Entomology, Ornithology & Herpetology
Ueno and Ueno, Entomol Ornithol Herpetol 2015, 4:3
DOI: 10.4172/2161-0983.1000159
Short Communication
Open Access

Host Approaching Behavior in a Parasitoid Wasp (Hymenoptera: Ichneumonidae) as Influenced by Physiological State and Host Type

Kanako Ueno and Takatoshi Ueno*

Institute of Biological Control, Faculty of Agriculture, Kyushu University, Fukuoka 812-8581, Japan

Abstract

The present study highlighted the interactions of host type and physiological state (i.e., the number of mature eggs a female carries) in determining a parasitoid's host-finding behavior, using the solitary endoparasitoid *Itoplectis naranyae* (Hymenoptera: Ichneumonidae). Females took much shorter time to approach and attack healthy hosts of high-value than empty hosts of no-value, discriminating between the host types from a short distance. Variance of the time was much greater for empty hosts. A striking difference was detected in the influence of physiological state on wasp behavior; females with greater egg loads approached an empty host more quickly in order to examine its suitability for oviposition whereas egg load effects were not found for healthy hosts. Thus, egg load was involved in variation of the host-finding behavior but its effects depended on host types. We discuss the adaptive significance of the context dependent effects of egg load on parasitoid behavior.

Keywords: Parasitic wasp; Motivation; Foraging theory; Host selection; Nutritional state

Introduction

Environmental and physiological factors affecting insect host-selection behavior have extensively been studied by focusing on the means or average values of behavioral events to examine the effects of such factors. It is however common that behavior of an insect species varies considerably among individuals, and much less attention has been paid to factors that cause variation in the behavior [1-4].

Host selection behavior in insects can be viewed as a problem in foraging theory, and various models have been developed to explain the adaptiveness and optimality of the behavior [5-7]. These models stress the need for experimental studies that connect physiological state and oviposition decisions and predict that variation in oviposition behavior can be an adaptive consequence in response to variation in physiological state. Such models assume that egg load (i.e., the number of eggs a female insect carries in her ovaries) is a major physiological factor.

In fact, egg load has been demonstrated to influence the ovipositon behavior of insect herbivores and parasitoids [7-10]. These studies have demonstrated that females with greater egg loads are more likely to oviposit. Thus, individual variation in host selection and oviposition behavior strongly relates to variation in egg load.

A question then arises: Does physiological state of an insect female (i.e., egg load) affect host finding processes other than host acceptance? Host-searching behavior by insect females is made at three major steps: (A) a choice of habitat in which to search (habitat choice), (B) a choice of a particular patch (plants etc.) on which to land (patch choice), and (C) choice to oviposit or not after finding a potential host in the patch (host acceptance) [10,11]. Further, between the second and third processes, female insects may choose a potential target to approach within a patch. Hereafter, this process is termed "host approaching" process, and host selection may still occur at this process.

Previous studies have focused on the host acceptance process; it is unclear whether egg load could affect the other host searching processes. However, response variation is commonly observed in searching processes, and such variation may be explained adaptively when egg load effects are taken into consideration. Accordingly, the present study examines whether egg loads can influence the "host approaching" process of a parasitoid for a short distance.

The present study also examines the interactive effects between host types and egg load because egg load effects may depend on host quality. The pupal parasitoid *Itoplectis naranyae* (Hymenoptera: Ichneumonidae) was used as a test insect. We discuss the importance and adaptiveness of egg load effects in determining host finding behavior of parasitoids and the mechanisms involved in host type selection from a short distance by *I. naranyae*.

Materials and Methods

Parasitoid and host

Itoplectis naranyae is a polyphagous solitary endoparasitoid [12,13]. It searches for its host during the daytime by flying or hopping from leaf to leaf or stem to stem. On the plant (leaf and stem), the parasitoid walks and drums the plant with its antennae to search for hosts. The females parasitize a variety of lepidopteran pupae by laying their eggs singly within them.

