J Ethol (2005) 23:43–49
DOI 10.1007/s10164-004-0126-2

ARTICLE

Kanako Ueno · Takatoshi Ueno

Effect of wasp size, physiological state, and prior host experience on host-searching behavior in a parasitoid wasp (Hymenoptera: Ichneumonidae)

Received: February 12, 2004 / Accepted: August 3, 2004 / Published online: November 11, 2004

Abstract Host-searching behavior in insects generally varies among individuals. A number of physiological and environmental factors can be involved in such individual variation. Here, a series of behavioral observations were made to highlight the importance of physiological state (i.e., number of mature eggs a female carries, amount of nutrient reserves, etc.) and learning state (i.e., prior host experience) on host-approaching behavior of parasitoids. *Itoplectis naranyae* (Hymenoptera: Ichneumonidae), a solitary endoparasitoid wasp attacking lepidopteran pupae and prepupae, was used as a test insect. The results show that female wasps with experience ovipositing on hosts 2 days before the test found hosts more quickly than did naïve wasps. Prior experience of host odor itself did not affect host-finding behavior, however. A single oviposition was enough for wasps to shorten time to find a host; additional experience had no significant effect on the efficiency of searching. The number of mature eggs a female carried had no effect on the time required to find a host regardless of prior host experience. The size of wasps, instead, was a significant factor when wasps had no prior host experience, and larger wasps found hosts more rapidly than did smaller wasps. Searching activity was not affected by how many hosts a female wasp had fed on before testing.

Key words Parasitic wasp · Host location · Pimplinae · Egg load · Nutritional state · Host feeding

Introduction

The behavior of insect parasitoids commonly varies among individuals within species, and such variation is generally observed even under laboratory conditions, where many possible factors can be carefully controlled (Lewis et al. 1990). Many recent studies have extensively examined factors causing behavioral variation in parasitoids. Informational (i.e., learning) and physiological states are among the factors to which growing attention has been paid (e.g. Charnov and Skinner 1988; Mangel 1987, 1989; Heimpel and Collier 1996; Dukas 1998).

Informational state is an important factor affecting oviposition behavior of female parasitoids. A striking difference is generally observed between experienced and naïve females. Females that have previous experience with hosts, host plants, or other host-associated stimuli are often more efficient in finding their host than are naïve females (e.g., van Alphen and Vet 1986; Lewis et al. 1991; Cortesero et al. 1995). Learning is accepted as the major mechanism causing the behavioral changes as the result of experience (van Alphen and Vet 1986; Papaj and Lewis 1993; Vinson 1998).

Recent host-selection models predict that variation in oviposition behavior can be an adaptive response to variation in physiological state among females, and that egg load (i.e., number of eggs a female carries in the ovary) is one of the most important physiological factors (Mangel 1987, 1989; Collier 1995; Heimpel and Collier 1996). Such models have stressed the need for experimental studies that connect physiological state and oviposition decisions.

Recent experimental studies have supported the model prediction: egg load has been demonstrated to influence the host-acceptance behavior of parasitoids (Collier et al. 1994; Heimpel and Rosenheim 1995; Ueno 1999) and herbivores (Odendaal and Rausher 1990; Prokopy et al. 1994). These studies show that egg load is variable even in controlled laboratory conditions, and that individual variation in host-acceptance behavior strongly relates to variation in egg load.

The present study focused on the effect of physiological and informational state on searching behavior in a parasitoid wasp. Host-searching decisions by insect parasitoids are made at three main levels: (1) where to search (habitat choice), (2) where to land (patch choice), and (3) whether to oviposit after finding a potential host in the patch (host acceptance). Further, between the second and third steps, which potential target she should approach from a short

K. Ueno · T. Ueno (✉)
Institute of Biological Control, Faculty of Agriculture, Kyushu University, Fukuoka 812-8581, Japan
e-mail: ueno@grt.kyushu-u.ac.jp

distance within a patch is included. This latter host-finding process was specifically the focus of the present study.

Previous studies addressing the effect of physiological state have focused on host acceptance. It is unclear whether egg load affects host finding. In addition, interactions among factors associated with host-finding behavior such as physiological state, information state, and female size have seldom been investigated (but see Rosenheim and Rosen 1991). The primary objective of this study was to examine whether physiological state can influence the host-finding process in a parasitoid. Further, interactions among female size, physiological state, and learning state were investigated.

