The Effects of Prior Host Experience and Egg Load on Host Acceptance Behavior of the Parasitoid Itoplectis naranyae (Hymenoptera : Ichneumonidae) on Empty Hosts

Ueno, Kanako
Graduate School of Bioresource and Bioenvironmental Sciences, Kyushu University

Ueno, Takatoshi
Faculty of Agriculture, Kyushu University

https://doi.org/10.5109/9282

出版情報：九州大学大学院農学研究院紀要. 52 (1), pp.63-67, 2007-02-28. Faculty of Agriculture, Kyushu University
バージョン：
権利関係：

J. Fac. Agr., Kyushu Univ., **52** (1), 63–67 (2007)

The Effects of Prior Host Experience and Egg Load on Host Acceptance Behavior of the Parasitoid *Itoplectis naranyae* (Hymenoptera: Ichneumonidae) on Empty Hosts

Kanako UENO[1] and Takatoshi UENO*

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

(*Received November 10, 2006 and accepted December 1, 2006*)

Oviposition behavior of parasitoids commonly varies among individuals even under controlled laboratory conditions. Some female parasitoids actively oviposit on many hosts whereas the others may show a weak response to hosts, accepting only a fraction of hosts for oviposition. Variation of egg load, i.e. the number of mature eggs that a female carries, can be a major source of such behavioral variation among female parasitoids. In the present study, we assessed the effect of egg load versus prior host experience on host acceptance behavior of *Itoplectis naranyae*, a major ichneumonid parasitoid wasp inhabiting in rice paddies. Here we used empty host cocoons (parasitized hosts after wasp emergence) to examine the wasps' responses to hosts that were not available for oviposition but contained useful host information to be learnt. More females that had oviposition experience attacked the test hosts than naïve females. Experienced females carried more mature eggs than naïve females, suggesting that the difference in host attack rate could be due to the difference either in egg load or in prior host experience. A multiple logistic regression analysis showed that egg load effect was significant while experience was not. Females with a greater egg load were more likely to attack hosts. Thus, egg load was the sole factor affecting the wasps' decision to attack empty hosts, and, at least in part, explained behavioral variation observed in *I. naranyae*. The importance of physiological state, i.e. egg load, in determining parasitoid foraging behavior was discussed.

INTRODUCTION

The oviposition behavior of insect parasitoids has been intensively studied because it should play a profound role in host–parasitoid population dynamics and because they are an excellent group of organisms as models for testing evolutionary theory (Charnov, 1982; Godfray, 1994; Ueno, 1999a; Hochberg and Ives, 2000). Much attention has been paid to the issues of host acceptance/suitability, clutch size and sex allocation, and a number of environmental factors affecting such behavior have been identified (Vinson and Iwantsch, 1980; Charnov, 1982; Waage and Godfray, 1985; van Alphen and Visser, 1990; Godfray, 1994). Less attention, however, has focused on variation of oviposition behavior in parasitoids, and a number of questions have been remained unsolved (Godfray, 1994; Heimpel and Collier, 1996; Ueno, 1999b; Babendreier and Hoffmeister, 2002; Ueno and Ueno, 2005). A main question that remains is factors affecting individual variation of oviposition behavior.

Optimal foraging theory emphasizes the importance of physiological state, i.e. egg load, hunger level, etc., in determining variation of parasitoid behavior. The robust prediction of the theory is that female insects with greater egg loads should express broader host ranges by ovipositing on hosts of lower quality (Mangel 1987, 1989; Godfray, 1994; Heimpel and Collier, 1996; McGregor, 1997). In fact, egg load has recently been suggested to influence the oviposition behavior of parasitoids (Heimpel and Rosenheim, 1995; Heimpel *et al*., 1996; Ueno, 1999b; Babendreier and Hoffmeister, 2002; Burger *et al*., 2004). These studies show that individual variation in host acceptance behavior can relate to variation in egg load. However, there are still a number of open questions, and the validity of egg load effects should be confirmed for other parasitoids with different life history traits.

Here, we focus on host acceptance behavior of the parasitoid wasp *Itoplectis naranyae* (Hymenoptera: Ichneumonidae). The parsitoid is widely distributed in East and South East Asia (Townes *et al*., 1965) and is commonly abundant in rice paddies where it attacks several lepidopteran pests (Yasumatsu and Watanabe, 1965). *I. naranyae* therefore plays an important role as a natural enemy in the ecosystem of rice fields. The females parasitize host pupae and prepupae by laying their eggs singly within them. Female *I. naranyae* produces relatively large, yolk–rich anhydropic eggs continuously throughout the lifetime (Ueno and Ueno, 2004). Thus, the female invests much material to eggs, and the reproductive trait should lead to a flexible behavioral decision in response to egg load. It is however not known whether egg load affects oviposition behavior of *I. naranyae*.

