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ASPECTS OF THE RELATIONSHIP BETWEEN BURYING BEETLES, *NECROPHORUS* SPP. AND THE MITE, *POECILOCHIRUS NECROPHORI* VITZ.

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INTRODUCTION

The various types of association between mites and other invertebrates, particularly insects, have been discussed by Vitzthum (1941) and Trägardh (1943), and more recently by Evans, Sheals & Macfarlane (1961). The associations fall into five broad categories, the parasitic and predacious mites being the best defined and studied. The other categories are commensals, phoretic species and exudate feeders, and detailed information on the relationships between the mites and other animals involved in these apparently harmless associations is lacking.

During a study of the biology of the carrion beetles, *Necrophorus humator* Ol. and *N. investigator* Zett. on the Farne Islands, Northumberland, in 1963 and 1964, it was found that all of these beetles carried large numbers of mesostigmatid mites, the commonest species of mite being *Poecilochirus necrophori* Vitz. The life history of these mites, associated with *Necrophorus humator*, has previously been studied by Neumann (1943), who indicated that the relationship is a loose one, the mite being a paraphage and symphorist, using the beetle for transport and feeding on the fly maggots and the carrion encountered by the host. Neumann obtained all stages of the life cycle of *Poecilochirus necrophori* from the host, and he found that a single generation lasted 8–9 days.

The present investigation aims at elucidating the interaction of *P. necrophori* with *Necrophorus* and demonstrates the complex interrelationship between these two animals as well as their interdependence.

FIELD STUDIES

Technique

Necrophorus beetles were caught on the Farne Islands in pitfall traps (1 lb jam jars about 5 cm across the mouth) sunk into the ground with their rims flush with the litter below the vegetation. Each trap was baited with 20 g of meat, normally sheep's lungs. The traps were emptied at least twice weekly and the beetles were individually preserved in Pampel's fluid. Before the beetles were dissected to determine the state of their gonads the mites were counted, examined and identified. The beetles were divided into immature, mature and spent, in accordance with their gonadal state.

Results

Necrophorus beetles show a high degree of social organization, a pair monopolizing a corpse (buried co-operatively by several beetles) and defending it. The larvae feed on

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the corpse, and the female beetle plays an essential role in their development by feeding them at the beginning of each of the three instars. The two beetle species, *N. humator* and *N. investigator*, are active at different times in the year, *N. humator* emerges in April, reproduces in May and June, and disappears in August. A new generation, which overwinters as adults, appears in September. *N. investigator* is active from July until September and reproduces in August, overwintering as a prepupa (Pukowski 1933; Springett, in preparation).

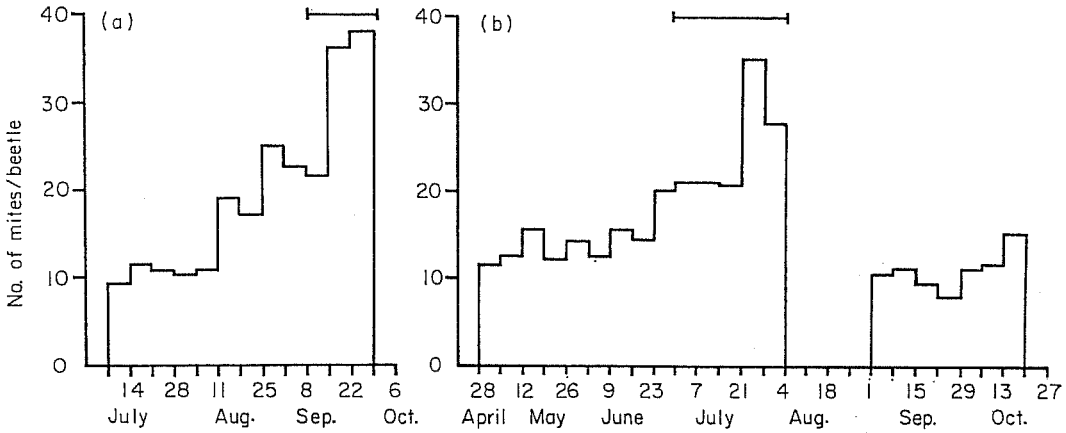

FIG. 1. The average numbers of deutonymphs of *Poecilochirus necrophori* found on (a) *Necrophorus investigator* and (b) *N. humator* in pitfall traps at weekly intervals during the flight season on Inner Farne. The period when the majority of beetles have spent gonads is indicated by a bar.

