Effect of Temperature and Intraspecific Allometry on Predation by Two Phenotypes of *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae)

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ABSTRACT *Harmonia axyridis* Pallas is a highly polymorphic coccinellid with a wide geographic distribution. Genetic polymorphism seems to be the strategy adopted for facing different habitats at different times. Many modifications, such as body shape, body size, and elytral patterns, may be adaptive through imparting increased tolerance to adverse conditions. Previous studies evaluating differences in the light-colored *aulica* and dark colored *nigra* phenotypes found differences in biological performances at 20°C. However, whether the predatory activity of the different phenotypes changes under different temperatures remains unknown. Relative consumption rate and predation activity of fourth instars and adults of *aulica* and *nigra* phenotypes were compared at 10, 15, 20, 25, and 30°C. Our results showed that temperature is a limiting factor to larval and adult relative consumption rate. The thermal optimum of *nigra* adults was 3.7°C lower than that of *aulica.* Both larvae and adults of *nigra* were more stenothermic than *aulica.* Close to the upper limit of tolerance (30°C), predation activity of *nigra* adults was more affected than *aulica.* In larvae body size and shape could explain the differences observed, because *aulica* is significantly bigger than *nigra* and thus *aulica* presumably can better control heat exchange.

KEY WORDS *Harmonia axyridis*, genetic polymorphism, phenotypes, voracity, ecogeographical Bergmann's rule

ORGANISMS EXHIBIT MORPHOLOGICAL, physiological and behavioral modifications in response to limiting factors. Many modifications increase tolerance to adverse conditions and therefore increase individual fitness. Within a species, shape and body size can vary considerably, and are strongly correlated with many life-history components. Thus allometric relationships not only describe differences in form and process, but also impact biological activities such as reproduction and predation (Begon et al. 1990, Ricklefs 1990, Calder 1996). A life-history trait involved in an allometric relationship that affects other life-history components can be a potent source of phylogenetic constraint (Begon et al. 1990).

Temperature is one of the main environmental abiotic factors that can induce morphological, physiological and behavioral modifications through natural selection (Dobzhansky et al. 1977, Ricklefs 1990, Sacarrão 1991). Species with a wide geographic distribution can exhibit ecotypes whose tolerance limits and thermal preferences differ, corresponding to adaptations to specific habitats. Geographic variation, for instance, appears to have adaptive significance as described by the so-called Ecogeographical Bergmann's Rule (Calder 1996). Thus, no single optimal phenotype exists and polymorphism should persist when different genotypes are selectively favored in different parts of the environment or at different times (Ricklefs 1990, Buskirk et al. 1997).

Harmonia axyridis Pallas is a polymorphic coccinellid with >100 elytral patterns of different colors (Tan 1946, 1949; Komai 1956), and different body sizes and shapes (Dobzhansky 1933, Soares et al. 2001). Phenotypes are classified in two groups, the *succinea* group, characterized by light reddish or brownish ground color and the melanic group. The latter includes the *conspicua, spectabilis,* and *aulica* sub-groups characterized by melanic elytral patterns of different sizes and shapes (Tan 1946, 1949; Komai 1956). *Harmonia axyridis* exhibits striking temporal and geographic variation in the relative frequency of elytral pattern phenotypes. Variations are generally related to geographic and seasonal factors (Kryltsov 1956, Abbas and Nakamura 1985, Abbas et al. 1988, Osawa and Nishida 1992, Hodek and Honek 1996). Precise factors determining geographical variation are, however, difficult to determine (Muggleton 1978). Macrogeographic variation in Asian populations of *H. axyridis* is related mainly to climatic factors, whereas microgeographic variation is related to food availability. Light and melanic phenotypes have different

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physiological adaptations to climatic conditions (Komai 1956), while the relative frequency of elytral pattern phenotypes vary with host plants supporting different aphid species (Komai and Hosino 1951). Seasonal variation in the proportion of dark and light forms in Japanese populations was also observed (Tan 1949, Osawa and Nishida 1992). Osawa and Nishida (1992) demonstrated a significant increase of light phenotypes during spring and early summer. Assortative mating may maintain the morph proportions observed under natural conditions. Long-time changes in relative frequency of elytral pattern phenotypes were observed in the Suwa population, Japan. Komai (1956) suggested that this change was because of natural selection, probably in response to milder climatic conditions in Suwa.

