

DIFFERENT RESPONSE IN RESPIRATION BETWEEN PREDACEOUS AND PHYTOPHAGOUS LADY BEETLES (COLEOPTERA: COCCINELLIDAE) TO STARVATION

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INTRODUCTION

Comparative physiological study on respiratory metabolism in animals has been little progressed in spite of IVLEV's (1939) earlier emphasis on its importance.

ITÔ (1964), working on a wolf spider, *Lycosa pseudoannulata*, found a notable fall of the respiratory rate of adults under starved conditions and suggested that this property was adaptive for predators with more difficult acquisition of food. Since then it has been shown that some spiders could survive for a long time under starved conditions (ANDERSON, 1974) and starved spiders reduced their respiratory rates (MIYASHITA, 1969; HAGSTRUM, 1970; ANDERSON, 1974).

In other studies on a wolf spider, *Pardosa astrigera*, (TANAKA and ITÔ, 1982) we have shown that the reduction in the respiratory rate of starved spiders was not due to their exhaustion nor senescence but possibly due to their adaptive behavioural change. We also suggested that the catabolized substrates under starvation were different from those under satiation.

If the strategy to tolerate starvation by saving the respiratory energy loss is peculiar to many predators, other predators will also take such a strategy. Coccinellid beetles, as they include both of predaceous and phytophagous species, are the most suitable material to elucidate the differences in strategies against starvation between predators and herbivores. Responses to starvation of an entomophagous lady beetle, *Coccinella septempunctata bruckii* MULSANT, and a phytophagous one, *Henosepilachna vigintioctopunctata* FABRICIUS, evaluated by changes in respiratory rates and body weights, are reported in the present paper.

MATERIALS AND METHODS

Insects

C. septempunctata, occurring throughout Palaearctica and some parts of the Oriental Region (HAGEN, 1962), normally preys on aphids in the field. Larvae of the first generation of *C. septempunctata*—the offspring of overwintering adults—were collected from experimental fields of Nagoya University in April and May, 1980. These larvae were reared in the laboratory supplied with living aphids, *Brevicoryne brassicae*, *Acyrtosiphon pisum* and *Megaura japonica*, collected from the field, and

newly emerged adults were used for the experiments.

H. vigintioctopunctata, belonging to the subfamily Epilachninae which has evolved phytophagy among Coccinellidae (HODEK, 1973), was chosen as a related species for comparison with *C. septempunctata*. Larvae of the first generation of *H. vigintioctopunctata* were collected from potato plant fields in Nisshin-cho, Aichi-gun, Aichi Prefecture in June, 1980. These larvae were reared in the laboratory supplied with leaves of potato plants and eggplants, and newly emerged adults were used for the experiments.

Rearing

Adult beetles of the two species were reared individually in polyethylene containers (2.5 cm in depth and 6 cm in diameter) under 25°C and 16:8 h light:dark photoperiod. *C. septempunctata* adults were daily fed on living aphids, *A. pisum* and *M. japonica*, collected from the field. These aphids were thought to be suitable food for *C. septempunctata*, because it was often observed that they were eaten by larvae and adults of *C. septempunctata* in the field.

H. vigintioctopunctata adults were fed on sliced potatoes. Food and rearing containers were renewed about every third day. According to KOYAMA (1962), the adults of *H. vigintioctopunctata* can be well reared on sliced potatoes. We observed that females of this species, fed only on sliced potatoes during the adult stage, laid a lot of fertile eggs. Hence sliced potatoes were thought to be suitable food for *H. vigintioctopunctata* adults.

The beetles of each species were divided into two groups, 'well-fed' and 'starved'. In the well-fed groups, the beetles were supplied with ample food, more than 30 aphids per individual every day for *C. septempunctata*; a piece of ca. 5 g sliced potato per individual every third day for *H. vigintioctopunctata*. Moist cotton was also supplied so that the beetles could drink water. In the starved groups, the beetles were supplied with ample food as well as the well-fed groups for ten days from the emergence, and hereafter they were supplied with no food but water.

