Patch Time Allocation by the Parasitoid *Diadegma semiclausum* (Hymenoptera: Ichneumonidae).

II. Effects of Host Density and Distribution

X. G. Wang^{1,2} and M. A. Keller¹

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*This study investigated the effects of host density and distribution on the patch-leaving behavior of *Diadegma semiclausum* (Hymenoptera: Ichneumonidae), a solitary endoparasitoid of larval *Plutella xylostella* (Lepidoptera: Plutellidae). Individual female wasps were released onto an experimental plant infested with host larvae at different densities and distributions, and were allowed to freely leave for an alternative host plant placed upwind of the experimental plant in a wind tunnel. The influence of host density and distribution, as well as within-patch foraging experience, on the parasitoid's patch-leaving tendency was analyzed by means of the proportional hazards model. This study aimed to test the predictions of a number of patch-leaving models, including the Marginal Value Theorem, "rules of thumb," and incremental or countdown mechanisms. The parasitoid's patch-leaving tendency decreased with increased host density, more clustered host distribution, and unsuccessful host encounter as a result of host defense, but increased with successful oviposition. None of the simple rules of thumb such as fixed time, fixed number of hosts parasitized, or fixed giving-up time was employed by this parasitoid. The results agreed with the general predictions of the Marginal Value Theorem that patch residence time and numbers of ovipositions by the parasitoid increased with increasing host density. The decreasing influence of oviposition on the parasitoid's patch-leaving tendency,*

¹Plant and Pest Science, School of Agriculture and Wine, University of Adelaide, SA 5064, Australia.

²To whom correspondence should be addressed at University of Hawaii, College of Tropical Agriculture and Human Resources, 7370 Kuamoo Road, Kapaa, Hawaii 96746. Fax: +1 808 822 2190. e-mail: xingeng@hawaii.edu.

regardless of host density or distribution, was consistent with the prediction of a countdown mechanism.

KEY WORDS: *Diadegma semiclausum*; foraging behavior; host density and distribution; parasitoids; patch-leaving behavior; patch time allocation; proportional hazards model.

INTRODUCTION

Because of time limitation in many parasitoids, optimal allocation of foraging time over host patches of different profitability should be under strong natural selection (van Alphen and Vet, 1986; Godfray, 1994; van Alphen *et al.*, 2003). Patch time allocation in parasitoids has received considerable attention, and many have used Cox's proportional hazards model (Cox, 1972) to analyze patch-leaving behavior in parasitoids (Hemerik *et al.*, 1993; van Roermund *et al.*, 1994; van Steenis *et al.*, 1996; Vos *et al.*, 1998; Driessen and Bernstein, 1999; Wajnberg *et al.*, 1999, 2003; Tenhumberg *et al.*, 2001; Wang and Keller, 2003, 2004). This statistical method provides a test of the relative importance of factors that may influence a parasitoid's patch-leaving tendency under various conditions (Haccou *et al.*, 1991), which usually have been considered separately in optimality models (Waage, 1979; Driessen *et al.*, 1995). Comparison of the results from statistically derived behavioral rules with the predictions of optimality models could provide important information for refinement of evolutionary and mechanistic behavioral models, and indicate directions for further testing or development of more realistic behavioral models (Godfray, 1994; Keller and Tenhumberg, 2000; Wajnberg *et al.*, 2000; van Alphen *et al.*, 2003).

A key question is how parasitoids acquire and process information about the abundance and distribution of their host resources in order to make the best decisions about when to leave a patch (van Alphen *et al.*, 2003). Optimal foraging models assume that foragers have either little or complete information about the abundance and distribution of resources (see Stephens and Krebs, 1986). Several simple behavioral 'rules of thumb' have been proposed for foragers having little information about the spatial distribution of resources. For example, a forager should leave a patch after a certain number of prey or hosts are attacked (fixed number rule), after a certain time has elapsed since it entered a patch (fixed patch time rule), or a certain time has passed since prey have been encountered (fixed giving-up time rule) (McNair, 1982; Green, 1984; Stephens and Krebs, 1986). However, empirical evidence of the use of these simple rules is rare in parasitoids (van Alphen and Vet, 1986; Godfray, 1994). On the other hand, when a forager is assumed to have complete information about patch quality prior to or during patch exploitation, the well-known

