Biological investigations on *Comperia merceti* (Compere), an encyrtid parasite of the cockroach *Supella longipalpa* (Serville)*

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**SYNOPSIS**

An account is given of the behaviour, host specificity and potential as a biological control agent of *Comperia merceti*, a hymenopterous parasite of cockroach oothecae.

**INTRODUCTION**

*Comperia merceti* (Compere), a small (1.5–2.5 mm. long) parasitic wasp that oviposits in cockroach oothecae, has been recorded from Africa, South America, the eastern United States, Arizona, the West Indies and Central and South America (Gomes, 1942; Musebeck *et al.*, 1951; Roth & Willis, 1960). Hosts which reportedly have been parasitised by *C.merceti* include the German cockroach, *Blattela germanica* (L.) (Muesebeck *et al.*, 1951; Gomes, 1942) and the brown-banded cockroach, *Supella longipalpa* (Serville)1 (Muesebeck *et al.*, 1951; Roth & Willis, 1954b and Lawson, 1954). Lawson (1954), however, was unable to induce parasitisation of the German cockroach by *C.merceti*.

Other Chalcids that parasitise cockroach oothecae have been shown not to be host specific: *Tetrastichus hagenowii* (Ratzburg), a Eulophid, parasitises *Euryctis floridana* (Walker), *Periplaneta americana* (L.), *P.australasiae* (F.), *Blatta orientalis* (L.), and *Neostylopyga rhombifolia* (Stoll) (Roth & Willis, 1954b); *Anastatus floridanus* Roth & Willis (Eupelmidae) has been reared from *P.americana, E.floridana* and *B.orientalis* (Roth & Willis, 1954a). The experiments described in this paper suggest that *C.merceti* is host specific on the brown-banded cockroach, *S.longipalpa*.

**MATERIALS AND METHODS**

Since *C.merceti* is not uncommon in buildings, females were easily collected from windows. The wasps were then placed individually in plastic vials (3 cm. diameter), to which cockroach oothecae were added. The wasps are extremely susceptible to desiccation (optimal R.H. appears to be 65–75 per cent.) and were therefore maintained in chambers with greater than 30 per cent. R.H., using a saturated solution of KCL (see Winston &

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1Formerly *Supella supellectilium* (Serville); see Gurney (1970) regarding name change.
Bates, 1960). Wasps in culture readily fed on diluted honey or sugar water soaked up in cotton.

In studies on host specificity a single ootheca was placed with an individual wasp or one ootheca was placed in a vial with several parasites and replaced daily. As soon as an ootheca was parasitised it was isolated, and the date and time of parasitisation was recorded. When more than one wasp was allowed to parasitise an ootheca this information was recorded. The isolated oothecae were kept at room temperature (22°–26° C.).

**RESULTS AND DISCUSSION**

**Mating behaviour**

Upon emergence from the oothecae, male and female wasps are photopositive. If mating fails to take place shortly after emergence (because of an overabundance of females), it occurs at the point of greatest illumination. Males are apparently attracted to females through visual and tactile stimuli. Courtship seems to be initiated by a male trailing a female until the latter stops, when the male nips at the terminal terga of the female’s abdomen. After five or six nips the male places his fore legs on the female’s abdominal tergum and thrusts his abdominal venter forward until contact is made; courtship and copulation require less than fifteen seconds. Males may mate with more than one female, whereas females mate only once during the course of a lifetime. Reproductively active female wasps display a negative phototaxis, which is probably correlated with ovarian development. After oviposition the females again become photopositive. Upon becoming reproductively active a second time the female wasp returns to a photonegative condition. It was not established precisely how many times the phototaxis would switch, but photonegativity is essential if the wasp is to find cockroach ootheca. Photopositivity is essential if the wasp is to disperse. Males are continually photopositive. The thresholds of light intensity that stimulate the phototactic response have not been established, but males and photopositive females are seen to be attracted to the strongest light available. Photopositiveness also probably increases the likelihood that all females will be mated. Flanders (1944) has observed that *Comperiella bifasciata* Howard, a parasite of *Aonidiella citrina* (Coq.) and *A.aurantii* (Maskell), also exhibits a differential phototaxis.