Determination of respiratory rate

Respiratory rate was determined by measuring CO₂ output using the titration technique used by ITÔ (1964). Preliminary experiments showed that, in both species, an adult beetle expired too small amount of CO₂ to measure precisely. Therefore measurements were made for couples of two individuals of the same sex with similar body weight (the maximum difference in body weights between the two was 5.74 mg). A respiratory chamber (plastic cylinder, 2.5 cm in diameter and 15 cm in length) was separated into two parts by a piece of plastic net. Two experimental beetles were individually introduced into each part of chamber, and it was connected to the CO₂-expelling tube including soda lime. After the air remaining in the chamber had been almost completely substituted by CO₂-free air, the chamber was put into a room maintained at 25°C and 16:8 h light:dark photoperiod for 24 h. Then the

chamber was connected to an apparatus for CO₂ output measurement and ventilated by CO₂-free air for 20 min. The CO₂ expired by a couple of experimental beetles was absorbed by N/20 KOH solution (20 ml in volume), and the absorbed CO₂ was titrated by neutralization with N/50 HCl solution of which factor was previously determined. The amount of CO₂ was calculated from the difference between amounts of HCl solution required for neutralization for experimental chamber and for empty control chamber. The results are expressed as mg CO₂ expired/mg body weight/h.

Each experimental beetle was weighed before and after the respiration measurement using the Chyo model C₃-100MD balance (minimum accuracy, 0.01 mg), then the mean of the two values was regarded as the live body weight at the time of measurement. No anesthetization was made in every experiment.

RESULTS

Survival time

Survival times of adults of *C. septempunctata* and *H. vigintioctopunctata* under well-fed and starved conditions are shown in Table 1. The figures for starved beetles in the table represent the number of days from the commencement of starvation to

Table 1. Survival times (in days) of *C. septempunctata* and *H. vigintioctopunctata*.

		Well-fed	Starved Mean ± SD ^a
<i>C. septempunctata</i>	Male	32(1) ^b , 47(1), 70< ^c (8)	21.3 ± 10.2(10)
	Female	65(1), 70<(9)	91.4 ± 27.2(10)
	Male	100<(10)	17.6 ± 6.0(10)
<i>H. vigintioctopunctata</i>	Female	100<(10)	22.9 ± 5.3(10)

^a Days from the commencement of starvation to the death of beetle. As experimental beetles were well-fed for first ten days since their emergence, true longevity is the values shown in this column plus ten days.

^b Figures in the parentheses indicate numbers of individuals.

^c See text for detail.

the death of beetle. True longevities of well-fed beetles were not determined because rearing was ceased before their death for some reasons. The well-fed *C. septempunctata* adults were reared for 70 days from the emergence and the well-fed *H. vigintioctopunctata* adults for 100 days. During these periods, two males and a female of *C. septempunctata* but none of *H. vigintioctopunctata* died.

Females of *C. septempunctata* survived for a long time, 91.4 ± 27.2 days, under starved conditions. On the other hand, males of the same species survived only for a time less than a fourth of the mean survival time of females under starved conditions. When starved, males and females of *H. vigintioctopunctata* survived for ca. 20 days, much shorter (less than a fifth) than the survival time of well-fed beetles.

These results suggest that *C. septempunctata* females have a strong tolerance to starvation, whereas *C. septempunctata* males and *H. vigintioctopunctata* males and females have relatively a weak tolerance.

Respiratory rate in relation to body weight

The respiratory rate (R) of animals can be expressed as a function of the body weight (W) by the following equation (EDWARDS, 1953):

$$R = aW^b$$

or $\log R = \log a + b \log W$,

where a and b are constants.