A laboratory colony of *I. naranyae* was established using adult parasitoids collected from Fukuoka City, Japan. Female and male parasitoids were placed in plastic containers (7.5 cm in diameter, 5.5 cm in height), together with tissue paper saturated with a honey solution. The tissue paper was replaced twice a week thereafter. The containers were kept at 20 ± 1°C, 60-70 % RH, and 16:8 LD. The colony was maintained on pupae of a laboratory host, Galleria mellonella (Lepidoptera: Pyralidae). The host was reared on an artificial diet [3,13]. Host cocoons containing fresh pupae were presented to female

***Corresponding author:** Takatoshi Ueno, Institute of Biological Control, Faculty of Agriculture, Kyushu University, Fukuoka 812-8581, Japan, Tel: +81 92-642-3036; Email: ueno@grt.kyushu-u.ac.jp

Received August 01, 2015; **Accepted** August 18, 2015; **Published** August 20, 2015

Citation: Ueno K, Ueno T (2015) Host Approaching Behavior in a Parasitoid Wasp (Hymenoptera: Ichneumonidae) as Influenced by Physiological State and Host Type. Entomol Ornithol Herpetol 4: 159. doi:10.4172/2161-0983.1000159

I. naranyae in plastic containers. Parasitized hosts were removed and held at 20 ± 0.5°C until wasp emergence. Newly emerged wasps were paired and placed in the plastic containers and maintained as mentioned above. Wasps of F2 or F3 generations since the collection of wild females were used for experiments, and the effect of artificial selection during laboratory rearing on wasp behavior was hence minimized.

Experimental settings and hosts

Test females were obtained as follows. Several newly emerged males and females were placed together in a plastic container. After three days from the wasp emergence, males were removed, and female wasps were transferred to a new container individually. Each female received two fresh host cocoons for two hours, and this treatment was repeated for the five consecutive days. These 8-day-old females were used in experiments, and each female was tested only once.

All experiments took place in a climate room (25 ± 5°C, 60-70% RH). The additional light source, a desk light, was placed right above the experimental arena (7.5 cm in diameter, 5.5 cm in height) to avoid variation in phototaxis. A fresh pupa enclosed within the cocoon (one-three days old since pupation) was used as a high value host in the experiments. An empty cocoon from which a wasp had already emerged was used as a low value host, and it was collected from the mass-rearing container at least one day prior to the experiment. Emergence holes made by greater wax moths and by parasitoid were easily distinguished. Test females were divided into two groups, and each female was given one of the two host types during behavioral observations.

In our experimental set-up, the walking activity of *I. naranyae* was high, and the majority of time in an experimental arena was spent walking or sitting still. A fresh or an empty host was introduced into the arena, and the behavior of a female was observed continuously during a test. The time needed for the parasitoid to find and attack a host after host introduction was measured. In some cases, female parasitoids passed by a host without showing any interest in it. Typical host-attacking behavior was that a female drilled into a host with her ovipositor after mounting on the host with antennal examination. All-tested-females were dissected immediately after the observation in order to count the number of mature eggs. Forewing length of tested-females was also measured. In all, 48 and 40 females were used for the empty and the healthy host groups. Data were analyzed with the aid of JMP version 8 [14]. When necessary, the data were log-transformed upon the analysis to apply parametric procedures; untransformed data were presented. Voucher specimens were deposited in Institute of Biological Control, Kyushu University.

Results

Great variations in egg load were found in *I. naranyae*. The egg load varied from 1 to 29 with a mean of 9.99 ± 5.67 (SD). The size of adult females explained variation in egg load to some extent (27%) (Regression analysis, r^2=0.27, df=1, F=23.18, P<0.0001). Likewise, host-searching behavior varied among test *I. naranyae* although they had reared under a controlled laboratory environment. Although all female wasps finally attacked hosts, the time between host introduction into an experimental arena and host probing initiation by a test female ranged from 39 to 6497 sec on empty host cocoons and from 50 to 1987 sec on host cocoons containing a fresh pupa. The mean time (with SD) differed markedly between the two host types (1697.63 ± 1683.08 sec versus 230.78 ± 391.98 sec for the empty and the fresh hosts, respectively; Welch's ANOVA, df=1, F=34.28, P <0.0001), and female wasps required much less time to approach and attack on the fresh- than the empty host cocoons (Figure 1). Evidently, some wasps quickly found the empty cocoons and attacked them whereas others took much time (Figure 1).