In this paper, experiments were designed to evaluate the effects of prior host experience and egg load on host acceptance decisions by *I. naranyae*. Empty hosts, i.e. host cocoons from which wasps of *I. naranyae* had already been emerged, were used here.

---

[1] Laboratory of Insect Natural Enemies, Department of Applied Genetics and Pest Management, Graduate School of Bioresource and Bioenvironmental Sciences, Kyushu University.

* Corresponding author (E–mail: ueno@grt.kyushu–u.ac.jp)

Although empty cocoons cannot be used as an oviposition site, they contain information of the host and the host–habitat cues, such as odors, physical features, place etc. Such host–associated information may be useful for host searching females if they can learn. Therefore, females may approach and attack empty cocoons even if they are of no value as an oviposition site. Then, the behavioral response should depend on the environment and physiological state of female wasps. By using empty host cocoons, we examined how wasps' behavior was flexible in response to environmental and physiological variables. Based on the results, we discuss the importance of egg load as a determinant of parasitoid oviposition behavior.

MATERIALS AND METHODS

Parasitoid and host

A laboratory colony of *Itoplectis naranyae* was established using adult parasitoids collected from Fukuoka City, Japan. Female parasitoids were placed individually 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.

The colony was maintained on pupae of a laboratory host, greater wax moth *Galleria mellonella* (Linnaeus) (Lepidoptera: Pyralidae). Host cocoons containing fresh pupae were presented to female *I. naranyae* in the 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.

The greater wax moth was mass–read in plastic boxes (20cm*30cm*5cm), bedded with a wheat–husk–based artificial diet (wheat husk, honey, bee wax, glycerin, and yeast). Containers were kept in a climatic camber, 25–35°C and 60–80%RH. Mature larvae were collected and placed in a pupation camber in order to obtain clean cocoons. Collected cocoons were stored in a refrigerator in order to prevent further development. It is possible to confirm pupation within cocoons by color.

Experimental procedures

From the fourth day to the eighth day from the emergence of wasps, females were subject to pre–experimental treatments. Two female groups were set up. For one group, female wasps for testing were given host experi–ence. A female in the plastic container was allowed access to two fresh host cocoons for two hours. Two cocoons were placed in a container at once, where a female was kept. Two hours later, host cocoons were removed from the container. This procedure was repeated for five consecutive days; each female for testing was allowed to experience a total of 10 host cocoons during the pre–experimental period. Females for another group experienced no hosts during the pre–experimental treatment. Thus, naïve females were prepared.

All experiments were taken place in a climate room (25±5°C). The additional light source, a desk light, was placed right above the experimental arena in order to prevent biased wasps' behaviors due to phototaxis. The same kind of the plastic container (7.5 cm in diameter, 5.5 cm in height) was used as the experimental arena. Tests were taken place on the ninth day from the emergence. A female wasp was placed in a new container prior to the test. In this experiment, an empty cocoon that considered relatively low in value was used as a reward. Cocoons from which wasps had already emerged, thus empty, were collected from the mass–rearing container at least one day prior to the experiment.

Test was initiated by presenting an empty host cocoon for a female wasp in the container. The direct observations started immediately after host introduction. Behavioral responses to the host were carefully observed. Whether or not the female attacked the host was recorded. Ovipositor drilling was regarded as 'host attack', and this type of behavior meant that female wasps accepted a host to see the suitability for oviposition. The observation was terminated after 2 hours from host introduction. After the test, all females were dissected under a microscope to count the number of mature eggs in the ovary. Forewing length was measured as an index of wasp size. In all, 121 female wasps were used for the experiment. Statistical treatments were made with the aid of JMP (SAS Institute, 1997).

RESULTS AND DISCUSSION

The proportions of females that mounted and attacked empty test hosts differed between the female groups (Chi–squared test; N=121, df=1, x^2=6.62, P=0.010). The majority of females with prior host experience (98.0 %) attacked test hosts whereas only 84.9% of non–experienced females did so (Fig. 1). The numbers of mature eggs that test female wasps carried also dif-