Insect body temperature is of paramount importance in determining its activity (Digby 1955), such as feeding in lady beetles (Gutierrez et al. 1982, Mack and Smilowitz 1982, Hodek and Honek 1996). Size, shape and surface area are important morphological traits in insect body thermal balance (Willmer 1982). Insects of small size and proportionately large surface area are especially vulnerable to temperature (Willmer 1982), and these traits can be important when temperature is a limiting factor. In small insects, the difference in body temperature over ambient air (the so-called temperature excess) is less than in larger insects (Willmer and Unwin 1981, Brakefield and Willmer 1985, Stewart and Dixon 1989). Larger insects attain higher temperature excess but take longer to reach it under constant conditions (Digby 1955, Willmer and Unwin 1981). Color differences between phenotypes appear to be an important factor influencing body temperature and lady beetle activity (Brakefield and Willmer 1985, De Jong et al. 1996). Melanic phenotypes of *Adalia bipunctata* L. have lower reflectance than nonmelanic phenotypes leading to higher temperature excess, faster warming-up, lower mean time to activity and faster walking speed (Brakefield and Willmer 1985, De Jong et al. 1996). Thus, variable levels of sunshine, especially at low ambient temperatures, are expected to favor melanic phenotypes (De Jong et al. 1996), but could be a disadvantage in summer when temperatures are high. It seems to be a consensus that body size is more important than color in thermoregulation, but Stewart and Dixon (1989) refer to the importance of both features in thermoregulation of *A. bipunctata.*

Thus, intraspecific variation in body size and shape at the same developmental stage may be adaptive. We hypothesized that: (1) at lower temperatures small adults (spherical shaped) exhibit higher feeding activity than large adults; (2) at higher temperatures the predation activity of large adults is negatively affected; (3) predation activity of larvae (elongate shape) is less affected by size; and (4) under extreme temperatures, predation activity of larger larvae is higher than that of smaller specimens. We therefore predicted that feeding performance of fourth instars is less affected by temperature than feeding performance of adults, which should be strongly temperature-dependent.

Materials and Methods

Harmonia axyridis individuals from *aulica* and *nigra* phenotypes were mass reared at 22 ± 1°C, 75 ± 5% RH and a photoperiod of 16L:8D, using fluorescent lamps (Philips ref.: TDL 23W/54 and TDL 18W/54). The *aulica* phenotype is characterized by the presence of confluent red areas that occupy nearly the whole elytra, leaving a narrow black border on proximal and external margins, and the *nigra* phenotype is completely black. Coccinellids were fed on a mixed diet of the aphids *Aphis fabae* Scopoli and *Myzus persicae* Sulzer, and eggs of *Ephestia kuehniella* Zeller. Field collected individuals were added regularly to avoid consanguinity. *Aulica* and *nigra* phenotypes occur naturally in our mass cultures. Before the experiment, we reared the *nigra* and *aulica* phenotypes separately to increase their number. Larvae and adults were weighed with a 10^{-4} mg Mettler AM 50 analytical balance.

Larval and Imaginal Voracity and Relative Consumption Rate. We evaluated the number of apterous females of *A. fabae* eaten in 24 h by fourth instar and adults of the *aulica* and *nigra* phenotypes of *H. axyridis.* Larvae and adults were 48-h old and had been starved for 24 h. All experiments were done at 75% RH, a photoperiod of 16L:8D under fluorescent lamps (Sanyo FL 40 SS W/37), and at constant temperatures of 10, 15, 20, 25, or 30°C. Coccinellids were provided with aphids in numbers exceeding daily consumption, as established in preliminary tests. At 10 and 15°C, 50 aphids were provided whereas at 20, 25, and 30°C, 100 aphids were provided. Predators and aphids were put in contact with aphids for 24 h in 39cc petri dishes (Ø: 4.5 cm, height: 2.5 cm). A minimum of 15 replicates was conducted per treatment. There were 12 control treatments of 50 aphids without predators for each temperature. Mortality in the controls was low for every temperature except 30°C where only 52.2% of the aphids survived.

