Departure Mechanisms for Host Search on High-Density Patches by the *Meteorus pulchricornis*

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**ABSTRACT.** Less attention has been paid to the parasitoid–host system in which the host occurs in considerably high density with a hierarchical patch structure in studies on time allocation strategies of parasitoids. This study used the parasitoid *Meteorus pulchricornis* (Wesmael) (Hymenoptera: Braconidae) and the Oriental leafworm, *Spodoptera litura* (Fabricius) (Lepidoptera: Noctuidae) as the parasitoids–host model system to investigate patch-leaving mechanisms as affected by the high-host density, hierarchical patch structure, and foraging behaviors on both former and current patches. The results showed that three out of eight covariates tested had significant effects on the patch-leaving tendency, including the host density, ovipositor insertion, and host rejection on the current patch. The parasitoid paid more visits to the patch with high-density hosts. While the patch with higher host densities decreased the leaving tendency, the spatial distribution of hosts examined had no effect on the leaving tendency. Both oviposition and host rejection decreased the patch-leaving tendency. The variables associated with the former patch, such as the host density and number of ovipositor insertions, however, did not have an effect on the leaving tendency. Our study suggested that *M. pulchricornis* females may use an incremental mechanism to exploit high-density patches to the fullest.

**Key Words:** behavioral mechanism, hierarchical patch structure, host density, host distribution, patch time allocation

Female insect parasitoids generally start searching for hosts shortly after emergence. However, most host species are not evenly dispersed over the habitat, but tend to occur in discrete, depletable patches in the environment. The parasitoid female, therefore, has to divide its time between different patches to maximize the number of offspring that she can produce during her short adult life (Godfray 1994). A number of theoretical models have been proposed to predict which strategy female parasitoids should use to make sure that they can allocate patch residence time optimally. The most well-known is the marginal value theorem (Charnov 1976), which states that the females should leave a patch when the instantaneous rate of fitness gain within the current patch drops below the maximum average rate that can be achieved in the environment. This model and its subsequent modifications also predict that females should stay longer on patches of higher quality (McNair 1982). Furthermore, patches of different quality should be reduced to the same level of profitability before leaving (Cook and Hubbard 1977, Wajnberg 2006). To accomplish this, female parasitoids of many species have developed proximate, rule-based behavioral mechanisms that appear consistent with the goal-based optimal patch time (van Alphen et al. 2003, Wajnberg 2006).

Time allocation to foraging behavior should be adapted to the density and spatial distribution of hosts in a patch. When a female parasitoid enters a host patch with an initial responsiveness (or tendency) level, its tendency to leave increases with time and oviposition, until a threshold is reached (Waage 1979). Each oviposition has an incremental influence on the current level of responsiveness and the total patch-residence time was increased. This proximate mechanism is usually called incremental effect (Waage 1979). By contrast, when an oviposition decreases the responsiveness level, the residence time will be reduced in the patch. This is called decremental effect or “count-down mechanism” (Iwasa et al. 1981). Iwasa et al. (1981) explains in their models, the mechanism with the host distribution. Their model suggests that the kind of mechanism that parasitoids use depends on the distribution of the hosts. Parasitoids foraging for hosts with an aggregated distribution should use incremental mechanisms, whereas those foraging for uniformly distributed hosts should use decremental mechanisms. Parasitoids foraging for Poisson-distributed hosts should be indifferent to the number of eggs that they have laid. This model is based on the assumption that the type of host distribution is constant over generations. However, when information about host availability is unreliable, an incremental mechanism would be expected (Driessen and Bernstein 1999). In addition, patch quality can also influence parasitoids in their patch-leaving tendency. Encountering a host in a poor patch should have a weaker incremental effect on the tendency to stay than encountering a host in a rich patch because more remaining hosts are expected in a rich patch than in a poor patch (Muratori et al. 2008). Even the quality of the former patch may also play a strong role in response to both chemical cues and oviposition events by the parasitoid when expiating a patch (Louâpre et al. 2011).