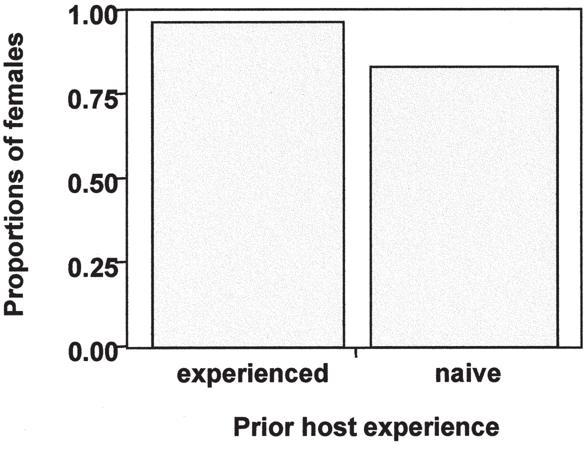

Fig. 1. The effect of prior host experience on the proportions of female wasps that attacked a test host during the observation. The proportions differ significantly between the groups (Chi–squared test; P=0.01).

fered significantly between the groups (ANOVA; df$=1$, $F=82.29$, $P<0.0001$), and the experienced females had greater egg load than naïve females (Fig. 2). Wasp size, measured with forewing length, did not differ between the groups (ANOVA; df$=1$, $F=2.26$, $P=0.14$).

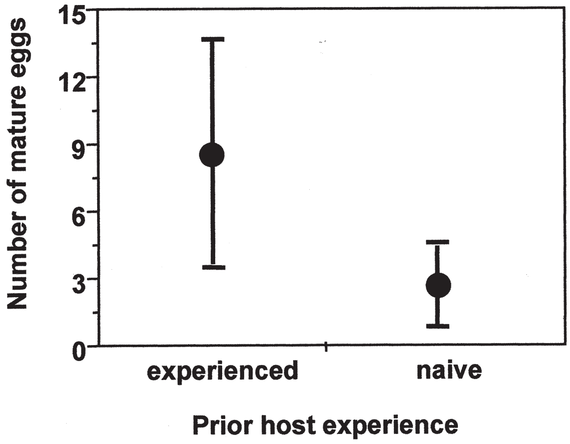

Fig. 2. The effect of prior host experience on the number of mature eggs that a female wasp held in the ovary. The mean numbers differ significantly between the groups (ANOVA; $P<0.0001$). The data are shown as means ± SD.

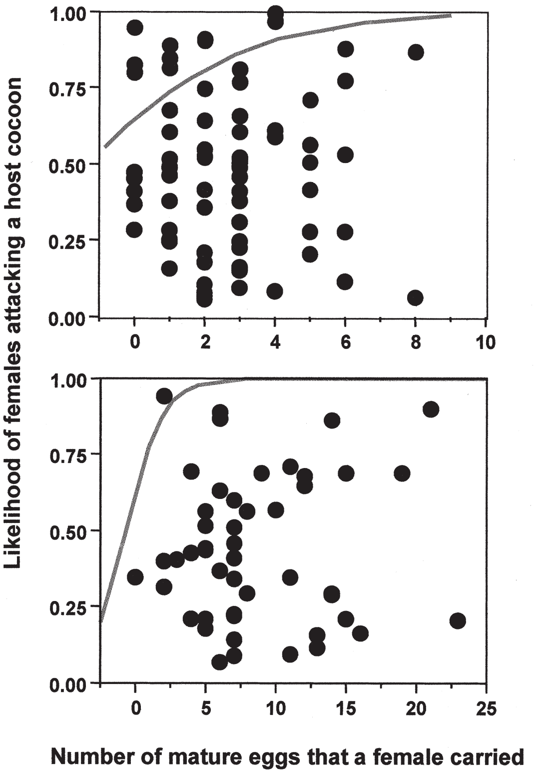

Fig. 3. Logistic regressions showing the relationships between egg load and likelihood of females attacking a test empty host (Above: naïve females, below: experienced females). Also see Table 1 for the result of a multiple logistic regression analysis that evaluates the effects of host experience versus egg load.

Table 1. Multiple logistic regression analysis for evaluating the effect of prior host experience and egg load on the likelihood of female wasps attacking a test host during the observations

Factors	χ^2	*P* values
Egg load	6.89	0.009
Prior experience	0.33	0.56

The whole model constructed is highly significant (N$=121$, $r^2=0.173$, df$=2$, $\chi^2=13.51$, $P=0.0012$). Interaction term is not included because it is not significant.