Itoplectis naranyae (Hymenoptera: Ichneumonidae) is a parasitic wasp widely distributed in East and Southeast Asia (Townes et al. 1965). A solitary endoparasitoid, *I. naranyae* is commonly found in rice paddies, where it attacks several lepidopteran pests (Yasumatsu and Watanabe 1965). The females parasitize host pupae and prepupae by laying their eggs singly within them; this parasitoid produces relatively large, yolk-rich anhydropic eggs continuously throughout its lifetime (Ueno and Tanaka 1994). As a host-feeding parasitoid, *I. naranyae* uses materials gained from the host for egg production (Ueno 1998; Ueno and Ueno 2004).

I. naranyae searches for its host during daylight, flying or hopping from leaf to leaf or stem to stem. During flights, the parasitoid uses cues that can be recognized from a relatively long distance to find a plant individual where hosts may be present. After landing on the plant, the parasitoid walks and drums the plant (leaf and stem) with its antennae to locate a host. During this stage of search, *I. naranyae* probably uses host-associated cues that can be perceived from a short distance.

In this article, we investigate (1) whether learning is involved in host finding in *I. naranyae*, and (2) how host-finding behavior of *I. naranyae* is influenced by egg load and nutritional reserves. In addition, the effect of female size is examined. Based on the results, factors affecting host-finding process in *I. naranyae* are discussed.

Materials and methods

Parasitoids

Wild female *I. naranyae* were collected on the shores of the Umigawa River at Higashi-ku, Fukuoka City, in late spring 2001. Offspring were thereafter reared continuously in the laboratory with occasional introductions of newly captured adult wasps. Pupae of the greater wax moth, *Galleria mellonella* (L.), were used as hosts. Although *G. mellonella* is not a natural host of *I. naranyae*, wild-caught females readily oviposited on it and the offspring were successfully obtained. Wasps and parasitized hosts were kept in an incubator [20°C, 60–80% realtive humidity (RH), and 16 : 8 h light : dark]. Tissue paper saturated with a honey-water solution was placed in rearing containers as a food source.

Host

The greater wax moth was mass reared in plastic boxes (20 × 30 × 5 cm), bedded with a wheat-husk-based artificial diet (wheat bran, honey, beeswax, glycerin, and yeast). Containers were kept in a climatic chamber at 25–35°C and 60–80% RH. Mature larvae were collected and placed in a pupation chamber to obtain clean cocoons. Cocoons were stored in a refrigerator to prevent further development. It is possible to confirm pupation within cocoons by color. Fresh pupae enclosed within the cocoon (1–3 days from pupation) were used as test hosts in the experiments.

Effect of prior host experience

We first set up a simple experiment to assess the effect of prior host experience on searching behavior of female *I. naranyae*. For this purpose, wasps with and without prior oviposition experience were prepared.

Experimental female wasps were obtained as follows. Several newly emerged males and females were placed together in a plastic container (7.5 cm in diameter and 5.5 cm in height) and allowed to mate. Three days after wasp emergence, male wasps were removed, and each female wasp was transferred to a new container to experience host-exposure treatments for the next 5 consecutive days.

Wasps were divided into two groups: experienced and naïve wasps. From the 4th to the 8th day after eclosion, females were subjected to host-exposure treatments. A female in the "experienced" group was allowed access to two fresh cocoons for 2 h. Two cocoons were placed together in a container where a female was kept. Two hours later, the cocoons were removed from the container. This procedure was repeated daily for 5 consecutive days; thus each female was allowed to experience ten cocoons during the pre-experimental period. "Naïve" female wasps were not allowed access to any hosts. The test was conducted with 10-day-old wasps, and each female was tested only once.

All experiments were conducted in a climate room (25 ± 5°C, 60–70% RH). An additional light source, a desk light, was placed directly above the experimental arena to prevent biased wasp behaviors due to phototaxis. Plastic containers (7.5 cm in diameter and 5.5 cm in height) were used as experimental arenas. A fresh host cocoon was placed in an arena, and the observation was started. The behavior of a female wasp was observed continuously during a test. Time required until each wasp attacked and oviposited on a host was recorded. In addition, the number of encounters with a host was recorded. Antennation of a host was considered to be an encounter with a host. In all, 76 female wasps were used in the experiment.

