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Patch Time Allocation and Oviposition Behavior in Response to Patch Quality and the Presence of a Generalist Predator in *Meteorus pulchricornis* (Hymenoptera: Braconidae)Sheng Sheng,^{1,2} Meng Ling,¹ Wu Fu-an,² and Li Baoping^{1,3}¹Department of Entomology, College of Plant Protection, Nanjing Agricultural University, Nanjing 210095, PR China²College of Biotechnology, Jiangsu University of Science and Technology, Zhenjiang 212018, PR China³Corresponding author, e-mail: lbp@njau.edu.cn

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ABSTRACT. Foraging parasitoids often must estimate local risk of predation just as they must estimate local patch value. Here, we investigate the effects of a generalist predator *Chlaenius bioculatus* (Coleoptera: Carabidae), has on the oviposition behavior and the patch residence decisions of a solitary parasitoid *Meteorus pulchricornis* (Hymenoptera: Braconidae) in response to the varying host quality of *Spodoptera litura* (Lepidoptera: Noctuidae) larvae (L2 and L4). *M. pulchricornis* attacked more L4 than on L2 hosts, with the difference in attack rate varying depending on predation treatments, greater in the presence (either actively feeding or not) of the predator than in the absence of it. The parasitoid attacked fewer L2 and L4 hosts when the predator was actively feeding than when it was not feeding or not present in the patch. *M. pulchricornis* decreased the patch leaving tendency with increasing rejections of hosts, but increased the tendency in response to the presence of the predator as compared with the absence of it, and furthermore, increased the patch leaving tendency when the predator was actively feeding as compared with when it was not. Our study suggests that *M. pulchricornis* can exploit high quality patches while minimizing predation risk, by attacking more hosts in high quality patches while reducing total patch time in response to risk of predation.

Key Words: foraging behavior, intraguild predation, parasitoid, patch time allocation, mortality risk

Insect parasitoids are excellent model systems to develop and test theoretical models in behavioral ecology (Godfray 1994, Hotchberg and Ives 2000, Wajnberg 2006). When foraging for hosts, insect parasitoids often face predation risks that influence the survival of both themselves and their offspring (Rosenheim et al. 1995, Heimpel et al. 1997, Brodeur and Rosenheim 2000, Meyhöfer and Klug 2002). They therefore should take into account risk of predation while exploiting host patches by making optimal patch-exit decisions (Roitberg et al. 2010).

Over the last few decades, studies of patch time allocation strategies in insect parasitoids have identified a number of factors affecting their patch leaving decisions (reviewed in Wajnberg 2006). Among those studies including predation risks, different responses of foraging parasitoids are displayed. For example, while some studies found that aphid parasitoids did not avoid predators or host patches harboring predators (Meyhöfer and Klug 2002, Bilu et al. 2006, Jazzar et al. 2008), other studies showed that aphid parasitoids responded to the presence or recent presence of a coccinellid predator by reducing the time it spent in a patch (Taylor et al. 1998, Martinou et al. 2009). However, few studies use caterpillar parasitoids as model systems to investigate time allocation strategies of foraging parasitoids in response to risk of predation in a host patch.

Meteorus pulchricornis (Hymenoptera: Braconidae) is a solitary endoparasitoid of free-living lepidopteran larvae exposed on plant foliage (Maeto 1989, 1990). Its hosts include some of the major agricultural pests, including *Helicoverpa armigera* Hübner (Liu and Li 2008), *Spodoptera exigua* Hübner (Liu and Li 2006), and *Spodoptera litura* Fabricius (Yamamoto et al. 2009, Chen et al. 2011). *S. litura* is one of the most destructive pests of soybean, cotton, and vegetable crops in eastern China (Hong and Ding 2007). It oviposits in egg masses, which result in high-density larvae (>100 per leaf) on plants (Sheng et al. 2014). *S. litura* eggs and larvae are often at risk of predation by the ground beetle *Chlaenius bioculatus* (Jiang et al. 1999). *C. bioculatus* larvae search for prey not only on the ground but also on plants. It is

long known that some ground beetles have plant climbing ability at larval stages (Vickerman and Sunderland 1975, Sunderland and Vickerman 1980, Lövei and Szentkirályi 1987, Lövei and Sunderland 1996), which often make the ground beetles with this ability more effective than those without (Renkema et al. 2013).

Here, we investigate effects of *C. bioculatus* on the oviposition behavior and the patch leaving decisions of *M. pulchricornis*. We manipulated *S. litura* larvae as either high (L4) or low (L2) quality host patches exposed to the parasitoid, and *C. bioculatus* larvae as either actively feeding or not in a patch. We examined oviposition behaviors performed and the patch leaving decisions made by *M. pulchricornis* in response to patch quality and risk of predation.

