

# Role of Visual Contrast in the Alighting Behavior of *Harmonia axyridis* (Coleoptera: Coccinellidae) at Overwintering Sites

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Environ. Entomol. 34(2): 425-431 (2005)

**ABSTRACT** The multicolored Asian lady beetle *Harmonia axyridis* (Pallas) is often a pest during autumn, when large numbers take flight and subsequently land on and enter buildings. Open field experiments were conducted during the autumn flight to examine the role of linear contrast in visually attracting beetles. White targets printed with 61 by 15-cm stripes that varied in orientation and degree of contrast were covered in insect adhesive, attached to a white background panel, and erected in sites known to be attractive to flying beetles. Flights occurred when temperatures rose above 21°C. Diurnally, peak flight occurred between 1400 and 1600 hours but shifted progressively earlier within that framework as the flight season advanced. Beetles significantly chose targets with high contrast, black stripes; the number of beetles landing on all other contrast levels did not differ significantly from controls. Vertically positioned stripes attracted more beetles than horizontal ones, but not significantly. The effects of high contrast were absolute rather than relative. The number of beetles landing on targets with 50% contrast stripes did not increase when these were the highest contrast targets available. Results suggest that visual intensity contrast is key to understanding the behavior of *H. axyridis* in autumn and call into question some commonly accepted ideas regarding choice of overwintering sites. First, during migratory flight, *H. axyridis* is not visually attracted to the color white per se, and second, it is unlikely that, during flight, pheromones are involved in beetle orientation.

**KEY WORDS** multicolored Asian lady beetle, migration, silhouette, orientation

IN THE UNITED STATES, the introduced lady beetle *Harmonia axyridis* (Pallas) is recognized as an effective predator of aphids in a variety of commodities, particularly pecan, apple, and citrus, but also Christmas trees, ornamentals, alfalfa, cotton, tobacco, soybeans, and small grains (e.g., Brown and Miller 1998, Dutcher et al. 1999, Michaud 1999). Despite these successes in agroecosystems, *H. axyridis* has received more attention because it is a problem in late summer, when adults feed on ripening fruit in some geographic locations (Koch et al. 2004), and in autumn, when large numbers alight on buildings then move into interior spaces, looking for dark, protected fissures to settle for the winter. The number of beetles that enter a given structure can be enormous, with estimates of tens or hundreds of thousands not uncommon (Kidd et al. 1995). In homes, the beetles encroach on eating, sleeping, and recreational activities. Their defensive secretions stain carpets, curtains, and furniture; they are malodorous, known to bite, and can trigger allergic reactions (Yarbrough et al. 1999, Heulsman et al.

2002). The beetles are also serious hazards in institutions that have a zero tolerance policy for biocontaminants. In North Carolina, the beetles have been reported in hospital operating rooms, in food processing plants, and in the testing facilities of pharmaceutical companies (M. Waldvogel, personal communication).

*Harmonia axyridis* is just one of many coccinellid species that overwinter in large numbers. The behaviors and mechanisms that bring large numbers of conspecific beetles to a particular overwintering site, however, are poorly known. Based on our previous observations of *H. axyridis* (e.g., Nalepa et al. 2000), we propose a series of five behaviors that result in beetle accumulation in overwintering sites. During their exodus from feeding and breeding locations, beetles first orient to macrosites, here defined as large-scale geographic features or visual landmarks, like buildings or mountaintops, detected at a distance by flying individuals. Second, the beetles alight on the surface of the macrosite. Third, they determine whether it is made of an appropriate substrate. Fourth, the insects begin a walking local search for microsites, i.e., cracks, crevices, recesses, or other acceptable microhabitats. Fifth, they settle within these microsites. The beetles may take flight and reinitiate the process

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if appropriate winter shelter is not detected during local search and evaluation.