**Parasitisation behaviour**

In the present study, on the basis of observations of 63 adult female wasps, five phases of behaviour were evident: (1) wandering, (2) searching, (3) exploring, (4) oviposition and (5) repulsion from the oothecae.

*Wandering activity* occupies most of the adult life except for periods of direct reproductive activity and is apparently random, with interspersed periods of quiescence. Experimental course tracing showed that no two trail patterns for females were superimposable; the patterns were similar, however, and appeared correlated with container shape. Since searching is not systematic, or alternatively the nature of the pattern cannot be established, it is likely that the wasps in the wandering phase are not seeking oothecae. When such wasps are presented with oothecae, they reject them; when wasps are isolated and not permitted to parasitise oothecae, wandering behaviour persists until death.

When female wasps become reproductively active and oothecae are present, wandering ends and *searching behaviour* is initiated. Searching behaviour is not random, but is restricted to areas within about 2 cm. of the oothecae. Searching is characterised by
Biological investigations on Comperia merceti 117

deliberate movements: the substrate is tapped with the antennae, and the wasp moves in the direction of the ootheca. As yet, it has not been possible to determine what initiates searching behaviour. Duration of the search phase is variable, but it seldom lasts more than one minute. The movements that characterise search behaviour are not seen at all if wasps are not confronted with oothecae.

**Exploration** of the cockroach egg-case is characterised by rapid, incessant tapping of the antennae over the surface of the ootheca. During exploration, the wasp constantly moves over the ootheca. The duration of this phase of behaviour is highly variable, requiring from 4 to 25 minutes. Often during exploration the female stops, dismounts from the ootheca, moves 1–2 cm. away and remains motionless with the antennae clamped together for 1–5 minutes before returning directly to the ootheca again. The function of discontinuing exploration at sporadic intervals is unknown.

Providing the ootheca is suitable to the wasp, oviposition occurs, requiring 35–50 minutes for completion. Under experimental conditions young and old female wasps require about the same time for completion of egg laying; and there is no lengthening of time required for parasitisation by wasps that have previously parasitised several egg capsules. After completing oviposition the wasp leaps away from the ootheca, thus completing the behaviour cycle. (For descriptions of the larval and pupal morphology see Lawson (1954)).

**Longevity in relation to parasitisation**

Adult wasps that were provided with a constant supply of oothecae lived longer than those in which oviposition was prevented (longevity refers to the length of adult life). Experiments were designed to test the longevity of female and male wasps maintained in bell jars with identical conditions of humidity, temperature, light and food. Light conditions were 16 hours of light followed by 8 hours of dark (LD 16 : 8), and water was provided through cotton plugged vials. One group of wasps was provided with oothecae from *S. longipalpa*, and the other group was allowed only the empty oothecae from which the brood had emerged. Using the Wilcoxon two-sample test (nonparametric), the difference in longevity proved significant \( P < 0.01 \). The mean and maximum longevities of wasps allowed to parasitise oothecae were 14.7 and 24 days; the mean and maximum longevities of wasps provided with empty oothecae were 6.39 and 11 days (fig. 1).

The explanation for such differential longevity is speculative, since at the present it is not clear whether behavioural satisfaction or a physiological need for oviposition accounts for the observed differences. Adults of *C. merceti* do not feed on the host, as many Chalcids do (cf. *Tetrastichus hagenowii* (Ratzburg), *T. flavigaster* Brothers & Moran (Roth & Willis, 1954b; Moran et al., 1969)), and such feeding therefore cannot be interpreted as affecting longevity in this instance. In a similar study Legner & Gerling (1967) demonstrated that longevity and fecundity of Pteromalids parasitising pupae of *Musca domestica* (L.) are correlated with host availability. In their study maximum longevity was achieved with *Spalangia cameroni* Perkins and *Nasonia vitripennis* (Walker) provided with hosts early in adulthood. A third species, *Muscidifurax raptor* Girault & Saunders, evinced maximum longevity only after being deprived of host pupae during the first four days of adult life. Adult females of all three Pteromalids feed on the host, and host feeding is presumably partially responsible for the greater longevity of adults having access to hosts. In a slightly different study, Wylie (1962) concluded that fecundity
and longevity of *Nasonia vitripennis* were influenced by the age of the host, both attaining their maximum when the female parasite feeds on *Musca domestica* pupae less than 48 hours old.

