

Review

When to leave the brood chamber? Routes of dispersal in mites associated with burying beetles

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ABSTRACT

Most nests of brood-caring insects are colonized by a rich community of mite species. Since these nests are ephemeral and scattered in space, phoresy is the principal mode of dispersal in mites specializing on insect nests. Often the mites will arrive on the nest-founding insect, reproduce in the nest and their offspring will disperse on the insect's offspring. A literature review shows that mites reproducing in the underground brood chambers of burying beetles use alternative routes for dispersal. For example, the phoretic instars of *Poecilochirus* spp. (Mesostigmata: Parasitidae) disperse early by attaching to the parent beetles. Outside the brood chamber, the mites switch host at carcasses and pheromone-emitting male beetles, where juvenile and mature burying beetles of several species congregate. Because they preferably switch to beetles that are reproductively active and use all species of burying beetles within their ranges, they have a good chance of arriving in a new brood chamber. Other mite associates of burying beetles (*Alliphis necrophilus* and Uropodina) disperse from the brood chamber on the beetle offspring. We suggest that these mites forgo the possible time gain of dispersing early on the parent beetles because their mode of attachment precludes host switching. Their phoretic instars, once attached, have to stay on their host and so only dispersing on the beetle offspring guarantees that they are present on reproducing burying beetles of the next season. The mites associated with burying beetles provide an example of multiple solutions to one life history problem – how to find a new brood chamber for reproduction. Mites that have mobile phoretic instars disperse on the parent beetles and try to arrive in the next brood chamber by host switching. They are independent of the generation cycle of a single host and several generations of mites per host generation are possible. Mites that are constrained by their mode of attachment disperse on the beetle offspring and wait until their host becomes mature and reproduces. By doing this they synchronize their generation time with the generation time of their host species.

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Key words: Silphidae, *Nicrophorus*, *Poecilochirus carabi*, phoresy, dispersal, host choice.

INTRODUCTION

The nests of brood-caring insects are virtually always colonized by a rich community of mite species (Costa, 1969; Hunter and Rosario, 1988; Eickwort, 1990,

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1994; Houck and O'Connor, 1991). Some of these mite species are only incidental associates that normally dwell in the environment of the nest. However, many are specialists that rely exclusively on the nourishment provided by the insects and their nests. Since insect nests are scattered in space and most of them are short lived, mites are not able to colonize them in a predictable way on their own. Phoresy (defined here as the attachment of an animal to the body of another animal for transport), therefore, is the principal mode of dispersal in mites specializing on insect nests. Often the mites will arrive in the nest on the nest-founding insect, reproduce there and their offspring will disperse on the insect's offspring.

By dispersing on the offspring of their hosts, the new generation of mites increase their chance of arriving in a nest that they can colonize. However, this also imposes constraints on the life history evolution of these mites. The mites become dependent on the offspring of their hosts for dispersal and are forced to synchronize their generation time with the generation time of the hosts (Costa, 1969; Hunter and Rosario, 1988; Eickwort, 1990). Mites that manage to use alternative routes of dispersal gain considerably more independence from their hosts.

Information about different routes of dispersal used by mites associated with nest-building insects is scattered in the literature and there are only few empirical studies focusing on this topic (e.g. Sakofski *et al.*, 1990; Schwarz and Huck, 1997). In this review we compile available information on routes of dispersal used by mites associated with burying beetles (Coleoptera: Silphidae: *Nicrophorus* spp.), a beetle genus that nests in subterranean brood chambers. Since by far the most data are available for one group of mites, the *Poecilochirus carabi* species complex (Mesostigmata: Parasitidae), we first focus on the dispersal behaviour in this group. We then ask how other mites differ from *P. carabi* and finally discuss the consequences of different routes of dispersal with respect to life history evolution.

