Temperature-Dependent Development in an Oregon Population of *Harmonia axyridis* (Coleoptera: Coccinellidae)

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ABSTRACT The multicolored Asian lady beetle, *Harmonia axyridis* (Pallas), an aphidophagous coccinellid, was first seen in Benton County, OR, in 1993. Coincident with the 1st occurrence of *H. axyridis*, we initiated a study on its temperature-dependent survival and development. Survival from 1st instar to adult emergence ranged from 83–90% between 18 and 30°C, and at 10 and 34°C was 42 and 25%, respectively. Mean time for complete development ranged from 14.8 d at 30°C to 81.1 d at 14°C. No eggs hatched at 10° or 34°C and no 1st instars transferred to 10°C survived. The mean lower threshold for egg-to-adult development of 11.2°C is typical relative to other temperate aphidophagous Coccinellidae and was not significantly different from 10.5°C calculated for a French population of this beetle. Conversely, the mean number of degree-days (DD) required for complete development was higher in the Oregon population (267.3 DD) than the French population (231.3 DD), although this may have been due in part to a different diet. Times for preimaginal development and values for thermal requirements suggest that the species is a thermal generalist in western Oregon.

KEY WORDS Coccinellidae, *Harmonia axyridis*, degree-days

THE MULTICOLORED ASIAN lady beetle, *Harmonia axyridis* (Pallas), was released in the United States as part of a classical biological control program targeting various arboreal, homopterous pests (Chapin and Brou 1991, Coulson 1992). This beetle is native to western and central Asia and was 1st observed in Oregon in 1991 (LaMana and Miller 1996). Intentional releases conducted in Washington of Japanese source-material (Coulson 1992) are the probable origin of *H. axyridis* populations in Oregon (LaMana and Miller 1996). Co-occurring with *H. axyridis* on various species of trees and shrubs in western Oregon are *Adalia bipunctata* (L.), *Calvia quatuordecimguttata* (L.), *Coccinella septempunctata* (L.), *Coccinella trifasciata* LeConte, *Cycloneda polita* Casey, *Hippodamia convergens* Guerin-Meneville, and *Olla v-nigrum* (Mulsant) (LaMana 1995). Furthermore, LaMana and Miller (1996) documented that *H. axyridis* comprised 70% of adult coccinellids observed in an arboreal habitat during 1994.

Temperature-dependent development of temperate-zone, aphidophagous coccinellids has been relatively well studied, and is an intrinsic trait affecting not only successful establishment of biocontrol agents but also subsequent predator-guild composition (Frazer and McGregor 1992, Rosenheim et al. 1993). Intraspecific variation in temperature-dependent developmental traits also has been shown in the Coccinellidae. For example, variation in temperature-dependent developmental rates among the progeny of individual females has been documented within a population of the convergent lady beetle, *Hippodamia convergens* Guerin-Meneville, (Rodriguez-Saona 1994) and *C. trifasciata* (Miller and LaMana 1996). Furthermore, Rodriguez-Saona and Miller (1995) showed that the developmental threshold of *H. convergens* changed in response to directional selection in the laboratory.

The recent establishment and range expansion of *H. axyridis* in the Pacific Northwest stimulated the 3 objectives of the current study. Our 1st objective was to assess the baseline temperature-dependent developmental profile of *H. axyridis* as an exotic biological control agent recently introduced into a new habitat where selection on intrinsic traits may occur. The 2nd objective was to determine whether temperature-dependent development differs between 2 disparate populations of this species, and we addressed this by contrasting *H. axyridis* in Benton County, OR, with a population introduced into France from China (Schanderl et al. 1985). Such a difference would be of interest not only to future biocontrol exploration but also as a measure of intraspecific phenotypic variability in Coccinellidae. And third, we compared this trait with that of other guild members for which this information is known. One reason for the sudden dominance by *H. axyridis* over endemic coccinellids in western Oregon may have been due in part to a rapid rate of development relative to that of co-occurring species.

Materials and Methods

Adult females of *H. axyridis* were collected during fall (November) 1993, spring (April) 1994, and fall

Table 1. Percentage of cumulative mortality of *H. axyridis* from 1st instar to adult at constant temperatures and fed *A. pisum*

Life stage	Temp, °C					
	14	18	22	26	30	34
Instar 1	NA[a] (102)[b]	NA (164)	NA (167)	NA (158)	NA (145)	NA (106)
Instar 2	30.4 (71)	11.0 (146)	7.2 (155)	9.5 (143)	11.0 (129)	35.8 (68)
Instar 3	34.3 (67)	11.0 (146)	8.4 (153)	9.5 (143)	14.5 (124)	40.6 (63)
Instar 4	34.3 (67)	11.0 (146)	9.6 (151)	9.5 (143)	15.2 (123)	46.2 (57)
Pupa	51.0 (50)	14.6 (140)	10.2 (150)	11.3 (142)	16.6 (121)	55.7 (47)
Instar 1 to adult	57.8 (43)	17.1 (136)	10.2 (150)	11.3 (142)	16.6 (121)	75.5 (26)

[a] Percent mortality initiated with 1st instars.