Marginal Value Theorem (Charnov, 1976) predicts that an optimal forager should leave each patch when the instantaneous gain rate (e.g., oviposition rate in parasitoids) falls to the average rate expected for the habitat. The general predictions of this model are that patch residence time as well as the total harvest rate per patch should increase with increasing patch quality or inter-patch distance, which qualitatively agrees with some empirical studies in parasitoids (e.g., Wang and Keller, 2003; Wang and Messing, 2003), although the model's assumptions are never fully met (Green, 1984; Stephens and Krebs, 1986; Godfray, 1994; Wang and Keller, 2003).

Insights obtained from empirical studies suggest that parasitoids may have limited prior information about the abundance and distribution of host resources, and thus have to rely on within-patch foraging experience to adjust patch-leaving decisions (Waage, 1979; Haccou *et al.*, 1991; Driessen *et al.*, 1995). The factors that influence the assessment of patch quality by parasitoids may include kairomones emitted from host feeding activities and direct encounters with hosts. Two behavioral models assume that a parasitoid has a basic tendency to leave a given patch as a response to the patch's kairomone concentration. In one model, ovipositions decrease this leaving tendency (incremental mechanism, Waage, 1979), while in the other model, oviposition increases its leaving tendency (countdown mechanism, Driessen *et al.*, 1995). Empirical studies have supported either of the aforementioned models (see van Alphen *et al.*, 2003). From an evolutionary point of view, which mechanism a parasitoid should use depends on the density and spatial distribution of its hosts (Iwasa *et al.*, 1981; Driessen and Bernstein, 1999). In an environment with low host density and a relatively uniform host distribution, increasing the tendency to leave the patch with each successful oviposition should be an adaptive strategy (Iwasa *et al.*, 1981). In contrast, in a rich environment with high host densities and clustered hosts, the incremental mechanism should be an adaptive strategy for a parasitoid unable to obtain a reliable estimation of initial patch quality (Driessen and Bernstein, 1999). Under natural conditions, the abundance and distribution of the hosts exploited by many insect parasitoids often vary considerably. For example, the abundance and distribution of the diamondback moth, *Plutella xylostella* (L.) (Lepidoptera: Plutellidae), vary considerably over time in the field (Wang, 2001). Could a parasitoid use different behavioral mechanisms when foraging for hosts in different environments?

This study investigated the effects of host density and distribution on the patch-leaving tendency of *Diadegma semiclausum* (Héllen) (Hymenoptera: Ichneumonidae), a parasitoid of larval *P. xylostella* (Wang and Keller, 2002). In a previous study, it was found that the parasitoid's

patch-leaving tendency increased with successful oviposition and unsuccessful search time since last oviposition, but decreased with increasing inter-patch distance and unsuccessful host encounter as a result of host defense (Wang and Keller, 2003). The aims of this study were to analyze the effects of host density and distribution, as well as within-patch foraging experience on the parasitoid's patch-leaving tendency using Cox's proportional hazards model (Cox, 1972), and test the predictions of optimal patch-leaving models.

MATERIALS AND METHODS

Insects, Host Plant and Experimental Setup

Colonies of both *P. xylostella* and *D. semiclausum* were established from field collections in Adelaide, Australia. *P. xylostella* was reared on cabbage plants, *Brassicae oleracea* L. var. *capitata* (cv, 'Green Coronet'), grown in pots (8 cm diameter), and *D. semiclausum* was reared on larval *P. xylostella* under laboratory conditions (25°C, 14L:10D, 50–70% RH). In all experiments, we used cabbage plants with five or six expanded leaves, second and third instar *P. xylostella*, and 2–3-day-old mated female *D. semiclausum*. For detailed procedures of insect culture and wasp handling prior to experiments see Wang and Keller (2002).

