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Some aspects of host selection in *Eucarcelia rutilla* Vill. (Diptera: Tachinidae)

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TABLE XL

Site of settlement of first instar maggots in 40 species of Tachinidae. For some species more than one site is listed. A figure between brackets refers to occasional settlement. For *Eucarcelia rutilla* foregut, mandibular muscles and the subcuticular position are mentioned.

| <i>Site</i> | <i>Number</i> |
|--------------------|---------------|
| haemocoel | 17 |
| segmental muscles | 8 |
| salivary gland | 5 + (2) |
| midgut | 5 |
| fat tissue | 4 + (1) |
| ganglia | 3 |
| mandibular muscles | 2 |
| foregut | 2 |
| subcuticular | 2 |

13.6. CONCLUDING REMARKS

The first question this study set out to answer was why the host list of *Eucarcelia rutilla* is restricted to only one or two pine dwelling species. It can now be stated that this is due to the combined influence of many different behavioural and physiological responses of this parasite to its natural environment. Host habitat selection, host finding, host acceptance, and host suitability all are involved in restricting the host list to *Bupalus piniarius* and *Semiothisa liturata*.

At several points the analysis of the interaction between *Eucarcelia* and *Bupalus*, its main host, also provided interesting indications that we are dealing here with a precariously balanced pair of species, each of which is under strong pressure to maintain and improve its adaptations against the other. A study of much wider scope would be required to do full justice to this aspect. Similarly, much further work remains to be done before we shall understand the physiological processes which determine whether or not a given potential host is suitable for *Eucarcelia*, not to mention the even subtler differences in suitability between sites of settlement in *Bupalus*. However, as far as the present author is aware there is not a single insect parasite for which we are less in the dark on these points than we still are with respect to *Eucarcelia rutilla*.

14. SUMMARY

Host finding, acceptance and suitability in *Eucarcelia rutilla* Vill. were studied in the field and in the laboratory.

The literature on nomenclature, morphology of adult and larva,

life history, hosts, synchronisation and geographical distribution is surveyed. The species is univoltine, well-synchronized with its two main hosts, *Bupalus piniarius* and *Semiothisa liturata*. It deposits macro-type eggs in which the maggots are ready to hatch.

Descriptions and relevant aspects of the biology of pine dwelling caterpillars and *Diprion* larvae are also given.

In the field gravid *Eucarcelia* females coincide mainly with *Bupalus* larvae in their second and third instar. Eggs were also found upon specimens of *Semiothisa liturata*, *Ellopija prosapiaria*, and *Thera obeliscata*. Superparasitism is not avoided under natural conditions.

Host selection was studied experimentally. Attention was paid to detectability and acceptability. A preliminary study of factors involved in host finding reveals that visual stimuli play an important role. In host acceptance stimuli originating from the host's surface are involved. Some evidence was found that these stimuli are mediated through receptors on the tarsi and ovipositor. In experiments there was no discrimination between parasitized and non-parasitized hosts. Pre-imaginal conditioning in oviposition preference was not noticeable.

The bigger the caterpillars, the greater the chance of detection and the greater the risk of parasitization. The resting position of the caterpillar upon the needle has a strong influence on its chance of being found by the parasite. Specimens resting at the base are almost exempt from attacks.

The detectability and acceptability of nine species of Lepidoptera and six species of Hymenoptera were tested. Only 4 differed significantly in detectability from *Bupalus*, but 10 were wholly unacceptable for oviposition. The reaction of the hosts towards attacking females and their eggs differed markedly among species.

Upon *Bupalus piniarius*, *Thera obeliscata*, *T. firmata*, and *Hyloicus pinastri* the eggs are deposited preferably on the thorax. In *Semiothisa liturata*, *Ellopija prosapiaria*, *Panolis flammea*, and Diprionidae other distributions were obtained. As regards the side of the host chosen, the wider its girth the less often the eggs are attached ventrally.

The risk of destruction of eggs upon the host's integument varies widely among species: *Panolis flammea* and *Eupithecia indigata* remove almost all the eggs, whereas in *Ellopija prosapiaria* no eggs were dislodged, and in *Hyloicus pinastri* almost none. *Bupalus piniarius*, *Semiothisa liturata*, *Thera obeliscata*, and *T. firmata* demonstrate a moderate reaction towards eggs placed upon the abdomen. In *Bupalus* the instars II and III have a stronger reaction than the other instars. Eggs laid dorsally on abdominal segments as a rule run a greater risk than those placed ventrally.

Eucarcelia can develop only in *Bupalus*, *Semiothisa*, and *Thera obelis-*

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cata. In about 20% of the cases *Thera firmata*, too, can give rise to full-grown parasite larvae.

Host suitability also depends on site of penetration. Posterior penetration into *Bupalus* lead to greater losses than anterior penetration.

The frequencies of settlement of maggots in wall of the foregut (intima), mandibular muscles, subcuticular sites, segmental muscles, and haemocoel were recorded for the various instars of *Bupalus*. Maggots which have settled in intima or in subcuticular sites must migrate at each moult of the host. This migration takes the maggot outside the host's body which it re-enters by piercing the integument at a sharply defined spot mid-dorsally in the membrane between head-capsule and first thoracic segment. Its main function certainly is to prevent removal with the shed intima or cuticle. In addition it is conjectured that migration may help the maggot to avoid exposure to the host's hormones in concentrations which might cause it to moult prematurely.

Mortality of maggots can be brought about by encapsulation by haemocytes or removal from the host. Larval mortality is higher in cases where more than one maggot has entered the host than when only one is present. Site of settlement exerts a considerable influence upon parasite mortality. Settlement in haemocoel or wall of the mid/hindgut is unfavourable. It is argued that the relatively high mortality of maggots penetrated into posterior segments of younger instars is due to lower suitability of the sites of settlement attained by these maggots.

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