A multiple logistic regression analysis was then made. The whole model obtained was highly significant (N$=121$, $r^2=0.173$, df$=2$, $\chi^2=13.51$, $P=0.0012$), and the analysis showed that egg load had a significant effect on wasps' behavior but prior experience did not (Table 1). Interaction between the two factors was not significant ($P>0.05$). Accordingly, simple regression analyses were performed to examine the relationship between egg load and host attacking decision. For the experienced female group, no significant regression was obtained simply because test females except one individual attacked empty cocoons (Fig. 3a; df$=1$, $\chi^2=3.41$, $P=0.065$). For naïve females, a significant relationship was detected between the egg load and the likelihood of females attacking empty hosts (Fig. 3b; df$=1$, $\chi^2=3.89$, $P=0.049$, also see Table 1). Test females with more than 4 eggs all attacked host cocoons while a high proportion of females with a few eggs did not respond to hosts presented.

Thus, our study has demonstrated that egg load is involved in host acceptance behavior in *I. naranyae*, and that females with a greater number of mature eggs show a higher tendency to attack empty hosts. The difference in host attacking rates between female groups appears to be explained by the difference in egg load between the groups.

Many species of female parasitoids that continue to mature eggs throughout the lifetime feed on hosts to gain nutrients required for egg production (Jervis and Kidd, 1986; Heimpel and Collier, 1996). Therefore, there should be a clear link between host feeding and egg production for such parasitoids. This is the case for *I. naranyae* (Ueno, 1998; Ueno and Ueno, 2004). In this situation, female *I. naranyae* that have previously been presented with hosts (i.e. experienced females) would use some portions of hosts for feeding purposes and gain additional nutrients for egg production. Such females are likely to produce new eggs during the pre–experimental period. The group of experienced females in fact carried more eggs than the naïve females group (Fig. 2). Then, prior host experience and egg load should be mutually confounding. The difference in proportions of females attacking hosts (Fig. 1) might arise from the difference in egg load or from prior experience with hosts.

To separate the effects of the two confounding factors, we used a multiple logistic regression analysis. The analysis assessed that host acceptance by *I. naranyae* was influenced by egg load and not by prior experience

(Table 1). Simple logistic regression analyses also supported the result (Fig. 3). The analyses demonstrated that females were more likely to find and attack test hosts during 2 hours observations, indicating that the motivation to oviposit was higher in females with greater egg load.

Optimal host selection theory robustly predicts that the decision to oviposit on a host should be linked to the number of mature eggs that a female carries (Collier, 1995; Heimpel and Rosenheim, 1995; McGregor, 1997; Burger *et al*., 2004). This prediction was empirically supported only for a few parasitoid species (Heimpel and Rosenheim, 1995; Heimpel *et al*., 1996; Ueno, 1999b; Babendreier and Hoffmeister, 2002). The present study demonstrates that the prediction also holds true for *I. naranyae* (Fig. 3).

An adaptive explanation for egg load effects is that a female parasitoid should not be choosy about hosts when she has many eggs because she may die before all eggs are laid. In contrast, a female insect should be choosy about hosts and select to oviposit on high quality hosts when she has relatively few eggs. This is because she may lose opportunities to oviposit on hosts of high quality due to egg exhaustion after she has laid eggs on hosts of low quality. Likewise, females with a great egg load should examine any type of hosts even if the hosts are seemingly unsuitable for oviposition. This is because such hosts should contain a number of information that can be useful for finding hosts that may be present adjacent areas. Learning such information will enhance efficacy of host searching thereafter. In fact, female *I. naranyae* learns host–associated information during an attack of empty, seemingly no–value hosts (Ueno and Ueno, unpublished).

Many researchers would notice that motivation to oviposit differs among individual females: Some females may show a broad host range in terms of host species and types while the others may select to oviposit on a limited range of hosts. In other cases, females may lay many eggs during a laboratory test but the others lay only a few eggs. In a laboratory condition in which many variables can carefully be controlled, less variation in oviposition behavior would be expected; in fact, one would still find a considerable variation.

Three major factors may be involved in behavioral variation: Genetic elements, physiological and informational states (Lewis *et al*., 1990). The experiments presented here were designed to evaluate the importance of the two factors, i.e. experience (informational state) and egg load (physiological state), in affecting the host attacking behavior of *I. naranyae* females. Our study has identified an involvement of egg load. Rapidity of behavioral responses varies among test females, and egg load difference explains at least in part the variation in rapidity. Until recently, most studies of foraging behavior have made the simple assumption that egg supply of foraging parasitoids is not limiting and that maximizing oviposition rate per unit time was the best strategy for them (e.g. Waage and Godfray, 1985; van Alphen and Visser, 1990; Godfray, 1994). Under this assumption, however, behavioral variation observed is not understood with adaptive interpretations. As theory stresses (e.g. Mangel 1987, 1989; Collier, 1995; Heimpel and Rosenheim, 1995; McGregor, 1997), a female parasitoid can maximize her lifetime reproductive success by making different decisions at different egg loads. Then, behavioral variation emerges as a consequence of adaptive responses. Understanding egg load effects on behavioral responses can contribute to the fundamental understanding of parasitoid foraging behavior, which has been molded by natural selection.

