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Patch Retention Time in an Omnivore, *Dicyphus hesperus* is Dependent on Both Host Plant and Prey Type

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We examined patch residence times for an omnivorous predator, Dicyphus hesperus *on a variety of plants and prey. Individual* D. hesperus *were placed in cages containing either mullein, tomato, pepper or chrysanthemum plants, and either no prey, Mediterranean flour moth eggs, greenhouse whitefly pupae or two-spotted spider mite adults. Patch residence times were typically greater than 24 h. The probability of remaining on the patch was greatest on mullein and tomato, followed by chrysanthemum and least on pepper, whereas probability of remaining on the patch was greatest when flour moth eggs were present, and least when no prey were available. Patch residence time in* D. hesperus *was determined by both the prey, and the species of plant, in an independent fashion. Our results reinforce the notion that for omnivores, the patch itself is as important as the prey that it harbors.*

KEY WORDS: Heteroptera; Miridae; biological control; retention; arrestment.

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INTRODUCTION

The distribution of insects in time and space is a fundamental concept in the field of ecology. Of course, these distributions are largely determined by behavior of individuals. In the case of insects associated with plants there are two major behavioral determinants of distribution, attraction and arrestment. Attraction generally derives from cues that either directly or indirectly signal site quality (Bell, 1991). Arrestment, on the other hand often depends upon direct assessment at the site (e.g. nutrient sampling by herbivores, prey capture rates by predators, etc.) (Bernays and Chapman, 1994).

Arrestment, the tendency to remain at a particular site (hence termed a patch), has been oft studied in recent years under the behavioral ecology lexicon of patch residence time. This is particularly true for parasitoids (see van Alphen *et al.*, 2003) to a lesser extent, predators (VanLaerhoven *et al.*, 2000; Jia *et al.*, 2002; Nakashima and Hirose, 2003) and to an even lesser degree in herbivores (Bernays and Chapman, 1994). Here the focus has been on the mechanisms that animals use to assess patch quality where the assumed utility that is maximized is fitness, mostly indexed as reproductive success (Roitberg *et al.*, 2001). Based upon such assessments, individual foragers choose to remain at a current patch or seek others.

Zoophytophagous insects that by definition feed on both animal and plant-based resources provide for an interesting twist on the arrestment-patch exploitation theme. First, while searching on plants, these foragers may simultaneously encounter two vastly different resources, plant and animal. Second, because of the different foraging and feeding modes associated with the two food resources, it is not clear how a patch is defined. The host plant could impact perception of patch quality indirectly by influencing prey quality or accessibility or directly via the nutrition that it provides (Treacy *et al.*, 1987; Chau *et al.*, 2005). The forager must locate prey within the host plant but is free to feed on the plant anywhere it chooses; however, within-plant quality can vary considerably among sites and structures (Karban *et al.*, 1997; Roitberg *et al.*, 1999). Statistically speaking, we expect prey and plants to be dependent in their effects on patch leaving time and we would therefore expect to see a plant by prey interaction on patch residence time.

Dicyphus hesperus (Hemiptera: Miridae) is a zoophytophagous mirid that feeds on a variety of host plants and prey (McGregor *et al.*, 1999; Gillespie and McGregor, 2000; Sanchez *et al.*, 2004). Adult and immature *D. hesperus* express preferences for some plant species over others, and feeding on different plant species has fitness consequences (Sanchez *et al.*, 2004). Although no preference data exists for prey, there is evidence that prey species affects development time and size of resulting females in *D. hesperus* (McGregor *et al*., 1999). We expect that *D. hesperus* will express different patch residence times on different plants, and in the presence of different prey. More importantly, we expect that *D. hesperu*s will express different patch residence times on different plants, depending on the prey available. This is the interaction term described above.

In this paper, we evaluate patch residence times for individual *D. hesperus* female adults on a variety of plants that harbor different species of prey. We show that both plant and prey species impact the length of time that individuals remain on a given host plant thus reinforcing the notion that for omnivores, the substrate itself is as important as the prey that it harbors.