NATURAL HISTORY OF BURYING BEETLES

Burying beetles reproduce on small vertebrate carcasses that they bury as a food resource for their larvae (Pukowski, 1933; Milne and Milne, 1976). Communal breeding of several beetles may occur, but in most cases a carcass is monopolized by a male and female beetle pair that chase away competitors by combat (Eggert and Müller, 1992; Trumbo, 1992). When the beetle pair bury the carcass, they remove the hair or feathers and gradually form it into a ball. Around the carcass ball they excavate a brood chamber and then the female lays her eggs into the surrounding soil. When the larvae hatch, they burrow into the brood chamber and congregate in a feeding hole that the parent beetles prepared on top of the carcass ball. Both male and female beetle remain in the chamber for several days to feed and guard their larvae. Usually, it is the male parent that stops brood care first and departs in search of a new carcass, followed a few days later by the female. When the carcass ball is completely spent, the larvae leave the brood chamber and pupate

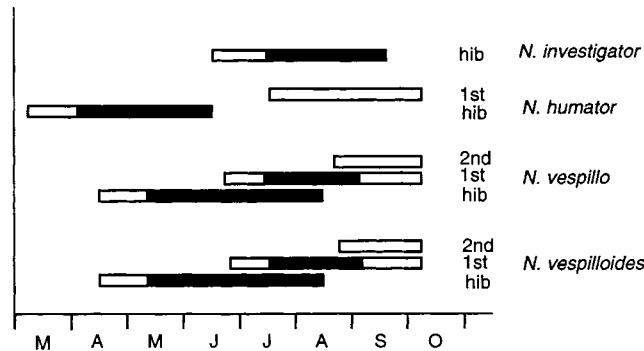


Fig. 1. Seasonality of burying beetles in central Europe. The bars indicate the flying season of four species of burying beetle. Black bars mark the periods when the beetles are reproductively active. 'hib' refers to hibernated beetles from the previous season. '1st' and '2nd' refer to the first and second generation offspring of the hibernated beetles, respectively. In *Nicrophorus investigator* the offspring of the hibernated beetles remain underground and overwinter as pre-pupae. In the other beetle species the young adults overwinter (Springett, 1968; Christie, 1981; Korn, 1983; Müller and Eggert, 1987; Rohner, 1990; Schwarz, 1992; Schwarz and Müller, 1992).

singly in the surrounding soil. When pupal development is completed, the adult beetles emerge, burrow their way out of the pupal cell and start to search for carcasses. In most species the young adults overwinter, but in some species the pre-pupae diapause and overwinter inside their pupal cells (Korn, 1983; Peck and Kaulbars, 1987).

If burying beetles arrive at a carcass that is too large to be buried, they only feed on it (Pukowski, 1933; Wilson and Knollenberg, 1984). In this case they are not aggressive and beetles of several species and different reproductive state may congregate. In central Europe, for example, beetles of three to four species may be at a carcass and two generations may be present for two of these species (Fig. 1). Burying beetles also aggregate at males that emit pheromones to attract females (Müller and Eggert, 1987; Eggert, 1992). Since these males are sometimes in the possession of a buried carcass, they are also visited by conspecific males and by burying beetles of competing species. At both large carcasses and pheromone-emitting males conspecific beetles copulate.

DISPERSAL IN THE *P. CARABI* COMPLEX

In and out of the brood chamber

Mites of the *P. carabi* complex are common associates of burying beetles worldwide (Brown and Wilson, 1992, 1994; Takaku *et al.*, 1994; Baker and Schwarz, 1997; Schwarz *et al.*, 1998). Their phoretic instars, the deutonymphs, occur on

almost every adult beetle and they usually arrive in the brood chamber with the parent beetles. Secondary colonization by mites may occur when competing burying beetles invade the brood chamber to chase away the resident beetle pair and take over the carcass (Wilson, 1983; Trumbo, 1990). Within hours of their arrival in the brood chamber the deutonymphs disembark from their hosts and moult into adults, which reproduce immediately. The non-phoretic instars of the mites dwell in the brood chamber where they live on the carcass and its associated microfauna. The phoretic deutonymphs of the new mite generation emerge and attach to a beetle before the brood chamber is abandoned (Korn, 1982a,b, 1983; Schwarz and Müller, 1992; Schwarz and Walzl, 1996).

The newly emerged deutonymphs have two principal alternatives for dispersal from the brood chamber: they can attach to one of the parent beetles or they can accompany the beetle larvae to their pupal cells and wait there until the adult beetles emerge. In field and laboratory experiments it was shown that most of the deutonymphs disperse by attaching to the parent beetles (Springett, 1968; Korn, 1983; Brown and Wilson, 1992; Schwarz and Müller, 1992; Schwarz *et al.*, 1998). This results in spectacular differences in infestation intensities, with the parent beetles carrying 100–250 deutonymphs while their offspring often carry less than five.

