

The dispersal behaviour of the phoretic mite *Poecilochirus carabi* (Mesostigmata, Parasitidae): adaptation to the breeding biology of its carrier *Necrophorus vespilloides* (Coleoptera, Silphidae)

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Summary. When the phoretic mite *Poecilochirus carabi* reproduces in the brood chamber of its carrier *Necrophorus vespilloides*, a beetle with biparental brood care, the first deuteronymphs of the new mite generation aggregate on the male beetle. They do not use sex-specific traits to discriminate between male and female beetles in the brood chamber, but traits that are related to the beetles' behaviour and may be displayed by both parent beetles. When the male beetle departs, it carries virtually all deuteronymphs then present in the brood chamber. Deuteronymphs that develop later congregate on the female, which leaves the crypt some days after the male. Only those deuteronymphs that miss the female's departure disperse on the beetle larvae, meaning they have to wait in their pupal chambers until the beetles have completed their development. On average, 86% of the deuteronymphs leave the brood chamber on the parent beetles, thereby gaining the advantage of an early departure. As soon as their carrier arrives at one of the beetles' meeting places, the deuteronymphs can transfer between the beetles present. Choice experiments revealed that the deuteronymphs tend to even out density differences between congregating carriers, and prefer sexually mature to immature beetles. Therefore, transferring between beetles results in a dispersion of deuteronymphs on the sexually mature beetles of the population.

Key words: Dispersal – Phoresy – Sex-preference – *Poecilochirus* – *Necrophorus*

Phoresy, i.e. the temporary attachment of an organism to the outer surface of another animal for dispersal, is a common phenomenon in mites and has evolved independently in different groups. It raises the migratory capacity of the mites and enables them to colonize discrete and ephemeral habitats. The commonest phoretic relations involve mites and insects. They range from unspecific euryxenous associations, where the mites use a variety of

insect species for transport, to stenoxenous associations, in which the mites depend on a single carrier species (Binns 1982; Athias-Binche 1990). Nesting in confined spaces and brood care by the carriers are amongst the conditions that favour the evolution of stenoxenous associations between mites and insects (Costa 1969; Lindquist 1975). The brood chamber or nest of the insect provides a stable and sheltered habitat where food is in plentiful supply, and mites reproducing in the nest improve the chances of their progeny finding a suitable carrier when reaching the phoretic stage.

Probably the most advanced form of brood care among subsocial insects is performed by the burying beetles of the genus *Necrophorus* (Coleoptera, Silphidae), which reproduce on small vertebrate carcasses. In most species of burying beetles, a suitable carcass is monopolized by one pair, which has often previously fought off competitors. The beetles bury the carcass, form it into ball shape, remove hair or feathers, and preserve it with oral and anal fluids. They build a brood chamber (crypt) around the carcass, in which both male and female beetles stay for several days to feed and guard their larvae. The larvae are located in a cavity excavated by the parents on top of the carcass. The male beetle usually leaves some days before the female, which stays in the crypt until the larvae have completed their development. After their parents' departure, the larvae disperse from the crypt and pupate in the surrounding soil (Pukowski 1933; Lengerken 1954; Bartlett 1988).

The pronounced brood care behaviour of burying beetles makes them ideal carriers for phoretic mites and they are associated with mite species from different systematic groups, e.g. Anoitidae (Scheucher 1959), Uropodina (Karg 1989), Eviphididae (Christie 1983), Macrochelidae (Hyatt and Emberson 1988), and Parasitidae (Korn 1983). The most ubiquitous mites living on *Necrophorus* are the large brown deuteronymphs of *Poecilochirus carabi* G. and R. Canestrini 1982 sensu Hyatt (1980) (Mesostigmata, Parasitidae), which can be found on almost every species of burying beetle in the world (Hyatt 1980; Wilson and Knollenberg 1987). In contrast to the resting stages of several other species of phoretic mites,

which cease feeding and locomotion during transport (Binns 1982; Hunter and Rosario 1988), *P. carabi* deuteronymphs stay active and share their carrier's meals (Neumann 1943; Korn 1983). At the same time they avoid losing contact with the beetle, on which they depend for transport. They do not disembark before arriving in a *Necrophorus* crypt, where they moult into adults and reproduce. The female mite hides her eggs in the surrounding soil, covering them with dirt (Korn 1982). While larvae and protonymphs move freely in the crypt feeding on the carcass and on nematodes, the deuteronymphs show a strong affinity for the beetles. Some hours after eclosion they attach either to the parent beetles or to the beetle larvae (Springett 1968; Korn 1983).

Recent studies have shown that *P. carabi* is a complex of sibling species and races, each of which has developed specific carrier preferences and specialized on one or only a few *Necrophorus* species (Wilson 1982, 1983; Müller and Schwarz 1990; Schwarz et al. 1991). In this paper we examine how the deuteronymphs of one of the *P. carabi* sibling species (P-vs-type, see Schwarz et al. 1991) are distributed on parent beetles and larvae in the crypt of their main carrier species, *Necrophorus vespilloides*. We analyze the behaviour causing this distribution, and compare the results with the seasonal fluctuation of mite frequencies in the field. The adaptive significance of the dispersal behaviour of *P. carabi* is discussed.

