Host Handling Time in a Polyembryonic Wasp is Affected both by Previous Experience and by Host State (Parasitized or Not)

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Abstract Foraging behavior for hosts in parasitoids resembles that of predators with respect to finding, evaluating and manipulating of the prey. Host handling time may depend on the life history of the parasitoid and can be affected by oviposition experience. Additionally, handling time can be affected by host aggregation, species, size and state (parasitized or not). We studied handling times in the egg-larval parasitoid wasp *Copidosoma koehleri*. We allowed naïve female wasps to oviposit into three consecutive unparasitized hosts, and measured time until oviposition, and the duration of ovipositor insertion. We recorded the same data for naïve females ovipositing into already parasitized hosts. We found that both previous experience by females and previous parasitism of hosts reduced handling time. The results suggest that host handling durations reflect the interplay between host state and parasitoid internal state.

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Introduction

Prey handling is an important component of foraging behaviour (MacArthur and Pianka 1966). Short handling enables an organism to increase the number of encounters with prey (Holling 1959) and to decrease predation risk (Sih 1993). Thus, there are many physiological and behavioral adaptations to decrease handling time (e.g. paralysis of prey; use of tools; group hunting, Alcock 2005). Handling time may vary according to prey type, and may also depend on the experience of the forager (Shettleworth et al. 1993).

Parasitoids resemble other foragers in the need to find, evaluate, and handle their prey (hosts), even though host tissues are consumed by the parasitoid's offspring, rather than by the foraging individual (Quicke 1997). Host handling by parasitoids may include: host examination, paralysis of the host, insertion of the ovipositor, release of eggs and host marking (Godfray 1994). Handling sequences and durations may depend on the life history of the parasitoid. For example, they may differ between idiobionts that often paralyze a host and koinobionts that do not; endoparasitoids that lay their eggs inside the host body, and ectoparasitoids that lay their eggs externally; gregarious parasitoids that lay many eggs per host and solitary parasitoids that normally lay a single egg in each host; and egg parasitoids that need to penetrate the egg chorion compared to larval parasitoids that penetrate the host cuticle (Vinson 1998).

Reduction in host handling time may increase reproductive success of female parasitoids that are limited in the time available to locate suitable hosts (Rosenheim 1999). Additionally, adult parasitoids may be prone to predation (Weisser et al. 1994; Heimpel et al. 1997), especially during oviposition, when females are less mobile. Thus, shorter handling times may reduce vulnerability to disturbance and mortality during host handling (Barzman and Daane 2001). Adaptations to decrease handling time may include: avoidance of hosts that are potentially difficult to handle (Slansky 1986; Kouame and Mackauer 1991), paralysis of hosts prior to oviposition (Vinson and Iwantsch 1980) and choice of an easy insertion location (Takasu and Hirose 1991; Barzman and Daane 2001).

Handling time was shown to decrease with experience in some parasitoids (Conti et al. 1997; Chow and Mackauer 1999; Nurindah et al. 1999), but not in others (Wiedemann et al. 2003; Keasar et al. 2006a). In addition to the effect of experience, the duration of host handling was shown to vary according to host characteristics. For example it may be affected by host aggregation (Mills and Kuhlmann 2004), host species (Chow and Mackauer 1999; Mansfield and Mills 2004), host size (King 1994), host age (King 1994; Ode and Strand 1995), host developmental stage (Bokononganta et al. 1995; Daane et al. 2005; Ardeh et al. 2005) and host state (parasitized or not) (Takasu and Hirose 1991). However, the relative contribution of parasitoid experience and host characteristics to handling duration has received little attention.

We studied oviposition behavior and handling durations in the polyembryonic egg-larval parasitoid wasp *Copidosoma koehleri* (Hymenoptera: Encyrtidae). This parasitoid exhibits a short and fixed sequence of host-handling behaviors. We were able to study the interplay of experience with host state by eliminating most variation among hosts (all were of the same species, developmental stage, size etc.),

and manipulating only the state of the host, i.e. parasitized or not. We conducted two experiments: to test for the effect of experience on handling time, we provided females with several unparasitized hosts in succession; to test for the effect of the host state on handling time we provided naïve females with either parasitized or unparasitized hosts. We observed the wasps closely, characterized their handling sequences, and measured the durations of different components of host handling.