Experimental observations were conducted in a wind tunnel (160 cm × 65 cm × 65 cm) under controlled conditions (24–25°C, 50–70% RH, balanced illumination provided by two 36 W fluorescent lamps on each side and two 18 W lamps on each end of the test section; Keller, 1990). The wind speed was set at 30–35 cm/s. For each observation, an experimental plant was placed 60 cm downwind of an extra plant in the tunnel. A female wasp was released 30 cm downwind of the experimental plant from a vial on a stand about equal height with the odor source from the experimental plant. Once the wasp arrived onto the experimental plant, its foraging behavior (attack, sting, and unsuccessful host encounter) and location on each leaf of the experimental plant were recorded continuously with an event recorder (The Observer 3.0 for Windows; Noldus, 1991), until the wasp left the experimental plant and landed on the extra plant. The recorded times were accurate to the nearest 1 s. The extra plant was placed to provide an alternative source of semiochemicals for the free-searching wasp to leave whenever it decided to do so (Wang and Keller, 2003).

The experiment consisted of five treatments of three different densities and two different distributions of host larvae on the experimental plant: (1) one larva per plant, with the larva placed on a randomly selected leaf; (2) three larvae per plant, with each larva placed on one of three randomly

selected leaves (even distribution); (3) three larvae per plant, with all larvae placed on one randomly selected leaf (clustered distribution); (4) nine larvae per plant, with the nine larvae distributed evenly to the leaves (i.e., one or two larvae per leaf); and (5) nine larvae per plant, with all larvae placed on one randomly selected leaf. For all treatments, the extra plant was always infested with three larvae that were distributed randomly on the plant. All the experimental and extra plants were infested with host larvae of the required density and distribution 24 h prior to the observations. Immediately prior to each observation, each plant was examined again for the number of host larvae present.

Immediately prior to release, each naive female wasp was held in an 8 cm Petri dish containing a piece of cabbage leaf with fresh feeding damage by one host larva for 5 min (the larva was removed just before the wasp was placed into the Petri dish). This exposure provided the wasp with experience of host-related cues and increased its orientation toward the experimental plant once released (Wang and Keller, 2002). All stung larvae were dissected after the observation to determine the number of eggs deposited into each larva. One or two female wasps were observed for each treatment in a random order on each observational date between 9:00 and 16:00 h. Each treatment was replicated 17–24 times.

Data Analysis

Mean numbers of attacks, ovipositions, and hosts parasitized by the parasitoid were compared among treatments using the Kruskal–Wallis test (JMP 4.0, SAS, Cary, NC). Here, an attack was defined as direct contact with a host. Patch residence time (the time between arriving on the experimental plant for the first time and leaving the experimental plant for the last time) and giving-up time (the time from the end of the last oviposition until the wasp left the experimental plant, or the patch residence time when no oviposition occurred; Waage, 1979) were analyzed using Bonferroni procedures for multiple comparisons on survival functions (log-rank test, survival analysis, JMP 4.0, SAS; Haccou and Meelis, 1994). In addition, oviposition intervals of individual wasps were calculated in each treatment to test if the instantaneous oviposition rate of the parasitoid decreased over time as is assumed in the Marginal Value Theorem (Charnov, 1976).

The effects of host density and distribution, as well as within-patch foraging experience on the parasitoid's patch-leaving tendency were analyzed using Cox's proportional hazards model (Cox, 1972). The model has been successfully used to analyze the patch-leaving tendency in parasitoids in many studies (see van Alphen *et al.*, 2003). Briefly, the probability per unit

Table I. Explanatory Covariates Selected and Tested in the Analysis of Patch-Leaving Tendency of *D. semiclausum* by Means of the Cox Proportional Hazards Model