Voracity (V_o) was calculated according to the following model:

$$V_o = (A - a_{24})ra_{24} \qquad [1]$$

where V_o = number of aphids eaten, A = number of aphids available, a_{24} = number of aphids alive after 24 h, and ra_{24} = ratio of aphids found alive after 24 h in the control treatment.

Relative consumption rate (*RCR*) was evaluated according to Schanderl (1987):

$$RCR_{(mg)} = (W_i/N)V_oPUC \qquad [2]$$

where $RCR_{(mg)}$ = relative consumption rate, W_i = total weight of aphids provided, N = number of aphids provided, V_o = number of aphids eaten, and *PUC* = prey utilization coefficient.

*PUC*s of *H. axyridis* fourth instars fed on *M. persicae* and *A. fabae* were previously estimated as 93% (Schanderl 1987). Schanderl (1987) determined the *PUC* (96.4%) for adults fed only on *M. persicae* aphids. Because larvae had a similar prey utilization coefficient against *A. fabae*, we estimated that of adults to be 96.4% against *A. fabae.*

Table 1. Mean weight (mg ± SE) of larvae and adults of *H. axyridis aulica* and *nigra* phenotypes

Temp, °C	Larvae						Adults					
	aulica	*nigra*	*N*	*F*	df	*P*	*aulica*	*nigra*	*N*	*F*	df	*P*
10	18.9 ± 0.6a*	16.4 ± 0.5b	61	11.6	1	0.001	28.9 ± 0.6a	30.2 ± 0.9a	61	1.6	1	0.213
15	25.1 ± 1.0a	22.7 ± 0.6b	60	4.1	1	0.047	32.1 ± 0.8a	34.2 ± 0.6b	67	4.1	1	0.048
20	21.8 ± 0.9a	16.4 ± 1.1b	28	14.1	1	0.0008	26.2 ± 1.0a	32.4 ± 1.1b	28	17.1	1	0.0003
25	20.2 ± 0.9a	19.0 ± 0.9a	41	0.6	1	0.432	25.0 ± 1.1a	32.1 ± 0.9b	28	25.3	1	≤0.0001
30	25.3 ± 1.9a	21.9 ± 0.5b	57	31.6	1	0.027	27.8 ± 1.1a	32.6 ± 1.0b	29	9.4	1	0.004

* Means within a row and within developmental stage followed by the same letter are not significantly different ($P < 0.05$).

Effect of Temperature on Predation Activity. Polynomial regressions were used to evaluate the effect of temperature on predation activity (JMP IN, SAS Institute 1996). Temperature limits of predation activity were evaluated by calculating the y intercept ($f(x) = 0$) of the polynomial. When ($f(x) = 0$) could not be evaluated, we considered the minimum obtained as the limit of tolerance. The first derivative of the polynomial function ($f'(x) = 0$) at the y intercept was calculated to evaluate the thermal optimum of predation activity (MATHEMATICA, Wolfram Research 1996).

Other Statistical Analyses. One-factor analysis of variance (ANOVA) was used to compare treatments of larval and imaginal weight, and relative consumption rate. Fisher Protected least significant difference (LSD) was used to compare RCR under different temperatures (Abacus Concepts 1989).

Results

Larval and Imaginal Weight. Larval body weight of the *aulica* phenotype was significantly higher than that of the *nigra* phenotype, while imaginal body weight of the *nigra* phenotype was significantly higher than that of the *aulica* phenotype (Table 1).

Larval and Imaginal Relative Consumption Rate. Relative consumption rate by larvae of the *aulica* phenotype was significantly higher at 10 and 30°C (Table 2). Relative consumption rate by adults of the *aulica* phenotype was significantly higher than that by adults of *nigra* phenotype, except at 20°C where there was no significant difference (Table 2).