Materials and Methods

Parasitoids and Hosts

C. koehleri parasitizes the potato tuber moth, *Phthorimaea operculella* (Lepidoptera: Gelechiidae), and serves as a biological control agent of this pest (Horne 1990; Kfir 2003). *C. koehleri* females oviposit into the moth egg, and their offspring develop inside the host as it grows through four larval instars. Toward the end of the host's development, wasp larvae start feeding actively on the host tissues until they fully consume it and pupate (Segoli et al. 2009). Polyembryony is a unique mode of development, which involves the production of several genetically identical embryos from each egg (Strand 2003). In *C. koehleri* around 40 individuals develop from one wasp egg (Kfir 1981; Segoli et al. 2009). Females typically lay one egg per oviposition event, but superparasitism is common (Doutt 1947; Keasar et al. 2006a). Superparasitism arises from repeated oviposition by one or more females, and may have significant consequences for the females' reproductive success (Keasar et al. 2006a).

A laboratory stock of *C. koehleri* was used in these experiments. The stock originated from field-collected individuals from South Africa (courtesy of Dr. R. Kfir, Plant Protection Institute, Pretoria). Parasitoids were housed at 27°C, natural daylight, and fed with honey. A laboratory stock of potato tuber moth (PTM) was housed at 27°C, natural daylight, and fed with honey and water. PTM eggs were collected daily and used within 24 h, since the egg's age is known to influence the parasitoid's oviposition decisions (Ode and Strand 1995). Wasps were used within 3 days of emergence.

Behavioral Observations

The experiments were conducted in the laboratories of Achva College, Israel, during 2007. At the beginning of each trial we placed one fresh host egg in the center of a Petri dish. We then placed one *C. koehleri* female inside the dish and directed it to the host. This was done by rotating the petri dish as the female was walking on its surface according to the direction of her movements, until she contacted the host with her antennae. Females attempted to oviposit into the host after probing it with their antennae. Occasionally, the female was unable to insert the ovipositor into the egg at the first attempt (the ovipositor was not placed against the egg, the egg moved or the ovipositor slipped on the egg surface). The female then turned around and re-initiated the process. The number of such unsuccessful insertion attempts prior to successful insertion was recorded. We observed the females under a dissecting

microscope throughout host handling. We measured the total time between first
contact with the egg and insertion of the ovipositor, including unsuccessful insertion
attempts ("time until insertion"). We calculated the average duration per insertion
attempt as the total time until insertion divided by the total number of insertion
attempts (number of unsuccessful attempts + one successful attempt). Additionally
we measured the duration of each insertion ("duration of insertion"). If a female did
not initiate oviposition during 3 min after the first contact, it was excluded from the
experiment. This decision was based on preliminary experiments indicating that
females that take more than 3 min from first contact until insertion eventually do not
oviposit. As soon as the female pulled her ovipositor out of the host egg, she was
transferred to a different petri dish with another host. The process was repeated until
each female oviposited into three hosts. We obtained data for "time until insertion"
from three consecutive ovipositions of 89 females, and for "duration of insertion"
from 86 females. To assess handling time during superparasitism, 30 host eggs that
were parasitized by naïve females were exposed to an additional naïve female, using
the same protocol as above, 2–6 h after the first oviposition. We used naïve females
as we were interested to know whether females adjust handling time to host
parasitism status, regardless of experience. Handling time of females presented first
to the host was compared to that of females presented to the already parasitized host.
All observations were conducted by the same observer.