Covariates
Is the host density one?
Is the host density three with clustered distribution?
Is the host density nine with even distribution?
Is the host density nine with clustered distribution?
Was the previous encounter unsuccessful?
Did the previous encounter involve an oviposition?
Did the previous encounter involve superparasitism?
Was a parasitized host rejected at the last encounter?
Cumulative number of unsuccessful host encounters
Cumulative number of ovipositions
Rate of last oviposition
Oviposition sequence (from first to the seventh oviposition)

of time (so-called cumulative hazard rate) that a female parasitoid leaves the patch, given that she is still on it, is determined by a joint function of the baseline leaving tendency (when there is no effect of any factors) and the effects of covariates (i.e., explanatory variables) (for a detailed description of the model, see Haccou *et al.*, 1991; Collett, 1994).

Host density and host distribution were the major variables considered. The treatment with three host larvae and an even distribution was taken as a reference. Other covariates that were associated with within-patch foraging experience and had been previously identified to influence the patch-leaving tendency of *D. semiclausum*, including unsuccessful host encounter, oviposition, and oviposition rate (Wang and Keller, 2003), were also considered in this analysis. In addition, each oviposition and its sequence, encounters with parasitized hosts, and superparasitism were also considered as potential covariates as they have often been treated so in other studies (e.g., Hemerik *et al.*, 1993; Driessen *et al.*, 1995). In total, 18 covariates were selected for this analysis (Table I).

We employed a standard likelihood ratio test through an iterative regression as used in other studies (Wajnberg *et al.*, 1999; Wang and Keller, 2003) to identify the significant variables influencing the parasitoid's patch-leaving tendency. All analyses were performed by the PHREG procedure of SAS software, Version 6.0 (Allison, 1997). The proportionality assumption of this model was verified by data stratification of the covariate under test and then plotting estimates of cumulative hazard rates at different levels of the covariate (Hemerik *et al.*, 1993), and the adequacy of the final fitted model was assessed by examining a plot of deviance residuals (Allison, 1997).

RESULTS

Patch Residence Time and Foraging Efficiency

Patch residence time by *D. semiclausum* increased with host density and with more clustered host distribution (Fig. 1). However, the patch residence times of parasitoids on plants containing one host larva were not significantly different from the times females spent on the plants containing three evenly distributed host larvae ($P > 0.05$).

The mean numbers of attacks and ovipositions, and mean attack rate per hour by *D. semiclausum* increased with host density and with more clustered host distribution (Table II). On the plant containing nine host larvae, both the mean number of attacks and the mean attack rate by the parasitoid were significantly higher when the hosts were clustered on one leaf than when evenly distributed over different leaves of the plant (Table II). Although there were no significant differences in the mean number of attacks and mean attack rate between the clustered and evenly distributed treatments of the plants with three host larvae, the mean number of ovipositions was significantly higher when the hosts were clustered than evenly distributed (Table II). The earlier results suggest that the clustered host distribution led to a higher searching efficiency by the parasitoid. Overall, the attack rate was higher than the oviposition rate across all the treatments (Table II), indicating that not every attack was successful (due to host

Fig. 1. Mean ($\pm$ SE) patch residence time by *D. semiclausum* as a function of host density and distribution of *P. xylostella* larvae (survival analysis, IMP, $P = 0.05$).

Table II. Mean $\pm$ SE Numbers of Attacks, Ovipositions, Attack and Oviposition Rate Per Hour by *D. semiclausum* on Host Patch Infested with *P. xylostella* Larvae at Different Densities and Distributions

