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Infection behavior of a parasitoid fly, *Emblemasoma auditrix*, and its host cicada *Okanagana rimosa*

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Abstract

Males of the cicada *Okanagana rimosa* (Homoptera: Cicadidae) that produce calling songs are parasitised by the parasitoid fly *Emblemasoma auditrix* (Diptera: Sarcophagidae). An ethogram of the infection behavior was extracted from videotaped experiments with tethered hosts. The infection behavior can be divided into three phases, each involving different sensory cues: long-range host detection via acoustic signals, visual short-range orientation, and a contact phase with tactile/chemical cues. After phonotaxis by flight, the fly lands on or near the host cicada. It walks around the host to identify the caudal end and squeezes underneath the wings (with a 64–67% preference of the left side). Finally, *E. auditrix* cuts into the timbal and deposits a larva into the sound producing organ of *O. rimosa*. This highly specific behavior restricts the host range to cicadas, only two species of which occur simultaneously with the parasitoid. During the infection behavior, the fly does not discriminate between male and female hosts. However, females were not successfully infected during the experiments. The host *O. rimosa* shows only weak defense behavior (mainly flapping their wings) and seems to rely on parasitoid avoidance. Production of the protest song does not prevent infection.

This paper includes one video that can be accessed at http://insectscience.org/4.36

Introduction

Host finding and selection often involves different processes such as habitat localization, host localization, host discrimination, and host acceptance (Vinson 1976). Such host finding and selection strategies are not very well understood in parasitoid Diptera (Feener and Brown 1997). Therefore we analysed host infection behavior in the sarcophagid fly *Emblemasoma auditrix* that parasitizes singing males of the cicada *Okanagana rimosa* (Soper *et al.* 1976b).

The parasitoid possesses an ear at the prothorax (Lakes-Harlan *et al*. 1999; Robert *et al*. 1999) and uses acoustic cues for host location (Soper *et al.* 1976b; Lakes-Harlan *et al.* 2000). The acoustic cue seems to be a major and sufficient cue for host finding, because flies can be attracted to loudspeakers broadcasting the calling song or song models (Soper *et al.* 1976b; Lakes-Harlan *et al.* 2000). The signal is a long-range signal allowing homing in on hosts from distances of 2–4 m (Köhler and Lakes-Harlan 2001). Furthermore, the neuronal networks are adapted to the characteristics of most likely a single species (*O. rimosa*), as can be seen in the specific phonotactical response (Lakes-Harlan *et al.* 2000; Köhler and Lakes-Harlan 2001). Specialized parasitoids can adapt to host-specific signals, which may be advantageous for host finding, compared to generalist parasitoids (Godfray 1994). Using the described system, our goals were to evaluate the specificity of host infection behavior, to identify possible sensory cues involved in the process, and to analyse the defense behavior of the host. Such an infection behavior has not yet been reported for sarcophagid flies. Therefore, experiments with tethered hosts were performed accompanied by field observations.

Materials and Methods

The natural host infection behavior was observed at six different times in northern Michigan between 1996 and 2002. In June 2000, experiments were set up in Emmet County, Michigan to videotape the parasitoid-host interactions. Experiments were performed at the margin of a forest where both host and parasitoid occur. A small portable box (30 cm × 50 cm) containing the electronic equipment was placed on the ground. A piezo loudspeaker was mounted into the lid of the box for broadcasts of a phonotactically attractive signal. A song model of the host calling song (for details on the signal and its generation, see Lakes-Harlan *et al.* 2000) was stored on a compact disc. The song model consisted of near rectangular sound pulses with a carrier frequency of 9 kHz and a repetition rate of 83 Hz. The signal was replayed with a discman

(Sony D-131) connected to a custom built amplifier and the loudspeaker (HT-Horn, Conrad Electronic, http://www.conrad.com). Sound intensity was adjusted to about 95dB SPL at one meter distance with a sound level meter (Bruel & Kjael 2203) equipped with a 1/2" microphone (Bruel & Kjael 4165). The battery-powered setup was directed upwards and covered with a sheath of cloth.

