Relationship between Female Size and Host-feeding Behavior in the Parasitoid Wasp Itoplectis naranyae (Hymenoptera : Ichneumonidae)

Ueno, Kanako
Laboratory of Insect Natural Enemies,Department of Applied Genetics and Pest Management,Graduate School of Bioresource and Bioenvironmental Sciences,Kyushu University

Ueno, Takatoshi
Institute of Biological Control,Faculty of Agriculture,Kyushu University

https://doi.org/10.5109/4567

出版情報：九州大学大学院農学研究院紀要. 49 (1), pp.77-84, 2004-02-01. Faculty of Agriculture, Kyushu University
バージョン：
権利関係：

J. Fac. Agr., Kyushu Univ., **49** (1), 77–84 (2004)

Relationship between Female Size and Host–feeding Behavior in the Parasitoid Wasp *Itoplectis naranyae* (Hymenoptera: Ichneumonidae)

Kanako UENO[1] and Takatoshi UENO*

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

(*Received October 31, 2003 and accepted November 14, 2003*)

The adult females of many parasitic Hymenoptera feed on their host insects to gain nutrients for egg production, a behavior known as host–feeding. Host–feeding is an essential component determining female fecundity for a number of parasitoid species. The size of adult females is widely recognized as a factor that intimately affects their fitness, including fecundity. Association between host–feeding and female size would then be expected but this has received poor attention so far. Here we studied the relationship between female size and host–feeding behavior, using *Itoplectis naranyae*, an ichneumonid endoparasitoid of many lepidopteran pests in rice paddies. During the early stage of female life, larger females fed on a greater number of hosts whereas the number of hosts oviposited did not differ among females of different size. In addition, larger females took larger host meal from single host individuals. Female size did not affect when females fed on a host for the first time. There was no significant relationship between the day of the first host–feeding and the number of hosts oviposited until that day. The age of females did not affect the size of host meal. We discussed the relationship among female size, fecundity and host–feeding and how female size affected egg production in the later stage of female life.

INTRODUCTION

The adult females of many species of parasitoid wasps feed on the hemolymph of their hosts (Jervis and Kidd, 1986; Heimpel and Collier, 1996). This behavior is called 'host–feeding'. Adult parasitoids therefore use the hosts as a food source and as well as an oviposition site. It is generally accepted that female parasitoids feed on hosts to obtain nutrients for egg production (Jervis and Kidd, 1986; Heimpel and Collier, 1996; Jervis *et al.*, 1996a). The importance of host–feeding has been recognized by many applied entomologists; host–feeding is an essential component determining female fecundity for a number of parasitoids that are good candidates for biological control (Leius, 1961, 1962; Sandlan, 1979; Collier, 1995; Ueno, 1999a; Ho and Ueno, 2002). Further, host feeding causes additional host mortality (DeBach, 1943; Flanders, 1953; Yamamura and Yano, 1988; Kidd and Jervis, 1989; Jervis *et al.*, 1996a, b; Ho and Ueno, 2002). Nevertheless, relatively little attention has been paid to ecological and physiological aspects of parasitoid host–feeding until recently (Heimpel and Collier, 1996).

---

[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)

The size of adult females is repeatedly shown to have an important effect on female fitness. Larger females in general are more fecund in many parasitoid species, regardless of whether they are pro–ovigenic or synovigenic (Waage and Godray, 1985; King, 1987; Godfray, 1994; Ueno, 1999b). For pro–ovigenic species, a positive relationship between female size and fecundity may intuitively be understood. The adult females of pro–ovigenic species emerge with a fixed number of eggs that are produced during the pupal stage based on nutrients gained from the host. Thus, larger females with greater fecundity are produced from larger hosts in which greater amount of nutrients for developing larvae is available.

For synovigenic species, in which oogenesis occurs continuously throughout adult female life, the mechanism of how female size relates the fecundity would be more complex (Ueno, 1999b). Nutrients stored during the larval stage may represent only a part of resources used for egg production; hence the availability of adult food can largely determine female lifetime fecundity. Then, for synovigenic parasitoids, greater fecundity in larger females may reflect higher ability of gaining food resources during adult female life. Alternatively, larger females may be capable of converting resources to eggs more quickly.