In this study, we focused on the patch time allocation strategy of the solitary parasitoid, *Meteorus pulchricornis* (Wesmael), using a caterpillar host, which formed a characteristic patch both in density and spatial distribution. *M. pulchricornis* (Braconidae) is an endoparasitoid of various free-living lepidopteran larvae that feed mostly on plant foliage (Maeto 1989). Its hosts include caterpillars that are either spatially dispersed, such as *Helicoverpa armigera* (Hübner) (Liu and Li 2008), or highly aggregated, such as *Spodoptera exigua* (Hübner) (Liu and Li 2006) and *Spodoptera litura* (Fabricius) (Yamamoto et al. 2009, Chen et al. 2011). The host used in this study was *S. litura*, which deposits eggs in a fairly large mass containing 100–200 eggs, leading to extremely high density (mostly >100 per leaf) of host larvae at the early stage. The hatching caterpillars form a dense cluster on a leaf at the first instar, then disperse to nearby leaves when molting into the next stage, and finally scatter to most leaves of the plant at the third stadium (Wang...
et al. 2005, Qin and Ye 2007). These spatial distributions of hosts form a hierarchical structure of patches from a leaf to a plant. The hierarchical nature of patches has, however, received less attention in studies of parasitoid foraging behaviors (Vos and Hemerik 2003). The aim of this study is to investigate how the patch-leaving tendency of *M. pulchricornis* is influenced by the high host density, hierarchical patch structure, and foraging behaviors on both former and current patches.

**Materials and Methods**

**Parasitoid and Host.** *M. pulchricornis* is thelytokous. The laboratory stock was obtained from rearing *S. litura* larvae collected in soybean fields in the suburb of Nanjing, China, and maintained using *S. litura* as hosts in the insectary (26 ± 2°C, 60–80% RH, 14:10 h light:dark photoperiod). Wasps were fed with a 10% honey solution as the supplementary food. The test parasitoids were from 6 to 8 days old. The host species, *S. litura*, was collected as larvae from soybean fields and reared in the insectary on the artificial diet (Shen and Wu 1995). *S. litura* is one of destructive pests on soybean, cotton and vegetable crops in eastern China, where four to six generations occur a year (Hong and Ding 2007). It can be attacked by *M. pulchricornis* at a rate of 20–30% in the soybean fields when application of pesticides is limited (Zhang et al. 2012). Adult moths were fed with a 10% sugar solution and provided with strips of paper as substrate for egg deposition in organza-covered cages (length by width by height = 20 by 20 by 30 cm). The female moths oviposit in egg masses each being composed of 100–200 eggs (Wang et al. 2005, Qin and Ye 2007). According to the field survey, females usually lay no more than one egg mass onto a soybean plant, and the hatched larvae do not diffuse to other plants until they are beyond the third instar (Wang et al. 2005). The test plants, soybean *Glycine max* (L.) (Nannong 84-4) were potted in the greenhouse and used for experiments when they were about 60 cm in height with 30–40 leaves.

**Experimental Setup.** The behavioral observation was conducted in a large transparent cage (240-cm long by 110-cm wide by 90-cm high). At two ends, there were ventilating holes covered by gauze, and a small fan was flowing from the one end to help the foraging parasitoid search for hosts. Three potted soybean plants, each being treated with one of three density levels, were placed in a random order in the wind direction (Fig. 1). The host density was manipulated as three broad categories: low, high, and control (without host), by following the range of host density in the soybean field. Due to realistic difficulties in hand-moving a large number of young larvae on to the plant, we attached the egg mass (100–120 egg) to the leaf. The low- and high-density treatments were obtained by attaching one and two egg masses, respectively. Though there was a slight variation in hatching rate among egg masses and in mortality of larvae between density treatments, the relative difference between the density treatments can still be maintained owing to broadness of the two categories. The hatching caterpillars formed a dense cluster on a leaf at the early stage (late first instar), then disperse to nearby leaves, when molted into the next stage, and finally scatter to most leaves of the plant at the third instar (Fig. 1). These three stages were treated as different treatments of the spatial distribution of hosts. By these manipulations, we set up a factorial combination of 3 by 3 (density, distribution) treatments. Although the host distribution was confounded by the host stage, the confounding effect should be minimal because host larvae at these stages are equally susceptible to parasitism and suitable for offspring development as showed in previous studies (Liu and Li 2006, 2008, Chen et al. 2011). A naïve female wasp was released into the cage at the upwind point. When the wasp alighted on any of the plants, timing was started. Patch residence time was defined as the total time from entering the current plant to leaving it. When the wasp occasionally returned to the plant within a few seconds after leaving it, the short excursions off the patch were still included within the same patch visit. When moved to the next plant and started foraging, it was treated as being on another patch. When the wasp landed on the wall of the cage and did not return to any of the plants within 15 min, this replication was terminated. For each treatment, 15–26 parasitoids were tested. The trials were made at the room temperature (24–25°C).

