

# Comparison of Respiration in Adult *Harmonia axyridis* Pallas and *Hippodamia convergens* Guerrin-Manaville (Coleoptera: Coccinellidae)

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**ABSTRACT** Specific metabolic heat rates ( $R_q$ ) and respiration rates ( $R_{CO_2}$ ) of adult *Harmonia axyridis* Pallas, the multicolored Asian lady beetle, and *Hippodamia convergens* Guerrin-Manaville, the convergent lady beetle, were measured in isothermal calorimeters at 5°C intervals from 0 to 40°C. Anabolic rates and  $R_q/R_{CO_2}$  ratios were calculated as functions of temperature from the calorespirometric data. The two species have similar heat and CO<sub>2</sub> rates from 0 to 10°C, but both rates are higher for *H. convergens* at all other temperatures. Anabolic rates and  $R_q/R_{CO_2}$  ratios indicated high-temperature stress in *H. convergens* at 40°C and at 35 and 40°C in *H. axyridis*. Anabolic rates and  $R_q/R_{CO_2}$  ratios for the two species differed markedly from 15 to 30°C, where *H. convergens* had a higher anabolic rate and lower  $R_q/R_{CO_2}$  ratio (i.e., greater metabolic efficiency) than *H. axyridis*. The data show that *H. axyridis* maximizes the anabolic rate, and therefore the biosynthesis rate, at low temperatures around 5°C and maximizes the catabolic rate at 25–30°C to support movement. In *H. convergens*, the optimum temperature range is the same for both biosynthesis (anabolic rate) and movement (catabolic rate), i.e., from 15 to 30°C. The ability of *H. axyridis* to more efficiently use periods of low temperature for development and reproduction and periods of mid-range environmental temperatures for searching for prey and feeding probably contribute to its competitive displacement of native North American coccinellid species.

**KEY WORDS** *Harmonia axyridis*, *Hippodamia convergens*, temperature response, calorespirometry, respiration

THE ESTABLISHMENT OF SEVERAL exotic coccinellid species in North America provides an opportunity to examine the impact of these species on native populations. *Harmonia axyridis* (Pallas) originates from the Far East, occurring in Korea, Japan, China, the Himalayas, and Siberia (Coderre et al. 1995), and was introduced into the United States in the late 1970s by the U.S. Department of Agriculture as a biocontrol agent for aphids and scales. *H. axyridis* has been established in the United States since the 1990s (Koch 2003). This species is an effective predator of a wide variety of aphids and other soft-bodied insects (Brown and Miller 1998, Kalaskar and Evans 2001). *H. axyridis* is more successful as a generalist predator than native coccinellids, possibly because of its broader diet (Reitz and Trumble 2002, Louda et al. 2003) and larger size. Although *H. axyridis* has had negligible effect on native coccinellids in some agroecosystems such as apple orchards (Brown 2003), in some environments *H. axyridis* has had a significant impact by competitive

displacement of resident coccinellids such as *Hippodamia convergens* Guerrin-Manaville (Elliott et al. 1996, Colunga-García and Gage 1998, Michaud, 2003).

Understanding the effects of temperature on introduced coccinellids (Acar et al. 2001, 2004) and comparisons with native species (Obrycki and Kring 1998) facilitate estimation of interspecific competition. This study compares the respiratory metabolism of adult beetles of two species to determine if physiological differences in temperature responses of metabolism contribute to the displacement of the native species *H. convergens* by the exotic species, *H. axyridis*. Rates of respiratory metabolism are commonly reported as rates of O<sub>2</sub> consumption or CO<sub>2</sub> production, but simultaneous measurement of CO<sub>2</sub> production and metabolic heat rates is necessary to separate anabolic and catabolic rates and determine metabolic efficiency (Hansen et al. 2004). Nearly all metabolic heat is produced by the highly exothermic, oxygen-consuming reactions of catabolism, while anoxic anabolism is thermally neutral. CO<sub>2</sub> produced by the catabolic reactions is thus accompanied by significant amounts of heat, but the anabolic reactions are not. The heat rate thus serves as a label on the CO<sub>2</sub> that can be used to determine if it came from catabolic reactions or from anoxic anabolic reactions. Simultaneous measurements of heat and CO<sub>2</sub> rates ( $R_q$  and  $R_{CO_2}$ ) by calorespirometry thus enable calculation of the rates of both processes (Criddle and Hansen 1999). Further-

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more, defining the anabolic rate as the increase in potential energy per gram of biomass allows direct comparison of anabolic rates even when anabolic products with different chemical compositions are produced (Hansen et al. 1998).