Factors influencing the time were then analyzed. Among the three factors, wasp size was not a significant variable in a stepwise regression analysis. Thus, host type and egg number (hereafter, egg load) were used in the following analyses. An ANCOVA demonstrated that both factors were significant (Table 1). In addition, the analysis detected a significant interaction between the two factors (Table 1). Therefore, the relationships between egg load and the time required to start host probing were separately analyzed for each host type group with simple regression analyses. A significant negative relationship was detected between egg load and the time taken for host probing when host cocoons were empty (Figure 2) above; r^2=0.14, df=1, F=7.54, P=0.0086). Females with greater egg loads attacked the cocoons more quickly. Curiously, there was no significant relationship when host type was fresh cocoon (Fig. 2 below; r2=0.008, df=1, F=0.322, P=0.573). Females thus approached quickly to fresh cocoons regardless of the egg loads.

Discussion

In general, insect behavior varies among individuals even in a controlled laboratory condition [1,5,6]. Likewise, we have shown that searching activity in terms of the time required for host finding greatly vary among test females of *I. naranyae* (Figure 1) Great egg load variation is also found in *I. naranyae* (see the Results). Individual

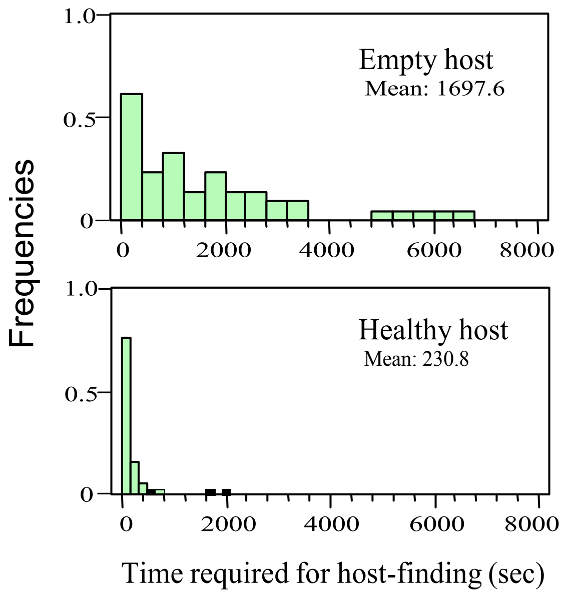

Figure 1: Variation in time that test wasps took to find and attack a host. Above: empty host cocoon with no value, below: high-value cocoons containing a fresh host pupa. Mean time and variance significantly differed between the two groups (Welch's ANOVA and Levene's test; P<0.0001).

Factors	t values	P
Egg load	-2.72	0.0079
Host type	4.69	<0.0001
Interaction	-2.46	0.016

The whole model: N=88, r^2=0.36, F=15.26, *P*<0.0001.

Table 1: Multiple regression analysis for examining factors influencing the time taken for host finding by *I. naranyae.*

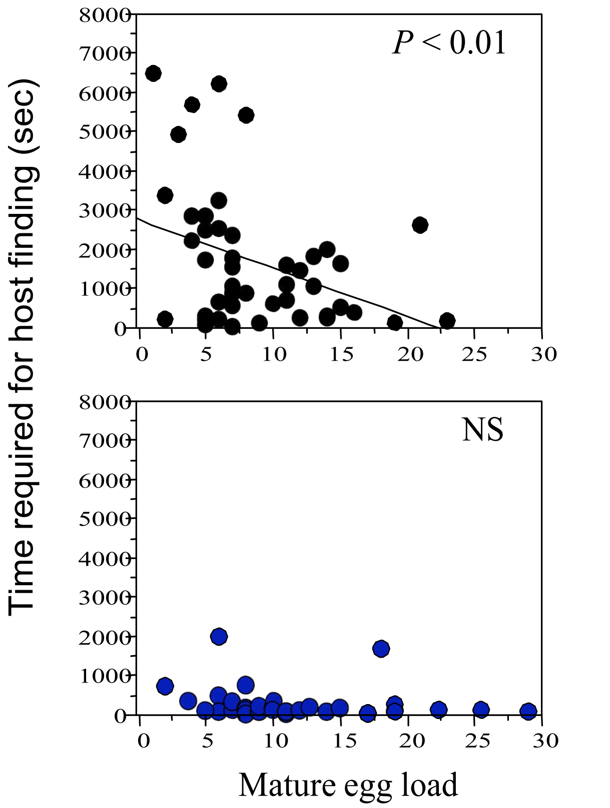

Figure 2: The relationships between egg load, the number of mature eggs that each female carried, and time taken for finding and attacking a test host. Above: empty host cocoon, below: fresh host cocoon.

variation in behavioral response may be explained by such egg load variation.

