Thermal Microhabitat Use by the Ladybird Beetle, *Coccinella septempunctata* (Coleoptera: Coccinellidae), and Its Life Cycle Consequences

KAZUNORI OHASHI,[1, 2] YASUYUKI SAKURATANI,[3] NAOYA OSAWA,[4] SHUICHI YANO,[1] AND AKIO TAKAFUJI[1]

Environ. Entomol. 34(2): 432–439 (2005)

ABSTRACT Most central Honshu populations of the ladybird beetle, *Coccinella septempunctata* L., pass the winter as quiescent adults. However, variations in life cycle within populations have been observed: hibernating and reproductive adults simultaneously coexist in the same habitat in winter. We studied microhabitat use patterns of this beetle in winter on a sunny slope of a southeast-facing riverbank. We found that, even though natural substrates were available, the beetle preferred to use artificial substrates such as metal cans (iron or aluminum), papers, and wooden materials discarded on the slope as oviposition and pupation sites. The artificial substrates were relatively easily warmed by solar radiation and were therefore used as thermal microhabitats by the beetle. Although ambient winter air temperatures of this region were not high enough for the beetles to complete their development, the use of thermal microhabitats enabled them to do so by thermal conduction. Prey aphids were also abundant during the winter. Thermal microhabitat use enables these beetles to complete an additional generation in winter.

KEY WORDS thermal microhabitat, oviposition site preference, pupation site preference, life-cycle polymorphism, human activity

---

MICROHABITAT SELECTION BY AN animal within a heterogeneous environment should maximize its fitness in terms of feeding rate, growth rate, and avoidance of natural enemies (Rosenzweig 1991). Thermal conditions of microhabitats are especially important for physiological and ecological performance (Huey 1991). As has been studied intensively in reptiles, ectothermic animals depend on the availability and distribution of thermal microhabitats to regulate their body temperatures (Christian and Tracy 1981, 1985, Waldschmidt and Tracy 1983, Tracy and Christian 1986, Adolph 1990, Diaz 1997, Rock et al. 2002). Although egg and pupal stages of insects are immobile, ovipositing females and wandering prepupal larvae should be able to seek out thermal microhabitats suitable for the subsequent life cycle stage. However, relatively few studies have examined this possibility (Rausher 1979, Williams 1981, Grossmueller and Lederhouse 1985, Rodriguez et al. 1992), although many studies have covered adult and larval thermoregulation behavior (see reviews in May 1979, Casey 1992 and Heinrich 1993).

Differences in microhabitat thermal conditions cause variations in demographic parameters such as larval developmental rate. Thermal microhabitat use by insects therefore affects their population dynamics and life cycles (Kingsolver 1979, Huey 1991). Grossmueller and Lederhouse (1985) suggested that a population of tiger swallowtail butterflies inhabiting an area where growth-degree-hours were insufficient for a second generation became bivoltine by ovipositing on branches exposed to sunlight. However, the impact of the availability of thermal microhabitats on life cycles of insects has not been widely examined.

The aphidophagous ladybird beetle, *Coccinella septempunctata* L., occurs most commonly on grasslands and has two generations per year in central Japan (34–38° N). First-generation adults (which emerge in spring) undergo summer diapause, whereas second-generation adults (which emerge in autumn) overwinter in a quiescent state, without entering winter diapause (Sakurai et al. 1981, 1983, 1986, 1987). Previous studies observed that these beetles laid their eggs (Banks 1954, Takahashi 1987, Sakuratani and Nakamura 1997) and pupated (Sakuratani et al. 1986) on dead leaves, stones, and various artificial substrates, such as discarded metal cans, in sunny grasslands during seasons of relatively low air temperature. This microhabitat use shortens developmental times because the temperature of these substrates rises above the ambient air temperature through absorption of

---

[1] Laboratory of Ecological Information, Graduate School of Agriculture, Kyoto University, Kyoto 606-8502, Japan.

[2] Corresponding author, e-mail: oohasi@kais.kyoto-u.ac.jp.

[3] Entomological Laboratory, Faculty of Agriculture, Kinki University, Nara 631-8505, Japan.

[4] Laboratory of Forest Ecology, Graduate School of Agriculture, Kyoto University, Kyoto 606-8502, Japan.

