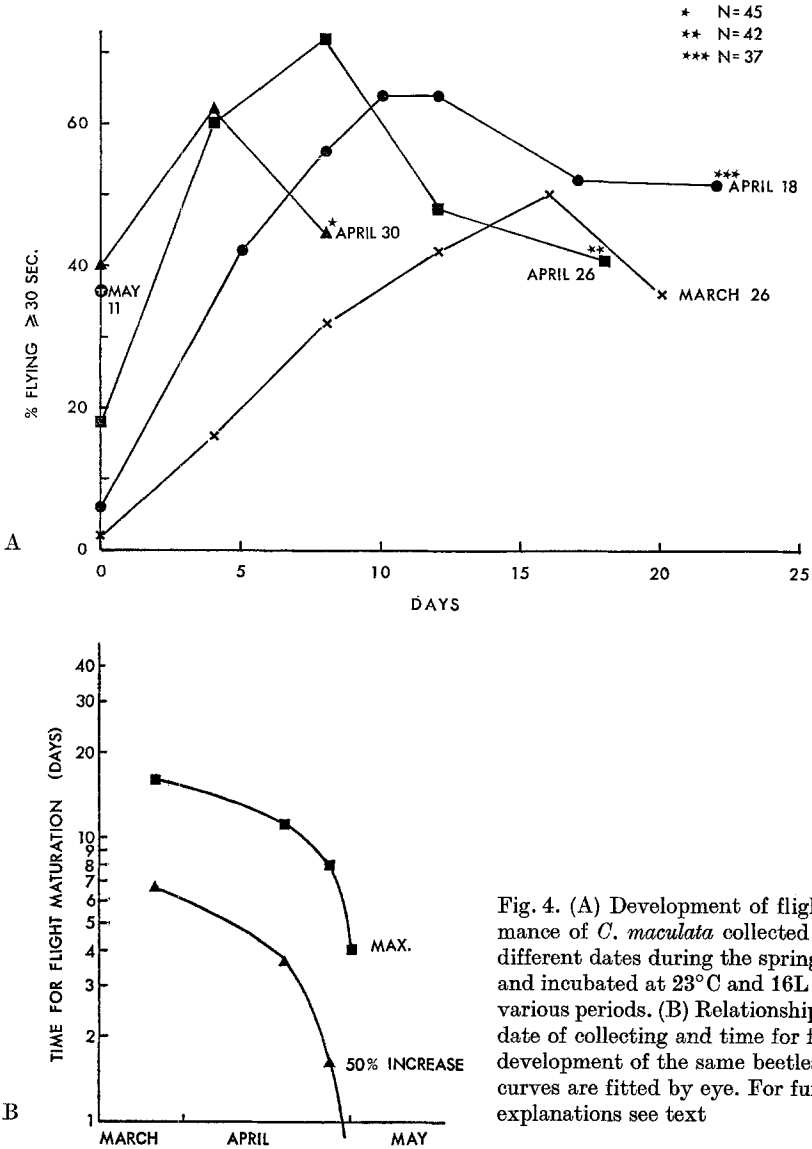


Fig. 4. (A) Development of flight performance of *C. maculata* collected at different dates during the spring 1973 and incubated at 23°C and 16L:8D for various periods. (B) Relationship between date of collecting and time for flight development of the same beetles. The curves are fitted by eye. For further explanations see text

The maturation of flight behaviour in *C. maculata* in the spring is undoubtedly strongly affected by the experience of increased temperatures over an extended period. As the temperature increases (in the range 19 to 31°C at least) the maturation process is speeded up (Fig. 3). It thus seems that *C. maculata* responds to an integrated value of temperature over time. One could probably make quite accurate predictions of the time for flight departure if data on "effective" temperatures in the hibernacula were available.

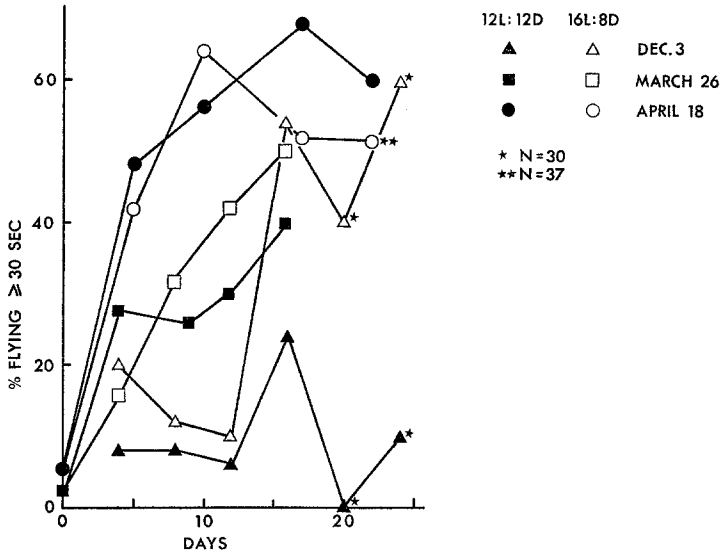


Fig. 5. Development of flight performance of *C. maculata* collected at the hibernation site on different occasions and then subjected to short-day (12L:12D) or long-day (16L:8D) conditions at 23°C while being flight tested at 3–5 day intervals