The beetles respond to a series of sensory cues during this stepwise sequence. There is evidence that initial orientation to macrosites is guided by hypsotaxis (Campan 1997): while in flight, the beetles are attracted to conspicuous, isolated features that form a contrasting silhouette on the horizon (Hagen 1966, Obata et al. 1986, Hodek et al. 1993). After arriving at macrosites, a combination of poorly characterized responses (geotaxis, hygrotaxis, phototaxis, thermotaxis, thigmotaxis, chemotaxis) influences the final selection of winter quarters (reviewed by Hodek 1967). The premise of this study is that a detailed description of the cues used by *H. axyridis* during massing and settling would provide a solid basis for devising methods to manage their choice of winter shelter.

Here we test whether visual contrast influences the landing behavior of beetles at macrosites (step 2). In natural habitats, *H. axyridis* typically spend winter in the cracks and crevices of granite outcroppings, bald rocky hills, large rocks, and in the spaces beneath small stones on slopes (Voronin 1969, Hodek 1973, Obata et al. 1986). We reasoned that buildings are full of contrasting linear elements that mimic the dark-on-light linear contrast of rock fissures on a sun-exposed cliffside. We also noted that beetles frequently land on the contrasting linear elements of buildings: gutters, drainpipes, siding, doorframes, window sashes and muntins, railings, patterns of brick and mortar, and the exposed frame elements of porches. If visual contrast does act as a behavioral cue for beetle approach and landing, it has implications not only for how homeowners plagued by the beetles may decide to paint, trim, and landscape their homes, but also for the visual design of potential traps.

### Materials and Methods

Each year there is a narrow window of opportunity for studying the behavioral basis of finding winter shelter in *H. axyridis*, because the beetles likely exhibit appropriate threshold levels of responsiveness only during the few weeks in autumn when they fly to overwintering sites. Open field experiments were conducted in October and November of 2000 and 2001 during the natural migratory flight in North Carolina. The insects were systematically presented with synthetic visual stimuli in the form of computer-generated targets attached to a large background panel; the panel was erected in sites known to be preferred by migratory beetles in previous years. Targets consisted of 61-cm<sup>2</sup> matte finish, heavyweight white paper squares (PCM 150 g Heavy Matte Paper, Roland DGA Corp., Irvine, CA) on which 15-cm-wide stripes were centrally located. Stripes were generated in Adobe Illustrator, ran the length of the target, and varied in orientation (horizontal versus vertical) and degree of black on white intensity contrast. Targets were produced on a wide format Roland or Novajet printer, heat laminated, and covered with a thin coat of Tanglefoot insect trapping adhesive. They were at-

tached, using Velcro self-adhesive hook and loop fasteners, to a 2.5 by 2.8-m white painter's tarpaulin used as the background panel. The tarpaulin was tautly spread between two polyvinylchloride pipes and erected upright in sites where the experiments were conducted. The bottom of the background panel was 51 cm (20 in) above the substrate.

At site 1, the tarpaulin was erected 2 m in front of the south-facing corner of a one-story storage building painted uniformly medium gray (estimated to be 25–50% black), with a similarly colored roof. This building was next to a two-story house of the same color, and situated next to a stream in a valley of the Appalachian Mountains in North Carolina near Weaverville (35.71° N, 82.45° W, 664-m elevation). The structure was backed by mixed deciduous forest and faced at least 4 ha of open pasture. At site 2, the tarpaulin was erected facing southwest 1 m in front of a 9.2-m tall, narrowly columnar red cedar tree (*Juniperus virginiana* L.) near the two-story brick NCDA and CS Beneficial Insects Laboratory in Cary, in the piedmont of North Carolina (35.79° N, 78.73° W, 146-m elevation). At this site, the tarpaulin faced at least 1.5 ha of open grassland surrounded by several different sized stands of mixed pine and hardwood. Site 1 is ≈340 km west of site 2 but is at comparable latitude. These locations were chosen because both had been excellent sites for collecting alighting beetles in previous years, and by working in two geographically disparate sites, we could increase the number of experimental replicates. Lady beetles characteristically arrive at overwintering sites over a period of several weeks on warm, calm days, but the timing of migration depends on altitude (Kidd et al. 1995). In North Carolina, initial flights of the season typically begin 11–18 October in the western, mountainous part of the state and 17–30 October in the piedmont.