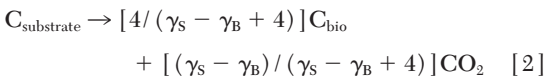
The biosynthetic reactions of anabolism are necessary for growth, development, and reproduction. Energy from catabolism powers both the endoergic reactions of anabolism and movement or activity required for hunting and feeding by predators. The more efficient a predator is in using this energy from catabolism and in using substrate in biosynthesis, the more fit it should be. However, fitness also depends on how well the organism fits with the environment. Measurements of metabolic heat rates ( $R_q$ ) and respiratory rates ( $R_{CO_2}$ ) at several temperatures with isothermal calorimetry permits calculation of both anabolic and catabolic rates, and thus, the optimum temperature ranges for activity and development. Calorespirometric methodology is much faster and provides much more insight into metabolic responses than direct observation of activity and development times. Direct observation can only show that something happened but does not provide any information on how the observation is related to metabolism (Criddle et al. 1997, Hansen et al. 1998, Acar et al. 2001).

### Materials and Methods

**Theory.** Respiratory metabolism can be divided into two types of overall reactions: oxidation reactions (oxidative catabolism) and disproportionation reactions (anabolism and anaerobic catabolism). The sum of the oxygen-consuming reactions can be represented as



where  $\gamma_S$  is the average chemical oxidation state of carbon in the substrate. The disproportionation reactions can be represented as



where  $\gamma_B$  is the average chemical oxidation state of carbon in the products of the reaction other than  $CO_2$ , i.e., in  $C_{\text{bio}}$ .

The rate of heat production  $R_q$  is given by the sum of the fraction of  $CO_2$  produced by each reaction multiplied by the enthalpy change for each reaction.

$$R_q = (-f_1\Delta H_1 - f_2\Delta H_2)R_{CO_2} \quad [3]$$

The  $\Delta H$  values are given by Thornton's rule (Thornton 1917, Battley 1999), i.e., the average heat of combustion of organic compounds is a constant equal to  $-455 \pm 15$  kJ when expressed per mole of  $O_2$ . Thus, in kilojoule per mole of  $CO_2$

$$\Delta H_1 = -455(1 - \gamma_S/4) \quad [4]$$

and

$$\Delta H_2 \approx 0 \quad [5]$$

The fraction of  $CO_2$  produced by oxygen-consuming catabolic reactions is therefore directly proportional to  $R_q/R_{CO_2}$  as shown in equation 6.

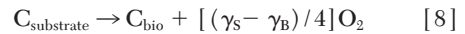
$$f_1 = (R_q/R_{CO_2})/[455(1 - \gamma_S/4)] \quad [6]$$

The fraction  $f_1$  varies from 0 to 1 and is equal to the ratio of aerobic to anaerobic respiration. Because  $\gamma_S$  is nearly always  $\leq 0$  in multi-celled organisms, i.e., the substrate is carbohydrate with  $\gamma_S = 0$ , protein with  $\gamma_S \approx -1$ , or lipid with  $-1 > \gamma_S > -1.8$ , ratios of  $R_q/R_{CO_2} < 455$  kJ/mol indicate the presence of an anaerobic component of respiration, i.e., anabolism or anaerobic catabolism. Values of  $R_q/R_{CO_2} > 455$  kJ per mole indicate the absence of anabolism or other anaerobic reactions and oxidation of a substrate more reduced than carbohydrate as the source of the  $CO_2$  (Hansen et al. 2004).

Whereas equation 6 provides values of the fraction of  $CO_2$  produced by oxygen-consuming reactions, the anabolic rate  $R_{AN}$  can be calculated from the difference between  $R_{CO_2}$  and  $R_q$  (Hansen et al. 1994, 2004).

$$R_{AN}\Delta H_B = 455(1 - \gamma_S/4)R_{CO_2} - R_q \quad [7]$$

Equation 7 gives the anabolic rate as the rate of storage of chemical energy (i.e., enthalpy) in anabolic products ( $R_{AN}\Delta H_B$ ) with the substrate as the reference energy state of carbon.  $\Delta H_B$  is the enthalpy change for the reaction



The value of  $\Delta H_B$  is dependent on the oxidation states of both substrate and biomass produced and is endothermic if the substrate is carbohydrate (Ellingson et al. 2003).

**Test Insects.** Field collected *H. axyridis* and *H. convergens* adults were purchased from Rincon-Vitova Insectaries (Ventura, CA) and maintained as described by Hamilton et al. (1999). Green peach aphids (*Myzus persicae*, Sulzer) were reared on Cherry Belle radishes (Carpenter Seed Co. Provo, UT) growing in a greenhouse with a temperature of 22°C and 70% humidity.