Statistical Analyses

We used repeated measures analyses to avoid pseudo-replication and to remove
variation that stems from the individual wasp (von Ende 1993). The assumptions
needed for a parametric test were not met in this data set, thus we used Friedman's
ANOVA (a non-parametric, repeated-measures test) to compare time until
oviposition between three successive ovipositions by the same female. Similarly
we used Friedman's ANOVA to compare the total number of oviposition attempts
(unsuccessful + 1 successful), the average time per oviposition attempt and duration
of oviposition. Wherever required, we applied sequential Bonferroni adjustments for
multiple comparisons (Rice 1989). We used Wilcoxon signed-ranks test to test for
differences in time to insertion, and duration of insertion, between two successive
ovipositions into the same host.

Results

Upon first contact with the host, the female usually examined it with her antennae.
The female turned around and held the host with one or both of her hind legs, and
placed her ovipositor against the host. The female then rotated her ovipositor and
inserted it into the host with drilling movements. As soon as the ovipositor was
pulled out of the host, the female touched the host with the full length of her
ovipositor from several directions. The female was then separated from the host to
avoid superparasitism. This sequence was similar for all ovipositions, regardless of
the female's previous experience and egg parasitism status. Time until insertion was
significantly affected by the experience of the wasp (Fig. 1, Friedman's ANOVA, $n=$
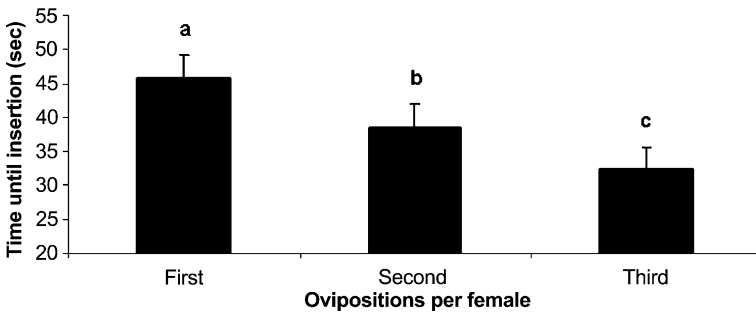
Fig.1 Mean and SE duration (sec) from first contact with the host (egg of *Phthorimaea operculella*) to insertion of ovipositor into the host, by a polyembryonic parasitoid female (*Copidosoma koehleri*), for first, second and third experience (*n*=89). Different letters indicate significant differences, according to posthoc tests.

89 females, χ_2^2=12.8, *p*=0.02). The number of oviposition attempts was also negatively affected by experience (1st experience- 1.75±1.14 attempts (average ± sd), 2nd experience- 1.47±0.97, 3rd experience- 1.36±0.72; Friedman's ANOVA, *n*=89 females, χ_2^2=8.6, *p*=0.013,). Similarly, the duration per attempt was negatively affected by experience (1st experience- 27.1±13.2 s (average ± sd), 2nd experience- 26.3±17.6, 3rd experience- 22.4±16.3; Friedman's ANOVA, *n*=89 females, χ_2^2=9.6, *p*=0.008). In addition, the duration of insertion was significantly and negatively affected by experience (Fig. 2, Friedman's ANOVA, *n*=86 females, χ_2^2=13.8, *p*=0.001).

The Effect of Previous Parasitism

Females that were presented with a previously parasitized host (*n*=30) never used a previous drilling hole. Time until insertion did not differ between first and second ovipositions by different females into the same host (Wilcoxon signed-ranks test, *n*= 30 hosts, mean ± SD=46.3±26.3 for first oviposition and 63.4±47.9 for second oviposition, Z=1.3, *p*=0.2). Insertion duration, however, was significantly shorter for the second oviposition by a different female into the same host (Fig. 3, Wilcoxon signed-ranks test, *n*=30 hosts, Z=−2.9, *p*=0.004).
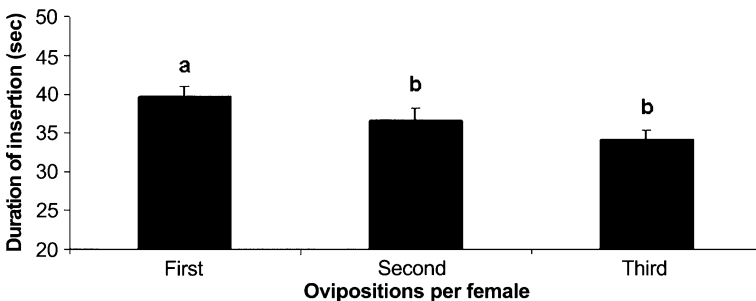