Host density (distribution)	<i>N</i>	No. of attacks	No. of ovipositions	Attack rate (per hour)	Oviposition rate (per hour)
1	17	1.6 $\pm$ 0.47 a	1.0 $\pm$ 0.31 a	6.6 $\pm$ 1.93 a	4.4 $\pm$ 2.52 a
3 (even)	24	2.5 $\pm$ 0.33 b	1.3 $\pm$ 0.20 a	9.0 $\pm$ 1.17 b	6.4 $\pm$ 1.28 a
3 (clustered)	22	3.6 $\pm$ 0.52 b	2.0 $\pm$ 0.27 b	9.2 $\pm$ 1.31 b	7.2 $\pm$ 1.42 a
9 (even)	16	7.4 $\pm$ 1.01 c	4.5 $\pm$ 0.68 c	11.9 $\pm$ 1.62 c	7.7 $\pm$ 1.13 a
9 (clustered)	17	13.8 $\pm$ 1.07 d	7.5 $\pm$ 0.45 d	18.6 $\pm$ 1.44 d	12.0 $\pm$ 1.55 b

Note. Values followed by different letter within same column were significantly different (Kruskal–Wallis test, $P < 0.05$).

defenses). However, the mean oviposition rate was not significantly different among treatments, except for the treatment of nine larvae per patch with a clustered distribution in which the oviposition rate was significantly higher than that of all other treatments (Table II).

The mean number of hosts parasitized by *D. semiclausum* also increased with host density and with more clustered host distribution (Table III). Self-superparasitism occurred, but the frequency was low and no difference was observed across treatments (Table III).

The cumulative number of ovipositions by *D. semiclausum* increased linearly with elapsed patch residence time, except for the treatment of nine larvae with a clustered distribution in which the cumulative number of oppositions showed an increasing but negatively accelerated gain function of patch time (Fig. 2). Giving-up time by the parasitoid varied largely among individual wasps within each treatment, and there was no significant difference in the mean giving-up time among treatments ($P > 0.05$) (Fig. 3).

Table III. Mean $\pm$ SE Number of *P. xylostella* Larvae Parasitized and Percentage of Superparasitism by *D. semiclausum* on Host Patches Infested with Hosts at Different Densities and Distributions

Host density (distribution)	<i>N</i>	No. of hosts parasitized	% Superparasitism
1	17	0.6 $\pm$ 0.12 a	24.5 $\pm$ 8.6 a
3 (even)	24	1.1 $\pm$ 0.16 b	16.1 $\pm$ 6.1 a
3 (clustered)	22	1.7 $\pm$ 0.19 c	13.6 $\pm$ 6.1 a
9 (even)	16	3.9 $\pm$ 0.49 d	12.5 $\pm$ 6.8 a
9 (clustered)	17	6.5 $\pm$ 0.33 e	12.6 $\pm$ 6.6 a

Note. Values followed by different letters within the same column were significantly different (Kruskal–Wallis test, $P < 0.05$).

Fig. 2. The relationship between cumulative number of ovipositions and elapsed patch residence time by *D. semiclausum* on host patches infested with larval *P. xylostella* at different densities and distributions.

Patch-Leaving Tendency

The patch-leaving tendency of *D. semiclausum* increased with the number of successful ovipositions, but decreased with the number of

Fig. 3. Mean ($\pm$ SE) giving-up time since the last oviposition by *D. semiclausum* on host patches infested with larval *P. xylostella* at different densities and distributions (survival analysis, JMP, $P = 0.05$).

Table IV. Estimated Regression Coefficients (β), Standard Errors (SE) and Hazard Ratios, $\exp(\beta)$, for the Final Fitted Model that Included all the Significant Covariates Affecting the Patch-Leaving Tendency of *D. semiclausum*

Covariates	β	SE	χ^2	P	$\exp(\beta)$
Three host larvae with clustered distribution	-0.981	0.424	5.4	0.0205	0.375
Nine host larvae with even distribution	-1.443	0.501	8.3	0.0040	0.236
Nine host larvae with clustered distribution	-1.718	0.460	14.0	0.0002	0.179
Unsuccessful host encounter	-0.931	0.355	6.9	0.0087	0.394
Cumulative number of ovipositions	0.040	0.015	7.3	0.0071	1.041

Note. The treatment of three host larvae with even distribution was taken as a reference. χ^2 correspond to the likelihood ratio tests ($\alpha = 0.05$). All of them were estimated with all other significant terms present in the model.

unsuccessful host encounters resulting from host defenses, increasing host density, or more clustered host distribution (Table IV). All the other covariates listed in Table I had no significant effect. A group of five covariates was finally fitted into the model, which fitted the data well as indicated by the symmetrical distribution of the deviance residuals around zero (Fig. 4).