The results of counting deutonymphs of *Poecilochirus necrophori* on each beetle during the flight season are expressed graphically in Fig. 1. The mean number of deutonymphs per beetle (±S.E.) on *Necrophorus humator* rises from 11·5±1·6 in April to 23·5±2·2 in July, with 11·8±1·7 in September and October when a new generation of beetles emerges. Similarly the mite infestations on *N. investigator* range from 10·5±1·3 in July to 23·0±2·5 in September. These infestations are large compared with an average

Table 1. *The numbers (and standard errors) of deutonymphs of* Poecilochirus necrophori *found on both sexes of two species of* Necrophorus *according to the reproductive state of the beetle*

	No. examined	Immature	Mature	Spent
Necrophorus humator	164	15·0±1·8	16·4±1·6	31·8±5·1
N. investigator	386	11·4±1·5	11·7±1·3	32·9±4·7

six to seven mites/beetle found by Costa (1963), but small compared with the average of 158/individual found on *Geotrupes stercorarius* L. (Hyatt 1959). The four specimens of *Geotrupes* examined by Hyatt (1959) carried two, twelve, 129 and 488 mites of eight species, but *Poecilochirus necrophori* was not among them.

The data also show how infestations increase as the flight season of the beetles progresses. The periods when the majority of beetles have spent gonads are indicated in Fig. 1, and further analysis (Table 1) shows that spent beetles had two or three times as many mites as immature or mature specimens. This strongly suggests that the mites reproduce underground at the same time as the beetle.

LABORATORY STUDIES

Techniques

A series of experimental cultures was set up to study the behaviour of *Necrophorus* in relation to infestations of *Calliphora* larvae, their chief competitors for corpses (Elton 1966), and in addition these cultures provided data on the behaviour of the mites.

The control culture consisted of a pair of beetles with a normal mite infestation of between ten and twenty deutonymphs of *Poecilochirus necrophori* and a standard corpse, an eviscerated wood mouse (*Apodemus sylvaticus* (L.)) in a 1000 ml crystallizing dish containing soil. The culture chamber was covered with a glass plate. The *Calliphora* eggs were obtained by exposing meat to gravid flies, and carefully transferring suitable numbers of eggs from the meat to the corpse. The eggs were placed in the mouth and in the body cavity of the eviscerated corpse, in batches of fifty. *Calliphora* larvae were obtained from meat in the same way, and thirty larvae were placed on each corpse. Live mites were obtained by brushing them from *Necrophorus humator*, about thirty deutonymphs being used for each culture. The combinations of animals used in the cultures were as follows:

A. Corpse, thirty mites, 100 *Calliphora* eggs.

B. Corpse, thirty mites, 100 *Calliphora* eggs, one male and one female *Necrophorus investigator*.

C. Corpse, thirty mites, one male and one female *N. investigator*.

D. Corpse, 100 *Calliphora* eggs.

E. Corpse, one male and one female *Necrophorus investigator*.

F. Corpse, 100 *Calliphora* eggs, one male and one female *Necrophorus investigator* (no mites).

The control cultures for this series were groups B and C which probably represent the normal conditions in the field, and each culture was replicated four times in 1963 and four times in 1964. In addition, another set of cultures was studied in 1966, in which the *Calliphora* eggs were replaced by small (3 mm) *Calliphora* larvae. In all other respects these later cultures were similar to the original set; eight replicates of each were set up. The cultures were examined daily and scored as successful depending on which species reproduced.

Results

The results from the cultures in 1963 and 1964 using *Calliphora* eggs were similar in both years, and have been combined in Table 2. The results indicate that, in cultures where mites were present (B, C), *Necrophorus* reproduced successfully. In the cases where only *Necrophorus* were present (E), reproduction was also successful, but in the cultures where *Calliphora* eggs were present and mites were absent (F), the *Necrophorus* were entirely unsuccessful. It is also striking that the mites reproduced successfully when *Necrophorus* were present (B, C) but not when *Necrophorus* were absent (A). *Calliphora* eggs hatched only when mites were absent (C, D), the reason being that when introduced into the culture the mites run rapidly over the corpse and, on finding a batch of *Calliphora* eggs, immediately stop, pierce the eggs with the chelicerae and eat the contents. A corpse is normally clear of *Calliphora* eggs in less than 4 h, and *Necrophorus* can reproduce without the presence of their chief competitors.