The mechanism of how larger females of synovigenic parasitoids produce and store more eggs has poorly been investigated. Further, relationships between female size and food gaining ability have seldom been examined. Given that hosts are an important food source for many parasitoids, it would be valuable to investigate the relationship between female size and host–feeding behavior. Accordingly, we addressed here how female size affected host–feeding behavior in a parasitoid wasp.

The solitary endoparasitoid wasp *Itoplectis naranyae* Ashmead (Hymenoptera: Ichneumonidae) is a polyphagous species attacking a variety of lepidopterous pupae and prepupae in paddy and grassy fields of Japan and Asia (Townes *et al.*, 1965; Yasumatsu and Watanabe, 1965; Ueno and Tanaka, 1994). Since *I. naranyae* is a major parasitoid of lepidopterous pests in rice paddies, its role in suppressing lepidopterous populations in rice paddies would be great. Female *I. naranyae* produces relatively large yolk–rich eggs, and have a relatively few number of mature eggs at any one time during oviposition periods (Ueno and Tanaka, 1994). Production of such large, yolk–rich eggs should be costly for the female wasp, and adult nutrition would then be important for *I. naranyae*. Previous studies have demonstrated that this parasitoid is typically synovigenic and is a host–feeder (Ueno, 1998).

Like many parasitoids, larger females of *I. naranyae* carry more mature eggs in the ovary (Ueno, 1998). We suspected that host–feeding behavior should have a great contribution to the positive relationship between female size and fecundity in this parasitoid. In the present study, we conducted laboratory tests to investigate the relationship between female size and host feeding behavior in *I. naranyae*. Based on the results, we discussed the importance of host–feeding in determining the fecundity of *I. naranyae* in relation to female size.

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 (10 cm in diameter, 4.5 cm in height), together with tissue paper saturated with a honey solution. The tissue paper was replaced twice a week thereafter. The cups were kept at 20±1 °C.

The colony was maintained on pupae of a laboratory host, *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.

Host–feeding behavior

Host–feeding behavior of *I. naranyae* is as follows. Female *I. naranyae* that feeds on hosts uses the ovipositor to make holes for extracting host fluids. After thrusting a host with the ovipositor, the female circulates round her abdomen and thereby her ovipositor, with the ovipositor inserted in that host. This movement causes the hole made on the host to be enlarged, and hence facilitates host fluids exuding from the hole. The female then sips the fluids. This series of behaviors is repeated until the female has satisfied. Consequently, there are a number of ovipositor holes on hosts, and hosts are heavily damaged with conspicuous marks of host body fluids exuded. *I. naranyae* is thus a destructive host–feeder.

Host–feeding experiments

We used the following protocol to determine whether host–feeding behavior could be influenced by female size. Newly emerged females of *I. naranyae* were individually placed in plastic containers together with a male. Tissue paper saturated with honey solution was also placed in the container, and was replaced every two days thereafter to provide females with fresh food. Females of *I. naranyae* emerge with no mature eggs and hence reproductively inactive when they are 0–1 days old. Therefore, experiments were started with 3 days old females.

On the third day since female emergence, females for testing were provided with two fresh host cocoons for 2 hours and were allowed access to the hosts freely. Hosts were then removed from the container and were examined under a binocular microscope to count the oviposition and host–feeding holes left by females. The holes made with the ovipositor were easily detected on the surface of a host pupa. It was also examined whether host hemolymph was exuded from hosts to determine whether the hosts had been fed upon. When hosts were with conspicuous marks of host body fluids exuded, we classified them as a ‘fed’ host. This procedure was repeated for 5 consecutive days, and thus a 5–day experimental period was used for each test female.

After the experimental period had been ended, forewing length of test females was measured under a binocular microscope to use as an index of female size. A total of 41 females were used in the experiment, and no test females died during the experimental period.

Statistical analyses

Statistical treatments were made with the aid of JMP (SAS Institute, 1997). Basically, linear regression analyses were applied to examine the relationships between female size and behavioral activity. One–way ANOVA was used to evaluate the effect of female age on amount of host meal.