The relationships of respiratory rate per individual to live body weight in the two species were known from data on ten days old well-fed beetles (Fig. 1). Figure for *C. septempunctata* suggests that there were linear relationships between the respiratory rate and live body weight on double logarithmic scales, though there was no significant correlation ($P > 0.05$). The respiratory rate of males tended to be much higher than females. In *H. vigintioctopunctata*, there was no difference in respiratory rates between sexes (Fig. 1b), so that the combined regression was calculated. The correlation coefficient was significantly different from zero ($P < 0.01$).

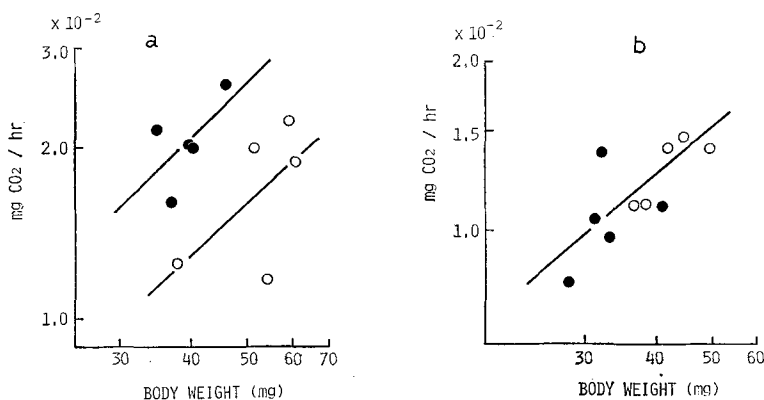


Fig. 1. Relationships of respiratory rate to live body weight in *C. septempunctata* (a) and *H. vigintioctopunctata* (b) under well-fed conditions. ●: males, ○: females. Although two individuals were coupled for measurement, relations between mean of body weights of the two and mean respiratory rate per individual were plotted. The regression lines are: $\log R = 0.985 \log W - 3.263$ ($r^2 = 0.376$) for *C. septempunctata* males, $\log R = 0.931 \log W - 3.352$ ($r^2 = 0.371$) for *C. septempunctata* females and $\log R = 0.844 \log W - 3.253$ ($r^2 = 0.532$) for *H. vigintioctopunctata*.

In both species the slopes of regression lines were close to unity. It indicates that the respiratory rate per unit body weight is almost constant regardless of body weight. Hence, in the present paper, the respiratory rate is represented as CO₂ output in mg per unit body weight per hour.

Changes in respiratory rates and live body weights under starved conditions

Fig. 2 shows changes in mean respiratory rates and mean live body weights

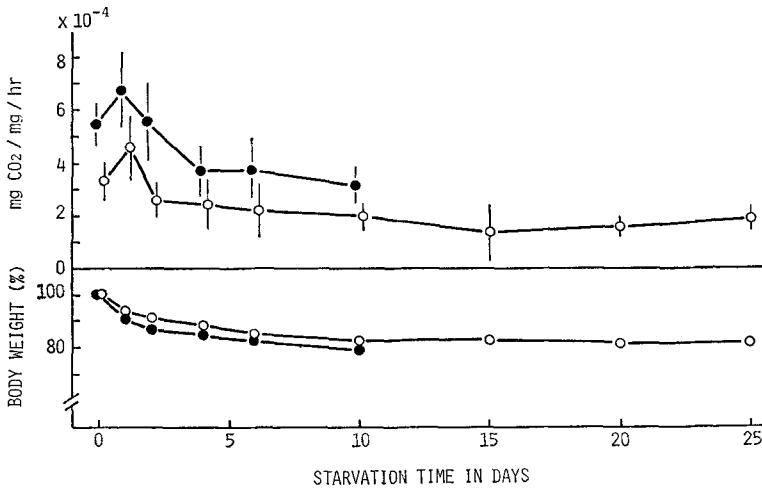


Fig. 2. Changes in mean respiratory rates and mean live body weights of *C. septempunctata* under starved conditions. Vertical lines show the standard deviations of mean respiratory rate. ●: males, ○: females. The mean respiratory rates were calculated from data on five couples of beetles, that is, from five values, but the mean live body weights from data on ten beetles, that is, from ten values.

of *C. septempunctata* during starvation. The changing patterns in mean respiratory rates of males and females resembled each other throughout experiments. The rates increased on the first day of starvation by 24% in males and 37% in females, but hereafter rapidly decreased till the fourth day, keeping an almost constant levels thereafter. On the tenth day, the rates were 56.4% in males and 58.5% in females of initial values.

