



## Flight potential and oxygen uptake during early dormancy in *Coccinella septempunctata*

Oldřich Nedvěd<sup>1,2</sup>, Piotr Ceryngier<sup>3</sup>, Magdalena Hodková<sup>1</sup> & Ivo Hodek<sup>1,\*</sup>

<sup>1</sup>Institute of Entomology, Czech Academy of Sciences, Czech Republic; <sup>2</sup>Faculty of Biological Sciences, University of South Bohemia, Branišovská 31, 370 05 České Budějovice, Czech Republic; <sup>3</sup>Institute of Ecology, Polish Academy of Sciences, Dziekanów Łeśny, 05-092 Lomianki, Poland; \*Author for correspondence

Accepted: March 15, 2001

**Key words:** diapause, energetic reserves, fat body, flight duration, flight tendency, migration, ovaria, respiration

### Abstract

Two flight parameters (take-off and duration) and respiration level were measured, in two years in summer and early autumn, in dormant *Coccinella septempunctata* L. (Coleoptera: Coccinellidae) collected while hidden in grass tussocks in hibernation sites (HID) and in beetles collected on plants (PLA). The duration of tethered flight of HID beetles measured in the laboratory in late August and September 1995 (range of geometric means 190–440 s) was slightly longer than the flight of PLA beetles (80–310 s), both being much longer than trivial flight recorded in beetles foraging for prey during the breeding season (35 s). In general, the flight performance had a tendency to increase in September and to decrease in October.

The oxygen consumption in HID beetles increased throughout September 1994 from 430 to 780  $\mu\text{l g}^{-1} \text{h}^{-1}$  and throughout October 1995 from 710 to 1060  $\mu\text{l g}^{-1} \text{h}^{-1}$ . This increase is ascribed to a concomitant decrease in diapause intensity. A similar increase was observed also in PLA beetles in 1994 and oxygen consumption was always higher than in HID beetles, most probably due to feeding and digestion in PLA beetles.

Laboratory feeding of HID beetles on aphids induced maturation of ovaries and increased oxygen uptake (from 680 to 1110  $\mu\text{l g}^{-1} \text{h}^{-1}$ ). Feeding on honey and pollen left their oxygen uptake unchanged. Effect of feeding on the flight parameters was mostly not significant. In agreement with its less suitable body shape and usually less distant dormancy sites, *C. septempunctata* was found a less apt flier than long-distance migrating coccinellid species.

### Introduction

As with many other migratory insect species (Gatehouse, 1997), prediapause migration occurs also in coccinellids (Hodek et al., 1993). Although flight in coccinellid species that undertake long distance migrations (and form large aggregations during dormancy), such as *Hippodamia convergens* and *Ceratomegilla* (syn. *Semiadalia*) *undecimnotata*, has been adequately studied (Hagen, 1966; Rankin & Rankin, 1980a,b; Ipert, 1986), no such studies exist in *Coccinella septempunctata*, a species with less spectacular migration behaviour. In contrast to the long distance fliers *H. convergens* and *C. undecimnotata* which have a more 'aerodynamic' and less convex body shape, the half-spherical adults of *C. septempunctata* might be

supposed to possess lower flight abilities. In Johnson's (1969) categorization of migration the species belongs to class IIIa (hibernate within its breeding area) while *H. convergens* is in class IIIb (hibernate far beyond the breeding area). *Coccinella septempunctata* indeed remain for their dormancy mostly in the lowland near the breeding habitats (Hodek & Honěk, 1996, p.274) although hibernation sites have also been reported from mountains (Hodek et al., 1977; Honěk, 1989). To study the predicted lower flight performance, we measured flight duration for the first time in this species. In other studies of *C. septempunctata* only flight tendency (take-off) has been recorded (Okuda & Hodek, 1989; Honěk, 1990).

Heterogeneous populations of *C. septempunctata* consisting of potential bivoltine individuals and oblig-

atory univoltine individuals occur in most temperate European regions (Hodek et al., 1977; Hodek & Ružička, 1979; Hodek & Honěk, 1996, p. 294). In central Europe, many individuals arrive at the dormancy sites already in late July/early August while other beetles can still be found on vegetation in October (Hodek, 1960, 1962; Hodek et al., 1977; Hodek & Honěk 1996, p. 289). On identical autumnal dates the individuals from dormancy sites differ characteristically from those on plants in the state of gonads, fat body, and gut (summarized in Hodek & Honěk, 1996). We also found that females sampled in autumn outside the dormancy shelters can be induced to mature ovaries by adequate rearing conditions more readily than those that are already dormant in shelters (Hodek, 1962).

The aim of this study was to find out whether individuals with two contrasting types of autumnal behaviour differ also in their flight performance and metabolic rate (oxygen consumption) and whether these parameters change with the season. By keeping beetles with ample aphid food we investigated whether a decrease might occur in flight performance similar to that in *H. convergens* (Rankin & Rankin, 1980a).

Dingle (1996, p. 421) advocated a complex approach to understanding migration, by studying "physiological mechanisms underlying migratory behaviour and ecological consequences". We combined measuring two flight parameters and oxygen consumption in field samples of two subpopulations in order to increase our understanding of migration in *C. septempunctata*.

## Materials and methods

**Beetles.** Adults of *Coccinella septempunctata* L. were tested in 1994 from August through September and in 1995 from July through October. Dormant individuals (HID) were collected while hidden in grass tussocks in a hibernation site on an isolated prominent hill (Raná, 500 m a.s.l., about 200 m rel. altitude), northern Bohemia. Beetles sitting on plants without aphids (PLA) were sampled in a lowland area next to this hill (1994) and in lowland localities in the vicinity of České Budějovice, southern Bohemia (1995). PLA beetles were less homogeneous than HID beetles. The dissections (see below) showed that they differed in completion of pre-dormancy feeding.