Factors affecting searching behavior

We designed the second experiment to analyze factors influencing wasps' searching behavior. Female wasps were allowed to experience two hosts on the 7th day after wasp emergence. The two hosts were removed from the container after a 2-h exposure time. With this pre-experimental treatment, about half of the test females oviposited in at least one host while the remaining females did not. Test females that did not oviposit, however, experienced the odors of hosts during the treatment. Thus, it was possible to evaluate whether experience of host odors by itself caused the reduction in searching time until host encounter. The test was conducted on the 9th day after wasp emergence (i.e., 2 days after the first host experience).

A test was conducted as with the first experiment. All tested females were dissected to count the number of mature eggs in the ovary. Forewing lengths of tested females were measured under a binocular microscope. Voucher specimens are deposited at the Institute of Biological Control, Kyushu University.

Data analysis

Data were analyzed with the aid of JMP (SAS Institute 2001) and StatView (SAS Institute 2000). Data from the behavioral study were first subjected to tests of homogeneity of variance to determine the suitability of analyses with parametric statistical procedures. Accordingly, Wilcoxon's signed rank test was used to assess the effects of prior host experience on time in the first experiment. The results of the second experiment were first subjected to multiple regression analyses, and the relationships between time until host finding and egg load or wasp size were examined using simple regression analyses.

Results

Effect of prior host experience

The majority of time in the container was spent walking, preening, or sitting still. A highly significant difference was detected between experience and the time required to find a host (Wilcoxon's test; $Z = 5.94$, $P < 0.0001$). Female wasps that had no oviposition experience required a much longer time to find a host than those with oviposition experience (Fig. 1). In addition, an *F*-test showed that variation in the time differed between the groups ($F = 0.58$, $P < 0.0001$). Thus, prior host experience strongly affected host-searching behavior in *I. naranyae*.

Factors affecting searching behavior

Actively walking wasps that approached a host typically mounted the host and antennated it. However, wasps occasionally passed by a host without attacking. Accordingly, the number of approaches made until attack on a host was compared between experienced and naïve wasps. Mean number of approaches (±SE) was 1.36 ± 0.52 and 2.15 ± 0.48 for experienced and naïve wasps, respectively. There was no significant difference between the groups (analysis of variance; $F = 1.24$, $P = 0.28$).

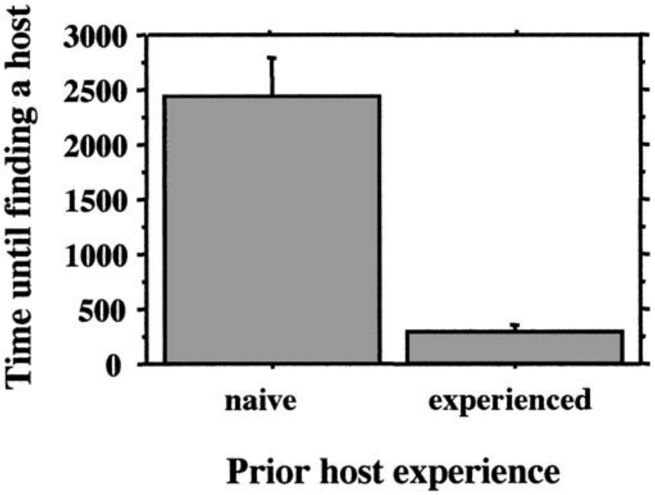

Fig. 1. Effect of prior host experience on time required to find a host by *Itoplectis naranyae*. Means significantly differed between the wasp groups (Wilcoxon's test; $P < 0.0001$). *Error bars* indicate standard errors

Table 1. Multiple regression analysis for factors affecting time required by *IItoplectis naranyae* to find a host

Factors[a]	*F*	*P*
Naïve females		
Forewing length	5.719	0.028
Egg load	0.148	0.705
Experienced females		
Forewing length	0.864	0.375
Egg load	0.266	0.617
Number of ovipositions	0.798	0.393
Number of host feedings	1.828	0.207

[a] No interactions were found to be significant ($P > 0.05$)

The time required to find and attack a host was again much longer for naïve wasps than experienced wasps (mean ± SE; 2,122.8 ± 574.4 s for naïve females; 151.7 ± 18.3 s for experienced females), and the difference was highly significant (Wilcoxon's test; $Z = -4.18$, $P < 0.0001$). In addition, the time to attack markedly varied among naïve female wasps (Fig. 2).