Table 1. Oviposisiton sites of *C. septempunctata* in the habitat

Year	Kind of substrates	No. egg batches (position[a])			Total no. eggs	No. eggs hatched	Egg-batch density/100 cm^2
		Under	Upper	Total			
1996	Wood	43	1	44	2,101	163	—
	Paper	14	0	24	851	136	—
	Brick	18	0	18	574	167	—
	Iron	15	0	15	624	172	—
	Concrete	8	0	8	248	57	—
	Nylon	5	2	7	229	16	—
	Dead plant leaf	1	0	1	41	1	—
	Glass	1	0	1	19	9	—
	Live plant leaf	0	0	0	—	—	—
	Total	115	3	118	4,687	721	
			***				
1997–1998	Paper	15	0	15	419	118	1.40
	Iron	11	0	11	411	205	2.06
	Wood	6	1	7	132	35	1.19
	Brick	5	0	5	130	30	0.60
	Aluminum	2	0	2	110	48	0.59
	Expanded polystyrene	1	0	1	44	21	0.49
	Nylon	1	0	1	17	8	2.31
	Dead plant stem	1	0	1	31	0	0.0097
	Live plant leaf	0	1	1	12	0	0.0041
	Total	42	2	44	1,306	465	
			***				

[a] Asterisks show significant deferences from a uniform distribution as 1:1 by binomial test (***$P < 0.0001$).

solar radiation (Sakuratani and Nakamura 1997). Not only active adults, but also eggs and pupae, of *C. septempunctata* were found in such thermal microhabitats, even in winter, when many adults were quiescent in nearby overwintering quarters (Sakuratani 1988). These observations strongly suggest that thermal microhabitat availability can modify the life cycle of *C. septempunctata* populations.

We studied oviposition and pupation site preferences of *C. septempunctata* with regard to thermal microhabitats during winter. The life cycle consequences of thermal microhabitat availability in the field for this beetle are discussed.

Materials and Methods

Study Site. The grassland habitat (10 m above sea level) consisted of a flat, dry riverbed ($\approx$15 m in width) and riverbank slope ($\approx$6 m in width, 30° slope) of the Katsura River, running northeast to southwest near Kyoto (34.9° N, 135.7° E) in central Honshu, Japan. The study site was dominated by herbaceous plants such as *Brassica juncea* (L.) Czern, *Vicia angustifolia* L., *Solidago altissima* L., and several Gramineae species; the ground surface was partly exposed by periodic mowing in early summer and late autumn. In spring and autumn, the first and second generations of *C. septempunctata* occurred mainly on the flat riverbed. During winter, rosulate *B. juncea* dominated the site, and three aphid species, *Lipaphis erysimi* (Kaltenbach), *Brevicoryne brassicae* (L.), and *Myzus persicae* (Sulzer), occurred mainly on these plants and only on slopes facing southeast. Above the bank was a road from which much trash and waste such as metal cans, papers, and wooden materials were discarded onto the slope.

Field Censuses. Field censuses were conducted on the sunny slope of the southeast-facing bank from January to May 1996 and from December 1997 to April 1998. Nine plots (70 by 70 cm) were established within the 6 by 45-m area of the slope; each contained discarded trash. The four corners of each plot were pegged, providing no obstacle to free movement of beetles and aphids among the plots. At approximately weekly intervals, the plots were searched for egg batches and pupae, and the nature of their substrates was recorded. Also noted were their positions, that is, whether they were fixed to the upper or lower side of the substrate; this allowed a rough estimation with regard to wind exposure. Newly observed egg batches and pupae were identified by painting markers close by on the substrate. The numbers of eggs laid, hatched eggs, and pupae, and the pupal eclosion rates were assessed on each census day. The number of aphids in each plot was directly counted by eyes without distinguishing species or developmental stages.

Oviposition and Pupation Site Preference. To determine the relative abundance of substrates within plots, we estimated area coverage of each substrate. Photographs of nine plots were taken in 1998. Then, area of each substrate within the nine plots was calculated using the pictures and squared papers. Substrates were classified into one of four categories: (1) live plants, mainly *B. juncea;* (2) dead plants, mainly *B. juncea, S. altissima,* and several Gramineae species; (3) soil surface and stones; and (4) artificial substrates, such as discarded waste and trash (listed in Tables 1 and 2). As most wooden substrates were waste-derived, these were included in the artificial category. We examined whether the beetles preferred the artificial substrates for oviposition or pupation site: whether observed numbers of egg batches and pupae

Table 2. Pupation sites of *C. septempunctata* in the habitat

Year	Kind of substrates	No. pupae (position)[a]			No. pupae eclosed	Pupal density/100 cm^2
		Under	Upper	Total		
1996	Wood	22	8	33	24	—
	Iron	14	9	23	19	—
	Brick	12	3	15	11	—
	Paper	7	0	7	7	—
	Nylon	5	0	5	4	—
	Live plant leaf	0	2	2	2	—
	Plastic	1	0	1	1	—
	Total	61***	22	83	68	—
1997–1998	Paper	23	3	26	19	2.42
	Dead plant stem or leaf	4	7	11	3	0.11
	Iron	0	4	4	1	0.75
	Stone	2	0	2	1	0.61
	Aluminum	1	0	1	1	0.29
	Live plant leaf	0	0	0	—	0.00
	Total	30*	14	44	25	—

[a] Asterisks show significant differences from a uniform distribution as 1:1 by binomial test (***$P < 0.0001$; *$P < 0.05$).

on each substrate of the four categories differed from expected number of those based on the area of each substrate were analyzed using χ^2 test. To further examine whether beetles preferred certain substrates with higher thermal qualities for oviposition or for pupation, regressions between the mean effective temperatures of each substrate and the density of eggs and pupae per unit area were performed.

Microhabitat Temperature Measurements. Ambient temperatures on the slope were determined every 30 min from 0600 to 1800 hours on a sunny day, 15 February 2003, which is within the coldest period in this part of Japan. The temperatures on 12 substrates recognized as oviposition and/or pupation sites (artificial substrates, $n = 3$–5; *B. juncea* leaves, $n = 10$) were recorded using a radiation thermometer. The air temperature at 1.5 m above the habitat ($n = 1$) and that of an airspace (within 1–2 cm height) between a wooden block board ($\approx$20 by 36 by 0.3 cm) placed on the slope and the ground surface, where eggs and pupae were actually exposed to the air ($n = 1$), were recorded with a thermistor thermometer. The differences in the changing patterns of temperatures between an artificial substrate (wood) and a natural substrate (*B. juncea* leaves) were analyzed using repeated measures of analysis of variance (ANOVA). The effective cumulative temperatures for growth of the beetle during the day (degree-hours) on each substrate were calculated based on the species' lower developmental threshold (egg, 11.2°C; pupa, 13.5°C; Kawauchi 1990). The data were subjected to one-way ANOVA testing to reveal whether cumulative temperatures differed among substrates. In addition, the expected developmental times on each substrate were estimated based on the total effective temperature for growth (egg, 38.8 DD; pupa, 56.2 DD; Kawauchi 1990).

Factors Determining Egg Temperature. To illuminate factors determining the egg temperature, the ambient temperatures were measured under various temperature conditions on 15 February 2003. The temperatures of the egg batches (egg-batch temperature) and the oviposition sites (substrate temperature) were recorded with a radiation thermometer, and the air temperatures within 10 cm of the eggs (ambient temperature) and at 1.5 m above the habitat (air temperature) were recorded with a thermistor thermometer. Multiple linear regression analyses were used to study the relationship between egg-batch temperature (the dependent variable) and substrate temperature, ambient temperature, and air temperature (the independent variables; StatSoft 1999).

Results

Microhabitat Use by the Beetle. The total numbers of egg batches observed were 118 in 1996 and 44 in 1997–1998 (Table 1). Eighty-three pupae were observed in 1996 and 44 in 1997–1998 (Table 2). Most egg batches and pupae were found on artificial substrates (Tables 1 and 2), including wooden wastes (mainly block boards or scantlings), papers, bricks (chips of terra cotta flower pots), and iron pieces. The density of egg batches was highest on these artificial substrates and lowest on dead and live plants. The density of pupae was highest on paper. Eggs and pupae were significantly more abundant on the underside of the substrates (Tables 1 and 2; binomial test). Egg hatch and pupal eclosion were observed during the censuses (Tables 1 and 2); eggs and pupae were obviously developing even during the winter.

Diurnal Changes of Microhabitat Temperature. The air temperature at 1.5 m above the habitat slightly exceeded the lower developmental threshold of *C. septempunctata* eggs (11.2°C), but did not over that of the pupal stage (13.5°C; Fig. 1). However, temperatures on artificial substrates (e.g., the wooden substrates shown in Fig. 1) exceeded 30°C during the day owing to substrate absorption of solar radiation. Daytime airspace temperatures also increased >20°C. The patterns of temperature change were significantly different between wooden waste and *B. juncea* leaves (repeated measures of ANOVA: $F = 206.48$; df = 1,312;