In all the cultures inoculated with fly larvae, *Necrophorus* failed to rear a brood

(Table 3), although in some cases eggs were laid. Only where fly larvae were absent was *Necrophorus* able to reproduce successfully. In many cultures containing *Calliphora* larvae, beetles were observed to search the corpse and eat fly larvae, and in some cases where many small fly larvae were placed on a corpse, the mites attacked and killed some of them. However, *Necrophorus* never succeeded in killing all the fly larvae and the mites attacked only larvae less than 5 mm long; large larvae were disregarded and eventually the fly larvae would invade the corpse and *Necrophorus* would abandon it.

Table 2. *The results of experimental cultures set up to examine the relationship between* Necrophorus investigator, Poecilochirus *and eggs of* Calliphora (*eight replicates of each combination and a standard corpse* (Apodemus) *were used*)

Type	Combination	No. of successful *Necrophorus* cultures	No. of successful mite cultures	No. of successful *Calliphora* cultures
A	Corpse, thirty mites, 100 *Calliphora* eggs	–	0	0
B	Corpse, thirty mites, 100 *Calliphora* eggs, pair of *Necrophorus*	6	8	0
C	Corpse, thirty mites, pair of *Necrophorus*	7	8	–
D	Corpse, 100 *Calliphora* eggs	–	–	8
E	Corpse, pair of *Necrophorus*	8	–	–
F	Corpse, 100 *Calliphora* eggs, pair of *Necrophorus*	0	–	8

Table 3. *The results of experimental cultures set up to examine the relationship between* Necrophorus investigator, Poecilochirus *and larvae of* Calliphora (*eight replicates of each combination and a standard corpse* (Apodemus) *were used*)

Type	Combination	No. of successful *Necrophorus* cultures	No. of successful mite cultures	No. of successful *Calliphora* cultures
A	Corpse, thirty mites, 100 *Calliphora* larvae	–	0	8
B	Corpse, thirty mites, 100 *Calliphora* larvae, pair of *Necrophorus*	0	0	8
C	Corpse, thirty mites, pair of *Necrophorus*	8	8	–
D	Corpse, 100 *Calliphora* larvae	–	–	8
E	Corpse, pair of *Necrophorus*	8	–	–
F	Corpse, 100 *Calliphora* larvae, pair of *Necrophorus*	0	–	8

In the successful cultures, it was observed that the third instar larvae of *Necrophorus* came to the surface and were very active for about 2 days before descending to pupate. During this time, which was presumed to be a dispersal phase similar to that shown by the larvae of *Calliphora* and *Lucilia* (Cragg 1955), the *Necrophorus* larvae had deutonymphs of *Poecilochirus necrophori* clinging to their dorsal shields. These deutonymphs descended underground with the larvae, and remained active within the pupal cell throughout the pupal period (2 months in *Necrophorus humator*, 10 months in *N. investigator*). During this time it was impossible for the mites to free themselves from the cell and the beetles emerged as adults bearing the deutonymphs.

The infestations on spent females of both species of *Necrophorus* from cultures were enormous, for example approximately 800 deutonymphs were counted in a single spent female of *N. humator*. The mean infestations (with their standard errors) in these conditions were 200±31 in *N. humator* and 250±36 in *N. investigator*. Infestations of this size were never found in the field, and simple experiments, consisting of releasing deutonymph-laden spent female *Necrophorus* in a large glasshouse and allowing them to fly freely for 5 min, showed that over 90% of the deutonymphs were dislodged during this period of activity. These results may account for the low number of mites on spent beetles caught in pitfall traps, compared with the high numbers of mites found on the spent females from the enclosed cultures.