Cicadas (males and females of *O. rimosa;* n = 10 each) were collected from nearby trees immediately before each experiment. They were checked for any injuries, in males especially at the timbal, and were pinned to the top of a cloth-covered loudspeaker with a needle through the thorax. Occasional field observations and initial experiments using cicadas attached with a thread did not show any differences in the infection behavior. The animals were checked again after each experiment and injured animals were replaced. Hosts were used for a maximum of 5 interaction sequences with the parasitoid. Male *O. canadensis* (n = 4) were collected in Mackinac County and transferred to the site of experiments. A digital video recorder (Canon MV 10) was placed on a tripod to tape the experiments from above.

After a fly arrived at the experimental box, the sound was stopped and its behavior was recorded until the fly left the experimental arena. When flies paused for periods of more than 2 minutes, the sound was turned on again and usually the flies immediately continued with infection behavior and the sound was turned off again. After each experiment the host was checked for the presence of a larva or indications of infection (ruptures in the timbal). Parasitoids were caught only in a minority of the experiments, because they usually suddenly left the host and flew away. In order to minimize pseudoreplication, we waited for approximately five minutes before starting the next experiment, disturbed the nearby vegetation in order to scare flies away and changed the location, each about 200 m apart, after 5–7 experiments.

Notes and videos were carefully analysed and an ethogram of the infection was extracted. Hosts were preserved in 70% ethanol and later dissected under a dissection microscope (Leica M5). Special attention was given to injuries of the timbal and the presence of larvae within the abdomen. Additionally, a sample of infected male cicadas collected in June 1999 in the same area was also dissected. Timbals were photographed with a CCD camera (1048*768 pixel) attached to the dissecting microscope.

Some timbals of cicadas and the abdomen of the parasitoid were viewed with scanning electron microscopy. Tissue was dehydrated, critical point dried and gold sputtered. Preparations were viewed with a Leo 438VP microscope and digital pictures (1024*768 pixel) were obtained.

In June 2002 an additional experiment was performed to test the alertness and defense behavior of unrestrained hosts. Male (n = 50) or female (n = 40) cicadas were carefully approached in the habitat ensuring that they did not react to the approaching person. Generally males continued singing or females continued laying eggs. A 30 cm long thin wooden stick (diameter 2 mm) with a thickened end (4 mm) was then used to mimic the infection behavior of the parasitoid. We tested whether it was possible to approach the cicada from behind, to touch the left wings, to lift the wings and to squeeze underneath the wings near the first abdominal segment, simulating infection behavior.

T-test and chi-square tests were conducted using Prism software (GraphPad, www.graphpad.com/).

Results

Behavioral sequence of infection

Videotaped experiments with restrained hosts revealed that the behavioral sequence for infection of *O. rimosa* by the fly *E. auditrix* was divided into three parts with respect to the distance to the host, and probably involved sensory cues (Fig. 1A). From long-range distance, *E. auditrix* is attracted by the directional acoustic cue towards the host. The fly lands either directly onto the host (35%; n = 79), or nearby (65%; often closer than 5 cm to the host; the short range). In the latter case, the parasitoid approaches the host by walking even when the acoustic signal is stopped. At about a distance of 1–2 cm from the cicada, the fly usually moves sidewise (approx. 80% of all approaches by walking) facing the host. The lateral movements continue until it reaches the caudal end of the host (Fig. 2, Video 1). The fly often continues moving until it faces the cicada from the other side and then returns to the caudal end of the wings. This suggests the use of visual cues during short-range host finding. After identifying the abdomen, the parasitoid accesses the host by squeezing underneath the wings using a caudal approach. In this contact phase, *E. auditrix* pushes underneath the wings of one side of the host. The fly probes the ventro-lateral parts of the host with its abdomen and with tarsi of the front legs. Thereafter it positions itself with its head dorsally between both pairs of wings and performs lateral movements of its abdomen to cut the timbal of the host. A larva is then deposited and the fly immediately flies away. This behavioral sequence, described from experiments with restrained hosts, was corroborated by occasional field observations.

If the fly lands directly on the host or if it jumps onto the cicada after landing nearby it also immediately attempts to squeeze underneath the wings. It can squeeze underneath the wings caudally, ventrally or dorsally and continues with the contact phase behavior as described above. This behavior indicates that the fly is able to locate the timbal from different approaches. In cases of incomplete behavior, it either starts over again at any position of the sequence or leaves the host (Fig. 1A).