Field samples of HID and PLA beetles (number of individuals ranging from 10 to 36) were investi-

gated within two days after collection. For measuring oxygen consumption in 1994, the PLA beetles were starved a week under outdoor conditions to bring them nearer to HID beetles which, of course, do not feed in their shelters. A sample of HID beetles for the food experiment was collected on 13 September 1994 and then kept for two weeks in outdoor cages before investigation. These beetles were either starved or fed on either essential food (i.e., enabling reproduction), the aphid *Acyrtosiphon pisum* (Harris), or alternative food (i.e., serving only as a source of energy; see, e.g., Mills, 1981, Evans et al., 1999), honey and sunflower pollen, under natural photoperiod and temperature. Temperature was recorded inside the cage where the beetles were kept.

**Respiration.** Oxygen consumption was measured at 26 °C by the conventional technique with the Warburg apparatus (Sláma, 1960). Respiratory vessels of about 10ml volume were employed with sodium calcite to absorb carbon dioxide. The recorded value of oxygen consumption of each individual at rest represented an average from three 0.5 h readings which were taken on the same day in the same individuals that were subsequently tested for flight and finally dissected. Oxygen consumption was related to fresh weight.

**Flight.** The flight activity was measured as the tendency to fly (take-off = TOF), and the duration of the flight (DUR). Measurements were performed at 25 °C in autumn 1994, and at 32–33 °C in 1995, after 0.5 h acclimation at that temperature. Because of low values of flight duration recorded in 1994 the temperature was increased in 1995. The beetles arrive at the hibernation sites by flying at such ambient temperatures (Figure 2C). Illumination was performed by eight 15W fluorescent tubes situated 50 cm above the animals.

Latency of flight take-off was recorded when the ladybird beetle was released onto a 50 mm lid of a Petri dish. The time preceding the attempt to fly ranged from 1 to 60 s, or the trial was discontinued if no flight occurred (Okuda & Hodek, 1989). The trials were executed in a cage and each individual was tested ten times ( $n=23-36$ ). Ten individuals were checked in one series, so that each individual rested 9 min between two trials. TOF was recalculated as number of take-offs per minute ( $\text{TOF} = 60/\text{time} - 1$ ).

Flight performance was measured as duration of tethered flight using the technique of Dingle (1966), modified after Rankin & Rankin (1980a,b), as de-

scribed in more detail elsewhere (Nedvĕd & Hodek, 1995). A ladybird was attached by wax on its pronotum to a pin head. Flight was initiated by moving the insect rapidly through the air and maintained by a mild air current (30 cm from 35 W fan). Durations of ten trials for each individual were pooled ( $n=23-36$ ). The individuals rested 5–10 min between two trials.

Due to high variability and skewed distribution within many samples, it was not always appropriate to use parametric comparative statistics based on arithmetic means. We tried to use the most informative parameter and the most robust test available for each particular set of data. We calculated medians for samples collected in the field in 1994, and means for samples fed with diverse food. The distribution of values in 1995 followed a lognormal distribution (Kolmogorov–Smirnov test, STATISTICA distribution fitting). Thus, we recalculated the individual values using decadic logarithm ( $LTO=\log(TOF+1)$ ;  $LDU=\log(DUR+1)$ ). The descriptive and comparative statistics were computed using the logarithmic parameters, but the group mean values in the text and table are expressed again as recalculated to the original parameters for easier readout. The arithmetic means of LTO and LDU are in fact close to the geometric means of TOF and DUR.

*State of organs.* The state of organs was evaluated by dissection under Ringer solution. The state of ovaries was scored in arbitrary categories from 1 (undeveloped) to 5 (chorionized eggs) (see Okuda & Hodek, 1989), the content of gut from 0 (empty) to 3 (full), the size of fat body from 1 (small, diffused) to 4 (hypertrofied). The volume of dorso-longitudinal flight muscles was measured in a Bürker chamber, an instrument that is also used for counting blood elements. It consists of two glass plates, the lower hollowed. The space is 0.1 mm deep and provided with a precise net of lines, which allows for accurately measuring the volume of organs.

## Results

*State of organs.* The PLA beetles had a full gut in July whereafter the gut content gradually decreased until September. The size of fat body increased simultaneously during the season (Figure 1). All HID beetles had a large fat body and an almost empty gut, except in the latest sample (Figure 1). Ovaries were undeveloped (score 1) in both HID and PLA bee-

gles. Flight muscle volume of HID beetles gradually increased from early September to late October.

*Respiration.* In HID beetles, oxygen consumption was low in early and mid-August 1994 (430 and 460  $\mu\text{l g}^{-1} \text{h}^{-1}$ ) and increased to intermediate values in September (675 and 780  $\mu\text{l g}^{-1} \text{h}^{-1}$  on two dates) (Figure 2A). In PLA beetles from northern Bohemia, the pattern was similar, but the mean values were higher. The oxygen consumption increased from low values in early August (620  $\mu\text{l g}^{-1} \text{h}^{-1}$ ), through intermediate values in late August (760  $\mu\text{l g}^{-1} \text{h}^{-1}$ ), to high values in September (1130  $\mu\text{l g}^{-1} \text{h}^{-1}$ ) (Figure 2A). After several days of starvation, the oxygen consumption of PLA beetles decreased to the level similar to that of HID beetles (430  $\mu\text{l g}^{-1} \text{h}^{-1}$  in early August, 600  $\mu\text{l g}^{-1} \text{h}^{-1}$  in late August, 840  $\mu\text{l g}^{-1} \text{h}^{-1}$  in September) (Figure 2A).