**Covariates.** Many variables could be tested for having an effect on the parasitoid’s leaving tendency. We took into account the biology of *M. pulchricornis*, factors found to be important in other braconid parasitoids and some factors assumed to be important in patch-leaving models. It is of importance, at which scale the patch is defined. Our exploratory observation of foraging behaviors showed that the parasitoid first landed on the leaf with host larvae, attacked a few hosts, and then walked to nearby leaves to continue searching. If failed to encounter the host on a few leaves, it flew away from this plant to the next. In consideration of both these foraging behaviors and the spatial distribution patterns of hosts tested in this study, we defined the patch to be a whole plant in our analysis. We, therefore, offered a plant without any hosts as a control in each replicate. The description of the covariates selected and the way coded were provided in Table 1.

**Data Analysis.** The Cox’s proportional hazard model was used to quantify the behavioral mechanisms used by the females to trigger their patch-leaving decision, owing to its flexibility, which enables one to statistically test the effect of any explanatory variable that is a priori believed to influence the patch-leaving tendency (Cox 1972, Haccou et al. 1991, Collett 1994, Wajnberg 2006). This model estimates the hazard rate at time *t*, which can be interpreted biologically as a tendency to leave the patch. We estimated the effect of the different factors on the
Multiple pairs of covariates were included in the model as well to test patch-leaving tendency. The hazard rate \( h(t) \) at time \( t \) in the patch is given by:

\[
h(t) = h_0(t) \exp \left( \sum_{i=1}^{n} \beta_i z_i \right)
\]

where \( h_0(t) \) is the baseline hazard function to leave the patch depending only on the time spent on it when all covariates \( z_i \) are set to zero, and \( \beta_i \) is the regression coefficients that give the relative contributions of the \( n \) covariates \( z_i(t) \). If the expression \( \exp(\sum_{i=1}^{n} \beta_i z_i) \) is lower than one, the patch-leaving tendency is reduced, resulting in an increase in the residence time, whereas a hazard ratio greater than one increases this tendency, resulting in a decrease of the residence time (Cox 1972, Haccou et al. 1991).

To estimate the influence of these covariates on the patch-leaving tendency under all the conditions tested, the effect of each variable and the overall significance of the fitting model were assessed using the likelihood ratio test (Collett 1994). This test was used through an iterative procedure to identify the parameters having a significant influence on the females’ patch-leaving tendency (Wajnberg et al. 1999). Multiple pairs of covariates were included in the model as well to test possible interactions between them. The adequacy of the final fitted model can be assessed by making residual plots (Wajnberg et al. 1999, Outreman et al. 2005). All the analyses were carried out using R 2.15.2 software (R Development Core Team 2012).

**Results**

The parasitoid performed characteristic foraging behaviors. It flew against the wind from the releasing point, when it started foraging in the cage. Upon landing on the plant, the foraging parasitoid began actively searching for leaves with hosts. The parasitoid traveled between plants or noncontact leaves by flying, which usually took less than 5 s. When neonate larval hosts were highly aggregated on one leaf, the parasitoid traveled between leaves by flying, which usually took less than 5 s. When neonate larval hosts were highly aggregated on one leaf, the parasitoid often landed first on a leaf without hosts, where it attacked the hosts on a contiguous leaf. When host larvae dispersed to adjacent leaves after moulting, the wasp often directly landed on the leaf containing hosts.

Among the eight covariates tested for their influence on the patch-leaving tendency, three were found to have a significant effect (Table 2); the other covariates examined did not significantly influence the patch-leaving tendency according to the likelihood ratio test, thus leaving out from the final model (Table 3). The parasitoid performed more visits to the plant with the high host density (72 visits) as opposed to the low (51) and the control (27; \( \chi^2 = 30.38 \), df = 1, \( P < 0.001 \)). The patch-leaving tendency significantly decreased on the patch with hosts as opposed that without (control), and on the patch with the high density as opposed the low density (Fig. 2). The Cox regression analysis showed that the host distribution did not have a significant effect on the leaving tendency (\( \chi^2 = 2.87 \), df = 2, \( P = 0.24 \)). The patch-leaving tendency decreased by a factor of 0.87 with each ovipositor insertion into hosts, and by a factor of 0.80 with each host rejected. A significant interaction between stings and host rejections was found to increase the leaving tendency (\( \chi^2 = 7.29 \), df = 1, \( P < 0.01 \)). Let \( S_1 \) be the stings, and \( R_1 \) the host rejections, and \( \gamma \) the estimated coefficient of the interaction term between these two effects. According to the equation, the corresponding hazard ratio should be \( \exp\{0.14 \times S_1 - 0.14 \times R_1 + 0.006(S_1R_1)\} = 0.80 \) (Table 2), leading to a decrease in the leaving tendency.