METHODS

Insect Origins and Rearing

Laboratory colonies were established using *D. hesperus* collected from white stem hedge nettle, *Stachys albens* A. Gray (Lamiaceae) in the foothills of the Sierra Nevada Mountains at an elevation of ca. 300 m near Woody, CA USA (Lat 35°42.9′ N, long 116°49.1′ W). These colonies were maintained at 25.0 ± 0.5°C, 23.0 ± 0.5% RH and a 16 h daylength. *Dicyphus hesperus* were reared on tobacco *Nicotiana tabacum* L. (Solanaceae) with *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae) eggs provided *ad libitum*.

Patch Retention

Meshcages (60 cm^3) were set up with 9 plants of a single type per cage set into a 3 × 3 grid, so that the leaves of neighboring plants did not touch one another. The experiment consisted of a full factorial design using 4 plant and 4 prey types. The plants were either mullein, *Verbascum thapsus* L. (Scrophulariaceae) tomato (*Lycopersicon esculentum* Mill. cv. Patio (Solanaceae), pepper, *Capsicum anuum* L. cv. Enza 444 (Solanaceae) or chrysanthemum, *Chrysanthemum coronarium* L. (Asteraceae). All plants were seedlings less than 6 months old. Mullein was a rosette (ca 20 cm diameter). Tomato was 10 to 30 cm tall, with at least 4 leaves but no flowers or fruit. Pepper was upright, 10–30 cm tall, with no flowers or fruit. Chrysanthemum was spreading, 15–30 cm high, with no flowers. Leaves on the mullein and chrysanthemum plants were removed so that they had similar leaf areas to the pepper and tomato plants . The prey treatments were either Mediterranean flour moth eggs (*E. kuehniella*), greenhouse whitefly pupae (*Trialeurodes vaporariorum* (Westwood) (Homoptera: Aleyrodidae)), two-spotted spider mite adults (*Tetranychus urticae* Koch (Acari: Tetranychidae)) or no prey. Flour moth eggs were stored frozen and were obtained from (company), whitefly pupae were removed from tobacco leaves obtained from Applied Bionomics (Sidney, BC, Canada), and spider mites were reared on the respective plant hosts for one generation before being used in experiments. Flour moth egg (ca. 200) and whitefly pupae (ca. 40) were presented on Post- it® notes (3M, St. Paul MN USA) cut into 5 mm strips and placed on the center plant. Due to difficulty gluing spider mites to strips, the mites were allowed to infest the center plant, but prevented from spreading by the use of white petroleum jelly on the pot margins. Prey were replaced every other day to ensure a steady supply of prey on the center plant. Female *D. hesperus* were approximately 7 days post-eclosion and had been held during this time in a mass rearing cage, with males. Although fertility was not checked directly, previous experience has shown that all females thus held are mated and will begin to produce eggs within a further 7 days. These females were removed from the mass cage, and held individually, without prey, on tomato leaflets, for 48 h prior to being used in experiments. One female *D. hesperus* was placed on the center plant of each cage and checked daily at midmorning. Previous research examining diel foraging behaviour of *D. hesperus* demonstrated that foraging for prey is higher at night (VanLaerhoven *et al.*, 2003) and between plant movements occur most often during the day (VanLaerhoven *et al.*, in review). *Dicyphus hesperus* rarely makes multiple between plant movements within a 24 period (VanLaerhoven *et al.*, in review). Once a female left the centre plant, the total time she remained on the plant was recorded and the female was removed from the cage. Each of the 16 treatment combinations were repeated 40 times, although some observations were discarded because of contamination of cages with prey species other than the test species, or with supernumerary *D. hesperus*, or because of plant wilting due to failure of the irrigation system.