**Host specificity**

In demonstrating parasitism of *S.longipalpa* by *C.merceti*, cockroaches were cultured and all oothecae were of known age. Wasps displayed no preference among oothecae of *S.longipalpa* less than two weeks old, but capsules older than two weeks were not parasitised and were apparently not attractive to *C.merceti*. Female wasps subjected to crowded conditions (six wasps per vial) parasitised single capsules, with as many as four wasps observed ovipositing in a single ootheca simultaneously. Single wasps presented with a single capsule parasitised the capsule at each encounter, even over a number of days. This would imply that *C.merceti* is unable to detect previously parasitised hosts, or that the host state has no influence on the wasp. When a fresh ootheca was provided at eight hour intervals to isolated individuals no individual wasp was observed to parasitise more than one ootheca during a 24 hour period.

Fertility of cockroach oothecae does not affect successful development of *C.merceti*; Gould & Deay (1940) found that capsules of *S.longipalpa* were only 35–45 per cent. fertile under conditions similar to those of the present study. Multiple parasitisation of capsules always yielded larger broods, but all members of such broods were smaller than progeny from capsules parasitised only once. Development time was not significantly influenced by the number of times a capsule was parasitised (Table 1). The mean development time for wasps emerging from 42 oothecae was 33.4 days. Lawson (1954) indicated that the development period for *C.merceti* was 30–41 days. Under comparable conditions Edmunds (1955) noted that *T.hagenowii* required 31–60 days to complete development in oothecae of *P.americana*.

Brood size is variable for *C.merceti*, singly parasitised oothecae yielding a maximum of 14 progeny. When more than one wasp parasitised a capsule, or the same female laid eggs in a capsule on consecutive days, the oothecae yielded a maximum of 32 individuals. In contrast, *T.hagenowii* yields between 12 and 187 progeny per ootheca, depending upon the number of wasps parasitising it (Edmunds, 1955).
Biological investigations on Comperia merceti

Table 1. Development time and brood size of C.merceti (22°–24°C.; RH = 41 per cent.).

<table>
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<tr>
<th>Development time (days)</th>
<th>No. of oothecae</th>
<th>Brood size</th>
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<tr>
<td>Oothecae parasitised once</td>
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</tr>
<tr>
<td>44</td>
<td>1</td>
<td>11</td>
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<tr>
<td>41</td>
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<td>37</td>
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<td>35</td>
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<td>11, 14</td>
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<td>34</td>
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<td>33</td>
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<td>31</td>
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<td>29</td>
<td>2</td>
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</tr>
<tr>
<td>27</td>
<td>1</td>
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\[ \bar{Y} = 34.52 \]

<table>
<thead>
<tr>
<th>Oothecae parasitised more than once</th>
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<tr>
<td>37</td>
<td>1</td>
<td>25</td>
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<td>36</td>
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<td>28, 25, 19</td>
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<td>33</td>
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\[ \bar{Y} = 32.40 \]

In establishing the host spectrum of C.merceti, several cockroach species may be eliminated on behavioural grounds. Willis et al. (1958) have categorised cockroach species on the basis of ovipositional behaviour as being: I. falsely ovoviviparous species that retain the ootheca in the uterus and give birth to nymphs internally; II. oviparous species that deposit oothecae shortly after production; and III. oviparous cockroaches that carry oothecae externally until shortly before nymphal emergence.

Falsely ovoviviparous cockroaches, which include species such as Blaberus craniifer Burmeister, Byrsotria fumigata (Guérin), Leucophaea maderae (F.), Pycnoscelus surinamensis (L.) and Gromphadorhina laevigata Saussure & Zehntner, are ecologically eliminated as possible hosts for C.merceti, since the wasp is a parasite of oothecae. On two occasions females of L.maderae, in colony, aborted oothecae. These oothecae were presented to reproductively active wasps but were rejected.