Beginning in mid-October, the tarpaulin with attached targets was erected by noon on warm, calm, sunny days, and disassembled between 1700 and 1730 hours in the afternoon or when >100 beetles had landed. Previous experience indicated that few beetles fly in the hour or so before sunset. The number of insects on all targets was noted at half-hour intervals during most trials. At the conclusion of each trial, a sheet of clear acetate on which a 76 by 76-mm (3 in) grid had been printed was superimposed on each target, and the number and distribution of beetles in each square of the grid was recorded. Data from days when <30 beetles landed on the experimental set-up were not included in analysis. Weather data were taken from the National Weather Service Climate Report for Raleigh-Durham International Airport, situated ≈10 km from site 2.

**Experiment 1: Influence of Stripe Orientation and Contrast.** The first experiment was designed to test the relative attractiveness of stripes of varying orientation and contrast. We tested two orientations of the stripe, horizontal and vertical, and five levels of intensity contrast, black, white (control), and three levels of gray. These will be referred to by the proportion of black in relation to white in the stripe: 100 (black), 75,

50, 25, and 0% (white). Treatments represented a 4 by 2 factorial (contrast and orientation), plus control. Targets were randomly arranged on the background panel in a 3 by 3 square; each target was separated from those adjacent to it by 15 cm. The experiment was replicated six times during the autumn of 2000; two replications in site 1 and four replications in site 2. Statistical analysis was done using Proc GLM of SAS (SAS Institute 2001). Variation in the number of beetles landing on a target increased with the mean; therefore, a square-root transformation of the data was employed before analysis. Treatment effect was partitioned into control versus factorials and main effects and interaction effects for contrast and orientation. The analysis of variance (ANOVA) included site (site 1 versus site 2) and replications within a site as factors in addition to the treatment factors. It was noted that insects tended to favor the top row of targets; the factorial ANOVA was therefore modified to include a factor "location" that designated the position of the target on the background panel (top row, middle row, bottom row). Because of the significant location effect, least square means were used for subsequent treatment comparisons. To determine if beetles favored a specific location on individual targets, a second ANOVA was carried out on just the high contrast targets with counts of beetles recorded for four zones corresponding to the stripe and three parallel 7.5-cm-wide zones at increasing distances on each side of the stripe. Zone was treated as a subplot or repeated measures factor in the ANOVA.

**Experiment 2: Role of Surrounding Levels of Contrast.** Based on the results of experiment 1, experiment 2 was designed to test if the beetles' preference for high contrast was absolute or relative, i.e., if the 100% contrast stripe was removed, would the beetles preferentially alight on the highest contrast stripe available? Two sets of targets were alternated. Set 1 consisted of targets with stripes of 50% contrast, 25% contrast, and a control; set 2 was made up of targets with 100% contrast, 50% contrast, and a control. All stripes were oriented vertically. The comparison of interest was between the number of beetles landing on a target of 50% contrast in two different contexts. Because experiment 1 indicated that the location of the target on the tarp was significant ( $F = 4.04$ ;  $P = 0.03$ ;  $df = 2,38$ ), experiment 2 was designed as replicated 3 by 3 Latin squares, with the two treatment sets replicated on alternate days over time; there was a new randomization of targets at each trial. Each set of targets was replicated four times in site 2 during the autumn of 2001. A combined ANOVA on all of the data included effects for sets, trials(sets), row(set \* trial), column(set \* trial), and treatment(set). A reduced model was run eliminating column effects because they were negligible.