OTHER ASPECTS OF THE RELATIONSHIP BETWEEN *POECILOCHIRUS NECROPHORI* AND *NECROPHORUS*

Beetles of genera other than *Necrophorus* were often caught in the pitfall traps, but the deutonymphs of *Poecilochirus necrophori* were not found on any but *Necrophorus*. An experiment was carried out to determine whether, if given a choice, the mites preferred *Necrophorus* to other beetles. Six mite-free *Necrophorus investigator* and six *Pterostichus* sp. beetles were placed in a large soil-filled tray and a known number of mites were shaken at random on to the soil surface. When the beetles were removed and inspected 6 h later, most of the mites were found on the *Necrophorus*, none on the other beetles. Similar results were obtained for each of five replicates (Table 4).

Table 4. *The results of preference experiments involving deutonymphs of* Poecilochirus necrophori, Necrophorus investigator *and* Pterostichus *sp., showing the distribution of the mites on the beetles after* 6 *h*

No. of mites released	No. of mites on *Necrophorus*	No. of mites on *Pterostichus*
150	150	0
100	98	0
50	43	0
80	79	0
40	38	0

Table 5. *The results of preference experiments involving deutonymphs of* Poecilochirus necrophori, Necrophorus investigator *and* Silpha carinata, *showing the distribution of the mites on the beetles after* 6 *h*

No. of mites released	No. of mites on *Necrophorus*	No. of mites on *Silpha*
40	36	0
53	50	0
92	92	0
86	85	0
154	152	0

It was thought that possibly another carrion beetle might be a suitable host, and *Silpha carinata* Herbst was used with *Necrophorus* in another set of five choice experiments (Table 5). Once again, the mites crowded on to *Necrophorus* and shunned the other beetles.

Certain other observations are useful indicators of the complexity and closeness of the mite–beetle relationship. On the Farne Islands many of the ground-nesting sea birds

suffer a heavy mortality in their young stages, and the corpses of these birds, particularly terns (*Sterna* spp.) are found in large numbers. Many of these corpses are utilized by *Necrophorus* for feeding and reproduction, and it was noticed that freshly dead corpses were free of *Poecilochirus necrophori* deutonymphs, and remained without mites until visited by *Necrophorus*. Corpses which had been visited by *Necrophorus* always had a few mites present, presumably left behind when the beetle departed. Where corpses were protected from *Necrophorus* by fine wire netting no *Poecilochirus necrophori* were found on the corpse.

On one occasion forty-three protonymphs of *P. necrophori* were obtained from a culture and placed in a small specimen tube in which an adult *Necrophorus* had recently regurgitated a drop of dark brown fluid, part of the contents of the fore-gut. The protonymphs rapidly gathered round the edge of the regurgitated drop and could be seen to insert their mouth parts into it. Within an hour the drop had vanished, the mites had dispersed and were wandering around the inside of the tube. When a drop of water was presented to these mites it produced no reaction, but when a further drop of the regurgitated fluid was placed in the tube the mites immediately gathered round it and fed. Although these mites were very active and difficult to pick up with a brush or forceps, it was discovered that once the same instruments had been used for handling *Necrophorus* the mites were attracted to them and could be handled easily. Presumably the strong smell of *Necrophorus* is very attractive to these mites.

DISCUSSION

Recently, Costa (1964) showed that although the biology of the scarabaeid dung beetle *Copris hispanus* L. was well known, the close association between it and a mite, *Parasitus copridis* Costa, had been overlooked. Costa (1963) pointed out that social organization and brood care by the host may be essential before successful association between insects and mesostigmatid mites can evolve. The present observations show that there is a close relationship between *Poecilochirus necrophori* and at least two *Necrophorus* species, *N. humator* and *N. investigator*. There appears to be no difference in the relationship of the mite to the two species of *Necrophorus*, and the pattern is as follows. The deutonymphs of *Poecilochirus necrophori* are carried by *Necrophorus* to carrion, where the mites leave the beetle and feed on dipteran eggs and small larvae. This behaviour is similar to that recorded by Filipponi (1955) for *Macrocheles muscaedomesticae* Scop. If the corpse is buried by the beetle for reproduction, the feeding behaviour of the mite, by killing eggs of flies, helps to ensure successful breeding of the beetle, and when the corpse is buried both beetles and mites reproduce underground. When the larvae pupate, the female abandons the corpse, and large numbers of mite deutonymphs are carried by the spent female beetle to another corpse, where the beetle feeds before dying. At the new corpse the mites stand a good chance of finding an immature *Necrophorus*, possibly one of a different species. The fate of deutonymphs which fail to encounter another host is unknown, but it is reasonable to suppose that they either die, or perhaps reproduce on the new corpse in the presence of the spent female *Necrophorus*. Continuity of the association is also maintained by the mite deutonymphs joining the beetle larvae when they pupate. This method ensures that newly emerged *Necrophorus* carry mites and that the relationship is continued through a new generation of beetles.