Statistical Analysis

Retention of an animal on a patch is analogous to longevity. Thus we used the well-accepted Cox proportional hazard analysis and

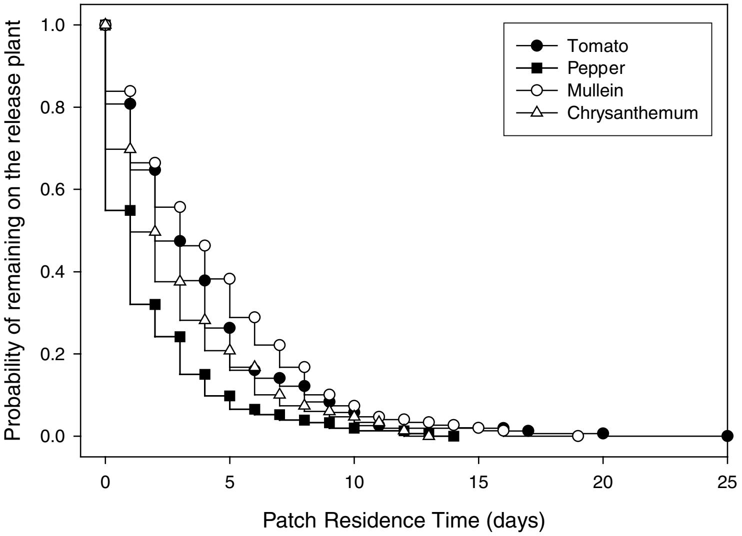

Fig. 1 Probability of *Dicyphus hesperus* Knight females moving off mullein, tomato, pepper or chrysanthemum plants over time.

log-ranked chi-square survivor analysis to analyze the rate of patch leaving (Haccou and Hemerik, 1985). For all tests, $\alpha = 0.05$. All statistical analyses were conducted using JMP IN version 5.0 (SAS, 1997).

RESULTS

The interaction between plant and prey type on patch retention time was not significant (Likelihood-ratio (LR) $\chi^2_{9,591} = 11.1$, $P = 0.3$). However, both main effects of plant (LR $\chi^2_{3,591} = 50.6$, $P < 0.0001$) and prey (LR $\chi^2_{3,591} = 104.1$, $P < 0.0001$) influenced the patch retention time. The probability of remaining on the release plant at any given time was the

Table I. Survivor Analysis of Retention Time of *Dicyphus hesperus* Females as Influenced by Host Plant Species

Main effect for plant type	log-rank chi-square	df	*P*
Mullein vs Tomato	2.0	1	0.2
Tomato vs Chrysanthemum	3.7	1	0.05
Chrysanthemum vs Pepper	8.4	1	0.004

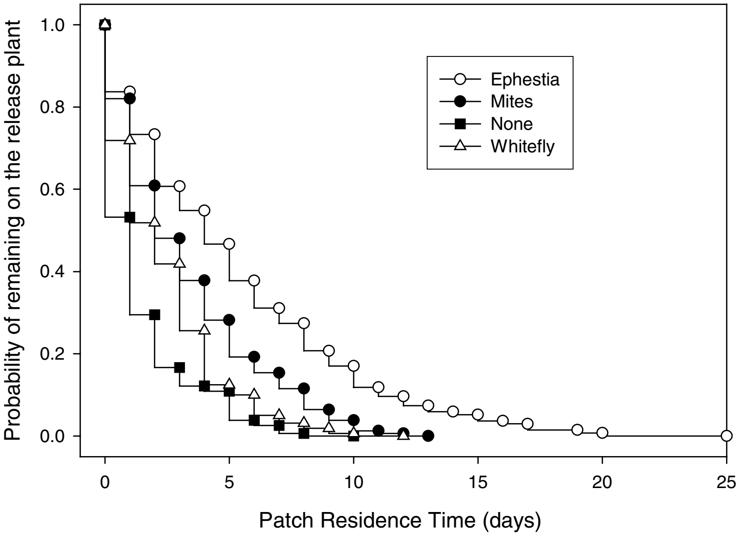

Fig. 2 Probability of *Dicyphus hesperus* Knight females moving off the center plant over time, with flour moth, whitefly, mites or no prey available.