**Results**

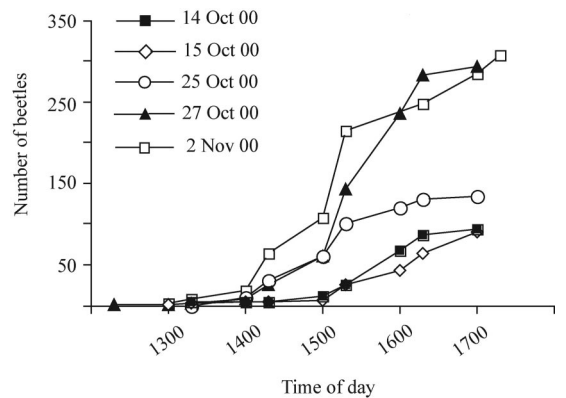
Temperature dramatically influenced flight activity in *H. axyridis*. Although there were some stragglers at lower temperatures, most beetles flew in central

**Table 1. Weather conditions for the week of 28 Oct. to 3 Nov. 2000 in Cary, NC, in relation to the total no. of *H. axyridis* landing on targets**

Date	Maximum temperature (°C)	Average wind speed (km/h)	Sky cover <sup>a</sup>	Number of beetles
28 Oct. 2000	27.0	3.9	0.32	651
29 Oct. 2000	19.4	5.6	0.05	3
30 Oct. 2000	21.1	4.4	0.14	2
31 Oct. 2000	21.1	2.8	0.00	3
1 Nov. 2000	21.1	1.3	0.10	10
2 Nov. 2000	23.0	1.1	0.20	308
3 Nov. 2000	25.0	1.5	0.40	1,591

<sup>a</sup> Averaged over daylight hours. Relatively high sky cover on 28 Oct. and 3 Nov. was caused by morning fog and intermittent scattered clouds in the afternoon.

North Carolina on calm, clear days when temperatures rose above 21°C (70°F; Table 1). There is a diurnal periodicity in flight behavior, with peak flight corresponding to maximum afternoon insolation. The majority of beetles landed on targets between 1400 and 1600 hours, with the onset of activity shifting to earlier in the day as the flight season progressed (Fig. 1). In a timed sequence during one of the peak flights (3 November 2000), we counted 731 beetles landing on 3.3 m<sup>2</sup> in 45 min, between 1330 and 1415 hours (16.2 beetles/min). This is the total number of beetles landing on all targets, some of which were less attractive than others. Subsequent landing activity diminished only slightly, with 15.7 beetles/min alighting between 1430 and 1500 hours. If these numbers are extrapolated to the south facing side of a typical two-story house (that of the first author, e.g., at 70 m<sup>2</sup>), ≈3,500 would land in a 10-min period, corroborating homeowner



**Fig. 1. Cumulative number of *H. axyridis* on all targets combined in relation to time of day (adjusted for Daylight Savings Time) on selected flight dates during autumn of 2000. Data for 14 and 15 October are from site 1 in the mountains of North Carolina; remaining data are from site 2, in the piedmont of the state. Between 14 October and 2 November, daylength decreased by 39 min, the azimuth of the sun decreased by 16.4°, and its altitude at noon decreased by 6.6°. The tendency for stronger flights as the season progresses should not be taken as a characteristic of *Harmonia* migration, because the pattern varies from year to year.**

**Table 2.** Comparison of mean no. *H. axyridis* alighting on targets with stripes of differing contrast and orientation

Percent contrast of 15-cm stripe <sup>a</sup>	Mean beetles <sup>b</sup>	Orientation of 15-cm stripe	Mean beetles <sup>b</sup>
100	39.5a	Vertical	28.6a
75	19.4b	Horizontal	20.6a,b
50	17.5b	Control	13.6b
25	21.9b		
0	13.6b		

<sup>a</sup> 100% contrast is a black stripe; 0% contrast is a pure white target (i.e., no stripe = control).

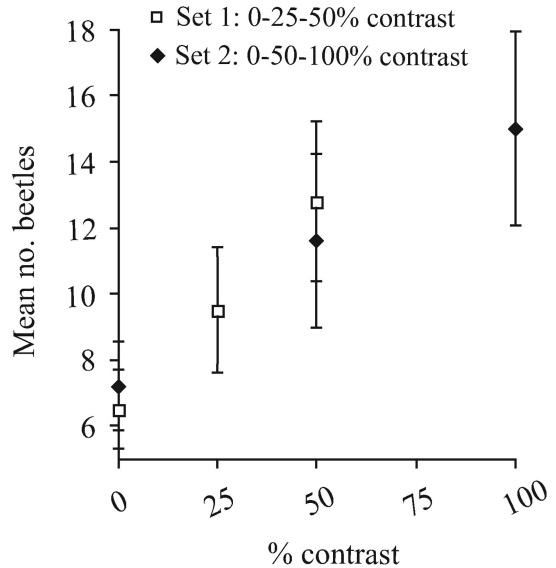
<sup>b</sup> Estimated using least square means; mean beetles within a category followed by different letters are significantly different based on analysis of square root transformed counts.