Materials and Methods

Insects. *M. pulchricornis* was obtained from rearing *S. litura* larvae collected in soybean fields in the suburb of Nanjing, East China and maintained using *S. litura* as hosts in the insectary [26 ± 2°C, 60–80% relative humidity, and a photoperiod of 14:10 (L:D) h]. *S. litura* was collected from soybean fields and reared in the insectary on the artificial diet (Shen and Wu 1995). Adult moths were fed with a 10% honey solution and provided with strips of paper as the substrate for egg deposition in organza-covered cages (20 by 20 by 30 cm). Adult parasitoids were fed with a 10% honey solution and used in experiments without parasitism experience at 6–8-d-old post emergence, the age with greatest daily oviposition (Wu et al. 2008). *C. bioculatus* was collected from soybean fields as larvae in 2011, and then maintained using young *S. litura* larvae as prey in the insectary. The soybean *Glycine max* (“Nannong 84-4”) was sown in plastic seed trays in the glasshouse and transplanted after 1 wk into plastic pots (20 cm diameter) filled with peat soils (Fanghua Horticulture Ltd., China). Soybean plants were used in the experiment at the height of 40–50 cm.

Experimental Setup. Parasitoid foraging behaviors were observed in a large transparent cage (240 by 110 by 90 cm, long by wide by

high), which was ventilated with holes (20 cm diameter) and covered by gauze at two ends. A small electric fan blowing at 0.5 m/s from the one end was used to help the foraging parasitoids search for hosts. A potted soybean plant with <10 leaves was placed in the middle of the cage. We manipulated *S. litura* caterpillars as either second (L2) or fourth (L4) instars, representing either low or high quality hosts, respectively. Both L2 and L4 are susceptible to parasitism, but the older is higher in quality for the development of offspring parasitoids (Liu and Li 2006, 2008; Chen et al. 2011). We manipulated predation risk as three categories: absence (control), presence without feeding, and presence with actively feeding, in the patch. The host quality and predation risk were crossed according to 2 × 3 factorial design. We moved 20 host larvae on the terminal leaf at the top of the potted soybean plant. These larvae mostly stayed on the leaf where they were released, often with some (especially L4) dispersed to nearby two leaves. We therefore treated host larvae on the three leaves (trifoliolate) as a host patch. When these larvae began nibbling leaves (about half an hour after the initial landing on leaves), we moved a *C. bioculatus* larva (second instar) to the host patch and then released a *M. pulchricornis* female at the upwind end of the cage.

Observations started when the wasp landed on the patch. Patch residence time was defined as the total time from entering to leaving the patch, including occasional excursions from the patch for a few seconds. Three foraging behaviors of the parasitoid in a patch were recorded, as they are correlated to patch quality and important in predicting patch residence time in other braconid parasitoids (Wajnberg 2006). These behaviors were: (1) the number of hosts stung once by a parasitoid using ovipositor, each stinging highly likely leading to an oviposition, (2) the number of hosts stung more than once, and (3) the number of hosts that were rejected after being touched with antennae. The predator behaviors in the patch were also recorded, and categorized as the three levels. When the parasitoid left the plant and did not come back within 15 s, the replicate was stopped. For each treatment 30 female parasitoids were tested and each female was used only once.

Data Analysis

We used the attack rate, as measured by the proportion of hosts stung by parasitoids among all hosts in a patch, to estimate the exploitation of a patch by the parasitoid, as each ovipositor sting highly likely results in an egg deposition (Zhang et al. 2013). We performed logistic model to analyze effects of host instar and predation risk on the attack rate. When detecting a significant interaction effect between the two factors, we analyzed effects of predation risk treatments separately for L2 and L4 hosts, using Tukey multiple comparison of parameters with the multcomp package for the R statistical environment (Bretz et al. 2010). We applied Cox proportional hazard model (Cox model) to the analysis of effects on the patch leaving tendency of fixed (host instar and predation risk) and time-dependent numerous covariates about parasitoid's foraging behaviors. Cox model has been successfully used to analyze patch-leaving decisions in parasitoids (van Alphen et al. 2003, Wajnberg 2006). To estimate the influence of testing covariates on the patch leaving tendency, we used the likelihood ratio test to assess the effect of individual variables and their possible two-way interactions (Collett 1994). Analyses were performed using R software version 2.15.2 (R Development Core Team 2012).