not significantly different for *D. hesperus* on mullein and tomato, but was significantly greater on tomato or mullein than chrysanthemum and greater on chrysanthemum than pepper (Fig. 1, Table I). The mean retention time was longest on mullein (5.0 ± 0.30 d) and tomato (4.4 ± 0.29 d), followed by chrysanthemum (3.6 ± 0.24 d) and shortest on pepper (2.6 ± 0.20 d). Probability of remaining on the release plant at any given time was significantly greater for *D. hesperus* preying on flour moth compared to mites, mites than whitefly, and whitefly than no prey (Fig. 2, Table II). The mean retention time was longest when flour moth eggs were present (6.1 ± 0.41 d), intermediate when mites (4.2 ± 0.23 d) or whitefly (3.3 ± 0.18 d) were present, and shortest when no prey were present (2.3 ± 0.23).

Table II. Survivor Analysis of Retention Time of *Dicyphus hesperus* Females as Influenced by Prey Species

Main effect for prey type	log-rank chi-square	df	*P*
Flour moth vs Mites	19.2	1	<0.0001
Mites vs Whitefly	10.0	1	0.002
Whitefly vs None	15.1	1	<0.0001

DISCUSSION

Patchresidence time in *D. hesperus* is not just determined by the prey, but also by the substrate, i.e., the species of plant, in an statistically independent fashion. This appears to be the first time this phenomenon has been demonstrated. Residence times did not completely correlate with the preference ranks found by Sanchez *et al.* (2004), who found that females preferred, in descending order: mullein, tomato, pepper and chrysanthemum. Similarly, residence times in the presence of different prey species did not correlate with effects of prey species on female size and nymphal development time found by McGregor *et al.* (1999), who found that females fed on either whitefly or flour moth eggs were significantly larger and developed more rapidly than females fed on spider mites.

We predicted a statistically significant interaction between plant and prey species. Why did we not see this expected interaction? On the one hand, these two estimates of patch used by the animal may be measured independently and not integrated. The animals responded very strongly to each of the factors, as demonstrated by the low *P*-values. This lack of integration is analogous to the labeled lines versus across-firing hypotheses of plant evaluation by herbivores (Bernays and Chapman, 1994). On the other hand, the animal may have been responding to qualities of the patch that we did not measure, for example, shelter and safety. These qualities may have obscured our ability to see the interaction. Risk of predation, for example, can be an important component of foraging decisions (Lima and Dill, 1990).

It is difficult to ascertain how common additive effects of disparate resources are in nature because we are not aware of many studies that used manipulative factorial designs to test for interactions (see Singer and Bernays, 2003). Eubanks and Denno (1999) showed that both high quality plant resources (pods) and aphid prey decreased dispersal of an omnivorous predator, *Geocoris punctipes* (Say) (Hemiptera: Geocoridae), from Lima bean plants, but their experiment did not specifically test for interactions between plants and prey. Prokopy *et al.*'s wide ranging work on apple maggot flies, *Rhagoletis pomonella*, (e.g. Prokopy *et al.*, 1994) does however demonstrate that food and oviposition cues can each affect patch residence in immature and mature female *R. pomonella* flies.

We concur with Singer and Bernays (2003) that a behavioural perspective is necessary to study omnivory. Here, we have demonstrated that plant-feeding omnivores may assess patches based on both plant and prey quality. Foraging decisions by omnivores seem to be based on many factors, but we have begun to unravel the rules omnivores use to make patch exit decisions.

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REFERENCES

Bell, W. J. (1991). *Searching Behaviour: The Behavioural Ecology of Finding Resources*. Chapman & Hall, New York.

Bernays E.A., and Chapman, R. F. (1994). *Host-Plant Selection By Phytophagous Insects*. Chapman & Hall, New York.

Chau, A., Heinz, K. M., and Davies, F. T. Jr. (2005). Influences of fertilization on population abundance, distribution, and control of *Frankliniella occidentalis* on chrysanthemum. *Ent. Exp. Appl.* **117:** 27–39.