Materials and methods

All laboratory experiments were performed at a temperature of 20° C. Beetles and mites were individuals from the first laboratory generation. They were kept at 20° C and a light/dark cycle of 18/6 hours.

Duration of brood care, and mite loads of beetles dispersing from the crypt

To assess how long beetles stay in the crypt, and how many mites they carry at dispersal, we used breeding boxes which were equipped with traps placed directly at the only exit point (Müller et al. 1990). The boxes were filled with peat and provided enough space for the beetle larvae to disperse and to pupate. At the start of the experiment a pair of burying beetles ($n = 38$ pairs) carrying a total of 10 deuteronymphs was put into the breeding box and supplied with a dead laboratory mouse (15 g). The minimum age of the beetles was 4 weeks, and the deuteronymphs were older than 10 days. Within 24 h the beetles buried the mouse, and both beetles and mites began to reproduce. Beetles emerging from the soil (i.e. parent beetles that had terminated brood care and, later, beetle offspring leaving the pupal chambers) were trapped in plastic tubes which were checked at 24 h intervals. They were subsequently anaesthetized with CO₂ and the mites they were carrying were counted.

Mite reproduction and development

P. carabi arrives in the crypts in the deuteronymphal stage, and the mites of the new generation have to leave by attaching to a beetle. We assessed the time required for reproduction and development by measuring the time span from the parental deuteronymphs' first

contact with the carcass, to the beetle-attachment of the new deuteronymph generation. For this purpose 14-day-old deuteronymphs were provided with a piece of liver to trigger the adult moult. Some hours later, the males, which develop faster than the females, had hatched and we were able to form pairs comprising one adult male and one female deuteronymph. Each pair ($n = 31$) was put into a plastic box (50 × 30 × 16 mm) lined with moist tissue paper, and containing a small piece of liver and peat. The boxes were checked daily for phoretic deuteronymphs by introducing a *N. vespilloides* which attracted them. The beetle was removed after 5 min and the attached deuteronymphs were counted. The boxes were stored in the dark. The experiment continued until the death of the female.

The number of eggs laid per day and the time from egg-laying to deuteronymph eclosion was determined in a similar set of experiments ($n = 7$); from the initiation of the adult moult to the death of the female, both male and female were transferred to new breeding boxes every 24 h. Each breeding box was checked for deuteronymphs at daily intervals.

To establish the time from adult moult to the start of egg-laying, and the duration of embryonic development, we performed a third set of experiments ($n = 14$), in which, during the first 24 h after the female's adult moult, the mite pair was transferred to a new breeding box every 3 h. After 24 h the mite pairs were transferred every 6 h. The boxes were stored in the dark and checked at 6-h intervals until the first larvae hatched.

Deuteronymph behaviour in the crypt

Three sets of experiments were performed to test whether the deuteronymphs discriminate between the adult beetles in the crypt. The general design of these experiments was as follows: A pair of burying beetles carrying a total of 10 mites was put into a plastic box (10 × 10 × 7.5 cm) containing 2 cm of moist peat and a dead mouse weighing 10–15 g. The box was stored in the dark. Under these conditions the beetles do not build closed crypts but construct an open bowl in which both beetles and mites reproduce. Each day, after the position of the beetles relative to the carcass was recorded, they were taken out of the box and anaesthetized separately. The adhering deuteronymphs were brushed off and counted. After counting the deuteronymphs were put back on their respective carrier, which was then returned to its original position in the breeding box. Anaesthesia and counting took no longer than 5 min and had no visible effect on the beetles' behaviour. Since the breeding boxes had no exit, the beetles were prevented from leaving and had to stay in the vicinity of the carcass. Beetles that had stopped caring for the brood, however, were recognizable by the fact that they were found hiding in the peat surrounding the carcass.

The first set of experiments corresponded to the normal situation in the crypt ($n = 19$). One male and one female beetle buried the mouse and raised their larvae. Apart from being anaesthetized and having their mites counted the beetles were not manipulated. In a second set of experiments ($n = 12$) the female was removed 4 days after the carcass was buried, and put into a small plastic container (50 × 30 × 16 mm) covered by wire mesh (mesh width 3 mm). The mesh permitted mites to pass but prevented the female from escaping. The container was placed in the crypt, in direct contact with the carcass. In every case the male took over caring for the brood after the female had been caged. A third set of experiments ($n = 10$) was performed with two females caring for the larvae. Under certain conditions (e.g. large carcasses, absence of males), two females may cooperate in brood care. In this situation one female will leave the crypt just as the male usually does (Müller unpubl.). This experiment differed from the previous two in that we used a mouse weighing 25 g, and, to facilitate identification, each beetle was of a different colour strain (Müller and Eggert 1988).

Choice experiments

N. vespilloides reaches sexual maturity about 14 days after emerging from the pupal chamber (Pukowski 1933). To determine whether deuteronymphs discriminate between sexually immature and mature beetles, two *N. vespilloides* of the same sex, one newly hatched from the pupa, the other 6 weeks old, were put into a test arena (10 × 10 × 7.5 cm, the bottom covered with peat). Each beetle carried 5 deuteronymphs. