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THE HYPOPE OF *HEMISARCOPTES COCCOPHAGUS*: DISTRIBUTION AND APOLYSIS

BY Sergey IZRAYLEVICH * & Uri GERSO*N*

ABSTRACT: Hypopodes (deutonymphs) of *Hemisarcoptes coccophagus* Meyer (Astigmata: Hemisarcoptidae), a parasite of armored scale insects (Homoptera: Diaspididae), had a contagious distribution while dispersing on their vector, *Chilocorus bipustulatus* (L.) (Coleoptera: Coccinellidae). When appearing in low numbers, most deutonymphs aggregated on one of the beetle’s elytra, whereas when occurring in higher numbers they were evenly distributed on both elytra. The hypopodes strongly preferred the subelytral margins (especially their anterior-lateral parts) for attachment. These areas lack microsetae which are dense at the elytras’ center. Deutonymphs were unable to complete their ontogenesis without staying a minimum of 48 hours under the vectors’ elytra. Optimal contact-time with the beetles was 4-6 days, a period which induced ca 30% hypopodial moltings. Host scales were not essential for apolysis, but their presence increased deutonymphal molting success. The significance of these results for enhancing the effectiveness of mite releases in the field is discussed.

RESUMÉ: On a observé une distribution *Hemisarcoptes* contagieuse des hypopodes (deutonymphes) de *Hemisarcoptes coccophagus* Meyer (Astigmata: Hemisarcoptidae), un parasite des pucerons à bouclier (Homoptera: Diaspididae), lors de leur dispersion sur leur vecteur, *Chilocorus bipustulatus* (L.) (Coleoptera: Coccinellidae). Lorsqu’elles figurent en petit nombre, la plupart des deutonymphes s’agglomèrent sur une des élytres de la coccinelle, alors qu’en plus grand nombre elles se répartissent de façon égale sur les deux élytres. Les hypopodes préfèrent de loin s’attacher aux marges subélytrales, et plus particulièrement à leurs parties antérieures-latérales. Ces zones manquent de microsetae qui abondent au centre des élytres. Les deutonymphes sont incapables de terminer leur ontogénese sans séjourner un minimum de 48 heures sous les élytres du vecteur. Le temps de contact idéal avec les coccinelles est de 4 à 6 jours et cette période induit à peu près 30 % de mues hypopodiales. Les pucerons hôtes ne sont pas nécessaires à l’apolyse, mais leur présence accroît le taux de réussite des mues des deutonymphes. On discute la signification de ces résultats afin d’augmenter l’efficacité des lâchers d’acariens dans les champs.

INTRODUCTION

The hypopus is the heteromorphic deutonymphal stage in the ontogeny of many Astigmata. The hypopus lacks functional mouth-parts but has various organs allowing phoresy through attachment to animals (HOUCK & OCONNOR, 1991).

Mites of the genus *Hemisarcoptes* (Astigmata: Hemisarcoptidae) are obligate parasites of armored scale insects (Homoptera: Diaspididae), and have been used in the biological control of pests belonging to this family (GERSON et al., 1990; HILL et al., 1993). Mite eggs are deposited on the host-diaspidid, on which the larvae, protonymphs, tri-
tonymphs and adults feed, causing scale death or reduction in fecundity. Hypopus occurrence in *Hemisarcoptes* is optional, as the mite may complete development without forming a deutonymph. However, when mite larvae and proto- 
tonymphs fed only on an insufficient diet such as moribund hosts, hypopodes were formed (Gerson & Schneider, 1982). The deutonymphs are attracted to, and transmitted by, coccinellid beetles of the genus *Chilocorus* (Gerson et al., 1990), which also feed on diaspids.

Factors promoting hypododial formation and termination in the Astigmata were reviewed by Gerson & Schneider (1982) and by Houck & O'Connor (1991). Termination of the deutonymphal stage by molt (apolysis) has been attributed to various factors: presence of fresh food, changes in osmotic pressure and high relative humidity (Cutcher & Woodring, 1969, and citations therein). Fain (1977) and Kuo & Nesbitt (1970) regularly obtained tritonymphs by exposing various hypopodes to very humid conditions. Hypododial termination was also influenced by temperatures (Capua & Gerson, 1983). Low humidities and high temperatures accelerated hypododial development of the stored-product mite *Lepidoglyphus destructor* (Schrank), but molting to the tritonymph was triggered by high humidity at a moderate temperature (Knülle, 1991). Little is known concerning the stimuli for the apolysis of astigmatic hypopodes parasitising invertebrates (Houck & O'Connor, 1991); Gerson & Schneider (1982) found no effect of relative humidity on the molting of *H. coccophagus* Meyer hypopodes. Herein we look at the distribution of the hypopodes of *H. coccophagus* on the elytra of its vector, *C. bipustulatus* (L.), and then discuss the effects of a diaspid host and the coccinellid vector on deutonymphal apolysis.

**Materials and methods**

**Distribution patterns**

A total of 785 *C. bipustulatus* adults, collected from ten citrus groves (22 samples), were examined for presence and attachment sites of hypopodes. Distribution pattern of hypopodes within beetle populations was estimated by Taylor's power law (TPL) (Taylor, 1961; 1984) describing the relationships between sample variance and mean ($s^2 = ax^b$). The distribution is clumped if either $a$ or $b$ of TPL exceeds unity (Horn, 1988). Another widely accepted method for estimating the distribution pattern of a given species is the negative binomial distribution (NB) (Southwood, 1978). If NB fits the data (as indicated by $\chi^2$ test) and the parameter $k$ (index of aggregation) is small [less than 8, according to Ruesnik (1980)] then the concerned species has a clumped distribution. We fitted the NB to observed frequencies of hypopodes/beetle by means of the maximum likelihood method developed by Bliss & Fisher (1953).

The subelytral surfaces of half a dozen beetles were separately observed. Houck (1994) suggested that the distribution pattern of subelytral microsetae of *Chilocorus* may affect deutonymphal preference for some areas there. Subelytral surfaces were therefore coated with palladium and examined by electron scanning microscopy (Jeol).

**Apolysis induction by the beetles**

Five *C. bipustulatus* beetles were placed on a hypopodes-producing mite culture maintained on latania scale, *Hemiberlesia lataniae* (Signoret), kept in the laboratory on potato tubers. After 48 hours ca 300 deutonymphs had been acquired and positioned under the beetles’ elytra. The beetles were then placed in a mite-free scale culture. Groups of 6-10 hypopodes/beetle were removed after 24 hr and then at 2, 4, 6, 9 and 11 days' intervals. Deutonymphs were placed in small plastic tubes padded with black filter paper and covered with microscopic glass slides, and incubated (22°C, 80% r.h.) till all hypopodes had molted or died. Each treatment consisted of 30-50 deutonymphs. A group of 60 deutonymphs which had no contact with the beetles served as controls. Percentage of apolysis and the longevity of unmolted individuals in all treatments were recorded.
Host-scale effect on hypopus detachment and apolysis

A group of hypopodes-bearing *Chilocorus* were used in the following two experiments (at 22°C, 80 % r.h.).

— Experiment 1: Several beetles carrying a total of ca 100 hypopodes were placed on a mite-free colony of latania scale, while a similar group of beetles was kept without any food. Numbers of hypopodes remaining on their vectors were recorded at 2-3 days’ intervals for 13 days, when all starving beetles had died.

— Experiment 2: Two groups of hypopodes, removed from the beetles, were placed on a potato tuber within glued plastic arenas. One of them contained a colony of latania scales while the other was empty. Percentages of aplysing deutonymphs were recorded after 5 days.

RESULTS

Distribution patterns

About half (369) of the 785 examined beetles carried a total of 1760 hypopodes on the ventral surfaces of their elytra. Around 90 % were attached to the margins of the ventral elytral surface (an region occupying about one third of the total elytral area), especially to its anterior-lateral part. The pattern seen in *C. bipustulatus* (Fig. 1) is similar to

![Fig. 1: (A) The venter of a left elytron of Chilocorus bipustulatus (× 40, SEM); (B) Anterior part of the elytron, showing dense setae at the central area (top) and their lack at the margins (bottom) (× 220); (C) Further magnification of a setae-dense area, unsuitable for deutonymphal attachment (× 2200); (D) Further magnification of setae-less area, the most suitable site for hypopodial attachment (× 2200).](image-url)
that shown by HOUCK (1994) for another Chilocorus sp., and deutonymphal dispersion in the present case may likewise be explained by microsetal distribution.

When hypopodes appeared on the beetles in low numbers (up to 6) most of them aggregated on the same elytron; when occurring in higher numbers they were more evenly distributed on both elytra (Fig. 2).

The regression between the samples' log mean and log variance was highly significant (Fig. 3) and its slope \( b \) of TPL exceeded unity \( (F = 25.9 \ P < 0.001) \), demonstrating the clumped distribution of the hypopodes. The frequency distribution of hypopodes/beetle (Fig. 4) fitted NB \( (\chi^2 = 9.44 \ P > 0.05 \ df = 5) \) with the \( k \) value being small (0.434). The contagious nature of hypopodial distribution within C. bipustulatus populations is thus evident.

Apolysis induction by the beetles

Hypopodes which had not stayed for any time on the beetles did not molt. One-day contact with the vector likewise had no effect, but after two days' residence a few deutonymphs molted. By the fourth day the frequency of apolysis increased substantially, remained relatively high on day 6, but decreased by day 9 (Fig. 5). This decline may be explained by the increased detachment of hypopodes which had already received their required molt-induction (HOUCK & OCONNOR, 1991). The
longevity of deutonymphs which failed to molt was affected by the treatments: the longer they had stayed on the beetles, the longer they survive (Fig. 5).

![Graph showing effect of residence period of Hemisarcoptes coccophagus hypopodes under the elytra of Chilocorus bipustulatus (induction time) on percentage of apolysis (bars), and on the longevity (mean days ± SE) of hypopodes which failed to molt (line).](image)

**Fig. 5**: Effect of residence period of *Hemisarcoptes coccophagus* hypopodes under the elytra of *Chilocorus bipustulatus* (induction time) on percentage of apolysis (bars), and on the longevity (mean days ± SE) of hypopodes which failed to molt (line).

**Host-scale effect on hypopus detachment and apolysis**

Hypopodes on beetles placed on host-scales left their vectors at a slightly higher rate than deutonymphs on beetles kept without scales (Fig. 6). However, when the beetles died (by days 9-10) the deutonymphs left them within 2-3 days (Fig. 6). This was probably due to the desiccation of the dead beetles: placing mite-bearing *Chilicorus* elytra at 100 % r.h. precluded deutonymph departure for more than ten days. More than twice as many hypopodes molted in the scale-containing arena than in the scale-free one (Table 1). Most moltings took place on the second day. All exuvia were found very close to scale shields, suggesting that apolysis had occurred just before host penetration.

![Graph showing percentages of hypopodes of *Hemisarcoptes coccophagus* remaining on *Chilocorus bipustulatus* when beetles were presented with a colony of latania scale, and when kept without scales. Arrow denotes beginning of beetle mortality.](image)

**Fig. 6**: Percentages of hypopodes of *Hemisarcoptes coccophagus* remaining on *Chilocorus bipustulatus* when beetles were presented with a colony of latania scale, and when kept without scales. Arrow denotes beginning of beetle mortality.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>N</th>
<th>Molted (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Scales present</td>
<td>102</td>
<td>44 (43.14)</td>
</tr>
<tr>
<td>Scales absent</td>
<td>129</td>
<td>32 (24.8)</td>
</tr>
</tbody>
</table>

\[ \chi^2 = 8.67, \quad P = 0.003 \]