**Discussion**

This study showed that the host density, total number of ovipositor insertions and of hosts rejected on the current patch had an effect to decrease the leaving tendency of *M. pulchricornis* females, but the variables associated with the former patch, such as the host density and number of ovipositor insertions, did not have an effect on the leaving tendency. These results suggest that *M. pulchricornis* females may only use information gleaned from the current rather than former patch to make the decision of patch-leaving. Studies on the braconid *Asobara tabida* show that the information gleaned from visiting the previous patch can affect the parasitoid in making time allocation decisions on a

### Table 1. Covariates tested for having an effect on the patch leaving tendency

| Covariate                  | Description                                                                 |
|----------------------------|-----------------------------------------------------------------------------|
| 1. Host density            | The three broad categories of host density: 0, no host, the control; 1, low density from 1 egg mass; 2, high density from 2 egg masses (each egg mass contained ca 200 eggs). |
| 2. Host distribution       | The spatial distribution of hosts, a categorical variable. 1, dense cluster on a leaf at the late first stadium; 2, moderately dense cluster on a few contiguous leaves; 3, spreading cluster on most leaf of the plant. |
| 3. Sting                   | The total number of ovipositor insertions in the current patch, a numerical variable |
| 4. Host rejection          | The total number of hosts rejected after touching with antennae, a numerical variable |
| 5. Re-sting                | The number of hosts receiving \( \geq 2 \) successive stings, suggesting superparasitism, a numerical variable |
| 6. Visit degree            | The cumulative number of leaves visited in the current patch, a numerical variable |
| 7. Previous host density   | See item 1 for the explanation.                                             |
| 8. Previous sting          | The total number of ovipositor insertions on the former patch, a numerical variable |

### Table 2. Estimated regression coefficient (\( \beta \)) of a Cox proportional hazard model for tested covariates that have a significant effect (\( P < 0.05 \)) on the patch-leaving tendency of *Meteorus pulchricornis* foraging

| Covariate                  | \( \beta \) | SE(\( \beta \)) | exp(\( \beta \)) | \( \chi^2 (df) \) | \( P \) | Effect on leaving tendency |
|----------------------------|------------|----------------|-----------------|-----------------|-------|--------------------------|
| Host density               |            |                |                 |                 |       |                          |
| Control                    | 0          | 0.04           | 1               |                 |       |                          |
| Low                        | -1.68      | 0.45           | 0.19            |                 |       |                          |
| High                       | -2.08      | 0.44           | 0.12            |                 |       |                          |
| Sting                      | -0.14      | 0.02           | 0.87            |                 |       |                          |
| Host rejection             | -0.14      | 0.03           | 0.87            |                 |       |                          |
| Sting \times Host rejection| 0.006      | 0.002          | 1.006           |                 |       |                          |

Note: The treatment of three host density with empty was taken as a reference level. \( \chi^2 \) correspond to the likelihood ratio tests \( (\alpha = 0.05) \).

### Table 3. Summary of covariates which were removed from the model selection procedure according to the likelihood ratio test

| Covariate                  | \( \chi^2(df) \) | \( P \) |
|----------------------------|-----------------|-------|
| Previous stings            | 0.007 (1)       | 0.93  |
| Previous host density      | 1.11 (3)        | 0.78  |
| Re-stings                  | 0.47 (1)        | 0.49  |
| Visit degree               | 2.05 (1)        | 0.15  |
| Host distribution          | 2.87 (2)        | 0.24  |

Note: \( \chi^2 \) correspond to the likelihood ratio tests \( (\alpha = 0.05) \).
and high host densities. The host densities manipulated in our study were apply to the parasitoid in our study. It is well established that parasitoids decreased leaving tendency after host encounter. This argument may decreases, and parasitoids are expected to switch from an increased to a between kairomone concentrations at low host densities than at high-density patch, a Bayesian-like decision-making (van Alphen et al. 2003, Louâpre et al. 2011). Learning and memory are known to be adaptive when a forager needs to retain information from previous patches and retrieves it on arrival in a new patch (van Alphen et al. 2003, Eliassen et al. 2009). It informs a forager both on the average quality of the environment and on the estimate of patch quality relatively to that of others. However, the experience obtained from visiting the previous patch can not inform the forager of accurate quality of the current patch (Louâpre et al. 2011). For highly polyphagous parasitoids like *M. pulchricornis*, an accurate estimate of the patch quality could be adaptive, when potential host caterpillars can vary substantially in the spatial distribution. According to Driessen and Bernstein (1999), a parasitoid capable of making an accurate estimate of patch quality on arrival is likely to use the giving-up density rule to leave the patch because the residual quality of the patch is directly related to the initial estimate.