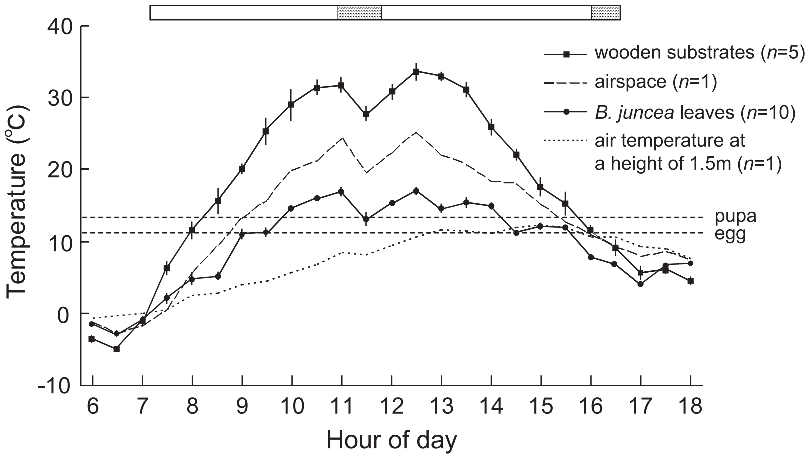

Fig. 1. Environmental temperatures measured on a sunny day in mid-February. Horizontal broken lines represent the lower developmental thresholds of beetle eggs (11.2°C) and pupae (13.5°C). The rectangle indicates the duration of illumination by solar radiation at the site; cloud cover is shown as absent (open area) or hazy (shaded area). Error bars indicate ±SEM.

$P < 0.0001$; Fig. 1). When it became cloudy, microhabitat temperatures fell rapidly, except for that of the air at 1.5 m above the study site.

Factors Determining Egg Temperature. Multiple regression analysis showed that egg batch temperatures depended significantly on the substrate temperature (Table 3). The coefficient value of the substrate temperature was 0.89, close to 1, and much larger than other coefficient values, indicating that thermal conduction from the substrate mostly determined the egg batch temperature.

Thermal Quality of Each Substrate. Figure 2 shows the effective cumulative temperatures (degree-hours) on the basis of temperature for a 12-h period on 15 February 2003 for eggs and pupal stages on each substrate. The mean effective temperatures differed significantly among substrates (ANOVA: egg, $F = 55.03$; df = 11,48; $P < 0.0001$; pupa, $F = 53.21$; df = 11,48; $P < 0.0001$; Fig. 2). Effective temperatures were higher on pieces of iron, stones, and bricks, but lower on nylons, plastics, and expanded polystyrenes. The temperatures of *B. juncea* leaves only slightly exceeded the developmental threshold (see Fig. 1), and the effective temperatures of natural substrates were very low (Fig. 2). The development times estimated from effective temperatures on *B. juncea* leaves were 46.7 and 150.7 d for the egg and pupal stages, respectively. This contrasts with development times on wooden wastes, where only 8.3 and 14.3 d were required for the egg and pupal stages, respectively (Fig. 2).

Table 3. Multiple regression analysis for the effect of three microenvironmental temperatures on egg-batch temperatures

Independent variable	Partial regression coefficient[a]	SE	t	P
Air temperature	0.2072	0.1586	1.3064	0.1989
Ambient temperature	−0.0299	0.0881	−0.3394	0.7360
Substrate temperature	0.8938	0.0436	20.5034	<0.0001
Intercept	−0.3353	1.4167	−0.2367	0.8141

[a] Adjusted $R^2 = 0.9848$, $F = 927.18$, df = 3,30, $P < 0.0001$, $n = 44$.

Oviposition and Pupation Site Preferences. Beetles significantly preferred artificial substrates as oviposi-

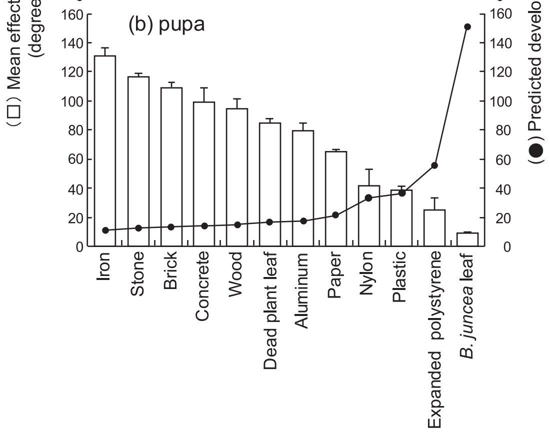

Fig. 2. Mean effective temperature (degree-hours) of eggs (a) and pupae (b) on various substrates measured on a sunny day in mid-February and expected egg and pupal developmental times based on each effective temperature. The number of *B. juncea* leaves measured was 10, while 3–5 representatives of other substrates were measured. Error bars indicate ±SEM.

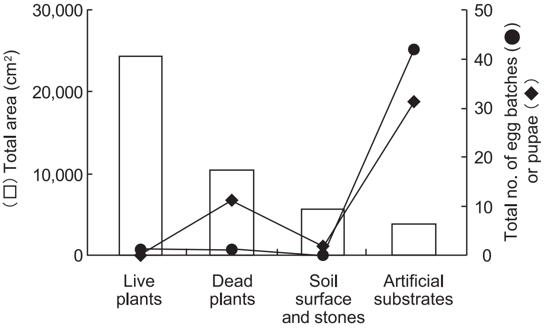

Fig. 3. Oviposition and pupation site preferences, showing relationships between the total areas of substrate and total numbers of egg batches or pupae observed within nine plots in 1997–1998.

tion and pupation sites (egg batch: $\chi^2 = 417.66$, df = 3, $P < 0.0001$; pupa: $\chi^2 = 219.88$, df = 3, $P < 0.0001$; Fig. 3). However, regression analyses between the effective temperature of each substrate (Fig. 2) and the density of egg batches and pupae (Tables 1 and 2) revealed no significant relationships (Table 4; $P > 0.05$). Although beetles strongly preferred artificial substrates as oviposition and pupation sites, they did not exhibit clear preferences for substrates with higher effective temperatures.