reports of thousands of beetles landing within a short time frame (Kidd et al. 1995). *H. axyridis* was typically the only coccinellid species landing on the experimental targets, but an occasional *Coleomegilla maculata lengi* Timberlake was also noted.

In testing the influence of stripe orientation and contrast in the alighting behavior of migrating *H. axyridis* (experiment 1), data were obtained from a total of 1,503 insects with beetles per replication ranging from 91 to 731. There were no significant differences between the two sites. Differences among replications were significant and may be attributed to the vagaries of beetle flight in relation to climatic conditions, the number of beetles already in winter shelter versus those still seeking it, and other factors. The degree of contrast influenced the number of *H. axyridis* landing on a target ( $F = 5.8$ ;  $P = 0.002$ ;  $df = 3,38$ ), with beetles significantly preferring the highest contrast, black stripes (Table 2); numbers of beetles landing on all other levels of contrast were not significantly different from the control. Vertical stripes were preferred over horizontal ones, although not significantly ( $F = 1.6$ ;  $P = 0.22$ ;  $df = 1,38$ ). There was no interaction between stripe orientation and level of contrast.

Within a target, no "edge effects," i.e., the tendency to preferentially land where the contrasting element meets the background, were evident, as in some insects (e.g., Allan and Stoffolano 1986). When targets of 100% contrast were divided into four zones based on distance from the central contrasting element, analysis indicated that the landing location of beetles was not significantly related to proximity of the black stripe ( $F = 1.67$ ;  $P = 0.19$ ;  $df = 3,30$ ). The number of *H. axyridis* landing directly on the black stripe compared with the mean for the other three zones was only weakly significant ( $t = 1.84$ ,  $P = 0.08$ ). These results were corroborated by observations of alighting behavior in a natural setting. At Pilot Mountain, a quartzite monadnock in Surry Co., NC, beetles were observed landing in the vicinity of crevices as well as flying directly into them (Fig. 1 of Nalepa et al. 2004).

The results of experiment 2 indicate that the preference for high contrast in alighting *H. axyridis* is absolute (Fig. 2). The number of beetles landing on a 50% contrast target in comparison with respective controls did not significantly increase ( $t = 0.74$ ,  $P = 0.46$ ) when 50% was the highest contrast choice avail-



**Fig. 2.** Number of *H. axyridis* alighting on targets of 50% contrast in two different contexts. In set 1 of the targets, 50% contrast was the highest contrast available; in set 2, 100% contrast was available. There is no significant difference between the number of beetles landing on targets of 50% contrast in the two target sets.

able ( $n = 751$  beetles, numbers per replicate ranging from 30 to 188).

## Discussion

As frequently cited in the literature, the contrasting silhouette of a distant macrosite serves to orient flying beetles to locations potentially suitable for overwintering. The results reported here indicate that, as beetles arrive in the vicinity of the macrosite, closer range black on white linear contrast attracts the beetles and acts as a stimulus for terminating flight. Thus, the second stage of aggregation behavior in *H. axyridis*, short range approach and alighting, is also strongly visual. Like other insects in search of resources (Markl 1974, Prokopy 1986), *H. axyridis* perceives and responds to its environment at several distinct levels. Silhouettes of macrosites are visual stimuli effective at long distance attraction. As beetles approach, buildings and mountains are resolved, step by step, into smaller contrasting units, until the goal resource, a crevice, is reached. A good analogy is that of pollinators seeking flowers. At a distance they orient to flowering fields, but as they draw near, the field is resolved into subpatches, individual plants, inflorescences, and finally individual flowers (Dafni et al. 1997).