In 1995, the oxygen consumption was only measured in HID beetles. It was intermediate in late August throughout September (710–820  $\mu\text{l g}^{-1} \text{h}^{-1}$ ) and increased to a high value in mid-October (1060  $\mu\text{l g}^{-1} \text{h}^{-1}$ ) (Figure 2B). Respiration was slightly positively correlated with the volume of flight muscles (variance explained: 5%,  $P=0.05$ ) (Figure 1). Neither sex, gut content, nor state of fat body was correlated with the level of respiration.

*Flight parameters in 1994.* Flight tendency (TOF) was very low in HID beetles in August (0–0.03  $\text{min}^{-1}$  – medians on two different dates), while it increased in September (3.4–8.2  $\text{min}^{-1}$ ). PLA beetles from northern Bohemia had intermediate TOF in August (2.1–3.7  $\text{min}^{-1}$ ) as well as in September (1.4–5.2  $\text{min}^{-1}$ ). PLA beetles from southern Bohemia had low median TOF at all times tested (0.2  $\text{min}^{-1}$  in August, 0.6  $\text{min}^{-1}$  in September; not shown).

The duration of flight (DUR) in HID beetles was very low in August (0.7–0.9 s), and increased slightly in September (1.2–3.7 s). DUR was variable in PLA beetles from northern Bohemia (medians 1.1–10.1 s in August, 1.3–9.5 s in September), and quite different in PLA beetles from southern Bohemia (1 s in August, 29 s in September; data not shown).

*Flight parameters in 1995.* PLA coccinellids showed a rather constant tendency to fly (TOF) from July to October (Figure 3A). HID beetles showed a changing TOF pattern. The geometric mean value was comparable to those of PLA beetles in August, but increased

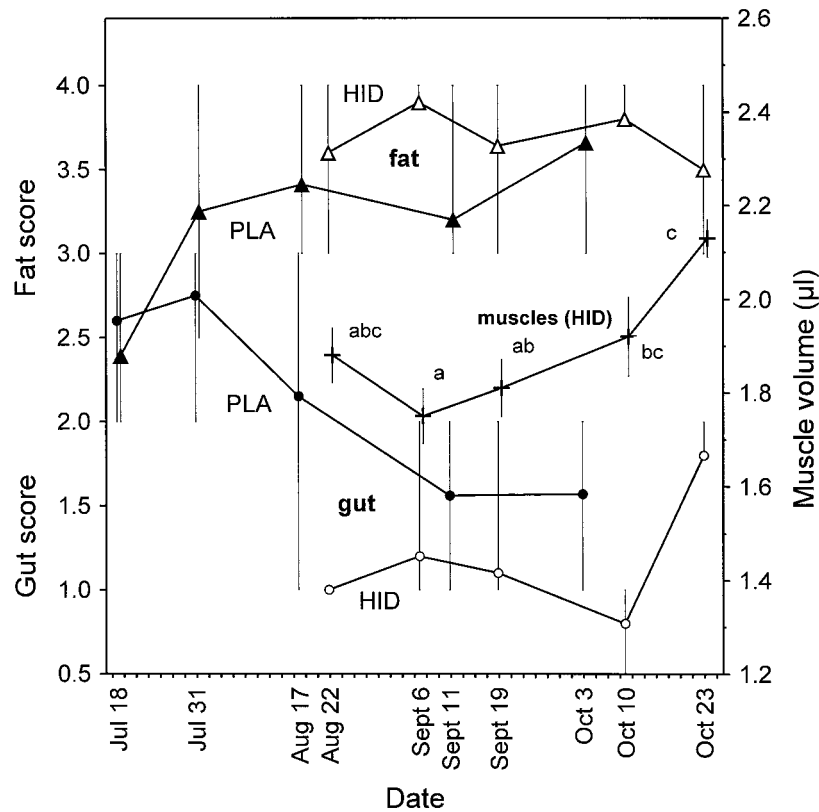


Figure 1. State of organs measured from July 18 to October 23 1995 in *Coccinella septempunctata* collected on plants (PLA, solid symbols) and hidden (HID, open symbols). Gut score = amount of 'food' in gut, categorized 0–3; fat score = size of fat body, categorized 1–4; means and quartils (25% and 75%) are plotted for both variables. Volume of flight muscles (only HID; mm<sup>3</sup>), means and S.E.; letters (a, b, c) group mean values not different from each other according post-hoc comparisons (LSD) at 5% level.  $n = 20-40$ .

thereafter till mid-September. During October, the TOF again decreased.

The duration of flight (geometric mean DUR) in PLA beetles increased from July to mid-September (Figure 3B), and decreased greatly in October. The DUR of HID beetles was quite high in August and even higher in September. However, it was low in October.

In spite of great variation, flight performance (DUR) of the two groups of beetles had rather unexpected similar seasonal dynamics (Figure 3B) and did not differ much in individual months although higher values of DUR were associated with HID beetles. Similar seasonal dynamics of DUR was also apparent when the beetles were divided into three groups: weak fliers (< 1 min), intermediate fliers (1–15 min), and strong fliers (>15 min). Thus, the incidence of strong fliers among HID beetles increased slightly from August (28%) and early September (31%) to

mid-September (39%) and then steeply decreased in October (3%).

None of the organ parameters were correlated with any of the flight parameters. TOF was generally higher in females than in males (ANOVA,  $P < 0.001$ ), but the course of changes in time was similar in both sexes. Flight duration (LDU) was negatively correlated to respiration at rest ( $P = 0.01$ , only 4% of the variance explained), and both flight parameters (TOF and DUR) were strongly correlated ( $P < 10^{-6}$ , 10% of variance explained).