**Calorimetric Measurements.** The five calorimeters used in this study were Hart Scientific (Pleasant Grove, UT) model 7707, differential, heat-conduction calorimeters operated in the isothermal mode at 5°C intervals from 0 to 40°C. Each calorimeter has three sample ampules and one common reference ampule. Calibration is done electrically with resistors embedded in the bases of the ampule holders. The detection limit caused by baseline reproducibility is 2–3  $\mu W$  at room temperature and  $\approx 5$   $\mu W$  at 0 and 45°C.

Each beetle was weighed before being placed in the 1-cm<sup>3</sup> calorimeter ampules. The average mass of the adult beetles was 41.5 mg for *H. axyridis* and 21 mg for *H. convergens* (Acar et al. 2001). At temperatures from 0 to 25°C, two beetles were placed in each ampule to get sufficient heat for accurate measurements of  $R_q$  and  $R_{CO_2}$ . At temperatures above 25°C, only one beetle was placed in each ampule. The beetles were kept from moving around or coming in contact with each other inside the ampule by placing a cage with paper separators over them. Cages were constructed by rolling 8-cm-long, 1-cm-wide, filter paper strips into a

cylinder that fit closely inside the ampule and gluing a nylon mesh screen over the top of the cylinder. Blank runs showed the cages did not produce measurable heat. Experiments were repeated 24 times (48 beetles were used in measurements at temperatures below and at 25°C and 24 beetles were used at temperatures above 25°C). One set of beetles was used for measurements at 20°C and then at 15, 5, and 0°C in sequence. Another set was used at 20 and 25°C. A third set was used at 30, 35, and 40°C in sequence. At the highest heat rates measured, i.e., at 40°C, up to one-half the oxygen was consumed during the ≈1-h measurement period, but respiration was not affected by either low oxygen or high CO<sub>2</sub> as shown by a constant heat rate during the measurements. Sample sets of raw data for each species can be seen in Acar et al. (2001, 2004). CO<sub>2</sub> rates were measured with 40 μl of 0.4 M NaOH in a vial inside the calorimeter ampule. CO<sub>2</sub> produced by the respiring tissues was absorbed by the NaOH to produce Na<sub>2</sub>CO<sub>3</sub>(aq) and liberate additional heat at a rate proportional to the CO<sub>2</sub> production rate (Criddle and Hansen 1999).

The heat rate shows an initial period (≈15 min) of changing power as the calorimeter approaches thermal equilibrium, followed by a steady-state rate with occasional spikes of 1- to 2-min duration caused by movement or spiracle breathing (Lamprecht and Schmolz 1999, Acar et al. 2001, 2004). The steady-state rate is indicative of the resting metabolic heat rate of the beetles. The NaOH trap was added ≈45 min after the initial measurement was begun. After another 45 min, the NaOH was removed and the heat rate measured again. The difference in heat rate produced by the sample with and without NaOH present represents the heat rate caused by CO<sub>2</sub> trapping, and consequently, the rate of CO<sub>2</sub> formation.

The rank-sum test was used to compare results on the two species. The rank-sum transforms data by replacing each observation by its rank in the combined data set.

**Results**

The measured metabolic heat rate (R<sub>q</sub>) of both species was relatively small and constant from 0 to 10°C, above which it increased continuously to 40°C (Fig. 1). The heat production rate in *H. convergens* was

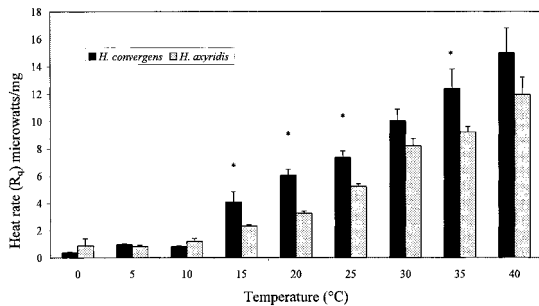


Fig. 1. Mean ± SD (n = 24) metabolic heat production rates (R<sub>q</sub>) of *H. axyridis* and *H. convergens*. \*Statistically significant differences in the values for the two species at a given temperature according to a rank-sum test (P < 0.05).