RESULTS AND DISCUSSION

When female *I. naranyae* feeds on a host for the first time

Itoplectis naranyae has a relatively long life span of ca one month, and the female oviposits on hosts throughout their lifetime except the earliest stage of female life (Ueno and Tanaka, 1994). As with most synovigenic parasitoids, newly emerged females of *I. naranyae* (i.e. 0–1 days old female) have no mature eggs (Ueno and Tanaka, 1994; Ueno, 1998). Our previous study has shown that the proportion of females that oviposit and host–feed quickly increases with increasing female age from 0 to 7 days old (Ueno and Ueno, unpublished). At the same time, the number of mature eggs increases quickly in

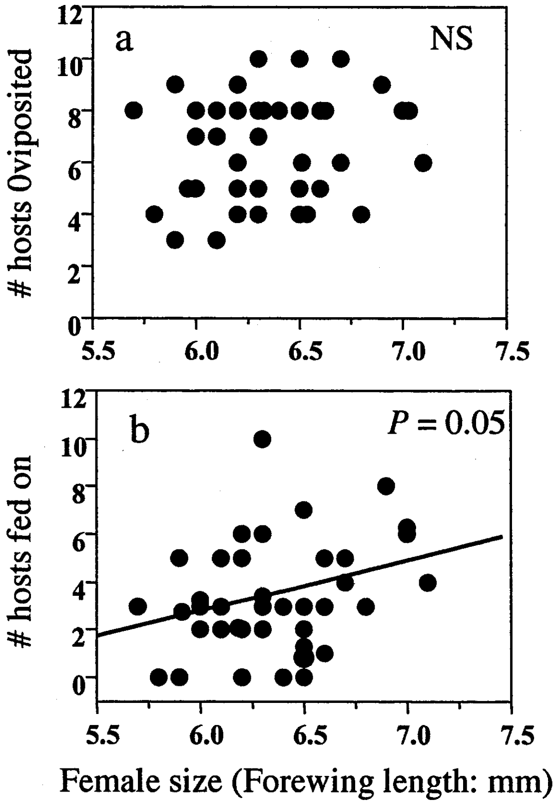

Fig. 1. Relationships between female size and how many hosts each female *I. naranyae* oviposited (a) or fed on (b). NS: Not significant ($P > 0.05$).

the ovary within this age class. We therefore expected that female size would have a significant impact on host feeding behavior within female age classes examined in the present study, i.e., 3 to 7 days old.

Based on the data obtained in the present study, we first analyzed the relationship between female size and number of hosts fed upon. Regression analyses were used for this purpose. There was no significant relationship between female size and number of hosts oviposited (N=41, $r^2=0.03$, $F=1.13$, $P=0.30$) (Fig. 1a). However, a marginally significant relationship was detected between female size and number of hosts used for host-feeding (N=41, $r^2=0.09$, $F=3.97$, $P=0.053$) (Fig. 1b). This result demonstrated that larger females could use a greater number of hosts for host-feeding during the early phase of their life. Feeding on more hosts should lead females to have more eggs in the later phase of their life.

To assess what factors caused the initial timing of host-feeding during female life, the relationship between female size and the day females host-fed for the first time was examined. A regression analysis showed no significant relationship between the two (N=41, $r^2=0.02$, $F=0.72$, $P=0.40$) (Fig. 2). Female size is thus not a factor affecting when female *I. naranyae* starts to feed on hosts.

In addition, no significant relationship was found between female size and number of oviposition marks on hosts before females started to host-feed (N=41, $r^2=0.002$, $F=0.06$, $P=0.80$) (Fig. 3). It is assumed that the number of oviposition marks on hosts positively reflects the number of eggs laid. Given this, the initial host-feeding during female life appears not to be determined by how many eggs a female laid until that point. Thus we could not find any factors affecting when females start to host-feed.

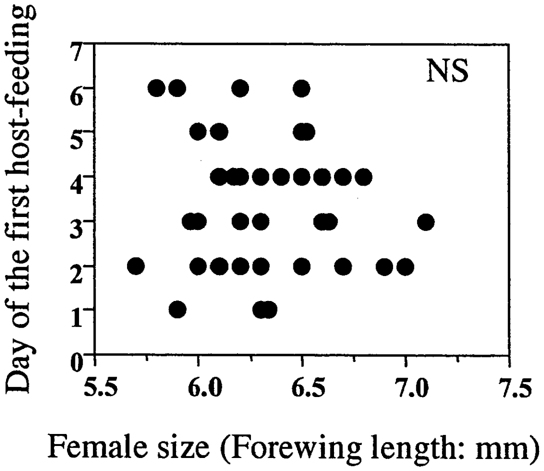

Fig. 2. Relationship between female size and the day when female *I. naranyae* host-fed for the first time. NS: Not significant (P>0.05).