*Effect of feeding on dormant (HID) beetles.* The values of take-off remained similar in beetles fed with aphids versus beetles tested soon after sampling, and increased in both starved and honey-fed samples. The mean duration of the flight remained low in beetles fed with aphids, but increased in those fed with honey. However, the difference among the two groups of beetles was not significant (Table 1). Oxygen con-

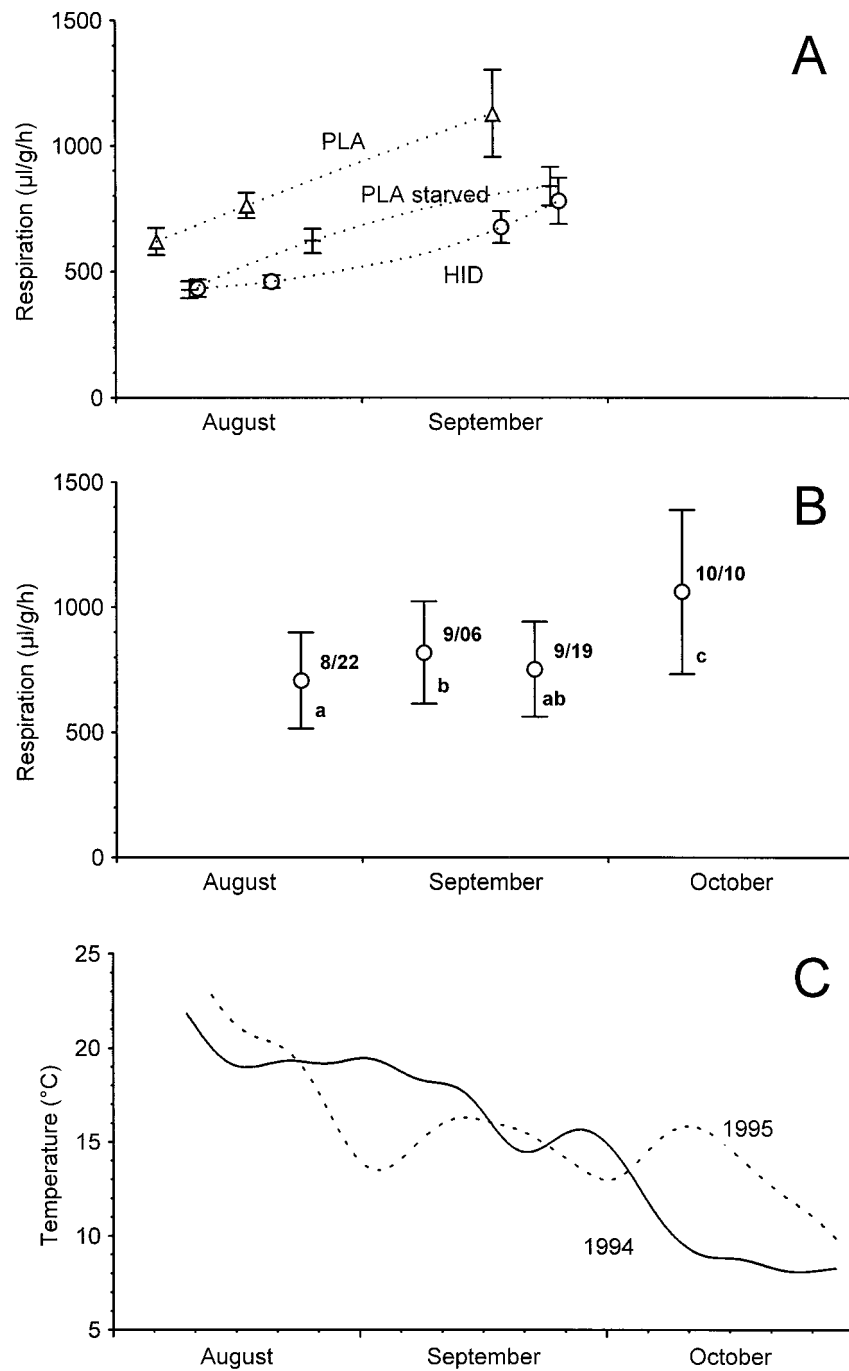


Figure 2. Oxygen consumption in *Coccinella septempunctata* ( $\mu\text{l g}^{-1} \text{h}^{-1}$ ; means  $\pm$  S.D.). (A) Samples in 1994: beetles collected on plants (PLA) just after sampling (triangles), and after a week of starvation (PLA starved, crosses), and hidden (HID) beetles just after sampling (circles). ANCOVA and Tukey test revealed a difference ( $F = 43.9$ ,  $P < 10^{-6}$ ) between PLA and the other two series. In each series separately, ANOVA showed an increase ( $F = 32.2$ ,  $P = 10^{-6}$ ) between the first and the last sample. (B) Samples in 1995, hidden beetles. Letters (a, b, c) group mean values not different from each other according post-hoc comparisons (LSD) at 5% level. (C) Outdoor temperatures in 1994 (solid line), and 1995 (dashed line); smoothed averages of 5-day periods.