Our study showed that *M. pulchricornis* female paid more visits to high-density patches and had a decreasing leaving tendency from there. Host density, closely associated with patch quality, has been found in many studies to have a decremental effect on the patch-leaving tendency of foraging parasitoids (Driessen et al. 1995, Wang and Messing 2003, Wang and Keller 2004). Hosts of *M. pulchricornis* include a wide range of free-living Lepidopteran species and their larval density can vary considerably in the fields (Maeto 1989, 1990). So, it is assumed that *M. pulchricornis* may lay great stress on the information about host density. By doing so, the parasitoid can exploit high quality patches to the full.

Our study showed that each oviposition had a strong effect on the patch residence time, leading to a significant decrease in the leaving tendency. This result suggested that an incremental mechanism should be used by the parasitoid to make the patch-leaving decisions, which is in line with the “incremental rule” as proposed by Waage (1979). Both theoretical models and empirical studies suggest that an incremental mechanism can only be adaptive under certain circumstances (Iwasa et al. 1981, Driessen and Bernstein 1999, Wajnberg 2006). Driessen and Bernstein (1999) argued that if a parasitoid could better distinguish between kairomone concentrations at low host densities than at high-host densities, as host density increases, the reliability of information decreases, and parasitoids are expected to switch from an increased to a decreased leaving tendency after host encounter. This argument may apply to the parasitoid in our study. It is well established that parasitoids use herbivore-induced plant volatiles to locate their herbivorous hosts (Vet and Dicke 1992). The host densities manipulated in our study were considerably high, which could provide heavy concentrations of kairomones by inflicting severe feeding damages to the plants, which may be perceived by the foraging parasitoid as manifested by its accurately landing position upon release, which was either close to or on the leaf with hosts. So, for *M. pulchricornis* females, each new oviposition may inform the wasp that other hosts still remain to be discovered, and in response, they must increase their foraging time correspondingly. This result was consistent with other parasitoids, which use the incremental mechanism (Sugimoto et al. 1987, 1990; Nelson and Roitberg 1995; Vos et al. 1998).

Fewer studies have examined the effect of rejecting a healthy or already parasitized host (Wajnberg 2006). Our study showed that the host-rejection had a decreasing effect on the leaving tendency. This result was in contrast with other studies, which found an increasing effect on the leaving tendency after rejection of a host (Wajnberg et al. 1999; 2003, 2004; Boivin et al. 2004; Wang and Keller 2004; Outreman et al. 2005). Our result was similar to Nelson and Roitberg (1995) in which *Opis dimidiatus* reduced the leaving tendency after encountering a parasitized host, and to Wang and Keller (2005) in which the patch-leaving tendency decreased with increased unsuccessful host encounter. The mechanism for ours, however, may be different from theirs. It is generally assumed that rejection of a host may inform the foraging female about the decreasing value of the patch and/or simply leads to a decrease in its motivation to continue searching (van Alphen and Vet 1986). In our model system, however, the host rejection may not be reliable information about the value of the patch for the foraging female on the following grounds. Though the laboratory study shows that this parasitoid can avoid self-superparasitism on the basis of host movement (Chau and Maeto 2008), superparasitism rate can still be as high as 31% in the laboratory (Fuester et al. 1993), and 23% in the field as well (Zhang et al. 2012). Therefore, the rejection of a host may not only provide the information about the decreasing value of the patch but also about the presence of competitors on the patch. This parasitoid often performed a special oviposition behavior by repeatedly stinging a healthy host, for which it was tested as a covariate in our model. This behavior did not necessarily realize more than one egg deposition as indicated by dissection in our exploratory trial. It is known that parasitoids frequently insert their ovipositor into a host but do not go on to lay an egg (Godfray 1994). So, we assume that the rejection of a host either owing to its low quality (parasitized) or just being probed may not only inform the foraging parasitoid of the decreasing value of the patch but also more of the presence of potential competitors. Theoretical models predict that foragers when exploiting a patch together should engage in a war of attrition and stay in the patch longer than when foraging alone (Haccou and van Alphen 2008). This prediction gains the support of experimental studies of some other parasitoids (van Alphen and Visser 1999, Visser et al. 1992).

Our study did not find an effect of the spatial distribution of hosts examined on the patch-leaving tendency. This result suggested that *M. pulchricornis* female might not change its leaving decision in response to the variation in distribution from a dense cluster on a leaf at the early life stage to a scatter over most leaves of a plant at the third stadium of *S. litura* caterpillars. One explanation is that high-density hosts provided the foraging parasitoid so sufficient information about the patch quality that the host distribution may be irrelevant, which guarantees the foraging parasitoid a maximum exploitation of the high-host-density patch.

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