The attacks are not qualitatively different on male or female cicadas until deposition of a larva. The short-range phase has a mean duration of 14 and 9 seconds, respectively (n = 15 each; Fig. 1B). The contact phase is about 36 seconds in males and 86 seconds in females (n = 24 for males, n = 33 for females; Fig. 1C). This significant difference ($t = 2.057$, d.f. = 61, $p < 0.05$) results from much longer probing and positioning on the female cicada and from defense behavior of the females (see below). The infection behavior on male and female host candidates differs in respect to the elements that are displayed. Flies show the "wing opening" and "probing" elements in both sexes; however, the percentage of the following elements is lower in females than in males (Fig. 1D). On male cicadas, 88% of the attacks include "positioning" and 74% include the behavior of "timbal cut." The latter behavior is seen as lateral movements of the abdomen at the place of the timbal; however, the timbal is injured and a larva is deposited in only 43% of attacks. On female cicadas, "positioning" is seen only in 42% of the attacks and attempts to cut the timbal only in 16%. No female was found injured and infected with a larva.

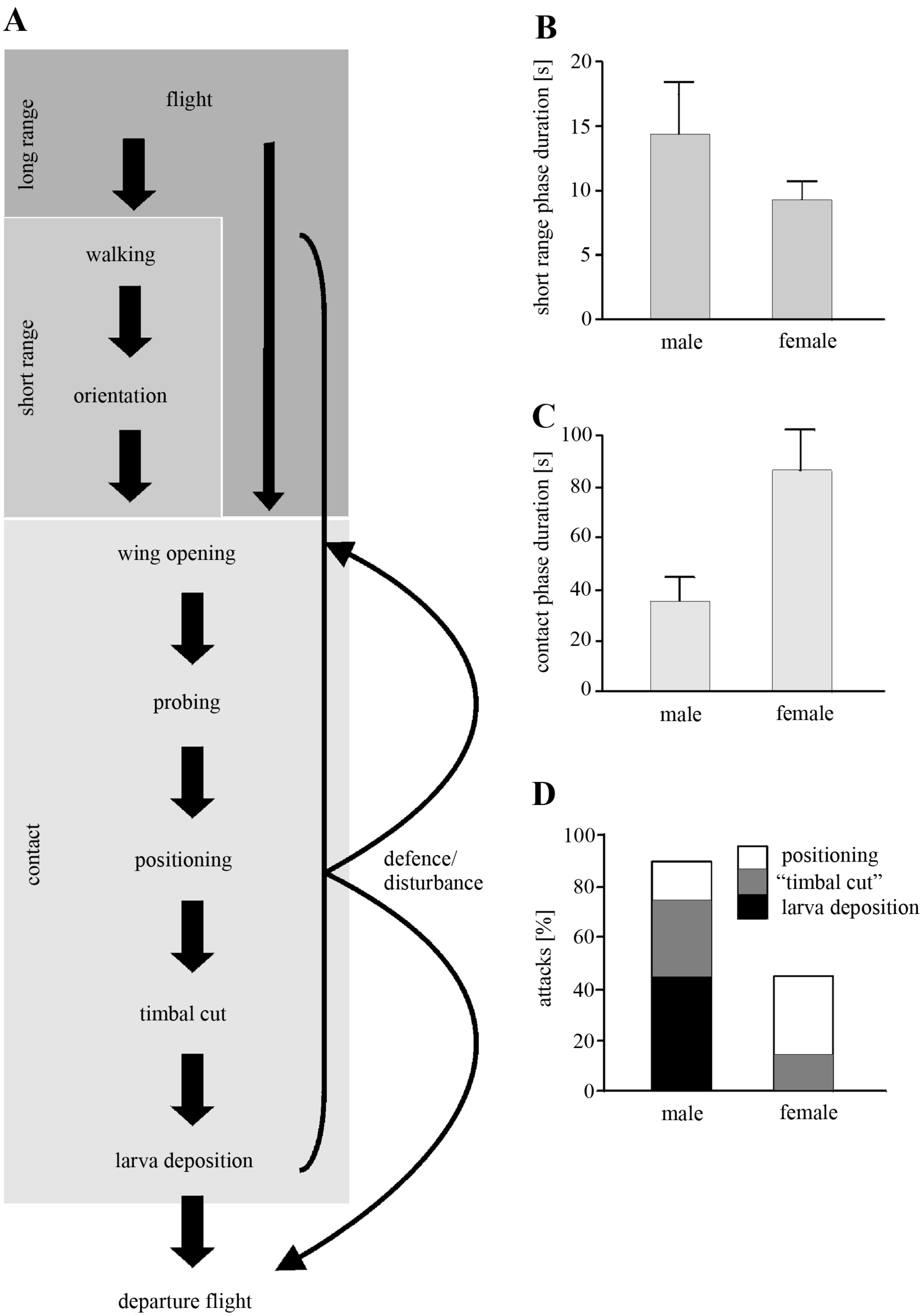

Figure 1. Infection behavior of the parasitoid *Emblemasoma auditrix* and the host *Okanagana rimosa*. **A** Ethogram illustrating the steps of the three different phases: long range host finding with acoustic signal and