Cockroaches that deposit oothecae shortly after completion of the capsule comprise the greatest number of species; these include all species of Periplaneta, as well as Neostylopyga rhombifolia, Blatta orientalis, and S.longipalpa, which are domiciliary and thus coincide with the habitat of C.merceti. Any potential host of C.merceti would have to fit into this group. To test this group for potential hosts, reproductively active wasps were given the opportunity to select their hosts in vials with oothecae of three cockroach species: P.americana, S.longipalpa and B.orientalis. Twenty-six replicates of this experiment were carried out with oothecae of various ages, and, in every instance the wasps successfully parasitised only S.longipalpa. Attempted oviposition into oothecae of P.americana was observed on two occasions, but penetration by the ovipositor was
not successful. The factor responsible for inhibiting successful parasitisation of _P.americana_ has not been established. Several oothecae were scraped with a scalpel, but the wasps showed no interest in altered oothecae. Similar experiments involving fewer replicates were conducted with oothecae of _Parcoblatta_ sp. but no oviposition attempts were observed.

Part of the reason for _C.merceti_ being a successful parasite of _S.longipalpa_ may be that the host is of tropical origin, whereas some other cockroach species examined (e.g. _Parcoblatta_ sp.) are not. _S.longipalpa_ in temperate regions is almost exclusively confined to artificially heated buildings (Cornwell, 1969). Similarly, _C.merceti_ has only been recorded from buildings in temperate regions and is extremely susceptible to cold temperatures, 100 per cent. mortality being recorded when the wasps are refrigerated at 7° C. for 24 hours (unpublished data). For this reason it seems unlikely that _C.merceti_ could survive as a parasite of endemic temperate or cold-tolerant tropical cockroaches belonging to category II unless the potential host is also domiciliary.

Egg capsules of _S.longipalpa_ are attached to the substrate with a mucilaginous substance by the gregarious adults in dark, dry places. Roth & Willis (1960) noted that the oviposition stimulus of parasitic wasps for cockroach oothecae is unknown, but Edmunds (1954) observed that _Prosevania punctata_ (Brulle) (Evaniiidae), also a parasite of oothecae, preferred capsules that were cemented to the substrate to oothecae that were not. _P.americana_ and _B.orientalis_ will occasionally attach their oothecae to the substrate but generally do not whereas _S.longipalpa_ consistently attaches its oothecae to the substrate. The host detection mechanism used by _C.merceti_ may therefore involve the mucilaginous secretion. If a particular odour consistently emanates from the secretion, _C.merceti_ might be attracted to _S.longipalpa_ in preference to other species tested. Experiments are being initiated to determine the validity of this hypothesis.

The preoviposition period for the brown-banded cockroach is 10·4 days, with an interval between oothecae of 6·4 days (Willis _et al._, 1958); most oothecae are produced during the fall (Gould & Deay, 1940). In addition, _S.longipalpa_ seems less productive of oothecae when subjected to constant temperature and light (personal observation). These data contrast sharply with the biological facts known for other potential cockroach hosts of category II. The interval between oothecae is shorter for _S.longipalpa_ than for most other cockroaches in category II. The shorter the period between oothecae, the greater the likelihood that a single female wasp can parasitise more than one ootheca. Since the wasps are short lived, the inter-ovipositional period assumes critical importance and could be responsible for host specificity.

The time required for host maturation is of critical importance when a new population of parasites is becoming established. Willis _et al._ (1958) found mean incubation time for the brown-banded cockroach egg capsules to be 39·9 days. Incubation time for _S.longipalpa_ increases with a decrease in temperature, and the optimal temperature appears to be 26° C. (Gould & Deay, 1940). Other cockroaches tested that belong to category II have comparable incubation periods (Willis _et al._, 1958; Roth & Stay, 1962; Bell, 1969). Since _C.merceti_ has a mean generation time of 33·4 days, any cockroach that has an egg development period of less than the minimum development time of the parasite is probably not suitable as a host.