REFERENCES

van Alphen, J. J. M. and M. E. Visser 1990 Superparasitism as an adaptive strategy for insect parasitoids. *Annu. Rev. Entomol*., **35**: 59–79

Babendreier, D. and T. S. Hoffmeister 2002 Superparasitism in the solitary ectoparasitoid *Aptesis nigrocincta*: the influence of egg load and host encounter rate. *Entomol. Exp. Appl*., **105**: 63–69

Burger, J. M. S., L. Hemerik, J. C. van Lenteren and L. E. M. Vet 2004 Reproduction now or later: optimal host–handling strategies in the whitefly parasitoid *Encarsia formosa. Oikos*, **106**: 117–130

Charnov, E. L. 1982 *The Theory of Sex Allocation*. Princeton University Press, Princeton, NJ

Collier, T. R. 1995 Host feeding, egg maturation, resorption, and longevity in the parasitoid *Aphytis melinus* (Hymenoptera: Aphelinidae). *Ann. Entomol. Soc. Am*., **88**: 206–214

Godfray, H. C. J. 1994 *Parasitoids: Behavioral and Evolutionary Ecology*. Princeton University Press, Princeton

Heimpel, G. E. and J. A. Rosenheim 1995 Dynamic host feeding by the parasitoid *Aphytis melinus*: the balance between current and future reproduction. *J. Anim. Ecol*., **64**: 153–167

Heimpel, G. E. and T. R. Collier 1996 The evolution of host feeding behaviour in insect parasitoids. *Biol. Rev*., **71**: 373–400

Heimpel, G. E., J. A. Rosenheim and M. Mangel 1996 Egg limitation, host quality, and dynamic behavior by a parasitoid in the field. *Ecology*, **77**: 2410–2420

Hochberg, M. E. and A. R. Ives 2000 *Parasitoid Population Biology*. Princeton University Press, Princeton

Jervis, M. A. and N. A. C. Kidd 1986 Host–feeding strategies in hymenopteran parasitoids. *Biol. Rev*., **61**: 395–434

JMP 1997 JMP version 3.2. SAS Institute Inc., Cary, NC

Lewis W. J., L. E. M. Vet, J. H. Tumlinson, J. C. van Lenteren and D. R. Papaj 1990 Variations in parasitoid foraging behavior: essential element of a sound biological control theory. *Environ. Entomol*., **19**: 1183–1193

Mangel, M. 1987 Oviposition site selection and clutch size in insects. *J. Math. Biol*., **25**: 1–22

Mangel, M. 1989 An evolutionary interpretation of the 'motivation to oviposit'. *J. Evol. Biol*., **2**: 157–172

McGregor, R. 1997 Host–feeding and oviposition by parasitoids on hosts of different fitness value: Influences of egg load and encounter rate. *J. Insect Behav*., **10**: 451–462

Townes, H., S. Momoi, and M. Townes 1965 *A Catalogue and Reclassification of the Eastern Palearctic Ichneumonidae*. Memoris of The American Entomological Institute No. 5.

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

Ueno, T. 1999a Host–size–dependent sex ratio in a parasitoid wasp. *Res. Popul. Ecol*., **41**: 47–57

Ueno, T. 1999b 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

Ueno, K. and T. Ueno 2004 Relationship between female size and host–feeding behavior in the parasitoid wasp *Itoplectis naranyae* (Hymenoptera: Ichneumonidae). *J. Fac. Agric., Kyushu Univ*., **49**: 77–84

Ueno, K. and T. Ueno 2005 Effect of wasp size, physiological state, and prior host experience on host–searching behavior in a parasitoid wasp (Hymenoptea: Ichneumonidae). *J. Ethol*., **23**: 43–49

Vinson, S. B. and G. F. Iwantsch 1980 Host suitability for insect parasitoids. *Annu. Rev. Entomol*., **25**: 397–419

Yasumatsu, K. and C. Watanabe 1965 *A tentative Catalogue of Insect Natural Enemies of Injurious Insects in Japan. Part 2. Host Parasite–predator Catalogue*. Entomol. Lab., Fac. Agric., Kyushu Univ., Fukuoka

Waage, J. K. and H. C. J. Godfray 1985 Reproductive strategies and population ecology of insect parasitoids. In *Behavioural Ecology: Ecological Consequences of Adaptive Behaviour* (R. M. Sibley and R. H. Smith eds.). Blackwell, Oxford, pp. 449–470