Results

Host instar and predation risk operated both independently and in interaction in affecting the attack rate (likelihood ratio test, host instar: $\chi^2 = 41.04$, $P < 0.001$; predation risk: $\chi^2 = 23.50$, $P < 0.001$; host instar: predation risk: $\chi^2 = 9.16$, $P < 0.001$). The attack rate was higher for L4 than for L2 hosts at each level of the predation risk, but the effect varied depending on the predation risk, being greater with predator's presence (a difference of 13.7% when the predator was not actively feeding, and 10.5% when it was) than without (6.2%). For the patch

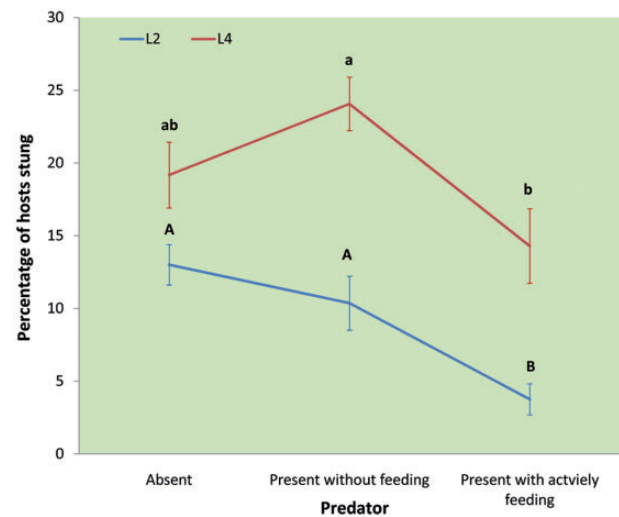


Fig. 1. Mean (\pm SEM) attack rate by *Meteorus pulchricornis* on *Spodoptera litura* L2 and L4 hosts at different levels of predation risk. Different lower and upper case letters indicate significant differences between predation risk treatments for the L4 and L2 hosts, respectively.

composed of the L2 hosts, the attack rate was lower when the predator was actively feeding than when it was not or absent in the patch, but did not differ between the latter two treatments (Fig. 1). For the patch composed of the L4 hosts, the attack rate was lower when the predator was actively feeding than when it was not, and was not different between the other two pairs (Fig. 1).

Both risk of predation and the number of hosts rejected affected the patch leaving tendency (likelihood ratio test, predation risk: $\chi^2 = 62.40$, $P < 0.001$; host rejection: $\chi^2 = 5.32$, $P < 0.05$). The patch leaving tendency increased by 10.5-fold when the predator is actively feeding, and by 2.5-fold when the predator was not actively feeding, as compared with the control (Table 1; Fig. 2). The patch leaving tendency, however, decreased by a factor of 0.87 for each increment in the number of hosts rejected (Table 1). The host instar (Fig. 3), the number of hosts stung once, and the number of hosts stung more than once did not affect the patch leaving tendency (Host instar: $\chi^2 = 0.49$, $P = 0.47$; No. hosts stung once: $\chi^2 = 0.009$, $P = 0.92$; No. hosts stung more than once: $\chi^2 = 0.004$, $P = 0.95$).

Discussion

Our results showed that *M. pulchricornis* adjusted its oviposition behavior in response to both host instar and the presence of the predator in a patch, attacking more L4 than L2 hosts but such effect varied depending on if the predator is present, being greater if the predator is present than if it is not. These performances suggest that *M. pulchricornis* regards the L4 as a higher valuable host in response to the presence of predation risk than it does in the absence of it. It is also interesting to note that *M. pulchricornis* decreased its attack in response to the presence of the predator which was actively feeding, as compared with the presence of the predator which was not feeding, but did not adjust its attack with regard to the difference between the presence of the predator which was not feeding and the absence of the predator. This observation suggests that the presence of the predator is estimated as a predation risk only when the predator is actively feeding by the parasitoid to make decisions on oviposition. The suggestion may explain why some other parasitoids pay scant attention to the presence of a predator. For example, Martinou et al. (2009) found that oviposition attempts of *Aphidius colemani* and mummified aphids were not affected by the presence of the predator on sweet pepper plants. Some studies showed that the presence of predators does not influence parasitoids' choice for

Table 1. Estimated regression coefficient (β) 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	β	SE (β)	exp (β)	Z value	P	Effect on leaving tendency
Predation risk						
Not feeding	0.91	0.25	2.50	3.62	<0.001	↑
Actively feeding	2.35	0.29	10.53	8.24		↑
Host rejection	-0.14	0.06	0.87	-2.25	0.025	↓

Note: The absence of the predator is the baseline. The upward arrow indicates increasing and the downward decreasing leaving tendency.