Cockroaches that retain their oothecae externally for a long period of time (_B.germanica_, _B.vaga_ Hebard) appear behaviourally unsuitable to be hosts for _C.merceti_, although Gomes (1942) claims to have reared _C.merceti_ from oothecae of _B.germanica_
and, as a result, Muesebeck et al. (1951) list the German cockroach as a host of C. merceti. Lawson (1954) was unable to induce parasitisation of this cockroach by C. merceti, but did not conclude that the wasp was not a parasite of B. germanica. On the basis of the following observations, however, it seems that C. merceti does not parasitise the German cockroach. (1) C. merceti failed to attack oothecae still retained by female cockroaches (Roth & Willis (1954a) have shown that a close relative, Anastatus floridanus Roth & Willis (Eupelmidae), readily oviposits into oothecae held externally by its host, Eurycotis floridanax). (2) In twelve attempts to induce parasitisation of oothecae freshly removed from female German cockroaches, female wasps were not attracted to the capsules. (3) Wasps placed in extremely cramped conditions with German cockroach oothecae repeatedly leaped away from them. (4) In choice experiments between German and brown-banded cockroach oothecae, the wasps always chose the oothecae of S. longipalpa (5) Finally, total embryonic development time for the German cockroach is 17 days; this is about one-half the time required for C. merceti to develop, making it unlikely that the parasite could successfully complete development. Although experiments were not conducted, it is probable that B. vaga and other cockroaches that retain the oothecae externally would not be suitable as hosts for C. merceti, since they also have incubation periods shorter than that of the wasp.

Sex ratio

Among 516 reared individuals of C. merceti, a sex ratio of three females to each male was noted. When broken into classes of single versus multiple parasitisation, the percentage of females present in both classes was almost identical (single parasitism 74.4 per cent. n = 121; multiple parasitism 77.2 per cent. n = 395). C. merceti is arrhenotokous, but mating takes place almost immediately after emergence. Other Chalids that mate just outside their hosts have a sex ratio similar to that of C. merceti. Anaphoidea nitens Girault (Mymaridae), a parasite of weevil oothecae, has a ratio of 3 : 1; Pleurotropis parvulus Ferriere (Eulophidae), a parasite of leaf-mining larvae, has a ratio of 13 : 4 (Hamilton, 1967). Although most Hymenoptera have a haplo-diploid sex determining mechanism, the ultimate sex ratio for a given species could be strongly influenced by the number of mated females from each brood.

Clausen (1923) has demonstrated that rate of oviposition influences sex ratio in some Eucharitids. The possibility exists that in C. merceti the sex ratio is likewise determined by rate of oviposition, but this seems unlikely, since the wasp requires a rather long period of time to oviposit. Differential mortality between males and females could also be implicated, but is probably not significant, since little larval mortality was noted during the present study.

C. merceti as a biological control agent

Zimmerman (1948) has indicated that Comperia falsicornis (= C. merceti) "has practically wiped out" the brown-banded cockroach from places in Hawaii. He also noted "nearly 100 per cent. parasitism of all oothecae located." Flock (1941) has observed that hymenopterous parasites could be of benefit in controlling S. longipalpa.

Although these reports are encouraging, S. longipalpa continues as a pest in many areas. Once an ootheca has reached a particular stage of maturity it is no longer attractive to the wasp. The time marking the onset of unattractiveness is variable, but seems to be approximately 14 days after deposition. Providing an ootheca less than two weeks old
is located, however, *C. merceti* is exceedingly efficient in curtailing cockroach development. From 27 oothecae yielding a mean of 12.9 parasites, no cockroaches emerged; from an additional two oothecae four and two parasites and one and two cockroaches emerged.

Another feature limiting success of *C. merceti* as a biological control agent is the failure of the wasp to respond to previous parasitisation of oothecae. Other species of Chalcids (e.g., *Trichogramma evanescens* Westwood and *Dahlbominus fuscipennis* (Zetterstedt) can detect previously parasitised hosts. The detection of previous parasitisation coupled with subsequent rejection could initiate further search behaviour. Since *S. longipalpa* tends to deposit its oothecae in aggregations, an ability to detect parasitised hosts would be beneficial from a control viewpoint.

**SUMMARY**

*Comperia merceti* (Compere) (Chalcidoidea), which parasitises the oothecae of *Supella longipalpa* (Serville), was found to be host specific when tested with representatives of five genera of cockroaches. Oothecae more than two weeks old were not parasitised. *C. merceti* appears unable to detect previously parasitised oothecae, and multiple parasitism of capsules always yielded larger broods. A sex ratio of three females to each male was noted, and wasps that parasitised oothecae lived longer than those that were not allowed to do so. Five distinct phases of parasitisation behaviour were categorised. Female wasps displayed differential phototaxis, depending on reproductive state; males were always photopositive.

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