Seasonal Changes in the Number of Beetles and Prey Aphids. Air temperature in this region seldom exceeded the developmental threshold of the beetle until March in 1996 and February in 1998 (Fig. 4, top). Two peaks of aphid abundance were observed (Fig. 4, middle). The observed number of newly emerged beetles for each census day is also shown in Fig. 4 (bottom). Eggs hatched from February to March in 1996 and from January to February in 1998. The peaks of adult beetle emergence were in early April in 1996 and late March in 1998. These results indicate that *C. septempunctata* had one generation during winter at this study site.

Discussion

The emergence of adult *C. septempunctata* in December or January has already been reported (Sakurai et al. 1983, Sakuratani et al. 1986). Oviposition continues for about 2 mo at 25°C (Kawauchi 1985), and therefore, adults emerging in December or January were considered to be late-hatching individuals of the second annual generation (Sakuratani et al. 1986). However, our study has shown that second generation adults lay eggs in winter and that these eggs develop into adults by early spring. This means that the beetle has another generation during winter. Although *C. septempunctata* has a bivoltine life cycle in central Honshu (Sakurai et al. 1983), the population at this study site seems to have a partly trivoltine life cycle.

Table 4. Relationships between mean effective temperature (degree-hours) (X) and the egg-batch or pupal density/100 cm² (Y) on each substrate

Stage	Regression equation	*n*	R^2	*F*	*P*
Egg	Y = 0.450 + 0.006X	9	0.0898	0.6908	0.4333
Pupa	Y = 2.082 − 0.013X	5	0.1521	0.5381	0.5164

In this habitat, most eggs and pupae were on substrates that were easily warmed by solar radiation. We showed that, in winter, the development of the eggs and pupae was possible only on artificial substrates but was almost impossible on the live plant leaves (Fig. 2). The temperature measurements of the microhabitats were conducted on a single day in mid-February, which is thought to be a typical winter day in Japan. Therefore, we concluded that the preference for thermal microhabitats as oviposition and pupation sites enabled development to be completed by thermal conduction even in the low temperature season. Egg hatchability was relatively low during both years (15.4% in 1996 and 35.6% in 1997–1998; Table 1), and the majority of egg mortality was caused by cannibalism rather than low temperature, because many eggshells caused by cannibals remained (K.O., unpublished data). Therefore, the cold hardiness of *C. septempunctata* eggs seems to be high, and they seem to survive even freezing ambient temperatures.

Females did not lay eggs on live plant leaves during winter at the study site, whereas they choose to lay their eggs mainly on leaves during warmer seasons (e.g., Hironori and Katsuhiro 1997). Such season-dependent changes in oviposition behavior suggest that ovipositing females are selecting substrates with suitable thermal conditions for their eggs. However, we could find no relationship between egg and pupal densities and the effective temperatures on each substrate. Instead the densities of eggs and pupae may be determined by factors such as the size and structure of the substrate and nearby prey density.

More rapid development is achieved when beetles oviposit and pupate at sites with direct radiation. In fact, Sakuratani et al. (1991) reported that, in spring and autumn generations, *C. septempunctata* pupae were attached to the upper sides of plant leaves at angles that allowed them to effectively receive solar radiation. In contrast, many pupae were observed on the undersides of substrates in the current study sites, at which the pupae were not insolated. These observations may be interpreted as behavioral plasticity of wandering larvae in response to air temperature conditions. De Jong et al. (1996) showed that body temperatures of thermoregulating insects dropped rapidly when they were exposed to cold wind. It is therefore possible that, during extremely cold seasons, wandering larvae prefer the undersides of substrates as pupation sites to avoid cold winds. In fact, we found that, during the day, the temperature of an airspace between a substrate and the ground surface was always higher than that of the air at 1.5 m above the plot. Female *C. septempunctata* also tended to lay their eggs on the undersides of substrates. It was reported that, in spring, eggs experimentally placed on the upper sides of substrates suffered heavy mortality from desiccation relative to those underneath (Sakuratani and

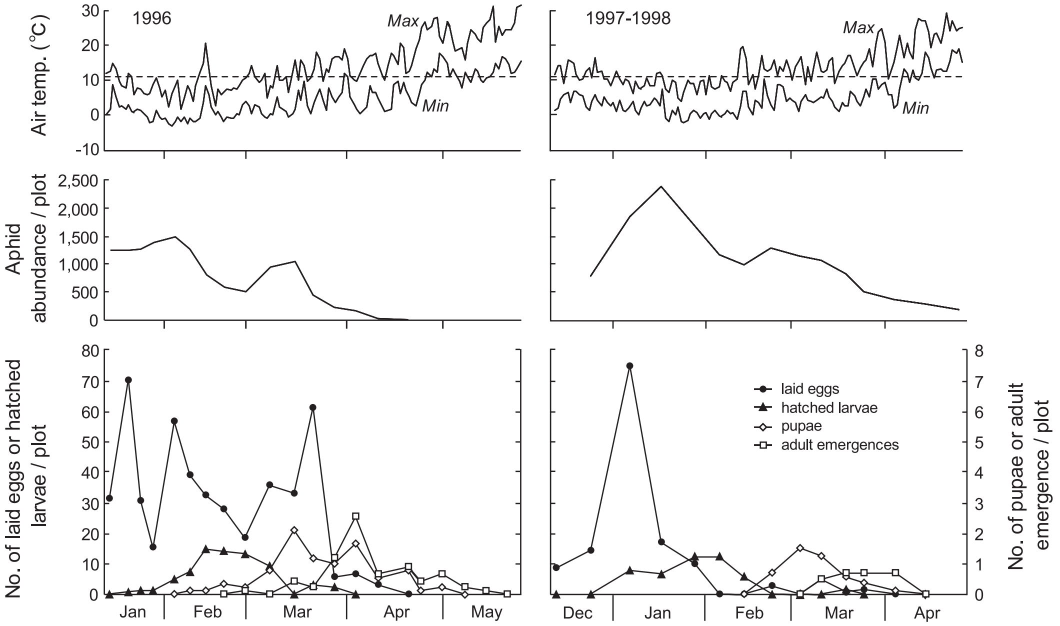

Fig. 4. Seasonal changes in daily maximum (Max) and minimum (Min) air temperatures in this region recorded by the Japan Meteorological Agency (top), seasonal changes in aphid abundance per plot (middle), and changes in the numbers of each developmental stage of *C. septempunctata* observed per plot (bottom) in 1996 (left) and 1997–1998 (right). Horizontal broken lines represent the beetles' lower developmental threshold (11.0°C; Kawauchi 1990) from egg to adult.

Nakamura 1997). Oviposition on the undersides of substrates in winter can also provide a selective advantage.

Prey aphids occurred throughout winter at the study site, which seemed to allow for development of the beetles. However, larval and ovarian developments were implausible under the observed low temperature of air. It has been reported that adult *C. septempunctata* thermoregulated on sunlit soil surfaces when air temperatures were low (Honěk 1985). During the course of this study, resting adults and larvae were often observed on both sunny and shaded sides of sunlit artificial substrates. Such behavior could also constitute thermoregulation, because beetles would be able to raise their body temperatures by conductive heat gain from thermal microhabitats, even on shaded sides. Thus, adult and larval beetles can develop in winter, at least on sunny days.

Intrapopulation variations in life cycles have been frequently observed in this coccinellid in several parts of Europe (Hodek and Honěk 1996), North America (Angalet et al. 1979), and in Japan (Sakuratani 1988, Ohashi et al. 2003). Such variations were considered to result from genetic differentiation and/or phenotypic plasticity of the individuals comprising the population in response to heterogeneous environments. In Japan, most central Honshu populations of *C. septempunctata* pass the winter as quiescent adults (Sakurai et al. 1981, 1983, 1986), and a life cycle polymorphism within populations has been observed: hibernating and reproductive adults simultaneously coexist within the same habitat in winter (Sakuratani 1988). Because the central Honshu populations have a short-day photoperiodic response (Hodek and Okuda 1997), they are potentially multivoltine, given a short-day photoperiod and favorable conditions. Both prey aphids and thermal microhabitats were available in our study site, and thus these conditions seemed to induce the reproduction of some-second generation adults, instead of entering the quiescent phase.

It is also noteworthy that this observed life history plasticity was induced by human activities. First, the artificially sunny slope of the riverbank produced warmer microclimates (e.g., Weiss et al. 1988). Second, herbaceous aphid-hosting plants such as *B. juncea* dominate the site owing to frequent environmental disturbance resulting from human activity (mowing); and third, human activity provided artificial substrates useful as thermal microhabitats.