Here, we have examined the effects of physiological state on behavioral process during host finding, i.e. host approaching and attacking. Our study has revealed the importance of physiological state (egg load) on the parasitoid host finding process. Egg load effects on the host approaching behavior however depended on host types (Table 1). Below we discuss the importance of egg load in determining parasitoid searching behavior and the mechanisms involved in host type discrimination from a short distance.

Effect of physiological state

Egg load variation is shown to link to variation in the ovipositional decision of female parasitoids including *I. naranyae* [3,8-10,15]. Thus, egg load influeces motivation to ovipposit. Similarly, in the present study, motivation to oviposit would be different among test females via an egg load effect, and the difference should affect the host-approaching process in *I. naranyae*. The results of experiments presented here support this idea (Figure 2).

Theory based on state variable models predicts that female insects should broaden their range of acceptable hosts as the egg load increases [5-7]. An adaptive explanation for this is that a female should not be choosy about hosts when she has many eggs because she may die before all eggs are laid. In contrast, a female should select to oviposit only on high quality hosts when she has a few eggs. This is because she can lose opportunities to oviposit on hosts of high quality, which may be subsequently encountered after she has spent eggs on hosts of low quality.

This prediction has been tested only in the process of host acceptance, i.e. ovipositional decision [4,7-9,15]. However, we emphasize that the prediction can be extended in host selection from a distance. Females with a great egg load should approach any potential host recognized from a distance to see the suitability for oviposition but those with a low egg load should avoid low-quality hosts without contact if they are able to assess host quality from a distance. Host range modification in response to egg load should take place during the host approaching process as well as the host acceptance process.

The variation in rapidity of host approaching response observed in the present study should be understood from an adaptive viewpoint of optimal foraging theory incorporating egg load effects. Thus, the present result agrees with the most important prediction in dynamic state variable models. Our finding would contribute to the understanding of the fundamental habits of parasitoid foraging behavior.

A striking result is that egg load effects arise only when hosts are of poor quality (Figure 2). The interpretation is that, regardless of the number of mature eggs available, females should examine the suitability of any hosts if they have once recognized the hosts could be of the highest quality. Test female *I. naranyae* had been allowed experience with fresh host cocoons before testing, and are likely to learn the host type as highly suitable [3]. Thus, learning enables test females to recognize the presence of a high quality host from a short distance. In fact, the time took for host recognition does not differ between the host types when naïve females are used (Ueno and Ueno, personal observations).

Empty cocoons should be less attractive probably because they would smell differently. Females with a high level of motivation then approach empty cocoons fast whereas those with low motivation due to a low egg load should spend a small proportion of their overall foraging time in examining poor quality hosts. Our finding provides good evidence that egg load effects are context-dependent.

Host selection from a distance

Here, we have shown that female *I. naranyae* take much less time to recognize and attack a healthy host than an empty host when they had past experience with healthy hosts (Figure 1). The results suggest that discrimination from a short distance occurs in the process of host finding or selection. Most parasitoid species can recognize host types, i.e. host size, age, stage and prior parasitism, which are associated with the quality of hosts in terms of offspring development and fitness, and show preference to hosts of higher quality [4,15]. The majority of studies have examined host-selection behavior of parasitoids after host encounter, however.

Host selection from a distance has received little attention so far; very little is known whether foraging parasitoids positively select hosts to be approached from a distance. Our study evidently demonstrates the presence of host selection by *I. naranyae* from a short distance. The females may use chemical (odors) and visual cues (shape, color etc) to recognize the presence of a potential host from a distance, as with the other members of pimpline parasitoids [16-19,20].

Females are slow to respond to the empty cocoons probably due to their weaker attractiveness. Because physical features of cocoons do not differ between the host types, odors emitted from cocoons are a most likely cue causing the difference in host-approaching responses. Empty cocoons may contain fewer host-derived volatiles in comparison with the fresh cocoons, which may result in the weaker attractiveness.