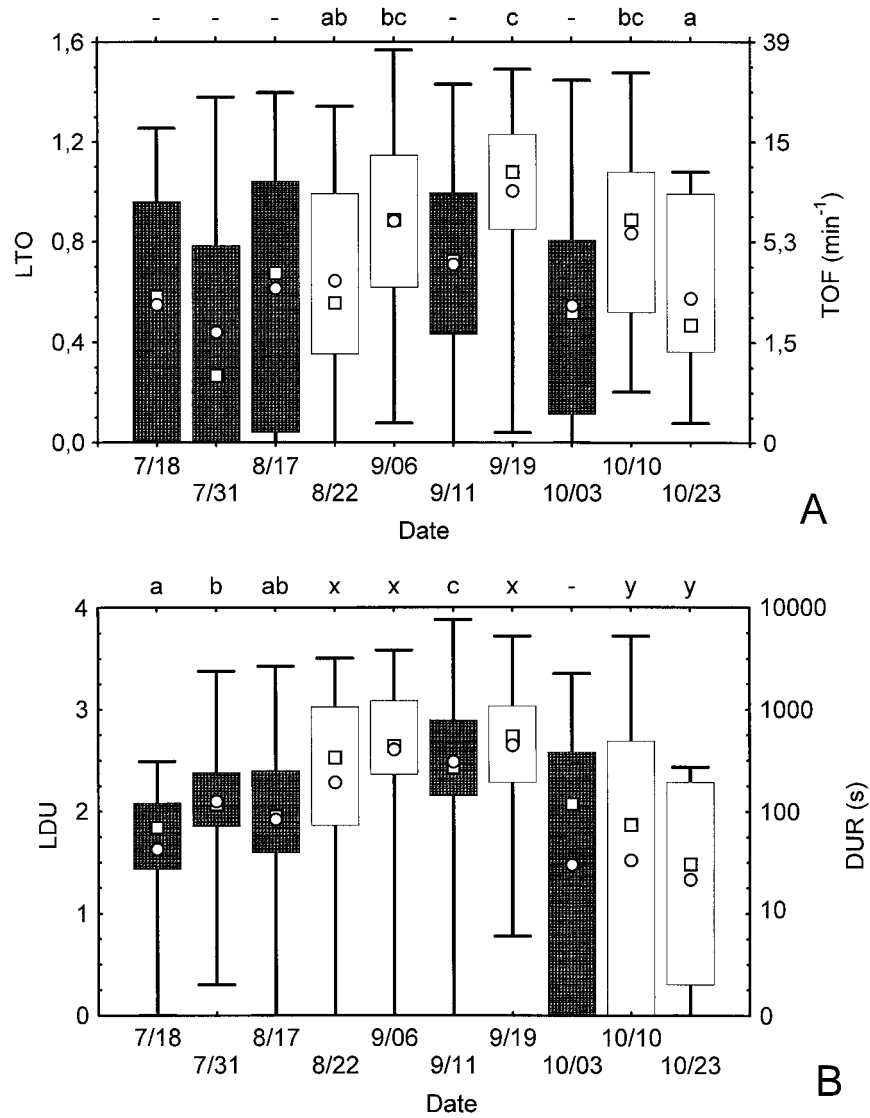


Figure 3. Seasonal changes in (A) take-off (TOF:  $\text{min}^{-1}$ , LTO – logarithmic scale), and (B) flight duration (DUR: seconds, LDU – logarithmic scale) of *Coccinella septempunctata* collected in 1995 on plants (PLA, hatched boxes) and hidden (HID, open boxes). Square = median, circle = geometric mean, box = quartiles (25 and 75%), bars = minimum and maximum values. Letters (a, b, c; x, y) group mean values not different from each other according post-hoc comparisons (LSD) at 5% level. In both variables, ANCOVA revealed a difference between PLA and HID beetles (LTO:  $F = 29.4, P < 10^{-6}$ ; LDU:  $F = 12.1, P = 6 \times 10^{-4}$ ). (A) No significant difference was found in take-off within PLA beetles; within HID beetles, the groups shown by Duncan test are marked. (B) Groups within both types of beetles are marked. The sample of 3rd October showed bimodal distribution and was thereafter excluded from the comparison.

sumption in starved and honey-fed beetles was similar to that recorded early after sampling, but oxygen consumption of beetles fed aphids was much increased (Table 1).

Starvation of HID beetles resulted in a decreased amount of food remnants in the gut. Feeding beetles with aphids led to an increase of the gut content, but it was still far from full (Table 1). Fat body volume

was similar in all combinations and generally well developed (about 2.7). Ovaries were involuted (state 1) in HID beetles, both soon after sampling and after two weeks of starvation or feeding with honey, but in aphid-fed beetles they contained ovarioles at different stages of development (average 3.0, most with vitellinized oocytes).

Table 1. Table 1: Effect of various kinds of feeding on *C. septempunctata*. Mean values and standard deviations are shown of the following parameters: fresh weight, oxygen consumption, gut content, state of ovaries, take-off (number of attempts to fly per minute), and duration of flight in hidden (HID) beetles immediately after sampling (mid-September 1994) and after two weeks in rearing conditions. Identical letters join values of rearing conditions not significantly different: fresh weight and O<sub>2</sub> – Tukey test,  $\alpha = 0.15$ ; take-off and duration – multiple Mann–Whitney tests with adjusted  $\alpha = 0.05$

| Rearing conditions | Fresh weight<br>(mg) | O <sub>2</sub><br>( $\mu\text{l g}^{-1} \text{h}^{-1}$ ) | Gut<br>(0–3) | Ovaria<br>(1–5) | Take-off<br>( $\text{min}^{-1}$ ) | Flight duration<br>(s) | N    |
|--------------------|----------------------|--|--------------|-----------------|-----------------------------------|------------------------|------|
| After sampling     | 325 ± 63             | a 675 ± 200  | a 0.7 ± 0.7  | 1               | 2.2*                              | a 21*                  | a 10 |
| Starved (controls) | 295 ± 50             | a 780 ± 290  | a 0.3 ± 0.5  | 1               | 9.0 ± 7.6                         | b 42 ± 55              | b 10 |
| Honey              | 352 ± 55             | a 710 ± 250  | a 0.9 ± 0.7  | 1               | 6.5 ± 5.5                         | b 81 ± 99              | b 20 |
| Aphids             | 469 ± 73             | b 1113 ± 433   | b 1.5 ± 0.9  | 3               | 1.4 ± 2.2                         | a 26 ± 39              | b 20 |

\*Medians; means and deviations not calculated because of very skewed distribution.