Rausher (1979) observed that egg and larval mortalities attributable to predation of two *Battus* and one *Parides* butterflies were greater in sunny habitats than in shady ones. A similar situation was also observed for the *Papilio* butterfly (Grossmueller and Lederhouse 1985). We did not observe *Harmonia axyridis* (Pallas), a coccinellid intraguild predator that usually attacks the immature stages of *C. septempunctata* (Takahashi 1989, Hironori and Katsuhiro 1997, Yasuda et al. 2001), or a parasitoid wasp (Hymenoptera: Tetrastichinae) that can cause pupal mortality (Kawauchi 1984) during our study (K.O., unpublished data). Moreover, other polyphagous enemies such as spiders (Yasuda and Kimura 2001) are likely to be inactive in winter. The winter environment may constitute an enemy-free space for *C. septempunctata.*

In more natural environments, the beetles lay eggs in thermal microhabitats such as dead leaves during early spring (Banks 1954, Takahashi 1987). This would have acted as a preadaptation for using artificial substrates for the same purpose during winter. For this beetle, winter reproduction has three benefits: fewer competitors, fewer natural enemies, and no risk of mortality during hibernation.

Acknowledgment

We thank three anonymous reviewers for valuable comments on this manuscript.

References Cited

Adolph, S. C. 1990. Influence of behavioral thermoregulation on microhabitat use by two *Sceloporus* lizards. Ecology. 71: 315–327.

Angalet, G. W., J. M. Tropp and A. N. Eggert. 1979. *Coccinella septempunctata* in the United States: Recolonizations and notes on its ecology. Environ. Entomol. 8: 896–901.

Banks, C. J. 1954. Random and non-random distributions of Coccinellidae. J. Soc. Brit. Entomol. 4: 211–215.

Casey, T. M. 1992. Biophysical ecology and heat exchange in insects. Am. Zool. 32: 225–237.

Christian, K. A., and C. R. Tracy. 1981. The effect of the thermal environment on the ability of hatchling Galapagos land iguanas to avoid predation during dispersal. Oecologia (Berl.). 49: 218–223.

Christian, K. A., and C. R. Tracy. 1985. Physical and biotic determinants of space utilization by the Galapagos land iguana (*Conolophus pallidus*). Oecologia (Berl.). 66: 132–140.

De Jong, P. W., S.W.S. Gussekloo, and P. M. Brakefield. 1996. Differences in thermal balance, body temperature and activity between non-melanic and melanic two-spot ladybird beetles (*Adalia bipunctata*) under controlled conditions. J. Exp. Biol. 199: 2655–2666.

Diaz, J. A. 1997. Ecological correlates of the thermal quality of an ectotherm's habitat: a comparison between two temperate lizard populations. Funct. Ecol. 11: 79–89.

Grossmueller, D. W., and R. C. Lederhouse. 1985. Oviposition site selection: an aid to rapid growth and development in the tiger swallowtail butterfly, *Papilio glaucus*. Oecologia (Berl.). 66: 68–73.

Heinrich, B. 1993. The hot-blooded insects. Harvard University Press, Cambridge, MA.

Hironori, Y., and S. Katsuhiro. 1997. Cannibalism and interspecific predation in two predatory ladybirds in relation to prey abundance in the field. Entomophaga. 42: 153–163.

Hodek, I. and A. Honěk. 1996. Ecology of Coccinellidae. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Hodek, I., and T. Okuda. 1997. Regulation of adult diapause in *Coccinella septempunctata septempunctata* and *C. septempunctata brucki* from two regions of Japan (a minireview). Entomophaga. 42: 139–144.

Honěk, A. 1985. Activity and predation of *Coccinella septempunctata* adults in the field (Col., Coccinellidae). Z. Ang. Entmol. 100: 399–409.

Huey, R. B. 1991. Physiological consequences of habitat selection. Am. Nat. 137: 91-S115.

Kawauchi, S. 1984. Ecological studies on the natural enemies of *Coccinella septempunctata brucki, Propylea japonica* and *Scymnus (Neopullus) hoffmanni* (Coleoptera, Coccinellidae). Kurume Univ. J. 33: 63–67.

Kawauchi, S. 1985. Comparative studies on the fecundity of three aphidophagous coccinellids (Coleoptera: Coccinellidae). Jpn. J. Appl. Entomol. Zool. 29: 203–209.

Kawauchi, S. 1990. Studies on the comparative ecology of three aphidophagous coccinellids. Kurume Univ. J. 39: 239–305.

Kingsolver, J. G. 1979. Thermal and hydric aspects of environmental heterogeneity in the pitcher plant mosquito. Ecol. Monogr. 49: 357–376.

May, M. L. 1979. Insect thermoregulation. Annu. Rev. Entomol. 24: 313–349.

Ohashi, K., S. Kawauchi, and Y. Sakuratani. 2003. Geographic and annual variation of summer-diapause expression in the ladybird beetle, *Coccinella septempunctata* (Coleoptera: Coccinellidae), in Japan. Appl. Entomol. Zool. 38: 187–196.