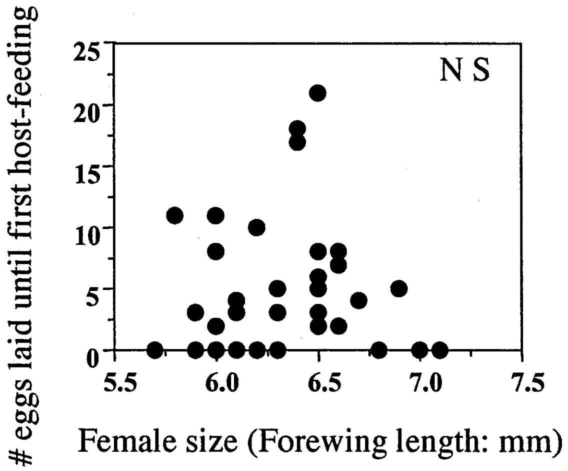

Fig. 3. Relationship between female size and number of eggs laid until the first host-feeding. NS: Not significant ($P>0.05$).

Female size and amount of host materials fed on

Although a number of studies examined host-feeding behavior of parasitoids (e.g. Jervis and Kidd, 1986; Collier, 1995; Heimpel and Collier, 1996; Jervis *et al.*, 1996a), no study so far has focused on how much materials a female parasitoid takes during a host-feeding event. Our study is first to assess this in terms of female size.

Female *I. naranyae* repeatedly drills into hosts to feed on host body fluids, as with many other ichneumonid parasitoids (Leius, 1961; Sandlan, 1979; Ueno, 1999a). It would therefore be expected that the number of drilling marks is much greater in hosts that have been fed upon than non-fed hosts. This was confirmed in the present observations. For example, the mean number of drilling marks was 2.5 on hosts used for oviposition purposes whereas that of fed hosts was 14.1 when female parasitoids were 7 days old.

By using a regression analysis, the relationship between female size and the number of drilling marks on fed hosts was examined. A significantly positive relationship was detected between the two ($N=77$, $r^2=0.05$, $F=4.23$, $P=0.043$) (Fig. 4). This suggested that larger females fed on more host fluids during each host-feeding event. By feeding on more host fluids, larger females can gain more materials for egg production, and, hence, carry a greater number of mature eggs at any one time.

The relationship between female age and the number of drilling marks on fed hosts was examined next. For this purpose, we performed one-way ANOVA, regarding female age as a categorized variable. The mean number of marks did not differ among female age classes ($N=74$, $F=099$, $P=0.40$) (Fig. 5). Given that the number of drilling marks on fed hosts should reflect how much host fluids female *I. naranyae* feeds upon, the amount of host meal taken from each host is constant regardless of female age at least within age classes examined in the present study.

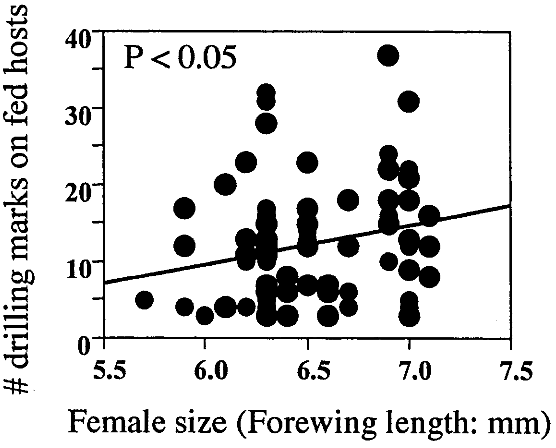

Fig. 4. Relationship between female size and number of drilling marks on hosts that were fed upon by female *I. naranyae*.