**TABLE 1**: Host scale effect on molting of hypopodes of *Hemisarcoptes coccophagus*.

**DISCUSSION**

The highly contagious distribution of *H. coccophagus* deutonymphs on the elytra of *C. bipustulatus* implies that relatively few beetles transferred most of the hypopodial populations. This overdispersion may be explained by heterogeneous accessibility and/or attractiveness of the beetles to deutonymphs. Some scale patches on citrus trees are spatially protected from mite (but not beetle) attacks (S. Izraylevich & U. Gerson, unpublished), which could bring about the clumped distribution pattern of *H. coccophagus*. Whatever the mechanism, such aggregative behavior is apparently beneficial for mite colonization of new habitats, since mating is essential for reproduction (Gerson & Schneider, 1982). The distribution of *Caloglyphus phyllophagianus* Oseto & Mayo hypopodes on many of their scarab beetle vectors was similar to that reported herein (Crocker et al., 1992). Deutonymphs of another mit, *Psylloglyphus uilenbergi* Fain, were also overdispersed during their phoretic association with the flea *Dinopsyllus lupus* Jordan, attacking the Nile grass rat (Schwan, 1993). The phenomenon of astigmatic mites with similar patterns of distribution on their vectors suggests that overdispersion may be a general property of the hypopus-insect interactions.

Houck & O'Connor (1991) reported that in a *Hemisarcoptes cooremani* (Thomas)-*Chilocorus cacti* (L.) system, hypopodes which did not encoun-
ter beetles could not complete their ontogenesis. Our data for another Hemisarcoptes-Chilocorus system were similar; in addition, the minimal and optimal contact-times required for mite apolysis (2 and 4-6 days, respectively) were established. Despite host-scale availability, a large number of hypopodes remained on the beetles for periods longer than optimal (Fig. 6). This may be due to large individual variance in the genetic system underlying length of hypopodial development, as reported by Knülle (1991) for a stored-product mite.

Most hypopodes of H. coccophagus were packed in the specific glabrous areas of the elytra. Such smooth surfaces allow better hypopodial attachment to the elytra, apparently required for the acquisition of some vital material(s) from the beetle (Houck, 1994). Our observations show that hypopodes arrive at their preferred sites soon after slipping under the beetles' elytra. The success of any given hypopus in occupying an optimal attachment site may affect its probability of molting, with latecomers restricted, at least temporarily, to the pubescent parts of the elytra. Hypopodial aggregation under the same elytron in the present case is somewhat surprising, since bilateral equality of deutonymphal distribution was observed in all hitherto studied hypopus-insect interactions (Houck & O'Connor, 1991, and citations therein). A possible benefit of such aggregative behavior could be an increased ability of deutonymphs to enhance the flow of apolysis-related materials in the beetles' elytra. The severity of asymmetric dispersion decreased as mite load increased (Fig. 2), suggesting that residency on a glabrous attachment site, on the unoccupied elytron, may become an important factor.

Our data demonstrate that scale vicinity was not essential for hypopodial apolysis, although its presence increased deutonymphal molting success (Table 1). The maximal rate of moltings in our experiments was ca 43%, which is only half that obtained by Houck & O'Connor (1990) for H. cooremani. Host scales differ in their suitability for the mite (Izraylevich & Gerson, 1993). Thus they may also differ as nutrients for Chilocorus. This in turn could affect the quality of the molt-inducing factor, and thereby rates of apolysis as well as optimal contact-time. These parameters may vary amongst different Chilocorus species and ages (M. A. Houck, personal communication).

Furthermore, apolysis success could be affected by hypopodial age. Chilocorus beetles are convenient means for transferring Hemisarcoptes to the field during biological control projects of pestiferous diaspidids (Gerson, 1967). Our study leads to optimization procedures of mite release, using beetle vectors. The following are conditions that should be met: optimal beetle-mite contact-time; occupation of the appropriate subelytral areas (avoidance of beetle overloading) and bringing the beetles with hypopodes to their host scales.

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