The sexual dimorphism in changing patterns in the respiratory rate was not found but the levels of rates were different between sexes. The mean rates in males were 1.47 to 2.14 times as high as those in females, and there were significant differences between the two at every time of measurement till the tenth day ($P < 0.01$ in Student's *t*-test).

The mean live body weight of *C. septempunctata* decreased rapidly till the second day of starvation, and then slowly (Fig. 2). Males and females lost their body weights by 20.2% and 17.8% of initial weights during the first ten days, respectively. Although the loss of body weight from the beginning to the first day may include the weight loss due to excretion of feces, the increase in respiratory rate per unit body weight on the first day did not only due to this, because the rate of weight loss was below 10% but the increase of respiratory rate was more than 20%.

As shown in Fig. 3, the changing patterns in mean respiratory rates of *H. vigintioctopunctata* during starvation were different from those of *C. septempunctata*. The mean respiratory rates did not significantly fluctuate during the first four days of starvation. After the fourth day the rates decreased slowly. On the tenth day,

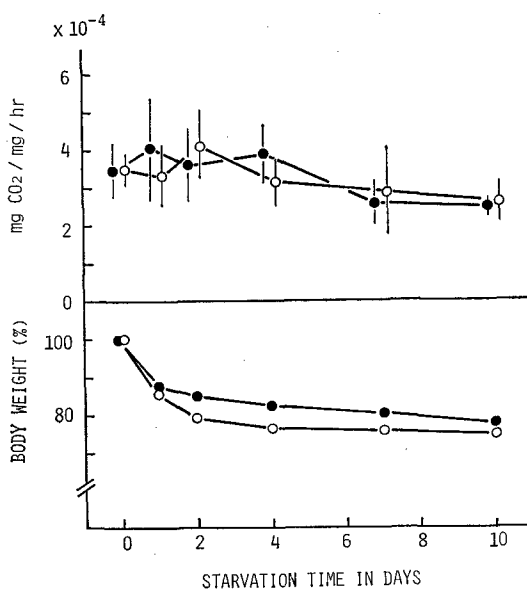


Fig. 3. Changes in mean respiratory rates and mean live body weights of *H. vigintioctopunctata* under starved conditions. Symbols and calculation methods of mean values are the same as Fig. 2.

the rates were 70.3% in males and 74.8% in females of the initial values, being much higher than those observed in *C. septempunctata*. The levels of rates were not significantly different between sexes.

The mean live body weight of *H. vigintioctopunctata* decreased rapidly till the second day of starvation, and hereafter slowly (Fig. 3). The losses of body weights accounted for 22.4% in males and 25.4% in females during the first ten days. The weight losses of *H. vigintioctopunctata* were significantly larger than those of *C. septempunctata*, suggesting, at least partially, the higher exhaustion rate against starvation in the former species.