The effect of host density and distribution on the patch-leaving tendency of *D. semiclausum* was also clearly shown when plotting the cumulative hazards rates (negative log-survivor) against the rank of searching periods for each host density or distribution (Fig. 5). The curves of host density one and three (even) were intertwined, suggesting that the

Fig. 4. Plot of the deviance residuals of the final fitted model with five covariates against the order of searching periods.

Fig. 5. Negative log-survival curves (cumulative hazards rates) for patch leaving by *D. semiclausum* as affected by host density and distribution of larval *P. xylostella*, i.e. a graphical test on proportionality assumption of Cox's proportional hazards model (Cox, 1972).

parasitoid did not distinguish between these two relatively low host densities. All the curves had a more or less concave shape, implying that the leaving tendency was an increasing function of the time already spent in the patch.

In order to verify the hypothesis that the effect of oviposition on the patch-leaving tendency could depend on the host density and distribution, i.e. 'switching rules,' a separate analysis for each treatment in which only the single covariate of the number of ovipositions was included was performed. It showed that the number of ovipositions consistently increased the parasitoid's patch-leaving tendency, regardless of host density or distribution tested (Table V).

Table V. Estimated Effect of the Number of Ovipositions on the Patch-Leaving Tendency of *D. semiclausum*

Host density (distribution)	β	SE	χ^2	P
1	0.129	0.235	0.30	0.5820
3 (even)	0.682	0.099	11.8	0.0006
3 (clustered)	0.507	0.171	8.8	0.0030
9 (even)	0.255	0.099	6.2	0.0131
9 (clustered)	0.635	0.159	15.9	0.0001

Note. Single covariate tests while all other covariates were not included in the model regression, β is the estimated coefficients and χ^2 correspond to the likelihood ratio tests ($\alpha = 0.05$).

DISCUSSION

The observed behavior of *D. semiclausum* agrees broadly with the general predictions of the Marginal Value Theorem (Charnov, 1976); patch residence times and cumulative numbers of ovipositions increased with increasing host density. However, the cumulative number of ovipositions was not always a diminishing function of elapsed patch time when the host density was lower than three larvae per plant or per leaf (i.e., the treatment of nine larvae per plant with an even distribution) (Fig. 2). Only when the host density was extremely high (i.e., nine larvae per leaf), did the oviposition rate of *D. semiclausum* appear to decrease with patch time (Fig. 2), which basically met the model's assumption.

In a previous study, it was shown that patch residence time and number of ovipositions by *D. semiclausum* increased with increasing inter-patch distance as predicted by the Marginal Value Theorem, but the model's assumption about decreasing oviposition rate over time was not met (Wang and Keller, 2003). Wang and Keller (2003) discussed several factors that could have caused large variation among individual oviposition intervals, particularly when host density was relatively low. Larval *P. xylostella* tends to avoid parasitoids by resting away from damaged plant parts after short feeding bouts, or dropping off a plant along a silk thread when attacked by *D. semiclausum*. In reaction, the parasitoid displays wide-area searching around damaged plant parts and waits for suspended hosts to climb back to the plant before attacking them again. The interaction between the host defense and the parasitoid counter-defense often results in many unsuccessful host encounters and a substantially variable host handling time (Wang and Keller, 2002, 2003). When host density is extremely high, for example, nine larvae per leaf in this study, the host larvae may be less likely to avoid the parasitoid by changing their feeding positions and are thus more likely to be located quickly by the parasitoid. As a result, the foraging efficiency by the parasitoid increased with host density and with more clustered host distribution (Table II). The period of waiting for a discovered host varies from several to over 1400 s (Wang, 2001; Wang and Keller, 2003). The period depends on the time that a host remains suspended. It may also depend on the behavioral decision of the wasp whether to wait for a discovered host to return to the plant, or to resume searching for new hosts. This decision should depend on the availability of hosts. When the attack rate is relatively higher in a host-rich environment, the parasitoid should give up waiting sooner. It was found that the mean waiting period on the lowest host density patches (515 ± 145 s, $n = 6$) was generally higher than on the highest host density patches that had a clustered host distribution (364 ± 160 s, $n = 24$).