## Discussion

**Oxygen consumption.** A higher oxygen consumption in PLA than in HID beetles (Figure 2A) is probably related to digestion and transformation of food into the reserves in the fat body. While HID beetles are starving in hibernacula, PLA beetles may occasionally feed. Indeed, the oxygen consumption decreased when PLA beetles were starved for several days after collection (Figure 2A). In contrast, the oxygen consumption slightly increased after several days of starvation in HID beetles (Table 1).

The oxygen consumption of HID beetles was low in August 1994 and intermediate in August 1995 (Figures 2A and 2B). It is not clear why the values were different as in the two years the outdoor temperatures on the dates of collection and also temperatures during measurement were similar; thus the difference cannot be explained by the effects of temperature change. In contrast to expectation, oxygen consumption did not decrease with length of stay of beetles in the hibernation sites. On the contrary, there was a tendency towards increased oxygen consumption in both 1994 and 1995. In October 1995, high values of respiration ( $1060 \mu\text{l g}^{-1} \text{h}^{-1}$ ) were recorded. A small non-significant increase in oxygen consumption recorded in HID beetles after several days of starvation (Table 1) is in accordance with the tendency for spontaneous increase in oxygen consumption.

The low metabolic rate recorded in HID beetles is consistent with the generally accepted adaptive function of diapause (Danks, 1987): the use of energetic reserves is lowered in spite of temperatures that are still high in late summer and early autumn. Such a depressed respiration rate in diapausing insects is relatively independent of temperature. For example, in

the diapausing adult chrysomelid *Ceratoma trifurcata* an increase in temperature from 25 to 30 °C does not change the oxygen uptake, although the same change in temperature considerably increases the metabolic rate in non-diapause chrysomelid adults (Schumm et al., 1983).

Three explanations might be offered for the surprising tendency of increasing oxygen consumption in the course of late summer and early autumn. (1) It might be a result of an inherent tendency of at least a part of the population to become active between aestivation and hibernation. Such trait is expressed in bivoltine populations of *C. septempunctata* living in warmer regions (Hodek & Honěk, 1996), but is normally precluded by our climatic conditions. (2) The relative independence of metabolism from temperature caused by diapause may gradually disappear with the decrease in diapause intensity; the impact of diapause is gradually replaced by depression of metabolism by low ambient temperatures. (3) Since all samples were measured at a high temperature of 26 °C, the increase of oxygen consumption recorded during autumn may result from an increase in temperature differences between the field and measuring conditions. This explanation may apply to the increase in oxygen consumption between August and late September 1994 (Figure 2A). However, outdoor temperatures were relatively high and similar in mid-September and mid-October 1995 (Figure 2C). The increase in oxygen consumption at least in HID beetles in October 1995 (Figure 2B) was apparently not caused by greater stimulation due to a temperature increase at transfer from outdoors to the laboratory.

**Flight performance.** The rather short migratory flight in *C. septempunctata* differs from that of a long

distance migrant, *H. convergens*. While Rankin & Rankin (1980a) reported that 60% of *H. convergens*, collected early after arrival, flew longer than 30 min when tested in the season of migration to dormancy sites, only in exceptional instances did we record DUR values of as much as 20 min in *C. septempunctata*. The highest average values were 15 min, while medians were only 9 min (Figure 3B). The highest incidence of strong fliers (>15 min of continuous flight) was 39%. The relatively weak flight performance of *C. septempunctata* matches the short distance of most dormancy sites from its breeding habitats. However, some estivo-hibernation sites of *C. septempunctata* were also observed in mountains (Hodek et al., 1977; Honěk, 1989). The great variation in flight performance with a few high maximum values may be related to the varying distance of dormancy sites from breeding areas. Although the duration of migratory flight of *C. septempunctata* recorded here is much lower than in *H. convergens*, it is still higher than the values for appetitive (trivial) flight in reproducing *C. septempunctata* foraging for prey in June (mean 77 s, median 44 s, geometrical mean 35 s – Nedvěd & Hodek, 1995).

The autumnal flight in *C. septempunctata* is similar to that in *H. convergens* in the differential effect of essential food, enabling maturation of ovaries, vs. alternative food. Thus our results on the stimulating effect of honey (vs. aphid) food are similar to higher flight activity in *H. convergens* when maintained on suboptimal (vs. suitable) food. Rankin & Rankin (1980a) recorded an important decrease in flight endurance of *H. convergens* females after six days of feeding on suitable food (living aphids) at 24 °C when long daylength stimulated reproduction. Feeding on aphids also initiated ovarian maturation in *C. septempunctata*; thus the respiration increased and the frequency of take off decreased. Flight duration remained similar to that of beetles tested just after sampling, and was shorter than in beetles fed on alternative food. Feeding on honey solution also increased duration of flight in the noctuid *Agrotis ipsilon* (Sappington & Showers, 1993). In contrast to both coccinellids, high flight performance was maintained until appearance of chorionated eggs in *Anthonomus grandis* (Rankin et al., 1994).