[b] Number beginning given life stage.

(September) 1994, and their F_1 progeny were used to assess developmental rates. Adults were reared individually in the laboratory at 22 ± 2°C and fed the pea aphid, *Acyrthosiphon pisum* (Harris), cultured in a greenhouse on fava bean, *Vicia fabae* L. Eggs from each of 25 field-collected females were placed as whole clutches into clear, paper-topped, 28-ml plastic cups within 12 h of oviposition, and systematically assigned to a temperature treatment to ensure equal representation of females. Upon eclosion, a sample of 1st instars from each female was retained for adult rearing.

Development through egg, larval, and pupal stages was observed at 7 constant temperatures: 10, 14, 18, 22, 26, 30, and 34°C under a photoperiod of 16:8 (L:D) h, and 50 - 70% RH. All individuals were monitored every 12 h for eclosion, molting, and mortality, at which time an excess of fresh, live pea aphids was provided. Newly hatched 1st instars were moved to 34° (n = 106) and 10°C (n = 52) because of egg death at those temperatures. Duration of pupation and each instar was calculated using only individuals that eclosed as adults. Thus, an individual that died as a pupa was not included in analyses. Each individual was weighed 24 h after pupation.

Statistical analyses were conducted to assess effects of temperature on mortality and developmental rates. Temperature dependence of mortality was assessed via a G test for independence (Sokal and Rohlf 1981). Differing developmental times among temperature treatments were differentiated with 1-way analysis of variance (ANOVA). Analysis of developmental rates of eggs, larvae, and pupae was via simple linear regression models (Statistical Graphics 1986). The inverse of development time for each life stage (1/days between molts) was used to represent developmental rates. The developmental rates were used as the dependent variable and constant temperatures as the independent variable in a linear regression model designed to calculate certain developmental parameters. The linear regression model estimates total degree-day requirements as the inverse of the slope of the regression line and the lower developmental threshold as the x-intercept of the regression line (Stinner et al. 1974). Differences in degree-day requirements (DD) and lower developmental threshold (D_{th}) were differentiated by 95% confidence intervals (CI) of these parameters. The best-fitting models for depicting growth rates were chosen by comparing the variance in developmental parameters among various linear models employing all temperature treatments included against models with extreme temperature treatments removed. Models were accepted as the best models based on the lowest levels of variance in predicting observed development times at respective temperatures by using extra-sum-of-squares F tests for additional variables (Ramsey and Schafer 1997).

Results and Discussion

Temperature-Dependent Mortality and Development. Total mortality differed among temperatures ($G = 73.7$, df = 4, $P < 0.01$). No eggs hatched at 10 or 34°C. Larval mortality was greatest at 34°C where all 1st instars died and 75.5% of the individuals transferred as 2nd instars failed to reach adulthood (Table 1). The lowest temperature tested, 14°C, was also unsuitable for survival with all 1st instars dying prior to molting and 57.8% of the individuals transferred as 2nd instars failing to reach adulthood. Mortality was generally low between 18 - 30°C, averaging 13.8%, but was lowest at 22°C; 10.2% of the individuals died in the pupal stage. No pupae died at 30, 26, or 22°C, and only 2.9% of pupae died at 18°C. The highest level of pupal mortality was at 14 and 34°C, reaching 14.0 and 23.4%, respectively.

Larval and pupal mortality in 2 species of native arboreal aphidophagous coccinellids is higher than that of *H. axyridis*. In Oregon, mortality in larvae and pupae of *H. convergens* reached 83% at 17°C and 100% at 13°C (Miller 1992). Likewise, mortality of *H. axyridis* did not surpass 17% between 22 and 30°C, whereas mortality in an Oregon population of *C. quatuordecimguttata* ranged from 30.2–44.4% within the same temperature range (LaMana and Miller 1995). We do not have corresponding data for the other arboreal coccinellid species in Oregon. Thus, compared with 3 of the 8 aphidophagous coccinellid species found in an arboreal environment, *H. axyridis* exhibited high levels of larval and pupal survival at lower and higher temperature extremes. Such enhanced survival may in part explain the relatively high abundance of *H. axyridis* in western Oregon.