Factors causing such variation in time were analyzed with a multiple regression analysis. Because no significant relationships were detected between wasp size and egg load (simple regression analysis; $r^2 = 0.06$, $F = 1.24$, $P = 0.28$ for naïve wasps; $r^2 = 0.10$, $F = 1.59$, $P = 0.22$ for experienced wasps), both factors were included in statistical models. The analysis showed that none of the factors examined significantly influenced the time required to find a host when females had had previous host experience (Table 1). No significant relationship was detected between the amount of host experience and time required to find a host (Table 1, Fig. 3). This indicated that a single oviposition experience was enough for female wasps to shorten the time. The effect of nutritional reserves on wasp behavior was evaluated by adding the number of hosts used for host feeding one day earlier as a factor. Again, the factor was not significant

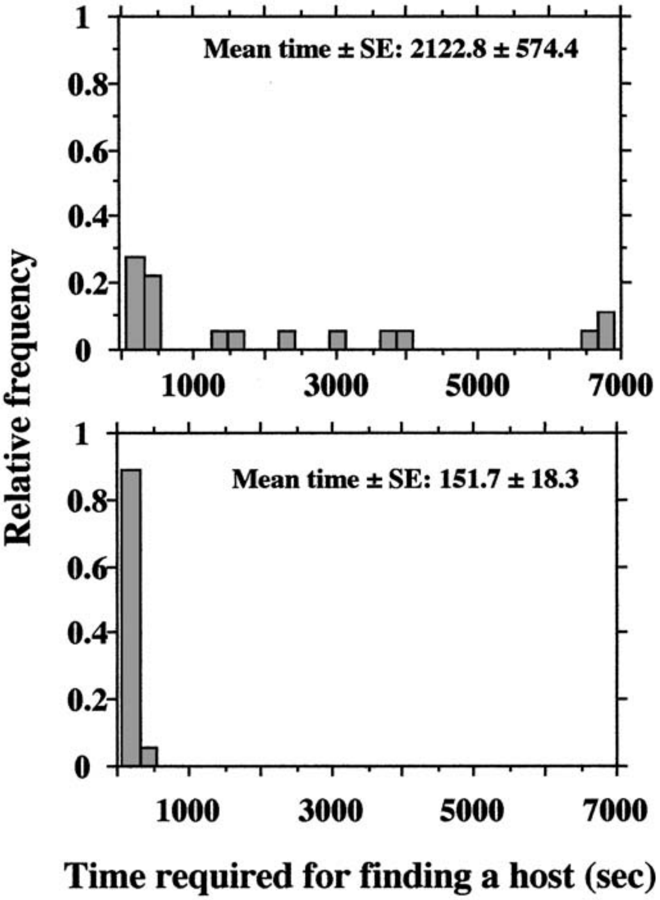

Fig. 2. Frequency distribution of time until *I. naranyae* found a host. The mean time differed significantly between the wasp groups (Wilcoxon's test; $P < 0.0001$). *Top* Wasps that experienced host odors but did not oviposit. *Bottom* Wasps that experienced oviposition once

(Table 1). Egg load and wasp size also did not have significant effects on host-finding behavior of experienced wasps (Figs. 4, 5).

Similarly, a multiple regression analysis was applied to analyze factors involved in time variation for naïve wasps. The analysis showed that egg load did not have a significant effect on time required to find a host (Table 1). Egg load thus had no significant effect on time to find a host regardless of prior host experience (Fig. 4). However, wasp size significantly influenced how quickly a female wasp found a host when she did not have prior host experience (Table 1). A simple regression analysis showed that larger wasps required less time to find a host (Fig. 5; $r^2 = 0.18$, $F = 6.95$, $P = 0.017$).