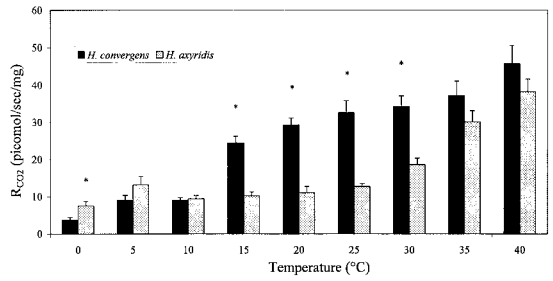


Fig. 2. Mean ± SD (n = 24) respiratory CO<sub>2</sub> rates of *H. axyridis* and *H. convergens*. \*Statistically significant differences in the values for the two species at a given temperature according to a rank-sum test (P < 0.05).

higher than that of *H. axyridis* at temperatures from 15 to 35°C (P = 0.04, 0.0001, 0.0001, and 0.11 at 15, 20, 25, and 35°C, respectively).

CO<sub>2</sub> rates in *H. convergens* were relatively constant from 0 to 10°C, increased sharply at 15°C, and increased steadily from 15 to 40°C (Fig. 2). In *H. axyridis*, CO<sub>2</sub> rates were relatively constant from 0 to 25°C and increased above 25°C. CO<sub>2</sub> rates were significantly higher in *H. convergens* at 15, 20, 25, and 30°C (P = 0.0001 at all four temperatures). Although the rates were statistically different at 0°C, the difference is probably not meaningful at this temperature.

In *H. convergens*, the R<sub>q</sub>/R<sub>CO2</sub> ratio was approximately constant from 0 to 10°C and increased from 10 to 40°C, with a maximum of 328 kJ/mol at 35°C (Fig. 3). In *H. axyridis*, the ratio decreased from 0 to 5°C, generally increased from 5 to 30°C with a maximum of 489 kJ/mol at 30°C, and decreased at 35 and 40°C. The decrease in R<sub>q</sub>/R<sub>CO2</sub> as temperature increased to 35 and 40°C indicates changes in metabolism caused by high-temperature stress. *H. axyridis* did not die during the 3-h exposure to the 40°C experiment, but died shortly thereafter. R<sub>q</sub>/R<sub>CO2</sub> was significantly greater in *H. axyridis* only at 15, 25, and 30°C (P = 0.0001, 0.0001, and 0.0003, respectively).

With the exception of the 35 and 40°C data, the anabolic heat rate (R<sub>AN</sub>ΔH<sub>B</sub>) reached a maximum at 5°C for *H. axyridis*, whereas the *H. convergens* maxi-

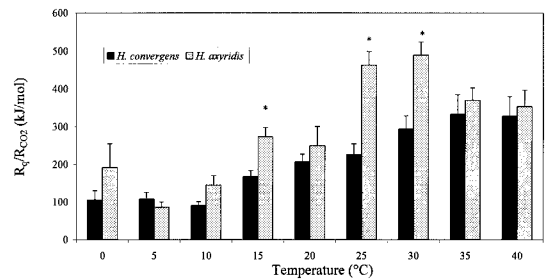


Fig. 3. Mean ± SD (n = 24) R<sub>q</sub>/R<sub>CO2</sub> ratios of *H. axyridis* and *H. convergens*. \*Statistically significant differences in the values for the two species at a given temperature according to a rank-sum test (P < 0.05).

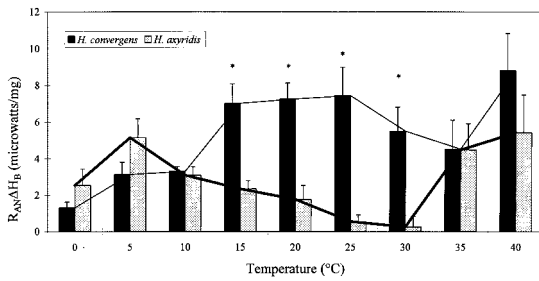


Fig. 4. Mean  $\pm$  SD ( $n = 24$ ) anabolic rates ( $R_{AN}\Delta H_B$ ) for *H. axyridis* and *H. convergens*. \*Statistically significant differences in the values for the two species at a given temperature according to a rank-sum test ( $P < 0.05$ ). The heavy line indicates the temperature response of *H. axyridis* and the light line that of *H. convergens*.

imum plateaued between 15 and 25°C (Fig. 4). The anabolic heat rate of *H. convergens* was significantly higher than that of *H. axyridis* between 15 and 30°C. The anomalous rates at 35 and 40°C for *H. axyridis* and at 40°C for *H. convergens* are presumably caused by high-temperature stress.  $R_{AN}\Delta H_B$  was significantly greater in *H. convergens* at 15, 20, 25, and 30°C ( $P = 0.0001, 0.0001, 0.0001$  and  $0.036$ , respectively).