approach by flight; short range host location in which the fly orientates visually and walks towards the host; contact phase leading to larva deposition and departure from the host. The long-range approach can also lead to direct contact. If the parasitoid is disturbed it either starts again at any position of the sequence or it leaves the host. **B** Duration of the short-range phase for male and female host candidates (n = 15 in both cases; no significant difference). **C** Duration of the contact phase (n = 24 for males and n = 33 for females; $p < 0.05$). **D** Percentage of attacks with completed behavioral elements of the contact phase (n = 23 for males, n = 29 for females). The shading indicates percentages of attacks with positioning, timbal cut and larva deposition. The element "timbal cut" is defined as abdominal movement, not as completed cut of the timbal. The latter was only seen with males where a successful larva deposition took place.

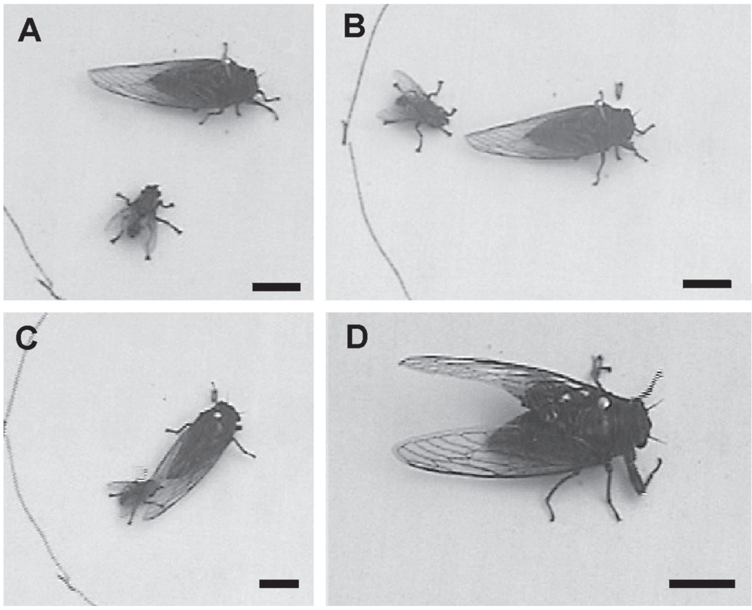

Figure 2. Four pictures from a video showing the infection behavior of *Emblemasoma auditrix*. A male cicada was attached on top of a loudspeaker. The fly approaches the host by walking (**A**), visually identifies the wings and the abdomen (**B, C**) and squeezes caudally underneath the wings (**C, D**). During the contact phase (**D**) it pushes the left wings aside, moves anteriorly with the head on top of the cicada and attempts to locate the timbal with its ovipositor. Scales: 1cm.