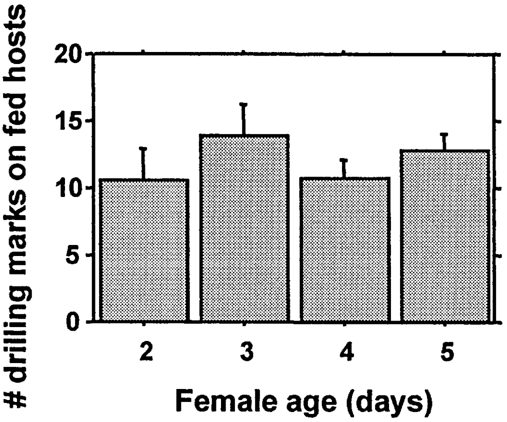

Fig. 5. Effect of female age on number of drilling marks on fed hosts. No significant effect was detected by one-way ANOVA ($P > 0.05$).

Taken together, the present results demonstrate that larger females of *I. naranyae* acquire and store a greater amount of host materials during the earliest phase of their life, and, as a result, larger females can carry a greater number of mature eggs during the later phase of their life. Female *I. naranyae* produced around 20–30 eggs without host feeding by using nutrients stored during the larval stage (T. Ueno, unpublished). The number of eggs produced without host-feeding may be greater in larger females. However, *I. naranyae* potentially produced more than 300–400 eggs during the lifetime (T. Ueno, unpublished). Therefore, female reproductive success should be determined by the number of eggs produced through adult feeding. Host feeding can thus contribute largely to mold the positive relationship between female size and fecundity.

REFERENCES

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

DeBach, P. 1943 The importance of host-feeding by adult parasites in the reduction of host populations. *J. Econ. Entomol.*, **36**: 647–658

Flanders, S. E. 1953 Predatism by the adult hymenopterous parasite and its role in biological control. *J. Econ. Entomol.*, **46**: 541–544

Godfray, H. C. J. 1994 *Parasitoids: Behavioral and evolutionary ecology.* Princeton University Press, Princeton

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

Ho, G. T. T. and T. Ueno 2002 Biology of *Hemiptarsenus varicornis* (Hymenoptera: Eulophidae), a parasitoid wasp of the leafminer *Liriomyza trifolii* (Diptera: Agromyzidae). *J. Fac. Agric., Kyushu Univ.*, **47**: 45–54

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

Jervis, M. A., N. A. C. Kidd, and G. E. Heimpel 1996a Parasitoid adult feeding behaviour and biocontrol – a review. *Biocont. News and Information*, **17**: 11–26

Jervis, M. A., B. A. Hawkins, and N. A. C. Kidd 1996b The usefulness of destructive host feeding parasitoids in classical biological control: theory and observation conflict. *Ecol. Entomol.*, **21**: 41–46

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

Kidd, N. A. C. and M. A. Jervis 1989 The effects of host feeding behaviour on the dynamics of parasitoid-host interactions, and the implications for biological control. *Res. Popul. Ecol.*, **31**: 235–274

King, B. H. 1987 Offspring sex ratios in parasitoid wasps. *Q. Rev. Biol.*, **62**: 367–396

Leius, K. 1961 Influence of food on fecundity and longevity of adults of *Itoplectis conquisitor* (Say) (Hymenoptera: Ichneumonidae). *Can. Entomol.*, **93**: 771–780

Leius, K. 1962 Effects of the body fluids of various host larvae on fecundity of females of *Scambus buolianae* (Htg.) (Hymenoptera: Ichneumonidae). *Can. Entomol.*, **94**: 1078–1082

Sandlan, K. P. 1979 Host-feeding and its effects on the physiology and behaviour of the ichneumonid parasitoid, *Coccygomimus turionellae. Physiol. Entomol.*, **4**: 383–392

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-feeding and reproduction in the parasitoid wasp *Pimpla nipponica* (Hymenoptera: Ichneumonidae). *Inverteb. Reprod. Develop.*, **35**: 231–237

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

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

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", eds. by R. M. Sibley and R. H. Smith, Blackwell, Oxford, pp. 449–470

Yamamura, N. and E. Yano 1988 A simple model of host-parasitoid interaction with host-feeding. *Res. Popul. Ecol.*, **30**: 353–369

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. Press, Fukuoka