Time for completion of egg-to-adult development differed at all temperatures (1-way ANOVA; $F = 147.4$, df = 591, $P < 0.001$) and ranged from 14.8 d at 30°C to 81.1 d at 14°C (Table 2). The mean proportions of the developmental period spent as egg, larva, and pupa

Table 2. **Life stage duration (in days) (mean ± SD) of *H. axyridis* completing pupation at constant temperatures and fed *A. pisum***

Life stage	Temp, °C					
	14	18	22	26	30	34
n	43	136	150	142	121	26
Egg	13.6 ± 1.5	6.3 ± 0.7	3.7 ± 0.3	2.8 ± 0.3	2.5 ± 0.2	NA[a]
Instar 1	11.6 ± 3.0	6.0 ± 1.1	3.5 ± 1.0	2.5 ± 0.5	2.0 ± 0.5	1.8 ± 0.4
Instar 2	7.8 ± 1.5	3.8 ± 0.6	2.3 ± 0.6	1.5 ± 0.4	1.4 ± 0.4	1.2 ± 0.3
Instar 3	8.3 ± 1.0	4.3 ± 0.6	2.7 ± 0.5	1.8 ± 0.3	1.5 ± 0.5	1.5 ± 0.3
Instar 4	20.8 ± 4.0	10.2 ± 1.5	6.3 ± 0.9	4.4 ± 0.6	3.8 ± 0.6	3.7 ± 0.7
Instar 1-4	48.5 ± 5.4	24.3 ± 3.1	14.8 ± 2.2	10.2 ± 1.0	8.7 ± 1.1	8.1 ± 1.2
Pupa	19.0 ± 1.5	10.6 ± 1.4	6.5 ± 0.6	4.5 ± 0.3	3.6 ± 0.3	3.4 ± 0.4
Egg-adult	81.1 ± 5.6	41.2 ± 4.3	25.0 ± 2.3	17.5 ± 1.1	14.8 ± 1.1	11.4 ± 1.0[b]

[a] No eggs hatched in 34°C. First instars were transferred from other temperatures.

[b] First instar to adult.

ranged between 14.9–17.1%, 57.7–59.8%, and 23.4–26.2%, respectively, and were similar to proportions previously reported for *H. axyridis* (Schanderl et al. 1985), *A. bipunctata* (Obrycki and Tauber 1981), *C. quatuordecimguttata* (LaMana and Miller 1995), and *H. convergens* (Miller 1992).

The lower developmental-threshold values and degree-day requirements for each life stage of *H. axyridis* were calculated (Table 3). Egg-to-adult development required a mean of 267.3 DD above a lower threshold of 11.2°C. The physiological time for egg hatch was 42.6 DD above a threshold of 11.0°C, and was similar to that for other aphidophagous coccinellids. For example, *A. bipunctata* required only 43 DD over a threshold of 9.2°C to complete egg development (Obrycki and Tauber 1981), whereas *H. convergens* required 45 DD over a threshold of 11.3°C (Miller 1992). Egg hatch at cool temperatures was studied by Frazer and McGregor (1992) for 7 species of aphidophagous coccinellids. Although their data show temperature ranges for egg hatch between 12 and 16°C, the extrapolation of threshold values ranging from 8.4 to 10.2°C cannot be compared with our developmental-threshold values because of differences in the overall range of temperatures used for linear regression and the extrapolation of D_{th}. Our study used a temperature range from 10 to 34°C whereas Frazer and McGregor (1992) used a range from 12 to 20°C.

The thermal requirements for completion of all larval stages and pupation in *H. axyridis* averaged 156 and 66.6 DD, respectively, above a common threshold of 11.2°C. These values are between those reported for the warm temperature-adapted species *H. convergens* (Miller 1992) and the cool temperature-adapted species *A. bipunctata* (Obrycki and Tauber 1981) and *C. quatuordecimguttata* (LaMana and Miller 1995). The consistency in the observed range in lower-threshold temperatures in *H. axyridis* (±0.3°C) is somewhat unusual for an aphidophagous coccinellid for which threshold values often increase 0.5–1.0°C with successive life stages (Orr and Obrycki 1990, Miller 1992).

Compared with the French population (Schanderl et al. 1985), the total degree-days required for egg-to-adult development was significantly higher in the Oregon population, averaging 36 DD (Table 3), whereas the developmental thresholds did not differ. One possible explanation for this difference may be differing prey items. The French population was reared on *Myzus persicae* (Sulzer), a much smaller aphid than the *A. pisum* used in the current study. Dietary influences on developmental rates have been demonstrated for *Hippodamia sinuata* Mulsant (Michels and Behle 1991). However, if future studies were to show that differences in development of *H. axyridis* in western Oregon and France were not due to diet, then temperature-dependent developmental rates could be useful for differentiating various populations.