More noteworthy in the present study is that some females nevertheless respond rapidly to empty cocoons that should be less attractive. As discussed above, females with high level of the motivation approach empty cocoons rapidly even when the cocoons are poor in attractive odors. Thus, host selection from a distance is context-dependent, and egg load modifies the response to odors from potential hosts. Our study highlights the importance of physiological state in determining the behavioral decision during the host approaching process by insect parasitoids.

Acknowledgment

We thank two anonymous reviewers for their helpful comments. This work was supported partly by grant No. 13760039 from the Ministry of Education, Culture, Sports, Science and Technology of Japan to T.U. and by JSPS Postdoctoral Fellowship to K.U.

References

1. Lewis WJ, Vet LEM, Tumlinson JH, Lenteren JC, Papaj DR (1990) Variations in parasitoid foraging behavior: Essential element of a sound biological control theory. Environ Entomol 19: 1183-1193.
2. Odendaal FJ, Rausher MD (1990) Egg load influences search intensity, host selectivity and clutch size in Battus philenor butterflies. J Insect Behav 3: 183-193.
3. Ueno K, Ueno T (2005) Effect of wasp size, physiological state and prior host experience on host searching behavior in a parasitoid wasp (Hymenoptera: Ichneumonidae). J Ethol 23: 43-49.
4. Hopper KR, Prager SM, Heimpel GE (2013) Is parasitoid acceptance of different host species dynamic? Funct Ecol 27: 1201-1211.
5. Mangel M (1989) An evolutionary interpretation of the 'motivation to oviposit'. J Evol Biol 2: 157-172.
6. Mangel M (2015) Stochastic dynamic programming illuminates the link between environment, physiology, and evolution. Bull Math Biol 77: 857-877.
7. Sirot E, Ploye H, Bernstein C (1997) State dependent super parasitism in a solitary parasitoid: egg load and survival. Behav Ecol 8: 226-232.
8. Collier TR, Murdoch WW, Nisbet RM (1994) Egg load and the decision to host-feed in the parasitoid, Aphytis melinus. J Anim Ecol 63: 299-306.
9. Heimpel GE, Rosenheim JA (1995) Dynamic host feeding by the parasitoid Aphytis melinus: the balance between current and future reproduction. J Anim Ecol 64: 153-167.
10. Ueno K, Ueno T (2007) The effects of prior host experience and egg load on host acceptance behavior of the parasitoid *Itoplectis naranyae* (Hymenoptera: Ichneumonidae) on empty hosts. J Fac Agric Kyushu Univ 52: 63-67.
11. Vinson SB (1998) The general host selection behavior of parasitoid hymenoptera and a comparison of initial strategies utilized by larvaphagous and oophagous species. Biol Cont 11: 79-96.
12. Ueno T (1998) Adaptiveness of sex ratio control by the pupal parasitoid wasp *Itoplectis naranyae* (Hymenoptera: Ichneumonidae) in response to host size. Evol Ecol 12: 643-654
13. Ueno T, Ueno K (2007) The effects of host-feeding on synovigenic egg development in an endoparasitic wasp, Itoplectis naranyae. J Insect Sci 7: 1-13.
14. JMP (2011) JMP version 8.0. SAS Institute Inc., Cary, NC.
15. Ueno T (1999) Host-feeding and acceptance by a parasitoid wasp (Hymenoptera: Ichneumonidae) as influenced by egg load and experience in a patch. Evol Ecol 13: 33-44.
16. van Alphen JJM, Vet LEM (1986) An evolutionary approach to host finding and selection. In: Waage J, Greathead D (eds) Insect Parasitoids. Academic Press, London, pp. 23-63.
17. Arthur AP (1981) Host acceptance by parasitoids. In: Nordlund DA, Jones RL, Lewis WJ (eds) Semiochemicals, their Role in Pest Control. Wiley, New York, pp. 97-120.
18. Sandlan K (1980) Host location by Coccygomimus turionellae (Hymenoptera: Ichneumonidae). Entmol Exp Appl 27: 233-245.
19. Schmidt JM, Carde RT, Vet LEM (1993) Host recognition by Pimpla instigator F. (Hymenoptera: Ichneumonidae): Preferences and learned response. J Insect Behav 6: 1-11.
20. Wackers F, Mitter E, Dorn S (1998) Vibrational sounding by the pupal parasitoid Pimpla (Coccygomimus) turionellae: an additional solution to the reliability-detectability problem. Biol Cont 11: 141-146.