There seems to be a threshold for this maturation process at about 15°C. Hodson (1937) noted that hibernating *C. maculata* started to move downwards in the leaves when the temperature was falling below about 15°C, which fits the idea of a threshold at about that temperature. Ipert (1966) found that the coccinellid *Semiodadalia undecimnotata* (Schneider) is reactivated to fly in the spring after minimum temperatures have been sufficiently high for several days, and Hodek (1960) found that the emergence of the same species seemed to be dependent on the ambient temperature, emergence occurring after the mean temperature had remained above 12–14.5°C for some time. These findings indicate a mechanism similar to that in *C. maculata*. The photoperiodic conditions in the spring do not seem to affect the flight maturation process. (The possibility of a photoperiodic effect at temperatures lower than 23°C cannot, however, be excluded.) However, there is an effect of photoperiod earlier in the winter, short photoperiods depressing the development of flight behaviour.

Are there other environmental factors involved in the regulation of the flight maturation process? Preliminary experiments indicate that the experience of starvation and possibly of high humidities in the late spring will cause an increase in the frequency of beetles making long flights. The effects, however, seem to be small compared to the temperature effect, and it is doubtful if these factors affect the maturation process per se. The humidity effect may just be the result of lowered viability among desiccated beetles. Further, the effect of starvation is probably only of importance after the beetles have dispersed from their hibernacula.



Summarizing our findings we can say that *C. maculata* has to go through a process during which flight behaviour develops, before it will fly from its hibernacula in the spring. Under natural conditions this process is mainly regulated by the accumulated effect of high temperatures over an extended period. The time for flight departure from the hibernation sites is thus determined by the maturation process by which flight-willing individuals are recruited *and* by the subsequent occurrence of weather conditions favourable for flight. Such a process may be fairly common among insects that hibernate as adults and migrate in the spring.

An insect that must move from a hibernation site to a breeding area in the spring faces two problems. First, it is dangerous to resume activity and fly before food is available (or as long as other environmental factors make life hazardous) in the breeding habitat. Second, it is advantageous to arrive in the breeding habitat as soon as living conditions permit, in order to breed as early as possible. Thus there ought to be a strong selective advantage for those individuals which have the best ability to synchronize their flight with the change from unfavourable to favourable living conditions (such as the appearance of food plants) in the breeding habitat.

While photoperiod often is the most accurate token stimulus for initiation of diapause (and probably of related reactions like prehibernation flights), temperature measured over a period is a stimulus which probably provides a better prediction about when to resume activity in the spring. Temperature undoubtedly shows a higher correlation with many phenological events in the spring than for example photoperiod, which does not change between years. For example, the beginning of flowering of many plants in the spring is highly variable from year to year, this variation being highly correlated with the summed effect of increased temperatures over a period (Daubenmire, 1967, pp. 185–186; Lindsey and Newman, 1956). One would thus expect that an integrated measure of temperature over a period would provide a more accurate prediction of environmental conditions in the breeding habitat in the spring than for example photoperiod. In addition to *C. maculata* such a temperature dependent maturation process for the initiation of spring dispersal flights has been described in *Limothrips cerealium* Haliday (Lewis, 1963) and a similar process occurs in *Leptinotarsa decemlineata* Say (LeBerre, 1962). Johnson (1969, p. 289) also thought that a temperature dependent rematuration period occurred generally.

Studies in progress on the flight behaviour of the bug *Lygaeus equestris* (L.) (Lygaeidae) strongly indicate a similar maturation process (Solbreck, unpubl.). It is striking that *C. maculata*, *L. equestris*, and *L. cerealium* all hibernate in sunexposed positions and frequently bask in the sun in the spring. They will thus attain very high body temperatures early in the spring, often long before it is safe to fly to the breeding habitat. An extended maturation process would thus provide a safety check against too early a departure from the hibernation site because of an occasional early warm and sunny day (*cf.* Lewis, 1963). One can also speculate about the significance of sunbasking behaviour of these insects in the spring. Maybe it allows the insect to "measure" a microclimate that is better correlated with the development of their food resources in the spring.