Differences in degree-day requirements between the Oregon and French populations of *H. axyridis* result in very different predicted times for development at several constant temperatures (Table 4).

Table 3. **Developmental threshold (D_{th}) and degree-day requirements (DD) (mean ± SE) of life stages of *H. axyridis* in Oregon and in France**

Life stage	Population	D_{th}	DD	Equation	r^2	*P*	*n*
Egg	O[a]	11.0 ± 0.2	42.6 ± 0.2	−0.25797 + 0.02346 (°C)	0.972	<0.001	969[b]
	F	10.7 ± 0.9[c]	42.4 ± 4.1	−0.25 + 0.024 (°C)	0.94	NA	NA
Larva	O	11.1 ± 0.5	156.0 ± 2.6	−0.07091 + 0.00641 (°C)	0.885	<0.001	591
	F	Na[d]	NA	NA	NA	NA	NA
Pupa	O	11.4 ± 0.4	66.6 ± 0.7	−0.17065 + 0.01502 (°C)	0.952	<0.001	591
	F	10.7 ± 0.1[c]	74.8 ± 4.2	−0.15 + 0.014 (°C)	0.98	NA	NA
Egg-adult	O	11.2 ± 0.3	267.3 ± 2.2	−0.04178 + 0.00374 (°C)	0.964	<0.001	591
	F	10.5 ± 0.4[c]	231.3 ± 8.2	−0.046 + 0.004 (°C)	0.94	NA	NA

[a] O, Benton County, OR; F, France (Schanderl et al. 1984).

[b] All eggs that hatched were used in this analysis, and many more hatched than larvae were reared.

[c] Only a partial estimate of threshold-temperature variance was possible from reported data.

[d] Data not available.

Table 4. Predicted days for egg-to-adult development at constant temperatures for 2 populations of *H. axyridis* and of some coccinellids co-occurring in western Oregon

Species	D_{th}	DD	Temp, °C				Reference
			16	20	24	28	
Calvia quatuordecimguttata	8.1	274.1	35a[a]	23a	17ab	14b	LaMana and Miller (1995)
Adalia bipunctata	9.0	262.8	37a	24a	18ab	14ab	Obrycki and Tauber (1981)
Harmonia axyridis (France)	(11.2)[b]	231.3	48ab[c]	26ab	18ab	14ab	Schanderl et al. (1984)
Harmonia axyridis (Oregon)	11.2	267.3	56bc	30c	20c	16c	Current study
Coccinella septempunctata	12.1	196.8	51bc	25a	17a	12a	Obrycki and Tauber (1981)
Hippodamia convergens	12.6	228.0	67c	31bc	20bc	15bc	Miller (1992)
Coccinella trifasciata	12.7	227.0	69c	31bc	20bc	15bc	Miller and LaMana (1996)

[a] Predicted times within a column are not significantly different (95% CI).

[b] The lower threshold for the Oregon population was used because it does not differ from that of the French population.

[c] Variation in predicted times for this population are slightly greater than shown because of limitations in reported data.

Based on reported values for D_{th} and degree-days, Oregon *H. axyridis* are predicted to develop significantly more slowly than the French population at temperatures between 17 and 32°C. For example, at 20°C the predicted developmental time of the French population is 4 d less than that of the Oregon population. Such rapid development in the French biotype of *H. axyridis* would be of interest given circumstances where population models predict a higher intrinsic rate of increase in populations with a shorter generation time (Hutchinson 1978).

Relative to aphidophagous coccinellids endemic to western Oregon, rates of development in *H. axyridis* were moderate. The cool, wet spring and fall and warm, dry summers of the Pacific Northwest provide the climatic variability upon which species-specific differences in temperature-dependent development may be 1 component of guild dominance. Species with lower developmental-threshold temperatures may initiate and complete development before species with higher minimum temperature requirements. Likewise, a reduced total degree-day requirement for development also will result in more rapid development when threshold temperatures are similar. At 16°C *A. bipunctata* and *C. quatuordecimguttata* complete pupation nearly 20 d faster than *H. axyridis*, whereas *H. convergens* and *C. trifasciata* are 11 and 18 d slower, respectively (Table 4). However, *C. septempunctata* develops more rapidly than *H. axyridis* at 28°C, as do *A. bipunctata* and *C. quatuordecimguttata*. The Oregon population of *H. axyridis* appears to be a thermal generalist based on predicted developmental times that are roughly equivalent to those of *H. convergens* at warm temperatures and *C. septempunctata* at cooler ones. Thus, *H. axyridis* is well adapted for development in either cool or warm temperatures, and is similar to indigenous species in developmental profile as indicated by its lower-threshold temperature and degree-day requirements.

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