Left-right asymmetry of infection

On their first attack, most flies squeeze underneath the host wings from the left side: 65% in males (n = 26) and 68% in females (n = 22). If the attack is interrupted or incomplete, the flies can also move to the right side. The bias to the left side is not induced by the artificial situation of the infection experiments because an analysis of a sample of infected cicadas from the same area confirmed the result. Cicadas infected with larvae of *E. auditrix* always had injuries in a timbal (n = 36) and in 64% the ruptures were in the left timbal. This asymmetry is statistically significant (d.f. 4.463, p = 0.0376).

Defense of the host

In field observations and during the experiments, little defense by the cicada was seen. Two defense behaviors are possible: to scare off the parasitoid and/or to escape. Scaring includes holding the fly with the wings, flipping the wings, and production of protest song. The effectiveness of each of the behaviors has not been determined due to the use of restrained hosts. During “holding,” the cicada presses the wings strongly against the fly and suppresses movements of the parasitoid. The holding is difficult to quantify, but the behavior seems to occur more often in females than in males. At least in some cases, the parasitoid leaves the host after the release without completing the infection. In about 13% of the infection experiments, both sexes of *O. rimosa* flipped their wings after contact of the fly (Fig. 3A). However, despite the movements the flies often manage to stay on the host. Occasional field observations in which flying cicadas were attacked show that even during flight the flies managed to stay on the host. When cicadas are handled or scared they often produce a protest song. Such songs were produced by *O. rimosa* in 32% of the experiments. This sound has a mean duration of 13 seconds (SEM 2.6; n = 8) and ceases thereafter although the fly is still in contact with the host.

By contrast, males of the related species *Okanagana canadensis* show more defensive behavior. In 85% of the attacks, male *O. canadensis* flip their wings (Fig. 3A) and they always produce a protest song as long as the fly contacts the host. However, even on this species flies manage to stay on the host, and no obvious influence of the protest song on the fly’s behavior has been detected.

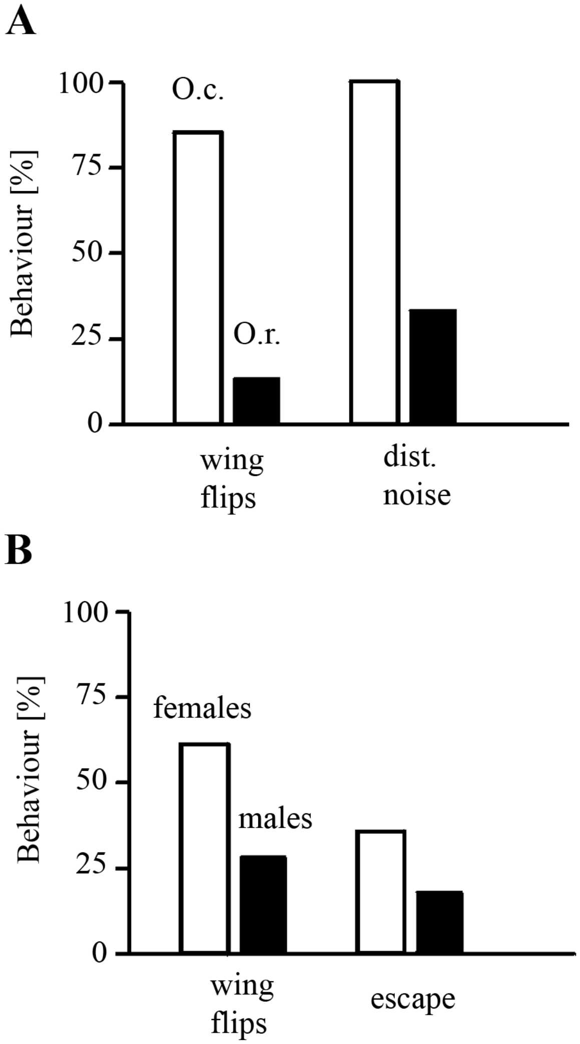

Figure 3. Defense behavior of the host candidates during the infection experiments (**A**) and experiments in which the animals were approached with a stick (**B**). **A** Comparison of two elements of defense behavior (display of wing flips and production of protest song; Dist. noise) between males of the sister species *Okanagana canadensis* (O.c.; n = 13) and *Okanagana rimosa* (O.r.; n = 24). **B** Defense behavior elements of males (n = 50) and females (n = 40) of *O. rimosa*.