None of the simple “rules of thumb” for leaving a “patch,” including fixed patch time, fixed number of ovipositions or fixed giving-up time since last oviposition could explain the observed pattern of patch-leaving behavior in *D. semiclausum* (Table II; Figs. 1 and 3). These simple rules do not consider the complicated effects of many within-patch foraging experiences on a parasitoid’s patch-leaving behavior. The agreement with the predictions of these rules maybe expected only under special conditions (Iwasa *et al.*, 1981). For example, Wang (2001) observed the foraging behavior of individual female *D. semiclausum* on a group of four host plants infested with different host densities, and examined the parasitoid’s leaving tendency at three different scales: a leaf, a plant and a group of four plants. It was found that successful oviposition always increased the parasitoid’s patch-leaving tendency across all spatial scales. However, at the level of the individual leaf, it was observed that *D. semiclausum* often immediately leaves after one successful oviposition (Wang and Keller, 2002), as if using the “fixed number rule” (Wang, 2001). In contrast, at the other two levels, the giving up time by this parasitoid was highly variable (Wang, 2001). Thus, the predictions of these rules may be influenced by a simple assumption about a parasitoid’s perception of ‘patchiness’ when it forages in an environment that is patchy at several different spatial scales (Wang, 2001).

The effects of unsuccessful encounter and oviposition on the parasitoid’s patch-leaving tendency were consistent with previous findings (Wang and Keller, 2003). The decrease in the patch-leaving tendency following unsuccessful host encounters could be an adaptive strategy for *D. semiclausum* to overcome its host’s defensive behavior (Wang and Keller, 2002, 2003). Oviposition consistently increased the parasitoid’s patch-leaving tendency, regardless of the host density and distribution, and there was no switch to use different rules under the conditions tested in this study. This confirms that *D. semiclausum* employs a countdown mechanism when foraging for hosts (Driessen *et al.*, 1995). Driessen and Bernstein (1999) argued that the countdown mechanism should be employed as long as a parasitoid can accurately assess the initial density of hosts in patches. *D. semiclausum* was observed to be more attracted to higher host density plants than lower host density plants when it was released into a group of plants infested with varying host densities (Wang and Keller, 2002). Quantitative responses of the parasitoids to varying kairomone concentrations are indicated by decreasing response of wasps to host-infested plants as inter-patch distance increases (Wang and Keller, 2003). Thus, there may also a link between kairomone concentration and perception of patch quality in *D. semiclausum*. The parasitoid may setup an expected patch-leaving tendency on a given patch based on its initial assessment of patch quality (Waage, 1979), but use actual foraging experience such as rewarding oviposition and

unsuccessful host encounter to adjust its patch-leaving tendency (Driessen and Bernstein, 1999).

The decreasing patch-leaving tendency with increasing host density and degree of host aggregation should lead to the same foraging behavior as is predicted by the Marginal Value Theorem (Charnov, 1976). A similar effect of host density on patch time allocation has been also found for other parasitoids searching for patchily distributed hosts (e.g., Waage, 1979; van Steenis *et al.*, 1996; Keller and Tenhumberg, 2000). The decreased leaving tendency in patches of abundant and clustered hosts could be a result of density-dependent presence of kairomone per unit area (Haccou *et al.*, 1991; Hemerik *et al.*, 1993; Nelson and Roitberg, 1995; Driessen and Bernstein, 1999). However, it is unknown if the presence of kairomone resources influences the patch-leaving tendency of *D. semiclausum*. This deserves further investigation.

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