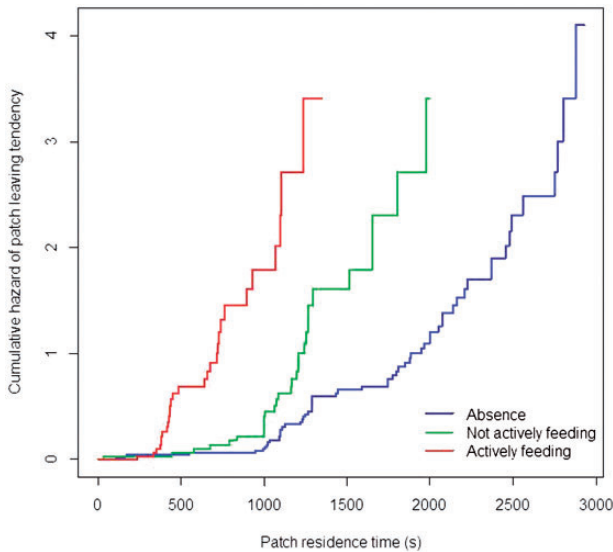


Fig. 2. The cumulative patch leaving tendency (hazard functions) of *M. pulchricornis* in response to the presence of the predator.

hosts even in cases where predator free plants are offered nearby (Bilu et al. 2006, Bilu and Coll 2007). A study on *Eretmocerus eremicus* (Hymenoptera: Aphelinidae) found that the parasitoid even increased its number of ovipositions in the presence of intraguild predator cues (Velasco-Hernández et al. 2013). We assume that in response to the predation risk *M. pulchricornis* may try to obtain more reproductive gains by allocating more time to attacking more high quality hosts, rather than by extending the patch residence time.

The results of our survival analysis showed that while *M. pulchricornis* decreased the patch leaving tendency with increasing number of hosts rejected, it increased the tendency in response to the presence of the predator, which was either actively feeding or not, as compared with the control (absence of the predator). These performances of *M. pulchricornis* are similar to some aphid parasitoids. It has been shown that aphid parasitoids can use trails left by intraguild predators on plant surfaces to avoid areas containing or already explored by predators (Nakashima and Senoo 2003, Nakashima et al. 2004). The presence of predators in a patch can make foraging aphid parasitoids increase their patch leaving tendency (Taylor et al. 1998, Raymond et al. 2000, Nakashima and Senoo 2003, Martinou et al. 2009, Meisner et al. 2011, Almohamad and Hance 2014, Velasco-Hernández et al. 2013). Furthermore, our study found that the patch leaving tendency increased more when the predator was actively feeding than when it was not. This result suggests that *M. pulchricornis* may regard the presence of the predator as a higher risk when it is actively feeding than when it is not. We assume that *M. pulchricornis* may perceive the

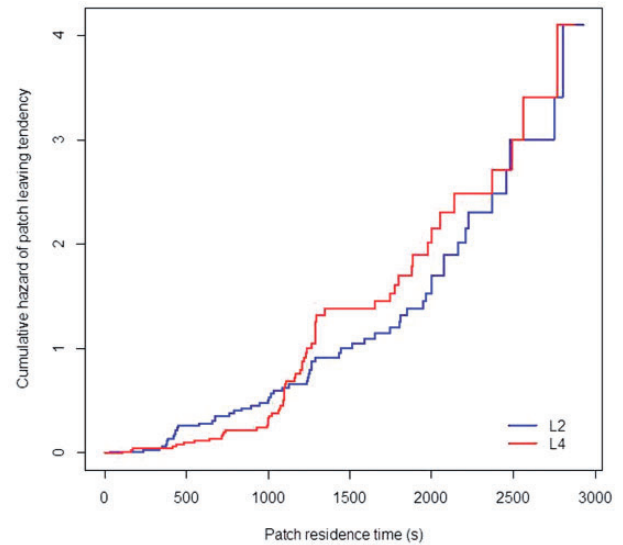


Fig. 3. The cumulative patch leaving tendency (hazard functions) of *M. pulchricornis* for L2 and L4 hosts.

predation behavior either visually or chemically (volatiles released from the prey-handling process such as host body fluids). Alternatively, it is possible that the predator induced the emission of visual or chemical cues from their prey. Although few studies have shown that caterpillars can produce alarm signals in response to the threat of predation, such behavior is well-known in aphids (reviewed in Vandermoten et al. 2012).

In addition to predation risk, host rejection also affected *M. pulchricornis* to make the patch leaving decision, decreasing the leaving tendency with increasing host rejections. This response to host rejections is same as shown in the previous study of this parasitoid where predation risk was not considered (Sheng et al. 2014). Theoretical models predict that to deal with competitors in a patch foragers should engage in a war of attrition and stay in the patch longer than when foraging alone (van Alphen and Visser 1990, Visser et al. 1992, Haccou and van Alphen 2008). We assume that the rejection of a host may inform foraging *M. pulchricornis* less about the decreasing value of the patch, as host density is generally much higher than needed, but more about the presence of potential competitors.

In conclusion, our study indicates that foraging *M. pulchricornis* attacks more L4 than L2 hosts in the presence of predation risk, and increases the patch leaving tendency with increasing host rejections and when the predator is actively feeding. Our results suggest that *M. pulchricornis* can exploit high quality host resources while minimizing predation risk, by attacking more hosts in high quality patches while reducing total patch time in response to risk of predation.

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