Escape seems to be the only effective behavior for parasitoid avoidance, and the difficulty to approach *O. canadensis* in the field is an indication for the alertness of the species.

In order to test the escape reaction and defense behavior elements in freely moving *O. rimosa*, a separate experiment was performed in the field. The animals were approached carefully with a thin stick from behind, attempting to lift the left wings and to touch the region of the timbal. Sixty-two percent of the females reacted with wing flips and 35% escaped by flight (Fig. 3B; n = 40). Males displayed wing flips in 28% of the experiments and only 20% escaped by flight (n = 50). In these experiments, 30% of the males produced a short protest song, a similar percentage to the experiments with restrained cicadas.

Morphology of the timbal and the ovipositor

Light microscopy and scanning electron microscopy were performed to analyse morphological structures involved in larval deposition. Female *E. auditrix* possess a sclerotized genital plate at the ventral abdomen, which is used to cut into the timbal (Figs. 4A, B). The plate is formed at the sternite of the fifth abdominal segment and has a curved shape without sharp teeth or other obvious structures (Fig. 4B). The ovipositor, dorsal of the genital plate, is covered with many hairs.

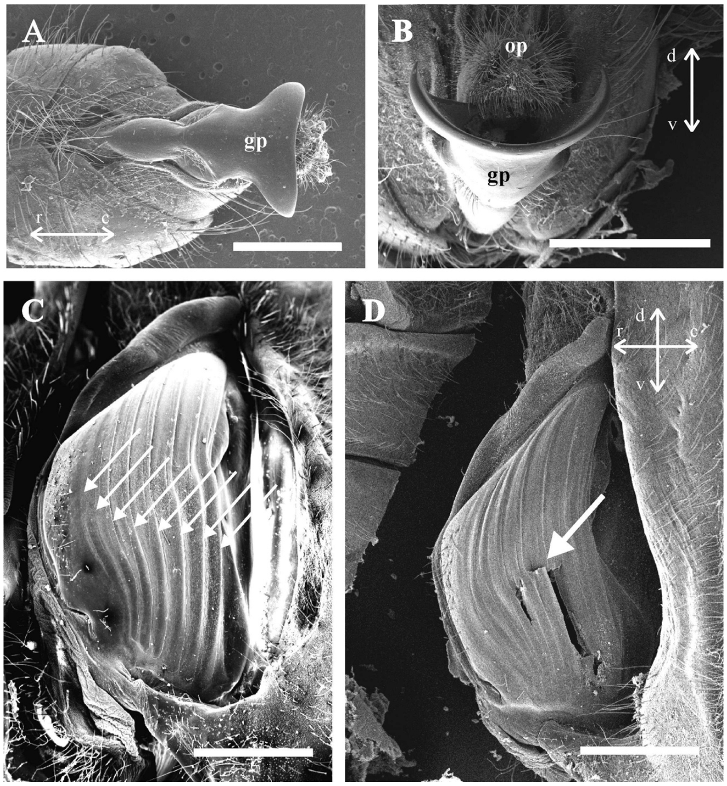

Figure 4. Scanning electron micrographs of structures involved in infection. **A, B** The genital plate (gp) of *Emblemasoma auditrix* has a curved shape and opens dorsally towards the ovipositor (op), which is densely covered with sensory hairs. **C** Timbal of an intact male of *Okanagana rimosa* showing the distinct ribs (arrows). **D** Timbal of a male with parasitoid infection. The timbal is lesioned and the rib number 6 is cut. Scales: 1mm.