Many insects are attracted to vertically striped, dark contrasting patterns (Markl 1974); Table 4 in Wehner (1981) lists 31 species in eight orders. The response to vertical contrast is documented primarily in herbivores and is implicated in guiding a variety of insects to plants, particularly trees (e.g., Borden et al. 1986). It makes sense, however, that coccinellid predators



seeking plant-associated insects like aphids may respond to similar cues; an attraction to vertical contrast is documented in *Coccinella septempunctata* (Collett 1988, Frantsevich and Zolotov 2001) and *Chilocorus nigritus* (Hattingh and Samways 1995). It is therefore possible that *H. axyridis* uses the same visual cues when they are orienting to overwintering sites as they do earlier in the year to find aphid prey on plants. Indeed, Hattingh and Samways (1995) suggest that all coccinellids respond to two classes of visual cues in a variety of contexts and spatial scales: vertical lines and dome shapes.

There are two common beliefs about autumn flight behavior in *H. axyridis* that this study calls into question. The first is that, while in flight, the beetles are both attracted to and land on the color white per se, or to bright, reflective surfaces (e.g., Koch 2003). This assumption is based on evidence from two sources. First, in a series of field experiments, Obata et al. (1986) erected different colored panels in the flight path of migrating *H. axyridis* and found that the majority (71%) of beetles landed on those painted white. The beetles' clear preference for light-colored panels was lost when clouds blocked the sun, leading to the conclusion that the insects favor reflective surfaces. While reflected light indeed decreases under cloud cover, intensity contrast is lost at the same time. Furthermore, these authors did not specify the color of the substrate against which these panels were displayed ("a slope of Mt. Shiroyama"). The results reported here support those of Sakurai et al. (1993), who found that *H. axyridis* preferentially chose black rather than white cinderblocks as overwintering sites; both our study and theirs contrast with the results of Obata et al. (1986) and point out the importance of taking background color into consideration when conducting studies of visual orientation.

The second reason it was assumed that beetles are attracted to pale colors is that they often land on white buildings and white objects. However, tan, gray, blue, brick, stone, cinderblock, and log buildings have also been reported as overwintering sites (K. A. Kidd and C. A. Nalepa, unpublished data), and a survey by Heulsman et al. (2002) found that house color was unrelated to beetle infestation problems. This variation in choice of macrosites by the beetles can be explained by an attraction to intensity contrast that operates at an ever finer scale until the insects alight. At the largest spatial scale, the beetles are responding to a silhouette, either on the horizon or against a contrasting backdrop. A large object of almost any color, however, forms a contrasting silhouette when viewed against the backdrop of a clear, bright, uniformly illuminated sky. Thus, a white church situated on top of a hill or a tall, dark, isolated cedar tree as in site 2 of this study both attract migrating beetles from a distance. It is probable that light-colored buildings and objects are often targeted because they are viewed by flying beetles against the dark backdrop of surrounding vegetation. Examples of the latter are the attraction of the beetles to white beehives facing an open space and backed by woods (Nalepa et al. 2000)

and the white panels against a presumably dark background in the Obata et al. (1986) experiments. Although this study showed that *H. axyridis* was attracted to black on white contrast, the reverse is probably also true if the cue for approach and landing is a sharp difference in intensity contrast, without regard to polarity, between two elements of the visual scene.