Fig. 2 Mean and SE duration (sec) of insertion of ovipositor into the host (egg of *Phthorimaea operculella*), by a polyembryonic parasitoid female (*Copidosoma koehleri*), for first, second and third experience (*n*=86). Different letters indicate significant differences, according to posthoc tests.
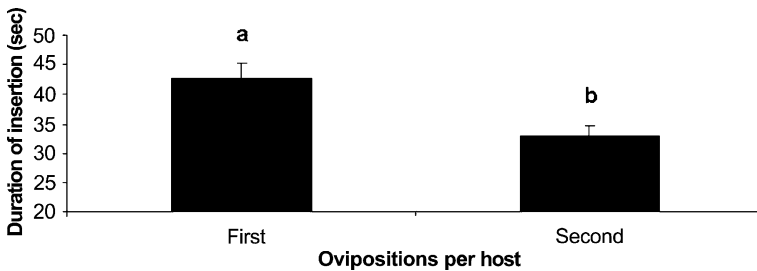
Fig. 3 Mean and SE duration (sec) of insertion of ovipositor into the host (egg of *Phthorimaea operculella*), for first and second ovipositions into the same host, by two polyembryonic parasitoid naïve females (*Copidosoma koehleri*), $n=30$. Different letters indicate significant differences, according to posthoc tests.

Discussion

We studied the effects of oviposition experience of the female and previous parasitism of the host on handling time in the egg-larval parasitoid *C. koehleri*. We found that both experience of female wasps and host state (parasitized or not) affected host-handling times. The results suggest that host handling durations reflect the interplay between host state and parasitoid internal state.

Wasps with previous experience reduced both time until insertion and the duration of insertion. The latter may be explained by mechanisms other than experience. For example, it is possible that the release of a first egg is mechanically or physiologically more difficult for a female than the release of additional eggs. The reduction in time until oviposition may reflect a change in the wasp's motivation to oviposit, which may be affected by its egg load (Rosenheim and Rosen 1991) or life expectancy (Roitberg et al. 1992). However, this is not likely for the experiments we performed, because both naïve and experienced females were of similar age, experienced similar conditions and had similar egg-loads at the time of exposure to hosts. The reduction in time until insertion is more probably a result of increased experience. The main difficulty for an egg parasitoid is to penetrate through the eggshell (chorion). Harder eggshells are more difficult to penetrate and this may be one of the reasons that female parasitoids prefer younger eggs with softer shells (Vinson 1998). We observed female wasps holding the egg with their hind legs while inserting the ovipositor, probably to restrict egg movement while drilling. This operation probably requires precision: standing at a wrong angle or distance from the egg may reduce insertion success. Indeed, females were able to reduce both the number of attempts and the duration of each attempt between successive ovipositions. Other examples of reduced handling time by experienced females in egg parasitoids include *Trichogramma australicum* while parasitizing eggs of the noctuid moth *Helicoverpa armigera* (Nurindah et al. 1999) and *Anaphes iole* while parasitizing eggs of *Lygus hesperus* embedded in green beans (Conti et al. 1997). In both cases, experienced females reduced the time until ovipositor insertion in comparison to naïve females.

It has been hypothesized that variable foraging conditions should promote the evolution of learning, because no single innate handling technique is adequate under

all conditions (Stephens 1993). Thus, parasitoids with a wide host range may benefit from the ability to adjust handling behavior to the host species. This may be demonstrated by a study on the ectophagous hyperparasitoid *Dendrocerus carpentari* that parasitizes various species of aphidiine wasps. One of the host species, which is relatively rare, pupates in a different location than the more common hosts (below rather than inside the mummified aphid). Experienced females reduced by half time required to locate the cocoon of the rare host as compared with naïve individuals (Chow and Mackauer 1999). In contrast, *C. koehleri* has a narrow host range (Guerrieri and Noyes 2005) and thus is not predicted to benefit from experience. Indeed, the sequence of host handling is largely stereotypic. Nevertheless, the effect of experience was significant and consistent.