Closer examination of the behavioural mechanisms that generate the distribution of mites on the beetles leaving the brood chamber showed that the deutonymphs not only prefer the parent beetles to their offspring, but also discriminate between the brood-caring parents themselves (Schwarz and Müller, 1992). Mites that are in the phoretic deutonymphal stage almost exclusively disperse on the first parent to leave which is usually the male. Only deutonymphs that emerge after the male's departure attach to the female parent. This may still be a considerable number because female mites lay their eggs over a period of several days and therefore many of their progeny develop too late to disperse on the male parent. Mites that reach the deutonymphal stage after both parent beetles have left use the beetle larvae for dispersal.

Switching between burying beetles at carcasses and at pheromone-emitting males

Direct observation and choice experiments have shown that the mobile deutonymphs of *P. carabi* readily transfer between beetles that come into direct contact (Korn, 1983; Brown and Wilson, 1992; Schwarz, 1996). They discriminate between the beetles olfactorily and transfer is highly directed. It was shown that the deutonymphs preferably transfer from immature or very old beetles to medium age beetles that are sexually mature (Korn, 1983; Schwarz, 1992; Schwarz and Müller, 1992) (Fig. 2). They also prefer certain species of burying beetle to others (Brown and Wilson, 1992; Schwarz, 1996) and there is evidence that this species preference changes with the reproductive season of the beetle species (Brown and Wilson, 1992). Therefore, when several beetles meet at carcasses and pheromone-emitting

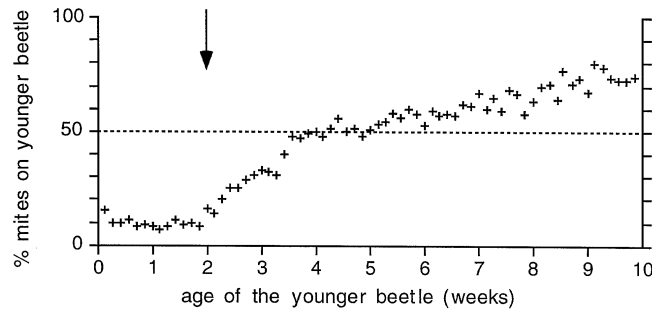


Fig. 2. The attractiveness of burying beetles (*Nicrophorus vespilloides*) changes with age. The results of experiments in which 20 beetle pairs, each carrying ten *P. carabi* deutonymphs, were kept for a period of 10 weeks are shown. Each pair consisted of two beetles of the same sex that differed in age by 4 weeks. The distribution of deutonymphs on the beetles was checked every day. The experiments started the day that the younger beetle emerged from its pupal cell. The arrow shows approximately when the younger beetles became sexually mature. Modified from Schwarz (1992).

males, deutonymph transfer will result in an accumulation of mites on beetles that are ready to reproduce.

Repeated findings of *P. carabi* deutonymphs on large carcasses in the absence of burying beetles suggest that the deutonymphs sometimes disembark when their host feeds at a carcass and later attach to a new host (Springett, 1968; Christie, 1981; Korn, 1983). It is unknown if this indirect mode of host switching occurs regularly or if the mites accidentally lose contact with their hosts. Christie (1981) and Korn (1983) observed that in the absence of a suitable host, deutonymphs may moult into adults at a large carcass and reproduce there. Adult mites die soon after reproduction (Korn, 1982b; Schwarz and Walzl, 1996). Their offspring have to reach the phoretic stage and attach to a host before the carcass decays.

Dispersal on hosts other than burying beetles

Occasionally, deutonymphs of *P. carabi* are found on silphid beetles other than *Nicrophorus* and on carabid and scarabaeid beetles (Micherdzinski, 1969; Olynyk and Freitag, 1979; Hyatt, 1980, 1990; Wilson and Knollenberg, 1987; Haitlinger, 1990; Takaku *et al.*, 1994). Mite abundance on these beetles, however, is much lower than on burying beetles and choice experiments have shown that they are only accepted if burying beetles are absent (Springett, 1968; Korn, 1983; Brown and Wilson, 1992). Because the non-*Nicrophorus* hosts are not known to invade the brood chambers of burying beetles but do visit carcasses on the surface of the soil, it is likely that abandoned mites use them to transfer between carcasses if theirs decays before a burying beetle arrives.