Discussion

Learning and host finding from a short distance

In the present study, we have shown that females of *I. naranyae* that had prior experience with hosts required less time to find a host than those without experience (Fig. 1). The results suggest that learning is involved in the process of host finding from a short distance. Many studies have demonstrated that foraging behavior of insect parasitoids

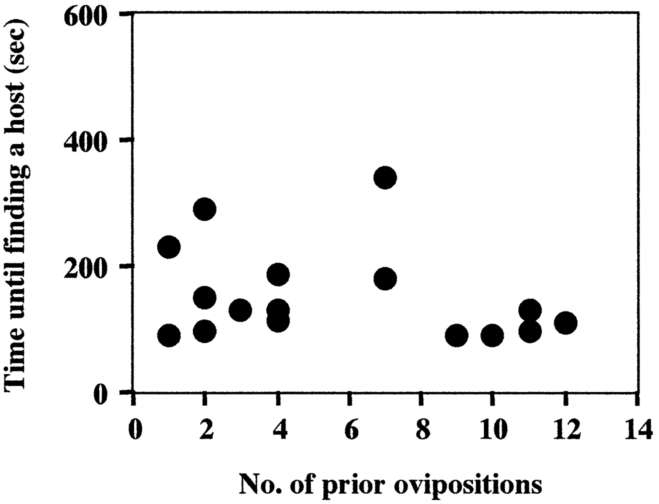

Fig. 3. Relationship between the amount of oviposition experience (number of prior ovipositions) and time required to find a host. No significant correlation was detected (Kendall's rank correlation test; $P > 0.05$)

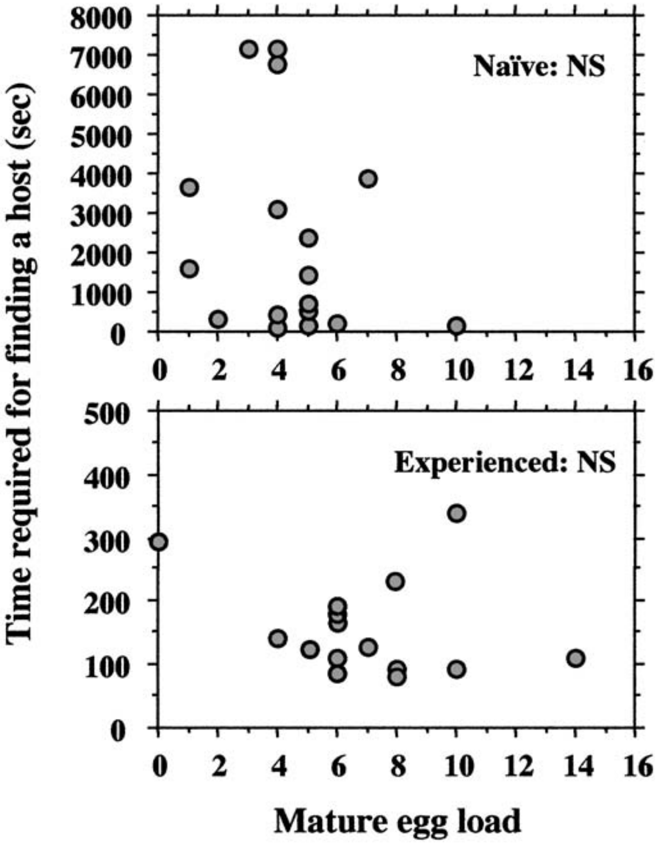

Fig. 4. Relationship between time until host was found and the number of mature eggs test females carried. No significant correlation was detected for either naïve (*top*) or experienced (*bottom*) wasps (Kendall's rank correlation test; $P > 0.05$)