As with *P. truncatus* (Fadamiro & Wyatt, 1995) the incidence of take-off was usually higher in starved coccinellids than in fed beetles. However, feeding of dormant *C. septempunctata* on the alternative food

of honey and pollen did not change the tendency to take-off in comparison with starved beetles.

The slow and weak decline in flight duration of HID *C. septempunctata* after their arrival at hibernation sites contrasts with the abrupt decrease in flight performance recorded in *H. convergens* in the first two months spent in the hibernaculum (Rankin & Rankin, 1980a). High values of flight duration in HID *C. septempunctata* collected in September are surprising, particularly as they are mostly higher than the values for PLA beetles in August. We suggest that the resumption of flight performance in HID beetles may be related to bivoltine trends, as mentioned in regard to oxygen consumption and as discussed in more detail below. Flight is, of course, precluded by low ambient temperature in the field but stimulated by higher temperature in the laboratory. The increase of flight muscle diameter in October recorded in this study as well as earlier (Okuda, 1983; Okuda et al., 1986) supports this assumption.

*Polyphenism of C. septempunctata and its diapause.* In Bohemia (and more generally in cold regions of temperate Europe) populations of the opportunistic species *C. septempunctata* are heterogeneous: while a great majority of individuals shows a strong tendency to a univoltine life cycle and arrives at hibernation sites already in summer (our HID beetles), in other beetles diapause is induced later. In a year-specific proportion of females that matured earlier in summer, the ovaries may start to mature (or even a partial second generation could be produced if conditions are favourable; Hodek, 1962, Tables 7.12 and 7.16 in Hodek & Honěk, 1996). Such beetles were sampled from plants (PLA) in our study. Beetles such as our PLA individuals have not consumed sufficient numbers of aphids and hence rove through the landscape; they feed on non-aphid foods and eventually enter hibernation anywhere as autumn temperatures fall.

Early after the arrival at hibernation sites diapause of coccinellid beetles is most intense. The intensity gradually decreases until about mid-winter (Hodek et al., 1977; Hodek & Ružička, 1979; Hodek & Honěk, 1996).

The present findings complete our understanding of the ecophysiological polyphenism in *C. septempunctata*. The polyphenism is most probably one of the main reasons for the plasticity of the species and its recent success in the colonisation of the Nearctic region (see, e.g., Obrycki et al., 1998; Evans, 2000).



The HID and PLA beetles differed in the characteristics measured: the beetles collected on plants (PLA) had higher respiration rate than the beetles hidden in dormancy sites (HID) but lower flight duration and flight tendency. Apparently the stronger fliers arrived at the typical high elevation hibernation site after accumulation of satisfactory reserves. They arrived so early in the season because their initiation of diapause is obligatory.

The seasonal dynamics in flight parameters and respiration rate were surprising. The increase in oxygen consumption with the progress in season (in one year even until early October) is ascribed to the decrease in endogenous inhibition of metabolism when the diapause intensity decreases due to diapause development (Hodek & Ružička, 1979). The values of take off increased from August to September and the flight was still long in mid-September.

The high flight duration in HID beetles in late August and September of 1995 is an interesting finding that should be followed further. It could be ascribed to a tendency to reactivation which remains unexpressed at our latitude. One might assume that aestivation and hibernation are separated by a period of reproduction in those Mediterranean regions where vegetation regrowth promotes population increase in aphids in late summer. Isolated cases of such a situation were reported from the coastal plain of Israel (Bodenheimer, 1943) and one locality in the French Riviera (Iperti, 1966). There are no data available from Spain or Italy, but a recent study from Greece (Katsyannos, 1997a,b) indicates that a shortage of aphid prey contributes there to inducing diapause in *C. septempunctata*: already in late June the beetles were found in dormancy sites, while their conspecifics reproduced at the same time in outdoor cages where ample aphid food was provided.

A detailed experimental study, combining the modification of physical and nutritive conditions with a histological analysis of flight muscles, should shed more light on this interesting problem which has also implications in biological and integrated control.

### Acknowledgements

The study was funded by the grant number A607103 of the Grant Agency of the Academy of Sciences, and ME 169 of the Ministry of Education of the Czech Republic. We feel obliged to three anonymous referees

for helpful suggestions and to Professor Edward W. Evans, Logan, USA for language improvements.