It is obvious that the relationship between these animals is not as simple as suggested by Neumann (1943). Costa (1963) suggests that social organization is a prerequisite for

successful associations between insects and mesostigmatid mites. *Necrophorus* have a complex social organization. From the present preliminary observations it is not possible to say that *Poecilochirus necrophori* is completely dependent on *Necrophorus* for successful reproduction, although it is possible to say that, without the mites, *Necrophorus* would be much less successful, particularly in competition with *Calliphora*. It is significant that the mites failed to reproduce without the beetle, although conditions were otherwise identical, and this indicates that the presence of the beetle may be very important to the mite. It is possible that, as in mites of the genus *Coleolaelaps* (Dermanyssidae) which feed on the dermal secretions of larval phytophagous scarabaeids, the larvae of *Poecilochirus necrophori* feed on the excretions of *Necrophorus* or on the regurgitated contents of the fore-gut with which the corpse is moistened.

The advantages of the relationship are obvious, the mites being carried from one food source to another, and reproducing safely underground in suitable conditions of temperature and humidity. Deutonymphs escape rigorous winter conditions by being enclosed in the subterranean pupal cell of *Necrophorus*, and the beetles enjoy freedom from competitors, which are eliminated by the mites. Experiments are now in progress which will determine the exact role of *Necrophorus* in the life cycle of *Poecilochirus necrophori*.

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SUMMARY

1. The nature of the association of the mite *Poecilochirus necrophori* Vitz. with the burying beetles *Necrophorus investigator* Zett. and *N. humator* Ol. was examined by means of field and laboratory studies on the Farne Islands, Northumberland.

2. Data obtained by trapping *Necrophorus* showed that infestations of from ten to thirty *Poecilochirus necrophori* deutonymphs/beetle were common. The infestations varied with the reproductive state of the beetle, and spent females were found to carry at least twice as many mites as immature or mature beetles.

3. In laboratory cultures containing a corpse of *Apodemus* and different combinations of mites, beetles and eggs or larvae of *Calliphora*, deutonymphs of *Poecilochirus necrophori* were observed to attack and eat the eggs and small larvae of *Calliphora* spp., although larvae larger than 5 mm were not attacked. *Necrophorus* failed to breed on corpses infested with *Calliphora* eggs unless mites were present, and, when *Calliphora* larvae more than 5 mm long were present, *Necrophorus* were unable to utilize the corpse successfully even in the presence of mites.

4. Large infestations (up to 800/beetle) of mite deutonymphs were observed on spent female *Necrophorus* in culture, but 90–95% of the mites were lost after the beetles had flown freely for 5 min.

5. Mite deutonymphs were observed to cling to pupating *Necrophorus* larvae, were observed within the pupal cell, and emerged with the adult beetles.

6. Experiments showed that *Necrophorus* were more attractive to deutonymphs of *Poecilochirus necrophori* than were ground beetles (*Pterostichus* sp.) or another carrion beetle (*Silpha* sp.). Larvae of *Poecilochirus necrophori* were observed to feed on droplets regurgitated by *Necrophorus*, and were attracted to the smell of *Necrophorus*.

7. Four species of mites were found on *Necrophorus* on the Farne Islands, and these are listed.

8. It is suggested that the relationship between *Necrophorus* beetles and *Poecilochirus necrophori* is probably obligatory. The presence of the mites ensures that *Necrophorus* breeds successfully, and the mite is apparently unable to breed in the absence of *Necrophorus*.

APPENDIX

Mites found on *Necrophorus* on the Farne Islands, Northumberland.

Mesostigmata: Parasitidae

Poecilochirus subterraneus Müller. Often present. Common as active deutonymphs.

P. necrophori Vitz. Always present and very common as active deutonymphs.

Mesostigmata: Eviphididae

Alliphis halleri Can. Often present.

Astigmata: Anoetidae

Pelzneria necrophori Duj. Often present as hypopi, found beneath the elytra in a compact clump.

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