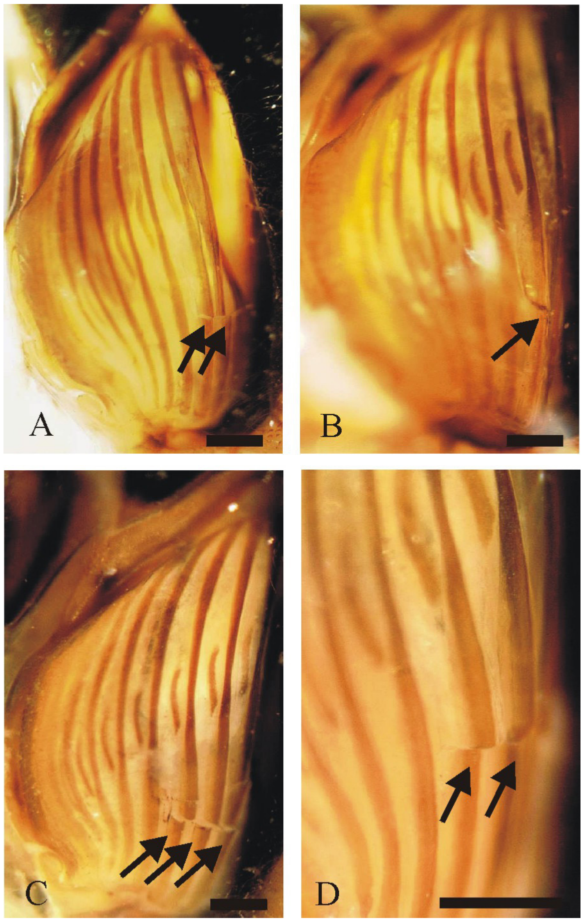

Figure 5. A-D Light micrographs of the timbal of infected *Okanagana rimosa.* The lesion occurs at the ventro-anterior part of the timbal. The micrographs demonstrate the variability of the lesion and the number of broken rips (arrows). Scales: 500µm.

Male cicadas have bilateral symmetrical timbals at the first abdominal segment that are used for sound production. The timbal of *O. rimosa* is a thin membranous structure supported by 7–8 dorso-ventrally running sclerotized ribs (Fig. 4C). Cicadas infected with a parasitoid larva always have injuries in a timbal. The injury occurs anterior-ventrally at one timbal (Figs. 4D, Figs. 5A–D). The larval deposition involves breaking of 1–3 rips (Figs. 5A–D) and rupturing of the membrane (Fig. 4D). An injury of the tympanum has been never been found even not in the females (which lack a timbal).

Discussion

We have studied the infection behavior of females of the sarcophagid parasitoid *E. auditrix*. The fly phonotactically locates its hosts, which are the singing males of the cicada *O. rimosa*. The infection behavior was only rarely observed in the field. Therefore we set up experiments with restrained hosts to analyse the behavior in detail. This experimental approach involves some possible differences compared to the freely moving hosts in the field: males did not produce the calling song by themselves, animals could not escape and the effectiveness of defense might be different from unrestrained animals. However, the occasional field observations confirm that the restraining does not change the behavior in general.

Specificity of infection behavior

E. auditrix is adapted to specific parameters of the calling song of the only known host species (Lakes-Harlan et al. 2000; Köhler and Lakes-Harlan 2001). This adaptation correlates with the highly specific infection behavior: the fly pushes underneath the wings from behind and injures the timbal of the male cicada for larva deposition. The parasitoid shows the same behavior when interacting with female cicadas. In the field a very low percentage of females were infected (Soper et al. 1976b). It is unknown how the larvae enter the female body, because females lack a timbal. Why are females not discriminated against, relative to males, for more efficient foraging? It is likely that the primary cue, the auditory signal from the male, makes it unnecessary to select for discrimination between males and females. Perhaps in crowded populations of cicadas the flies might be attracted by a calling male, but instead of finding the male, encounter a nearby female. In these populations new males can be located rather fast and a waste of energy is probably not a limiting factor. An infection via the timbal has further consequences: infected males cease to produce calling song, although it is not known whether this results from injury of the timbal. Therefore these hosts are not detected again and the parasitoid avoids superparasitism.

*T*his specific infection mechanism reduces the potential host range to male cicadas and up to now *E. auditrix* has only been found in O. rimosa. Other acoustically hunting parasitoids (tachinids) deposit their larvae either on the host, on the substrate nearby the host or even expel larva into the direction of the host (Wineriter and Walker 1990; Walker 1993; Fowler and Martini 1993; Adamo et al. 1995b; Allen et al. 1999). Deposition on the substrate reduces the larval survival (Allen et al. 1999) and, in all cases, the larva enters the host's body by itself. Whereas the tachinids have several hundred larvae (Allen et al. 1999), E. auditrix has a mean number of 35 larvae at the beginning of the season (deVries and Lakes-Harlan, unpubl. results). Thus, the low number correlates well to the specific infection behavior, which might allow a much higher survival rate of larvae.