DISCUSSION

Females of predaceous lady beetles, *C. septempunctata*, survived for a long time, 91.4 ± 27.2 days, accompanying the remarkable reduction in their respiratory rates under starvation. The similar results have been reported in various species of poikilothermal predators; e.g. fishes (IVLEV, 1939; GLASS, 1968, 1971), crabs (ROBERTS, 1957; VERNBERG, 1959; MARSDEN et al., 1973), spiders (ITÔ, 1964; MIYASHITA, 1969; HAGSTRUM, 1970; ANDERSON, 1974; TANAKA and ITÔ, MS) and leeches (MANN, 1956). In studies on a wolf spider, *Pardosa astrigera*, (TANAKA and ITÔ, MS), we found that the respiratory rate of adults increased during the first two days of starvation following a remarkable decrease from the third to the twelfth day but thereafter an almost constant level was retained. We consider that the spiders shall search for prey by active movement at the initial stage of starvation,

but when they cannot take food in spite of their efforts, they change their behaviour to be at rest waiting the recovery of food resources by immigration and/or emergence of prey without notable energy exhaustion. Since the similar results have been obtained in such diverse animals as mentioned above, it can be conceivable that to reduce the respiratory rate is an adaptive strategy in energy metabolisms against starvation and should be generally possessed by at least predaceous poikilotherms which depend on mobile prey. When spiders were supplied with ample food for five days after the starvation period, both the respiratory rates and the body weights recovered to almost the initial levels (TANAKA and ITÔ, MS). Thus, we concluded that the reduction in respiratory rate under starvation is not due to predators' exhaustion nor senescence but to the regulation of movement.

Contrary, a phytophagous lady beetle, *H. vigintioctopunctata*, did not remarkably reduce the respiratory rate nor survived for a long time under starvation. Only a few studies are available for understanding the respiratory responses to starvation in phytophagous and saprophagous animals. ITÔ (1964) reported that CO₂ output per individual of houseflies, *Musca domestica*, starved for 24 h was almost the same as that of well-fed flies, and considered that CO₂ output per unit body weight would be somewhat larger in the starved flies than the controls. He also showed that all the starved flies died till 77th h of starvation. RICHMAN (1958) showed that O₂ consumption per unit body weight of *Daphnia pulex* was remained at a constant level during five days of starvation but after six days the animals lost about 50% of their body weight. Thus it is suggested that many herbivores can not control the respiratory rate by starvation, so that they cannot survive long under starvation.

Such differences in responses to starvation between predators and herbivores suggest that the formers are supplied with more limited food resources in nature than the latters. The prey animals for predators are objects that their distributions are more scattered or discontinuous and their densities are susceptible to unpredictable fluctuations as compared with the food-plants for herbivores. On the other hand, small herbivores, especially phytophagous insects, generally live on their food-plants, which enable them to take food easily. Furthermore, since the plants often form large uniform colonies, even if herbivores eat up one plant or one clump of plants, they can easily move to another and eat it.

ITÔ (1976) postulated that in the terrestrial ecosystems, except the savannahs before the beginning of hunting by men, plants are generally in excess as food for the primary consumers (herbivores), so that a small proportion of plant tissue (presumably less than 5%) is consumed by herbivores and most of that is directly transferred to decomposers. On the other hand, the secondary or higher consumers (carnivores) are considered to consume a large proportion of the trophic level which they use as food, and it is probable that the number of carnivores is regulated by the shortage of food. PIANKA (1974) also estimated that nearly 90% of the net

production in the primary producers may be consumed by decomposers.

If these were true, predators had to face starvation more severely than herbivores; this condition, in turn, caused predators to evolve the adaptive character that they wait the recovery of food resources with reducing the respiratory energy loss when they have starved.

The respiratory rate once increased on the first day of starvation in both the wolf spider (TANAKA and ITÔ, MS) and the predaceous lady beetle, suggesting that early in the starvation period the predators take different responses from the later. DIXON (1959) reported that when female adults of a predaceous lady beetle, *Adalia decempunctata*, were supplied with small number of aphids, their activity became large. NAKAMUTA (personal communication) found that the activity of *C. septempunctata* adults rose ca. 4 h after the commencement of starvation and maintained around this level till 24 h (no observation was made after the 24th h). These facts suggest that the increase in the respiratory rate of *C. septempunctata* in the beginning of the starvation period were attributed to the active search for prey.