Eubanks M. D., and Denno R. F. (1999). The ecological consequences of variation in plants and prey for an omnivorous insect. *Ecology* **80:** 1253–1266.

Gillespie, D. R., and McGregor, R. R. (2000). The functions of plant feeding in the omnivorous predator *Dicyphus hesperus*: Water places limits on predation. *Ecol. Entomol.* **25:** 380–386.

Haccou, P., and Hemerik L. (1985). The influence of larval dispersal in the cinnabar moth, (*Tyria jacobea*) on predation by the red wood ant (*Forma polyctena*). An analysis based on the proportional hazards model. *J. Anim. Ecol.* **54:** 755–769.

Jia, F., Margolies, D. C., Boyer, J. E., and Charlton, R. E. (2002). Genetic variation in foraging traits among inbred lines of a predatory mite. *Heredity* **89:** 371–379.

Karban, R., Agrawal, A. A., and Mangel, M. (1997). The benefits of induced defenses against herbivores. *Ecology* **78:** 1351–1355.

Lima, S., and Dill, L. M. (1990). Behavioral decisions made under risk of predation: A review and a prospectus. *Can. J. Zool.* **68:** 619–40.

McGregor, R. R., Gillespie, D. R., Quiring, D. M. J., and Foisy, M. R. J. (1999). Potential use of *Dicyphus hesperus* Knight (Heteroptera: Miridae) for biological control of pests of greenhouse tomatoes. *Biol. Control* **16:** 104–110.

Nakashima, Y., and Hirose, Y. (2003). Sex differences in foraging behaviour and oviposition site preference in an insect predator. *Orius sauteri*. *Entomol. Exp. Appl.* **106:** 79–86.

Prokopy, R. J., Cooley, S. S., Prokopy, J. J., Quan, Q., and Buonaccorsi, J. P. (1994). Interactive effects of resource abundance and state of adults on residence of apple maggot (Diptera, Tephritidae) flies in host tree patches. *Environ. Entomol.* **23:** 304–315.

Roitberg, B. D, Boivin, G., and Vet, L. E. M. (2001). Fitness, parasitoids, and biological control: An opinion. *Can. Entomol.* **133:** 429–38.

Roitberg, B. D., Robertson, I., and Tyreman, J. (1999). Vive la variance: A new theory for the evolution of host selection. *Entomol. Exp. Appl.* **91:** 187–194.

Sanchez, J. A., Gillespie, D. R., and McGregor, R. R. (2004). Plant preference in relation to life history traits in the zoophytophagous predator. *Dicyphus. hesperus. Entomol. Exp. Appl.* **112:** 7–19.

SAS(1997). *JMP IN 5.0*. Sas Institute Inc., Cary, North Carolina.

Singer, M., and Bernays, E. (2003). Understanding omnivory needs a behavioral perspective. *Ecology* **84:** 2532–2537.

Treacy, M. F., Benedict, J. H., Lopez, J. D., and Morrison, R. K. (1987). Functional response of a predator (Neuroptera: Chrysopidae) to bollworm (Lepidoptera: Noctuidae) eggs on smoothleaf, hirsute, and pilose cottons. *J. Econ. Entomol.* **80:** 376–379.

van Alpen, J. J. M., Bernstein, C., and Driessen, G. (2003). Information acquisition and time allocation in insect parasitoids. *Trends Ecol. Evol.* **18:** 81–87.

VanLaerhoven, S. L., Gillespie, D. R., and McGregor, R. R. (2000). Leaf damage and prey type determine search effort in *Orius tristicolor*. *Entomol. Exp. Appl.* **97:** 167–174.

VanLaerhoven, S. L., Gillespie, D. R., and Roitberg, B. D. (2003). Diel activity pattern and predation rate of the generalist predator. *Dicyphus. hesperus. Entomol. Exp. Appl.* **107:** 149–154.

VanLaerhoven, S. L., Gillespie, D. R., and Roitberg, B. D. (in review). Deconstructing effects of plant community on natural enemies. *Ecol. Entomol.*