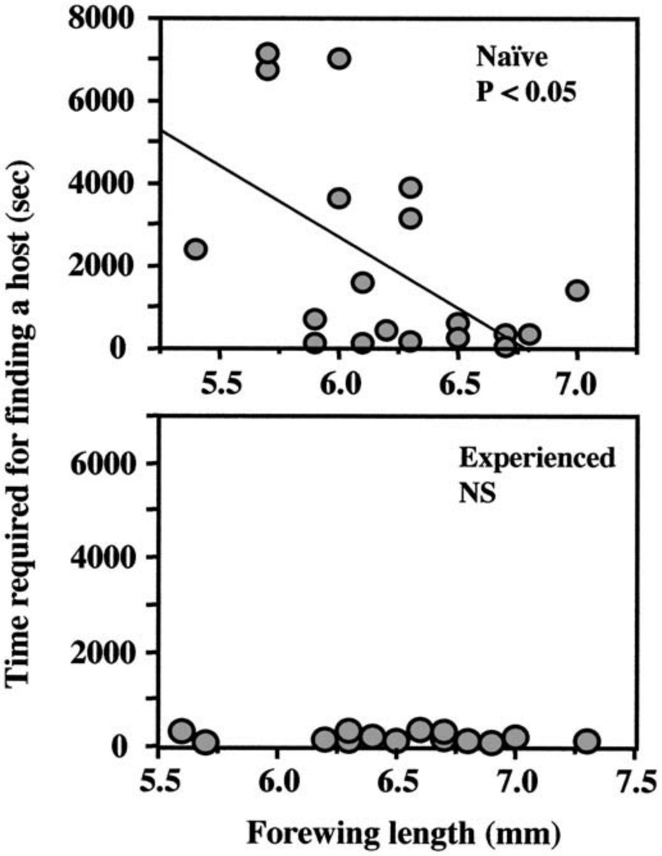

Fig. 5. Relationship between wasp size (forewing length) and time required to find a host. A negative correlation was detected for naïve wasps (*top*, Kendall's rank correlation test; $P < 0.05$) whereas there was no significant correlation for experienced wasps (*bottom*, $P > 0.05$)

differs between females with and without prior experience of oviposition, and that experienced females are more effective in locating their host (van Alphen and Vet 1986; Lewis et al. 1990; Vet and Dicke 1992; Godfray 1994; Vinson 1998). Learning is now accepted as the major mechanism that causes the behavioral changes as the result of experience. Such learning is widespread in parasitoids (van Alphen and Vet 1986; Papaj and Lewis 1993; Vinson 1998).

Our second experiment showed that experience with host odors itself did not result in reduction of time to find a host; oviposition experience was essential to evoke learning (Fig. 2). Experience with host-associated stimuli alone may alter parasitoid searching behavior and physiological state such as fecundity (e.g. Lewis et al. 1991). However, in many cases, oviposition is prerequisite to evoke learning (van Alphen and Vet 1986; Schmidt et al. 1993), and this appears to be the case for *I. naranyae*.

Parasitoids use a series of host cues that are possible to sense from a distance (Arthur 1981; Vet and Dicke 1992; Vinson 1998). Learning of host-location cues recognized from a relatively long distance is well documented for many parasitoids, and they use the learned cues during searching flight (e.g., Vet and Dicke 1992; Wackers and Lewis 1994). In our experimental set-up, *I. naranyae* mostly located a host by walking over a short distance. Our study therefore suggests that *I. naranyae* can learn to use host-location cues from a short distance. The cues may involve the color, shape, and/or odor of host cocoons, as for other related ichneumonids (Sandlan 1980; Schmidt et al. 1993).

Time to find a host did not depend on how many ovipositions each wasp had experienced (Fig. 3). This suggests that single oviposition experience is enough to evoke learning and to shorten the time for host finding. Although several studies have shown that the amount of experience positively affects learning behavior in parasitoids (Honda and Kainoh 1998; but see Poolman et al. 1992), this appears not to be the case for *I. naranyae*.

Factors causing behavioral variation

It is common for insect behavior and physiological state to vary among individuals even under controlled laboratory conditions. We showed that searching activity greatly varied among females of *I. naranyae* particularly when they had no prior oviposition experience (Fig. 2). In our study, we did not standardize the size of test female wasps. Therefore, wasp size may be an explanation for such behavioral variation. Alternatively, individual variation in behavior may be explained by variation in physiological state.

The effects of prior oviposition experience on host finding were evident in the present study. Variation in the time until female wasps found a host was wide when the wasps had no prior oviposition experience but a single oviposition experience made variation in time to encounter narrow (Figs. 2, 3). Wasp size had a significant effect on time to find a host, although this was the case only when female wasps had no prior oviposition experience (Fig. 5).

Naïve larger wasps were able to find a host more quickly than naïve smaller wasps (Fig. 5). There are two possible explanations for this. One is that larger wasps walk faster so that they find a host more quickly. The other explanation is that larger wasps have a greater ability to detect a host. In a related species, host-finding ability is suggested to be greater for larger wasps because larger wasps can produce larger sound vibrations to detect a host (Wackers et al. 1998; Otten et al. 2001).