Rausher, M. D. 1979. Laval habitat suitability and oviposition preference in three related butterflies. Ecology. 60: 503–511.

Rock, J., A. Cree, and R. M. Andrews. 2002. The effect of reproductive condition on thermoregulation in a viviparous gecko from a cool climate. J. Therm. Biol. 27: 17–27.

Rodriguez, L., M. B. Sokolowski, and J. S. Shore. 1992. Habitat selection by *Drosophila melanogaster* larvae. J. Evol. Biol. 5: 61–70.

Rosenzweig, M. 1991. Habitat selection and population interactions: the search for mechanism. Am. Nat. 137: S5–S28.

Sakurai, H., Y. Mori, and S. Takeda. 1981. Studies on the diapause of *Coccinella septempunctata bruckii* Mulsant. I. Physiological changes of adults related to aestivation and hibernation. Res. Bull. Fac. Agr. Gifu Univ. 45: 9–15.

Sakurai, H., K. Goto, and S. Takeda. 1983. Emergence of the ladybird beetle, *Coccinella septempunctata bruckii* Mulsant in the field. Res. Bull. Fac. Agr. Gifu Univ. 48: 37–45.

Sakurai, H., T. Hirano, and S. Takeda. 1986. Physiological distinction between aestivation and hibernation in the lady beetle *Coccinella septempunctata bruckii* (Coleoptera: Coccinellidae). Appl. Entomol. Zool. 21: 424–429.

Sakurai, H., T. Hirano, K. Kodama, and S. Takeda. 1987. Conditions governing diapause induction in the lady beetle, *Coccinella septempunctata bruckii* (Coleoptera: Coccinellidae). Appl. Entomol. Zool. 22: 133–138.

Sakuratani, Y. 1988. Overwintering stages of *Coccinella septempunctata bruckii* in Japan, pp. 79–82. *In* E. Niemczyk and A.F.G. Dixon (eds.), Ecology and effectiveness of Aphidphaga. SPB Academic Publishing, The Hague.

Sakuratani, Y., and N. Nakamura. 1997. Oviposition strategies of *Coccinella septempunctata* (Col.: Coccinellidae). Entomophaga. 42: 33–40.

Sakuratani, Y., K. Shimizu, and E. Shirouchi. 1986. Adult emergence of *Coccinella septempunctata bruckii* Mulsant (Coleptera: Coccinellidae) in winter in central Japan. Appl. Entomol. Zool. 21: 476–478.

Sakuratani, Y., K. Ikeuchi, and Y. Ioka. 1991. Seasonal changes of angle of pupation of *Coccinella septempunctata bruckii* in relation to solar altitude, pp. 259–264. *In* L. Polgar, R. J. Chambers, A.F.G. Dixon, and I. Hodek (eds.), Behaviour and impact of Aphidophaga. SPB Academic Publishing, The Hague.

StatSoft. 1999. Statistica 5.5 for Windows. StatSoft, Tulsa, OK.

Takahashi, K. 1987. Differences in oviposition initiation and sites of lady beetles, *Coccinella septempunctata brucki* Mulsant and *Harmonia axyridis* (Pallas) (Coleoptera:

Coccinellidae) in the field. Jpn. J. Appl. Entomol. Zool. 31: 253–254.

Takahashi, K. 1989. Intra- and inter-specific predations of lady beetles in spring alfalfa fields. Jpn. J. Entmol. 57: 199–203.

Tracy, C. R., and K. A. Christian. 1986. Ecological relations among space, time, and thermal niche axes. Ecology. 67: 609–615.

Waldschmidt, S., and C. R. Tracy. 1983. Interactions between a lizard and its thermal environment: implications for sprint performance and space utilization in the lizard *Uta stansburiana.* Ecology. 64: 476–484.

Weiss, S. B., D. D. Murphy, and R. R. White. 1988. Sun, slope, and butterflies: topographic determinants of habitat quality for *Euphydryas editha.* Ecology. 69: 1486–1496.

Williams, E. H. 1981. Thermal influences on oviposition in the montane butterfly *Euphydryas gillettii.* Oecologia (Berl.). 50: 342–346.

Yasuda, H., and T. Kimura. 2001. Interspecific interactions in a tri-trophic arthropod system: effects of a spider on the survival of larvae of three predatory ladybirds in relation to aphid. Entomol. Exp. Appl. 98: 17–25.

Yasuda, H., T. Kikuchi, P. Kindlmann, and S. Sato. 2001. Relationships between attack and escape rates, cannibalism, and intraguild predation in larvae of two predatory ladybirds. J. Insect Behav. 14: 373–384.

Received for publication 8 September 2004; accepted 20 December 2004.