Effect of Temperature on Predation Activity. Both relative consumption rate by larvae of the *aulica* phenotype (ANOVA, $F = 53.15$, df = 4, 111, $P \le 0.0001$) (Fig. 1A) and of the *nigra* phenotype (ANOVA, $F = 46.17$, df = 4, 136, $P \le 0.0001$) (Fig. 1B), increased significantly between 10 and 20°C and decreased significantly between 25 and 30°C. Relative consumption rate by adults of the *aulica* phenotype increased significantly between 10 and 30°C but there were no significant differences between 25 and 30°C (ANOVA, $F = 249.0$, df = 4, 106 $P \le 0.0001$) (Fig. 1C). The relative consumption rate by adults of the *nigra* phenotype significantly increased between 10 and 25°C and decreased significantly between 25 and 30°C (ANOVA, $F = 124.82$, df = 4, 107, $P \le 0.0001$) (Fig. 1D).

The minimal tolerance limit for relative consumption rate by larvae of the *nigra* phenotype was lower than that of the *aulica* phenotype, while the maximum tolerance limit for larvae of *aulica* was higher than that of *nigra.* Thermal amplitude for relative consumption rate was higher in both larvae and adults of the *aulica* phenotype (Table 3). There was no difference in the thermal optimum for the relative consumption rate of *nigra* and *aulica* larvae, but the adult thermal optimum of *nigra* was 3.7°C lower than that of the *aulica* phenotype (Table 3).

Discussion

In general, voracity increases with temperature, food availability and instar of an insect predator (Frazer 1988, Hodek and Honek 1996). Daily consumption rate of coccinellid larvae and adults increases with temperature in a range that favors their survival and development (Sundby 1966, Ives 1981). High values of voracity for *Chilocorus bipustulatus* L., *C. cacti* L., *C. distigma* (Klug), *C. infernalis* (Mulsant), *C. nigritus* (F.), and *C. simoni* (Sicard) on *Aspidiotus nerii* (Bouché) were observed at temperatures between 24 and 38°C (Hattingh and Samways 1994). Our results showed that the RCR of *H. axyridis* changes with temperature and differs between phenotypes.

Survival and development of coccinelids decreases drastically outside thermal tolerance limits, generally <15°C and >32–34°C (Kaddou 1960; Gawande 1966;

Table 2. Mean relative consumption rate (mg of aphids eaten ± SE) of larvae and adults of *H. axyridis aulica* and *nigra* phenotypes

Temp, °C	Larvae						Adults					
	aulica	*nigra*	*N*	*F*	df	*P*	*aulica*	*nigra*	*N*	*F*	df	*P*
10	10.5 ± 0.6a*	6.0 ± 0.6b	61	23.7	1	≤0.0001	3.7 ± 0.3a	1.9 ± 0.2b	61	13.5	1	0.0005
15	18.8 ± 0.9a	17.5 ± 0.4a	60	1.63	1	0.206	16.8 ± 1.0a	11.4 ± 0.6b	67	20.9	1	≤0.0001
20	33.2 ± 2.4a	29.4 ± 1.1a	28	1.9	1	0.170	27.8 ± 1.0a	28.3 ± 2.0a	28	0.05	1	0.824
25	38.3 ± 3.6a	36.0 ± 3.0a	41	0.23	1	0.631	44.4 ± 2.4a	32.9 ± 1.5b	28	16.4	1	0.0004
30	31.1 ± 1.5a	18.7 ± 1.3b	57	29.1	1	≤0.0001	41.5 ± 1.1a	17.7 ± 1.7b	29	123.4	1	≤0.0001

* Means within a row and within developmental stage followed by the same letter are not significantly different ($P < 0.05$).