Possible sensory cues in host infection

The described sequence of infection behavior might involve different sensory signals for host infection: in the long range the acoustic signal is most important, in the short range visual signals might be important, and in the contact phase mechanical and chemical signals may be involved. The sequence of different stimuli might elicit a chain of infection behavior, which is also seen in other parasitoids (e.g. Karamaouna and Copland 2000). However, the sequence does not represent a strict hierarchical order, for example, a visual identification of the wings and a subsequent caudal approach is not necessary, although often seen. The primary cue for host finding is certainly the auditory signal. A silent cicada in a quiet environment was never observed to be approached by a fly in the field. The secondary cue is probably a visual signal. Visual objects influence the phonotaxis response of *E. auditrix*, although the auditory signal is dominant (Schniederkötter and Lakes-Harlan 2001). The short-range approach with identification of the caudal end of the host, also involves visual input. This scanning of the host resembles to some extent the visual scanning behavior of honeybees (Lehrer *et al.* 1985). Generally, the visual system of Diptera is highly evolved and contributes to many different behaviors, including host location (Morehead and Feener 2000; Stireman III 2002; Yamawaki *et al.* 2002). In the tachinid *Homotrixa alleni,* visual cues enable females to find the direction of the host, but sound alone can trigger larviposition (Allen *et al.* 1999). It is not yet clear whether mechanical and chemical stimuli play a role in assessing host suitability and larva deposition. Chemical stimuli could be important for discrimination of hosts with existing infections of a fungus (Soper *et al.* 1976a) or other parasitoids. The tachinid *O. ochracea* deposits larvae on dead *Gryllus sp*., on plastic coated crickets and cricket models, suggesting that chemical cues are less important (Cade 1975; Adamo *et al*. 1995a). The importance of the different sensory cues for host infection and possible host discrimination has now to be tested experimentally.

Whether sensory cues are responsible for the asymmetry in the infection side is unknown. No anatomical correlate has been found on either the cicada or on the parasitoid. The biology of the host does not give any hints for a necessity of a lateral asymmetry. Both timbals are equally involved in sound production (Stölting et al. 2004) and also the behavior of the cicada does not suggest any lateral bias. Thus, so far the asymmetry in infection behavior remains unexplained.

Defense of the host

During the experiments and in observed parasitoid attacks in the field, *O. rimosa* usually showed only weak defense behavior. For defense, male cicadas could produce a protest song, flip their wings, hold the parasitoid with wings or escape. An internal defense (e.g., encapsulation of the parasitoid larva) has never been observed.

Interestingly, the production of the protest song does not seem to influence the parasitoid. Male *O. rimosa* produce it only for a short time, but also the long, ongoing noise of *O. canadensis* does not repel flies. For the attacked individual, rigorous movements, especially flipping of wings, are more effective. This behavior does not provide complete protection against parasitation because parasitoids manage to stay on the host. Nevertheless, such movements are a common strategy of defense (Godfray 1994) and might enhance the chances to escape parasitation at relatively low cost. Therefore, it is surprising that the frequency of individuals displaying such behavior is rather low.

Only early escape by flight seems to be an effective defense. However, the field data suggest that many cicadas do not escape. By contrast, the partly sympatric species *O. canadensis* is much more alert. It produces long protest songs, rigorously flips its wings, and readily escapes. No parasites have been found in this species; however, it is not known whether this defense is the only decisive factor. A low attractiveness of the acoustic signal might also be important (Lakes-Harlan *et al.* 2000). In *O. rimosa,* the rate of successful infections in the field is unknown. However, the limited possibilities to avoid infection suggest that the host relies more on avoidance of discovery by the parasites in the first place, again a common strategy in many insects (Godfray 1994). An absolute avoidance cannot be archived because the signal used by the parasitoid is also used for sexual behavior and reproduction of the host. Thus, the selective pressure by the parasitoid might act directly on the sound production of the cicada, which is subject to further studies.

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