One possible explanation may be that the relatively simple task of handling an immobile host can be easily improved, even after a single successful trial. In contrast, handling of larval or adult hosts may require more sophisticated behaviors. Hosts often defend themselves from parasitism, by secretions, increased movement, or by attacking the adult parasitoid (Hays and Vinson 1971; Kouame and Mackauer 1991; Gross 1993). Thus, overcoming the host defense and manipulating the host may involve a complex behavioral sequence of host handling, which may require many trials before it is significantly improved. A good example for such complex host handling comes from the wasp *Ampulex compressa,* which parasitizes adult cockroaches. Host handling in this wasp includes stinging, cutting the cockroach antennae, feeding on its hemolymph, leading the cockroach into a cavity, laying eggs and blocking the entrance to the cavity (Haspel et al. 2003; Libersat 2003). Handling time is not reduced with experience in this wasp, perhaps because it is too complex to be learned over the lifetime of a single individual (Keasar et al. 2006b). Alternatively, host defenses may select for an innate ability to parasitize hosts quickly to avoid the large costs of long handling time (Vinson 1985; Gross 1993). In this case as well, experience is not predicted to have a strong effect. Thus, the selective advantage of oviposition experience may depend on the combination of host variability, the complexity of the task and the risks of long handling.

The total reduction in handling time as a result of experience was 15 s on average. Although this does not seem to be a substantial decrease, it comprises 18% of the total handling time. This is similar to the proportion of reduction of handling time with experience in other egg parasitoids (Conti et al. 1997; Nurindah et al. 1999). Such a reduction may potentially increase encounter rate with hosts and decrease predation risk during oviposition. However, additional information regarding the distribution of the hosts in the field, host searching times and the risk of predation under natural condition is required to estimate the adaptive value of these responses.

Handling time of previously parasitized hosts may be reduced if a second female uses the same hole drilled in the host by the first female. This is the case in the wasp *Ooencyrtus nezarae*, which parasitizes the egg of a plataspid bug. In this species females prefer parasitized hosts probably since they require shorter handling time (Takasu and Hirose 1991). Similarly, in the wasp *Pachycrepoideus vindemmiae*, a generalist parasitoid, insertion into a parasitized host is shorter when females reuse previous oviposition holes (Goubault et al. 2004). In the current study, however, we did not observe any female using a previously drilled hole. Nevertheless, the duration of ovipositions into parasitized hosts was significantly shorter than into unparasitized hosts.

One possible explanation is that wasps released an egg less often after internal inspection of an already parasitized host. Indeed, survival of offspring is expected to be lower in already parasitized hosts, due to larval aggression (Giron et al. 2007). Nevertheless, *C. koehleri* females are known to superparasitize hosts regularly (Doutt 1947; Keasar et al. 2006a), and two-choice experiments indicate that females can discriminate parasitized from unparasitized hosts via external inspection (Segoli et al. unpublished data). In this study we did not dissect the hosts after oviposition, thus further investigation is required to determine the importance of post-insertion rejection in this species. An alternative explanation is that a first ovipositing female releases substances during oviposition that enhance parasitism success. Female parasitoids inject substances that suppress the immune system of the host or that affect host development (Vinson and Iwantsch 1980; Strand et al. 1986; Amaya et al. 2005; Andrew et al. 2006). A female ovipositing in a parasitized host may sense that these substances have already been released and may shorten oviposition accordingly.

Overall this study demonstrates that variable host handling times depend on both the experience of the parasitoid and the status of the host, and includes both innate and acquired components. Estimating the adaptive value of these responses under natural conditions remains a challenge for future studies.

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