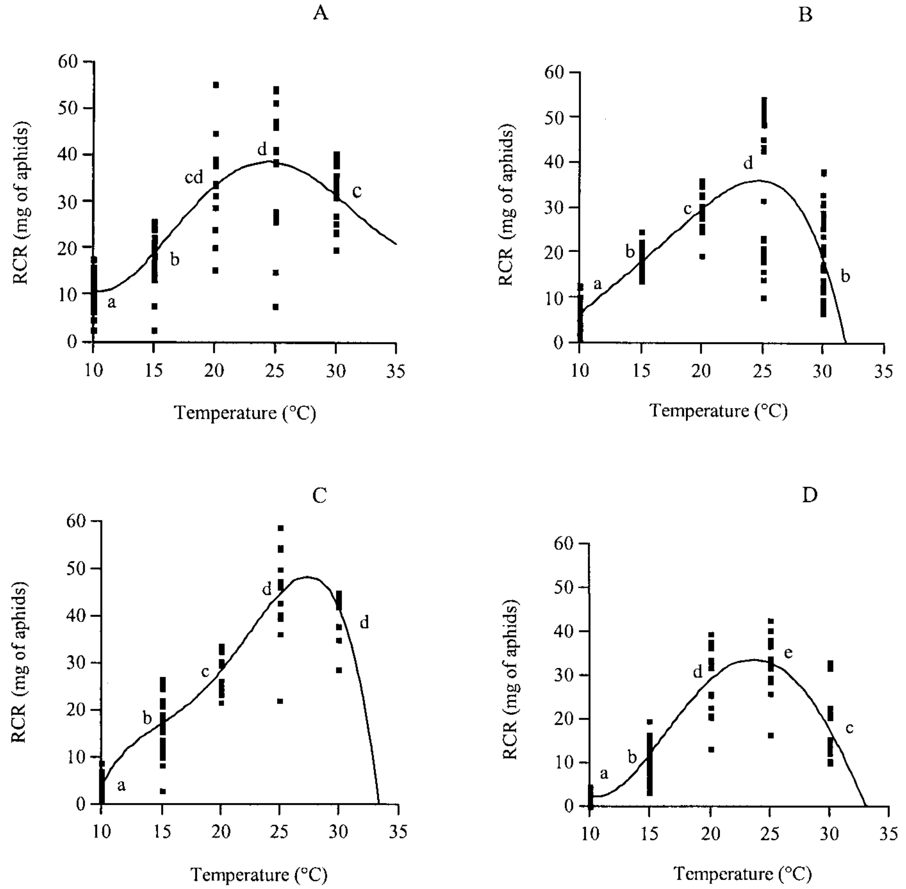

Fig. 1. Effect of temperature on relative consumption rate (RCR) of larval *H. axyridis aulica* (A; $RCR = 8.3 \times 10^{-4} t^4 - 78.65 \times 10^{-3} t^3 + 2.52 t^2 - 30.71t + 136.04$; $r^2 = 0.66$; $P < 0.0001$) and *nigra* (B; $RCR = -8.5 \times 10^{-4} t^4 + 5.2 \times 10^{-2} t^3 - 1.16t^2 + 13.51t - 56.63$; $r^2 = 0.58$; $P < 0.0001$), and adults *aulica* (C; $RCR = -2.17 \times 10^{-3} t^4 + 16.19 \times 10^{-2} t^3 - 4.34 t^2 + 51.92t - 221.3$; $r^2 = 0.90$; $P < 0.0001$) and *nigra* (D; $RCR = 8.2 \times 10^{-4} t^4 - 8.35 \times 10^{-2} t^3 + 2.78 t^2 - 34.6t + 145.2$; $r^2 = 0.82$; $P < 0.0001$) phenotypes. Means within panels followed by the same letter are not significantly different ($P < 0.05$; Fisher Protected LSD test).

Gurney and Hussey 1970; Ferran and Larroque 1979; Mack and Smilowitz 1982; Alikhan and Yousuf 1986; Michels and Behle 1991a, 1991b; Giroux et al. 1995). Our results showed that RCR decreased greatly at 10 and 30°C. This was more evident in spherically shaped adults, especially the bigger phenotype *nigra.* Both larval and adult *nigra* were more stenothermic than *aulica* and had narrower tolerance limits of predation activity. Despite significant differences of RCR near the tolerance limits, those differences were less accentuated at 10°C indicating that low temperatures have less of an affect of the feeding activity of the *nigra* phenotype than do high temperatures.