It should be noted that this study has been concerned with the response of a population. How is this related to the change in flight behaviour of the individual beetle, and what is the character of this change? One possible mechanism would be a gradual lowering of the temperature threshold for flight of the individual beetle. Studies on *L. equestris* have shown that such a gradual lowering of the temperature threshold for take-off occurs during the spring (Solbreck, unpubl.). A similar mechanism in *C. maculata* seems likely.

The mechanism regulating the rematuration of flight behaviour in *C. maculata* appears to be intimately interwoven with the general diapause development. Usually diapause is terminated fairly early in the winter, the subsequent dormancy (or continuation of the diapause in the sense of Mansingh) being maintained by low temperatures (e.g. Danilevsky *et al.*, 1970; Hodek, 1973; Mansingh, 1971). Similarly, in the early winter short photoperiods arrest the development of flight behaviour in *C. maculata*, while later temperature seems to be the main controlling factor.

Finally some words should be said about the dispersal capacity of *C. maculata*. Ewert and Chiang (1966) found that it moved about less and flew lower than the coccinellids *Hippodamia convergens* Guerin and *H. tredecimpunctata* (L.) in corn fields during the period mid-July to mid-September. The present study indicates that dispersal from the hibernation sites in the spring mostly takes the form of repeated rather short flights relatively close to the ground. However, some beetles were observed to exhibit a behaviour during exodus flight that took them high in the air. Further a small proportion of the tethered beetles flew for several hours. One specimen of *C. maculata* was collected by airplane at 500 feet in Illinois-Indiana during the period May 15–June 4 by Glick (1960). Twelve specimens were collected in southern United States during the summer months at altitudes ranging from 20 to 200 feet. The related species *C. floridianus* was even captured at 6000 feet (Glick, 1939, 1957). All these observations strongly suggest that at least a part of the population is able to disperse over considerable distances on winds high up in the air.

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### References

- Danilevsky, A. S., Goryshin, N. I., Tyshchenko, V. P.: Biological rhythms in terrestrial arthropods. *Ann. Rev. Ent.* **15**, 201–244 (1970)
- Daubenmire, R. F.: Plants and environment. A textbook of plant autecology, 422 pp. New York: Wiley 1967
- Dingle, H.: Migration strategies of insects. *Science* **175**, 1327–1335 (1972)
- Ewert, M. A., Chiang, H. C.: Dispersal of three species of Coccinellids in corn fields. *Can. Ent.* **98**, 999–1003 (1966)
- Glick, P. A.: The distribution of insects, spiders and mites in the air. U. S. Dept. Agric. Tech. Bull. **673**, 1–150 (1939)
- Glick, P. A.: Collecting insects by airplane in Southern Texas. U. S. Dept. Agric. Tech. Bull. **1158**, 1–28 (1957)

- Glick, P. A.: Collecting insects by airplane, with special reference to dispersal of the potato leafhopper. U. S. Dept. Agric. Tech. Bull. **1222**, 1-16 (1960)
- Hodek, I.: Hibernation-bionomics in Coccinellidae. Acta Soc. Ent. Čechoslov. **57**, 1-20 (1960)
- Hodek, I.: Biology of Coccinellidae, 260 pp. + 32 pl. Prague-The Hague: Academia-Junk 1973
- Hodson, A. C.: Some aspects of the role of water in insect hibernation. Ecol. Monogr. **7**, 271-315 (1937)
- Iperti, G.: Migration of *Adonia undecimnotata* in South-eastern France. In: I. Hodek, ed., Ecology of aphidophagous insects. Proc. Symp. Liblice near Prague Sept. 27-Oct. 1, 1965, p. 137-138. Prague-The Hague: Academia-Junk 1966
- Johnson, C. G.: Migration and dispersal of insects by flight, 763 pp. London: Methuen 1969
- Johnson, C. G.: Insect migration: Aspects of its physiology. In: M. Rockstein, ed., The physiology of insecta, 2nd ed., vol. III, p. 279-334. New York-London: Academic Press 1974
- LeBerre, J. R.: Les bases scientifiques des avertissements agricoles. Phytoma (Paris) **14** (Nov.), 14-18 (1962)
- Lewis, T.: The effect of weather on emergence and take-off of overwintering *Limothrips cerealium* Haliday (Thysanoptera). Ann. appl. Biol. **51**, 489-502 (1963)
- Lindsey, A. A., Newman, J. E.: Use of official weather data in spring time-temperature analysis of an Indiana phenological record. Ecology **37**, 812-823 (1956)
- Mansingh, A.: Physiological classification of dormancies in insects. Can. Ent. **103**, 983-1009 (1971)
- Park, O.: Studies in the ecology of forest Coleoptera. Ann. ent. Soc. Amer. **23**, 57-80 (1930)

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