In *C. septempunctata* the mean survival time of males was much shorter than that of females. The reason for this might be that the respiratory rate of males was essentially higher than that of females. CAMPBELL et al. (1980) also found that in a predaceous lady beetle, *Menochilus sexmaculatus*, the respiratory rate of males was higher than that of females under five constant temperatures from 1 to 37°C. This sexual difference may be related to the mating behaviour of these beetles. The different responses to starvation between sexes may reflect different roles in reproduction between sexes. As females should usually survive longer than males, it may be adaptive that the overall respiratory rate of female adults was lower than that of males.

SUMMARY

Survival times and changes in the respiratory rates and the live body weights of a predaceous lady beetle, *Coccinella septempunctata bruckii* MULSANT, and a phytophagous lady beetle, *Henosepilachna vigintioctopunctata* FABRICIUS, under starved conditions were compared.

1. Females of *C. septempunctata* survived for a long time, 91.4 ± 27.2 days, under starved conditions. On the other hand, males of *C. septempunctata* and males and females of *H. vigintioctopunctata* survived for 21.3 ± 10.2 , 17.6 ± 6.0 and 22.9 ± 5.3 days, respectively. These values were much shorter than that of *C. septempunctata* females.

2. The respiratory rate of starved *C. septempunctata* increased on the first day of starvation, but hereafter rapidly decreased till the fourth day, keeping an almost constant level thereafter. On the tenth day of starvation, the respiratory rates of *C. septempunctata* were 56.4% in males and 58.5% in females of initial values. The respiratory rate of males was 1.47 to 2.14 times as high as that of females, and

there were significant differences between the two.

3. Males and females of *C. septempunctata* lost their body weights by 20.2% and 17.8% of initial weights, respectively, during the first ten days of starvation.

4. The respiratory rate of starved *H. vigintioctopunctata* did not significantly change till the fourth day of starvation, and thereafter decreased slowly. On the tenth day of starvation, the respiratory rates of *H. vigintioctopunctata* were 70.3% in males and 74.8% in females of initial values. These values were much higher than those of *C. septempunctata*.

5. Males and females of *H. vigintioctopunctata* lost their body weights by 22.4% and 25.4% of initial weights, respectively, during the first ten days of starvation. Thus under starvation *H. vigintioctopunctata* underwent the larger weight loss than *C. septempunctata*.

6. Differences in strategies against starvation between poikilothermal predators and herbivores and their roles in population dynamics were discussed.

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捕食性および植食性テントウムシの飢餓に対する異なる呼吸反応

田中幸一・伊藤嘉昭

捕食者であるナナホシテントウと植食者であるニジュウヤホシテントウの飢餓条件下における生存期間、呼吸率の変化および体重の変化を比較した。

1. 飢餓条件下において、ナナホシテントウの雌は、長い期間(平均91.4±27.2日)生存したが、ナナホシテントウの雄およびニジュウヤホシテントウの雌雄は、長くは生存しなかった(平均約20日)。
2. 絶食したナナホシテントウの呼吸率は、絶食1日目には増加したが、その後4日目まで急速に減少し、4日目以後はほぼ一定のレベルを維持した。絶食10日目の呼吸率は、0日目に対して雄が56.4%、雌が58.5%であった。雄の呼吸率は、雌の1.47~2.14倍であり、両者の間には有意な相違があった。
3. ナナホシテントウの体重は、10日間の絶食中に、雄では20.2%、雌では17.8%だけ減少した。
4. 絶食したニジュウヤホシテントウの呼吸率は、絶食4日目まではほとんど変化せず、それ以後はゆっくり減少した。絶食10日目の呼吸率は、0日目に対して雄が70.3%、雌が74.8%で、ナナホシテントウより高かった。
5. ニジュウヤホシテントウの体重は、10日間の絶食中に、雄では22.4%、雌では25.4%だけ減少し、減少率はナナホシテントウより大きかった。
6. 捕食者と植食者の対飢餓戦略の相違および、その個体群動態における役割について論じた。