Several insect features, such as size, shape, and surface area influence heat gain and loss. It is more economical to generate and conserve heat within a large body than a small body (Willmer 1982). Body mass is important since the surface area:volume ratio of the animal determines the ratio of "heat dissipation capacity:heat content" (Schmidt-Nielsen 1997). Large animals have a lower surface area:volume ratio than small animals, and therefore cool (or warm) more

Table 3. Temperature limits and thermal optima for predation activity of larvae and adults of *H. axyridis aulica* and *nigra* phenotypes

Life stage	Phenotype	Temp, °C			
		Minimum	Maximum	Max.-Min.	Optimum
Larvae	*aulica*	10.4	36.2	25.8	24.4
	nigra	7.9	31.9	24.0	24.7
Adults	*aulica*	9.3	33.4	24.1	27.4
	nigra	10.4	33.0	22.6	23.7

slowly (Digby 1955, Willmer and Unwin 1981, Stewart and Dixon 1989, Calder 1996). Thus, one would expect adults to have a different relation to temperature than larvae. Our results suggest that higher metabolic heat production by bigger specimens of *nigra* adults, in addition to their thermally economic spherical shape, results in (1) a lower thermal optimum for predation activity, (2) a higher temperature excess near maximal thermal tolerance, with deleterious consequences on predation activity, and (3) greater tolerance at low temperatures than at high temperatures. Small spherical specimens such as *aulica* reach higher predation activity than bigger specimens near minimum thermal tolerance. Our results also suggest that the elongate body shape of larvae does not exhibit the same mechanism of thermoregulatory economy and conservation. For larvae, predation activity near the tolerance limits is less temperature-dependent and more size-dependent.

The thermomelanism hypothesis predicts that the internal temperature of dark forms should be higher than that of light color forms, resulting in increased activity, voracity, developmental rate, reproduction, and therefore fitness (Lusis 1961, Benham et al. 1974, Muggleton et al. 1975, Brakefield 1984). Our results showed that the thermal optimum of *nigra* adults is lower than that of larvae and *aulica* adults, consistent with the thermomelanism hypothesis. The dark color of adult *nigra* elytra may absorb solar radiation more efficiently than the elytra of *aulica.* This could give a significant advantage to the *nigra* phenotype in situations where low temperatures limit activity, as was found for *A. bipunctata* (Lusis 1961, Brakefield and Willmer 1985, De Jong et al. 1996, De Jong 1997). However all experiments were performed under fluorescent lamps that provide low radiation. Thus, our results suggest that beyond the body size and shape of the coccinelid, the thermal optimum for predation activity could be a genetically determined adaptation. In general, the relative frequency of melanic phenotypes in the cold regions occupied by Asian populations is high (Komai 1956). However, the precise factors determining geographical variation in relative frequencies of phenotypes are difficult to determine (Muggleton 1978). In Japan it seems that assortative mating, local climatic changes, relative humidity, geographic factors, and food availability also could determine also morph frequency in *H. axyridis* populations (Komai and Hosino 1951, Komai 1956, Osawa and Nishida 1992).

To avoid deleterious consequences in insects, only two main types of mechanisms can regulate body temperature; either by changes in metabolic heat production and internal redistribution of the heat generated (endothermy), or by heat exchange with the environment (Willmer 1982). The second mechanism is very important for immatures because they are true ecotherms (Willmer 1982). Avoiding exposure to solar radiation on warm sunny days greatly restricts the time available for foraging (Stewart and Dixon 1989), which could adversely affect the fitness of large coccinellids. However, intraspecific shape and size variation conferred by genetic polymorphism may permit a species to exploit much more finely graded habitats and microniches. Thus, different phenotypes could simultaneously exploit different parts of a highly stratified ecosystem. Given that polymorphism should persist only when different genotypes are selectively favored in different parts of the environment or at different times, we suggest that this results in increased tolerance to a wide range of temperatures.

The effect of temperature on individuals may differ either between species or between races of the same species (Begon et al. 1990). Our results suggest that size and shape of coccinelids could be important morphological modifications that influence its distribution and abundance, as predicted by the ecogeographical Bergmann's rule.

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