It was suggested that *P. carabi* deutonymphs may also use small mammals as transport hosts (Micherdzinski, 1969; Haitlinger, 1976). However, fatality is high

for small mammals caught in traps and therefore a better explanation is that the *P. carabi* deutonymphs arrived in the traps with burying beetles visiting the corpses (Christie, 1981; Ambros, 1995).

DISPERSAL IN OTHER MITE SPECIES ASSOCIATED WITH BURYING BEETLES

In Europe, seven mesostigmatic and three astigmatic mite species are regularly associated with burying beetles (Christie, 1981; Scheucher, 1957; Schwarz *et al.*, 1998). Similar numbers of species have also been recorded on North American beetles (Wilson and Knollenberg, 1987). However, information on the preferred routes of dispersal from the brood chamber is available for only a few of these species. The only mite (other than the *P. carabi* complex) known to prefer the parent beetle as a carrier out of the brood chamber is *Poecilochirus subterraneus* (Korn, 1983). Other mites clearly prefer the offspring: 74–93% of the phoretic *Alliphis necrophilus* adults dispersing from a brood chamber were found on the emerging offspring in field experiments (Schwarz *et al.*, 1998) and unidentified uropodine mites were reported to disperse on the offspring exclusively (Wilson and Knollenberg, 1987). No significant difference between the mite numbers dispersing on parent beetles and offspring was found in *Macrocheles nataliae*, but there seems to be a tendency to use the parents (Schwarz *et al.*, 1998).

Host switching between congregated burying beetles was only observed in *P. subterraneus*, either directly or by attaching to the larger and more mobile deutonymphs of *P. carabi* (Korn, 1983). Like those of *P. carabi*, the phoretic deutonymphs of *P. subterraneus* show behavioural host preferences (Korn, 1983). Sometimes they are found on carcass-visiting beetles other than burying beetles (Micherdzinski, 1969; Hyatt, 1980; Christie, 1981; Korn, 1983), which suggests that they can use them to transfer between carcasses. This may also be the case for *M. nataliae*, which is occasionally found on scarabaeid beetles (Hyatt and Emberson, 1988). The phoretic instars of *A. necrophilus* and of the uropodine species associated with burying beetles were not reported to switch host and are usually not found on hosts other than burying beetles (Christie, 1981, 1983; Athias-Binche *et al.*, 1993; Masan, 1994).

CONSEQUENCES OF ALTERNATIVE ROUTES OF DISPERSAL

The mites associated with burying beetles can use two alternative routes of dispersal from the brood chamber of their hosts (Fig. 3). They either disperse on the parent beetles or they accompany the beetle larvae to their pupal cells and attach there to the emerging adults. Outside the brood chamber, opportunities to switch host are at carcasses and pheromone-emitting males.

In the genus *Poecilochirus* most mites disperse on the parent beetles. By this they gain time because they emerge from the soil earlier than mites that wait in the pupal