Curiously, wasp size effects disappeared after experience with hosts (Fig. 5). Small wasps were able to find a host as rapidly as were large wasps. This suggests that small wasps experience a reduced disadvantage of being small after successfully finding a host. Thus, improvement in host-finding efficiency is estimated to be higher for smaller wasps (Fig. 6).

In addition, our results suggest that learning could potentially make a greater difference to the host-finding efficiency for smaller females. Smaller females shortened the time required for finding a host much more than did larger females (Fig. 5). The degree of improvement via experience was also higher in smaller females (Fig. 6). Although many studies have shown that learning and experience improve foraging efficiency of insects, very few have examined how improvement via learning can interact with other factors involved in insect behavior. The advantage of being large

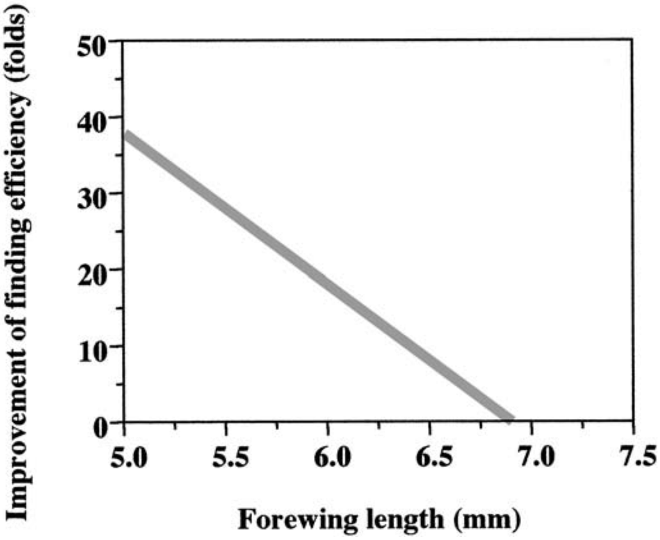

Fig. 6. Estimated improvement of host-finding efficiency in relation to wasp size for naïve *I. naranyae*

has been repeatedly demonstrated for many parasitoids with laboratory studies; larger females of many parasitoid species have greater fecundity, longer life span, and shorter handling time, among other advantages (van den Assem et al. 1997; Godfray 1994; Quicke 1997). Learning may, however, play a role in weakening the disadvantages of being small. Our result highlights the potential importance of learning in molding fitness/size function.

Motivation to oviposit generally varies among insect individuals. Variation in motivation is a feature that is often overlooked in insects. Factors involved in motivation can be egg load, nutritional reserves, and age of insects (Mangel 1987, 1989; Lewis et al. 1990; Sirot et al. 1997). Female *I. naranyae* that had no prior experience with hosts showed a great variation in time required for finding a host (Fig. 2). We suspect that such physiological factors could be involved in variation of time. The results show that physiological state, that is, egg load, had no significant effects on how quickly the female found a host (Fig. 5). Instead, our study shows that female size affected the efficiency of host finding (Fig. 4). Because it is common that wasp size positively correlate with egg load, the two factors are mutually confounding. It might be difficult to separate the effects of the two on searching behavior. In our study, correlations between wasp size and egg load were not significant, and multiple regression analyses were applied to evaluate the effects of the two factors. Nevertheless, our study suggests that egg load has no influence in the host-approaching process in *I. naranyae*. A close, positive relationship between egg load and motivation to oviposit was detected in host-acceptance decisions of *I. naranyae* (K. Ueno and T. Ueno, unpublished). Egg load effects may or may not arise depending on the process of host finding and acceptance.

Acknowledgements We thank two anonymous reviewers for helpful comments on earlier versions of the manuscript. This work was supported partly by grant no. 13760039 from the Ministry of Education, Science, Sports and Culture, Japan.