In *H. axyridis*,  $f_1$  decreased from 0 to 5°C to  $\approx 0.2$ , increased with temperature to a maximum value of 1 at 25 and 30°C, and decreased at 35 and 40°C (Table 1). In *H. convergens*,  $f_1$  had about the same minimum value at low temperature and also increased with temperature, but only to a maximum of  $\approx 0.7$  and at a higher temperature of 35°C.

### Discussion

Values of  $R_q/R_{CO_2} > 455$  indicate that substrate more reduced than carbohydrate is being oxidized in catabolism and that there is little or no net anabolism in *H. axyridis* at 25 and 30°C. Because there are no indications of temperature stress at these temperatures, we interpret this to mean that all the energy from catabolism is being directed to provide energy for activity in *H. axyridis* at these temperatures, and none is being used for biosynthesis. At temperatures below 25°C, this ratio indicates metabolism in

Table 1. Mean  $\pm$  SD (24 replications) fraction of  $CO_2$  produced by oxygen-consuming reactions of catabolism for two species of coccinellids as calculated from calorimetric data

Temperature (°C)	<i>Harmonia axyridis</i>	<i>Hippodamia convergens</i>
0	0.42 <sup>a</sup> $\pm$ 0.14	0.23 $\pm$ 0.05
5	0.19 $\pm$ 0.10	0.24 $\pm$ 0.04
10	0.32 $\pm$ 0.06	0.20 $\pm$ 0.02
15	0.60 $\pm$ 0.05	0.37 $\pm$ 0.04
20	0.55 $\pm$ 0.11	0.45 $\pm$ 0.04
25	1.02 $\pm$ 0.08	0.50 $\pm$ 0.06
30	1.07 $\pm$ 0.08	0.65 $\pm$ 0.08
35	0.81 $\pm$ 0.07	0.73 $\pm$ 0.11
40	0.78 $\pm$ 0.10	0.72 $\pm$ 0.11

Values are calculated with equation 6, assuming  $\gamma_s = 0$ .

*H. axyridis* is a mix of catabolism and anabolic biosynthesis. Because an  $f_1$  value of  $< 0.2$  is required to fully supply all of the ATP needed for biosynthesis (Hansen et al. 2004), respiration-driven biosynthesis is most efficient at temperatures around 5°C in both species (see Table 1). However, the anabolic rate is at a maximum in *H. axyridis* around 5°C (Fig. 4) indicating that *H. axyridis* engages only in biosynthesis at this temperature. In contrast, the anabolic rate is at a maximum in *H. convergens* at 15–25°C. These results indicate that the two species have different strategies for dealing with environmental temperatures and the expenditure of energy for both development and activity. As temperatures rise to around 25–30°C, *H. axyridis* rapidly redirects all of its energy to support activity. In contrast, *H. convergens* never directs all of its energy to activity, but carries on biosynthesis at all temperatures. The ratio between energy use for activity and biosynthesis does increase with temperature in both species, however. In nature, both species of lady beetles favor temperatures between 15 and 22°C (Lamana and Miller 1998). According to a recent study by Soares et al. (2003), the relative rate of consumption of prey by *H. axyridis* decreased below 10°C and above 30°C. These observations agree with our findings.

Our data predict that because they direct more of their energy to activity, multicolored Asian lady beetles will be more effective predators at temperatures between 10 and 30°C. They also will mature and produce reproductive structures more efficiently at temperatures around 5°C. However, their upper stress temperature is apparently lower than that of the native convergent lady beetle. Our data indicate the native North American species *H. convergens* tolerates temperatures above 25°C better than the introduced species, *H. axyridis*, and matures more rapidly in the mid-range of temperatures from 15 to 30°C. Metabolic responses to temperature thus apparently confer some competitive advantages on *H. axyridis* at the temperatures most prevalent over much of the summer season in most of North America.

Evaluation of other life history parameters also shows that *H. axyridis* has some advantages over native species such as *H. convergens* and *Cycloneda sanguinea*, and *H. axyridis* seems to be well adapted for competing with other coccinellid species (Michaud 2002). Field-collected adult *H. axyridis* weigh more than *H. convergens*. Based on the authors' observations, *H. axyridis* adults consumed more aphids in the laboratory than *H. convergens* adults. We observed a higher fecundity rate in *H. axyridis* as well, as did Michaud (2002) in a comparison of *H. axyridis* with *C. sanguinea*.

Measurements of both heat and  $CO_2$  rates by calorimetry provide a rapid means to estimate temperature responses that are apparently of value in predicting survival and establishment of introduced species. To this end, calorimetric data needs to be collected on several more species of coccinellids adapted to a wide range of climates.

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