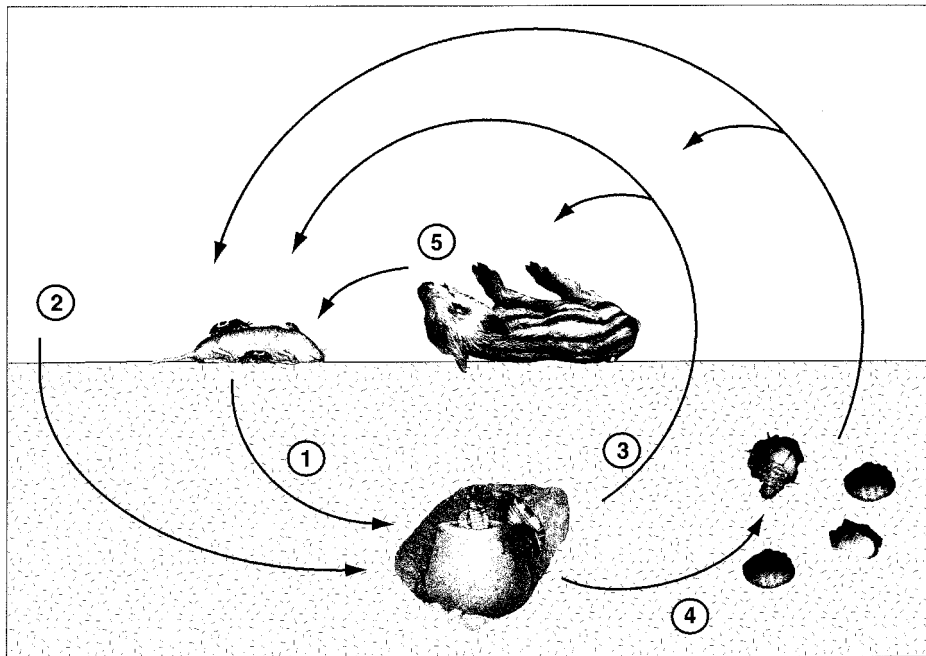


Fig. 3. Routes of dispersal in mites associated with burying beetles. (1) Mites arrive in the brood chamber on the nest-founding beetles. (2) Secondary invasion may occur via intruding beetles that try to take over the carcass. Mites can disperse from the brood chambers either on (3) the parent beetles or (4) the beetle larvae. Outside the brood chamber they can switch host at (5) large carcasses or at pheromone-emitting beetle males (not depicted). Parts of the figure adapted from *The Social Behavior of Burying Beetles* by L.J. Milne and M. Milne (1976). Copyright © 14 January 1997, Scientific American, Inc. All rights reserved.

cells until beetle development is completed. This time gain is considerable: 20–67 days, for example, in mites associated with beetle species that overwinter as adults (Schwarz and Müller, 1992; Sikes, 1996; Schwarz *et al.*, 1998) and up to 10 months in mites associated with beetle species that overwinter as prepupae (Springett, 1968). In addition, mites leaving on the parent beetles no longer rely on their host's offspring for dispersal. According to modern theory on the evolution of host–parasite interactions, this should allow for greater exploitation of their hosts (Ewald, 1983; Clayton and Tompkins, 1994). This is supported by experiments showing that *P. carabi* consume the eggs of their host beetle species (Beninger, 1993). However, there is also contrary evidence that under some circumstances *P. carabi* may benefit its host by destroying the eggs of competing flies (Wilson, 1983; Wilson and Knollenberg, 1987).

Once outside the brood chamber, the phoretic instars of *P. carabi* readily transfer between beetles. Because they preferably switch to beetles that are reproductively active and use all species of burying beetles within their ranges, they have the

chance of arriving in a new brood chamber as long as burying beetles are reproducing. By doing this they become independent of the generation time of a single host species and several generations per host generation are possible.

Springett (1968) suggested that mites dispersing on the parent beetles would suffer a high mortality because only a few of them would manage to hang on to the overloaded beetles during their flight. Observations by several authors, however, suggest that burying beetles carrying well over 100 mites do arrive at carcasses in the field (Starzyk, 1967; Costa, 1969; Hyatt, 1980, 1990; Schwarz and Müller, 1992; Schwarz *et al.*, 1998). Springett (1968) performed his experiments in a glass house and therefore in this case loss of mites was probably due to beetles hitting the glass windows when flying towards the light.

Despite the time gain and greater independence achieved by dispersing on the parents, the phoretic instars of *A. necrophilus* and the uropodine mites associated with burying beetles prefer their host's offspring for dispersal. The reason why this way out of the brood chamber is favoured by these species could be that their mode of attachment precludes host switching; the phoretic deutonymphs of the uropodine species attach with their anal pedicels (Faasch, 1967) and *A. necrophilus* lives in the first thoracic spiracles of the beetles where they are almost completely enclosed by the elytrae and the lobes of the pronotum (Christie, 1981; Schwarz *et al.*, 1998). It is likely that the phoretic instars of these species, once attached, have to stay on their host and so only leaving on the offspring guarantees that they will be present on reproducing burying beetles of the next season.

The mites associated with burying beetles provide an example of multiple solutions to the same life history problem. When the mites of the new generation disperse from the brood chamber, they must ensure that they will arrive in a new brood chamber where they can reproduce. Mobile mites disperse early on the parent beetles and switch host until they arrive in the brood chamber of another beetle pair. By this they can achieve several generations per host generation. Mites that are constrained by their mode of attachment disperse on the beetle offspring and wait until these become mature and reproduce. They forgo the chance of early reproduction and synchronize their generation time with the generation time of their hosts.

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