### References

- Bodenheimer, F.S., 1943. Studies on the life-history and ecology of Coccinellidae. I. The life-history of *Coccinella 7-punctata* in four different zoogeographical regions. Bulletin de la Société Fouad Ier d'Entomologie 27: 1–28.
- Danks, H.V., 1987. Insect Dormancy: an Ecological Perspective. Biological Survey Canada, Ottawa, 439 pp.
- Dingle, H., 1966. Some factors affecting flight activity in individual milkweed bugs (*Oncopeltus*). Journal of Experimental Biology 77: 335–343.
- Dingle, H., 1996. Migration. The Biology of Life on the Move. Oxford Univ. Press, New York-Oxford, 474 pp.
- Evans, E.W., 2000. Morphology of invasion: body size patterns associated with establishment of *Coccinella septempunctata* in western North America. European Journal of Entomology 97: 469–474.
- Evans, E.W., Stevenson, A.T. & D.R. Richards, 1999. Essential versus alternative foods of insect predators: benefits of a mixed diet. Oecologia 121: 107–112.
- Fadamiro, H.Y. & T.D. Wyatt, 1995. Flight initiation by *Prostephanus truncatus* in relation to time of day, temperature, relative humidity and starvation. Entomologia Experimentalis et Applicata 75: 273–277.
- Gatehouse, A.G., 1997. Behaviour and ecological genetics of wind-borne migration of insects. Annual Review of Entomology 42: 475–502.
- Hagen, K.S., 1966. Suspected migratory flight behaviour of *Hippodamia convergens*. In: Hodek I. (ed.), Ecology of Aphidophagous Insects. Academia, Praha & Junk, The Hague, pp. 135–136.
- Hodek, I., 1960. Hibernation-bionomics in Coccinellidae. Časopis Československé Společnosti Entomologické 57: 1–20 (in Czech, English abstract).
- Hodek, I., 1962. Experimental influencing of the imaginal diapause in *Coccinella septempunctata* L. (Col., Coccinellidae), 2nd part. Časopis Československé Společnosti Entomologické 59: 297–313.
- Hodek, I. & A. Honěk, 1996. Ecology of Coccinellidae. Kluwer Academic Publishers, Dordrecht, Boston, 464 pp.
- Hodek, I. & Z. Ružička, 1979. Photoperiodic response in relation to diapause in *Coccinella septempunctata* L. (Coleoptera). Acta Entomologica Bohemoslovaca 76: 209–218.
- Hodek, I., Iperti, G. & M. Hodková, 1993. Long-distance flights in Coccinellidae (Coleoptera). European Journal of Entomology 90: 403–414.
- Hodek, I., Iperti, G. & F. Rolley, 1977. Activation of hibernating *Coccinella septempunctata* (Coleoptera) and *Perilitus coccinellae* (Hymenoptera) and the photoperiodic response after diapause. Entomologia Experimentalis et Applicata 21: 275–286.
- Honěk, A., 1989. Overwintering and annual changes of abundance of *Coccinella septempunctata* in Czechoslovakia (Coleoptera, Coccinellidae). Acta Entomologica Bohemoslovaca 86: 179–192.
- Honěk, A., 1990. Seasonal changes in flight activity of *Coccinella septempunctata* L. (Col., Coccinellidae). Acta Entomologica Bohemoslovaca 87: 336–341.
- Iperti, G., 1966. Comportement naturel des Coccinelles aphidiphages du Sud-Est de la France. Leur type de spécificité,

- leur action prédatrice sur *Aphis fabae* L. Entomophaga 11: 203–210.
- Iperti, G., 1986. Ecobiologie des coccinelles aphidiphages: les migrations. Colloques de l'INRA 36: 107–120.
- Johnson, C.G., 1969. Migration and Dispersal of Insects by Flight. Methuen, London, 763 pp.
- Katsoyannos, P., Stathas, G.J. & D.C. Kontodimas, 1997a. Phenology of *Coccinella septempunctata* (Col. Coccinellidae) in central Greece. Entomophaga 42: 435–444.
- Katsoyannos, P., Kontodimas, D.C. & G.J. Stathas, 1997b. Summer diapause and winter quiescence of *Coccinella septempunctata* (Col. Coccinellidae) in central Greece. Entomophaga 42: 483–491.
- Mills, N.J., 1981. Essential and alternative foods for some British Coccinellidae (Coleoptera). Entomological Gazette 32: 197–202.
- Nedvěd, O. & I. Hodek, 1995. Confinement stimulates trivial flight in *Coccinella septempunctata* (Coleoptera: Coccinellidae). European Journal of Entomology 92: 719–722.
- Obrycki, J., Giles, K.L. & A.M. Ormord, 1998. Interactions between an introduced and indigenous coccinellid species at different prey densities. Oecologia 117: 279–285.
- Okuda, T., 1983. Anatomical and Ecophysiological Study of *Coccinella septempunctata* L. and *Semiadalia undecimnotata* Schneid. in Relation to Diapause. Ph.D. thesis, Academy of Sciences, Praha.
- Okuda, T. & I. Hodek, 1989. Flight tendency of 2 coccinellids, *Semiadalia undecimnotata* and *Coccinella septempunctata*, in relation to diapause. In: M. Tonner, T. Soldán & B. Bennetová (eds), Regulation of Insect Reproduction IV. Academia, Praha, pp. 385–400.
- Okuda, T., Hodková, M. & I. Hodek, 1986. Flight tendency in *Coccinella septempunctata* in relation to changes in flight muscles, ovaries and corpus alatum. In: I. Hodek (ed.), Ecology of Aphidophaga. Academia, Praha & Junk, Dordrecht, pp. 217–223.
- Rankin, M.A., Hampton, E.N. & K.R. Summy, 1994. Investigation of the oogenesis - flight syndrome in *Anthonomus grandis* (Coleoptera: Curculionidae) using tethered flight tests. Journal of Insect Behavior 7: 795–810.
- Rankin, M.A. & S.M. Rankin, 1980a. Some factors affecting presumed migratory flight activity of the convergent ladybird beetle *Hippodamia convergens* (Coccinellidae: Coleoptera). Biological Bulletin 158: 356–369.
- Rankin, S.M. & M.A. Rankin, 1980b. The hormonal control of migratory flight behavior in the convergent ladybird beetle *Hippodamia convergens*. Physiological Entomology 5: 175–182.
- Sappington, T.W. & W.B. Showers, 1993. Influence of larval starvation and adult diet on long-duration flight behavior of the migratory moth *Agrotis ipsilon* (Lepidoptera: Noctuidae). Environmental Entomology 22: 141–148.
- Schumm, M., Stinner, R.E. & J.R. Bradley, 1983. Characteristics of diapause in the bean leaf beetle, *Cerotoma trifurcata* (Forster) (Coleoptera: Chrysomelidae). Environmental Entomology 12: 475–477.
- Sláma, K., 1960. Oxygen consumption during postembryonic development of *Pyrrhocoris apterus* and its comparison with that of Holometabola. Annals of the Entomological Society of America 53: 606–610.