References

Alphen JJM van, Vet LEM (1986) An evolutionary approach to host finding and selection. In: Waage J, Greathead D (eds) Insect parasitoids. Academic, London, pp 23–63

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

Assem J van den, Iersel JJA van, Hartogh RLL (1989) Is being large more important for female than male parasitic wasps? Behaviour 108:160–195

Charnov EL, Skinner SW (1988) Clutch size in parasitoids: the egg production rate as a constraint. Evol Ecol 2:167–174

Collier TR (1995) Adding physiological realism to dynamic state variable models of parasitoid host feeding. Evol Ecol 9:217–235

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

Cortesero AM, Monge JP, Huignard J (1995) Influence of two successive learning processes on the response of *Eupelmus vuilleti* Crw (Hymenoptera: Eupelmidae) to volatile stimuli from hosts and host plants. J Insect Behav 8:751–762

Dukas R (1998) Cognitive ecology. University Chicago Press, Chicago

Godfray HCJ (1994) Parasitoids: behavioral and evolutionary ecology. Princeton University Press, Princeton

Heimpel GE, Collier TR (1996) The evolution of host-feeding behaviour in insect parasitoids. Biol Rev 71:373–400

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

Honda T, Kainoh Y (1998) Age-related fecundity and learning ability of the egg-larval parasitoid *Ascogaster reticulatus* Watanabe (Hymenoptera : Braconidae). Biol Control 13:177–181

Lewis WJ, Vet LEM, Tumlinson JH, Lenteren JCV, Papaj DR (1990) Variations in parasitoid foraging behavior: essential element of a sound biological control theory. Environ Entomol 19:1183–1193

Lewis WJ, Tumlinson JH, Krasnoff S (1991) Chemically mediated associative learning: an important function in the foraging behavior of *Microplitis croceipes* (Cresson). J Chem Ecol 17:1309–1325

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

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

Otten H, Wackers F, Battini M, Dorn S (2001) Efficiency of vibrational sounding in the parasitoid *Pimpla turionellae* is affected by female size. Anim Behav 61:671–677

Papaj DR, Lewis AC (eds) (1993) Insect learning. Chapman and Hall, New York

Poolman SMTT, Suverkropp BP, Vet LEM, de Moed G (1992) Comparison of learning in related generalist and specialist eucoilid parasitoids. Entomol Exp Appl 64:117–124

Prokopy RJ, Roitberg BD, Vargas RI (1994) Effects of egg load on finding and acceptance of host fruit in *Ceratitis capitata* flies. Physiol Entomol 19:124–132

Quicke DLJ (1997) Parasitic wasps. Chapman and Hall, New York

Rosenheim JA, Rosen D (1991) Foraging and oviposition decisions in the parasitoid *Aphytis lingananensis*: distinguishing the influence of egg load and experience. J Anim Ecol 60:873–893

Sandlan K (1980) Host location by *Coccygomimus turionellae* (Hymenoptera: Ichneumonidae). Entomol Exp Appl 27:233–245

SAS Institute (2001) StatView-J version 4.5. SAS Institute, Cary, N.C.

SAS Institute (2001) JMP version 4.0. SAS Institute, Cary, N.C.

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

Sirot E, Ploye H, Bernstein C (1997) State dependent superparasitism in a solitary parasitoid: egg load and survival. Behav Ecol 8:226–232

Townes H, Momoi S, Townes M (1965) A catalogue and reclassification of the eastern Palearctic Ichneumonidae. (Memoirs of the American

Entomological Institute, number 5). American Entomological Institute, Ann Arbor, Mich

Ueno T (1998) Selective host-feeding on parasitized hosts by the parasitoid *Itoplectis naranyae* (Hymenoptera: Ichneumonidae) and its implications for biological control. Bull Entomol Res 88:461–466

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

Ueno T, Tanaka T (1994) Comparative biology of six polyphagous solitary pupal endoparasitoids (Hymenoptera: Ichneumonidae): differential host suitability and sex allocation. Ann Entomol Soc Am 87:592–598

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

Vet LEM, Dicke M (1992) Ecology of infochemical use by natural enemies in a tritrophic context. Annu Rev Entomol 37:141–172

Vinson SB (1998) The general host selection behavior of parasitoid hymenoptera and a comparison of initial strategies utilized by larvaphagous and oophagous species. Biol Control 11:79–96

Wackers FL, Lewis WJ (1994) Olfactory and visual learning and their interaction in host site location by *Microplitis croceipes*. Biol Control 4:105–112

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 Control 11:141–146

Yasumatsu K, Watanabe C (1965) A tentative catalogue of insect natural enemies of injurious insects in Japan, part 2. Host parasite-predator catalogue. Entomological Laboratory, Faculty of Agriculture, Kyushu University, Fukuoka