The second common belief made questionable by results of this study is that migrating lady beetles are attracted to macrosites by long distance pheromones (e.g., Hawkes 1926, Edwards 1957, Savoiskaya 1965). This assumption is based on observations that beetles, first, have an odor distinctive to the human nose and, second, return to the same sites year after year. Dead beetles and persistent secretions are cited as the sources of an attractant that accounts for this site constancy (e.g., Yakhontov 1960). Although both *H. axyridis* and *H. conformis* return to the same locations year after year, this occurs only if the visual relief of the landscape remains the same (Anderson and Richards 1977, Obata et al. 1986). During autumn flight, coccinellids also readily mass on newly erected conspicuous objects (Hagen 1962), which are presumably pheromone free. Chemical signals do play a central role in the formation, cohesion, and regulation of aggregation in many species (Greenfield 2002). Despite a long history of attempts to prove their role in attracting lady beetles to overwintering sites (e.g., Hawkes 1926, Nalepa et al. 2000), however, no convincing evidence exists. A visual attraction of all flying *H. axyridis* individuals to similar high contrast stimuli can bring large numbers to the same macrosites and sufficiently near to each other so that close range communication or even meeting by chance may guarantee encounter of individuals (Markl 1974). If chemical attraction does play a role in *H. axyridis* massing behavior, it is most likely through short distance or contact pheromones. These may originate from conspecifics or their residues and function as arrestants rather than as attractants during the concluding, walking, and settling stages of the process (Nalepa et al. 2000).

Despite the results reported here, it is still not easy to predict why a particular house is targeted by beetles based on its visual characteristics alone. *H. axyridis* may descend on a particular house in a neighborhood full of homes similarly sized and colored, just as ladybird beetles may accumulate on one mountain summit and not on neighboring peaks of similar height (Edwards 1957). The way that we view a resource is unlikely to be strictly applicable to animals as small and mobile as airborne insects (Prokopy 1986), particularly in visually heterogeneous landscapes. Only the most straightforward type of visual contrast was tested here, but hue contrast, color saturation, and other optical stimuli may also be important (Hailman 1977), as well as nonlinear patterns of intensity contrast. Nonvisual, location-specific features also dilute or enhance the number of *H. axyridis* attracted to a given building. Structures in proximity to late-season aphid infestations consistently attract large numbers of bee-

ties, and the interaction of air currents and topography also have a significant effect (Balduf 1935, Hodek et al. 1993), particularly in high elevation complex terrain. Superimposed on this variation in visual and environmental stimuli is the behavior of the insect itself. Alighting during migratory flight often seems haphazard, with beetles landing on people, laundry, fences, and other sites inappropriate for overwintering. It may be that migrating *H. axyridis* explore any contrasting linear profile, with the sequence of take-off, flight, and alighting continuing until appropriate winter shelter is found. Reduced light, increased wind speed, and flight exhaustion may alter behavioral thresholds for flight termination.

The results presented here have implications for the management of *H. axyridis* at problematic overwintering sites. During step 2 of the behavioral sequence, contrasting linear elements on a building influence where the beetles approach and alight. Experiment 2 of this study indicated that this attraction to linear contrast is absolute, suggesting that the number of beetles massing on a structure may be lessened by decreasing the number of highly contrasting elements, like dark trim on a light house or vice versa. Unfortunately, in strong, directional afternoon sunlight, the only conditions in which these beetles fly, dark, linear shadows cast by gutters, drainpipes, windows, doorframes, overhangs, and other architectural features are also attractive to *H. axyridis*. It would be problematic to suppress shadow contrasts in a building of any color short of removing the offending elements. It is therefore doubtful that traps that relied on visual attraction, no matter how masterfully designed, would be able to compete successfully with contrasting elements already on a building. Contrasting linear features of a building may, however, be useful as guidelines in the precise placement of insecticides or beetle repellents that are in development (e.g., Riddick et al. 2000). Further examination of the cues used by *H. axyridis* during the entire range of behaviors resulting in massing at particular localities will no doubt help refine management strategies. Potential studies include exploration of additional aspects of contrast as a visual cue, the possible influence of first arriving beetles on those that follow, and a full characterization of the final, settling stages of the flight and assembly process.

#### Acknowledgments

We thank C. Revis for the use of his house as an experimental site, T. Jarrett (Agricultural Statistics, NCDA and CS) for making the targets, K. Maekawa for the translation of Japanese literature, and L. Blue, G. Cross, K. Kidd, and P. Rand for technical help, discussion, and/or review of the manuscript.

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Received for publication 15 June 2004; accepted 20 December 2004.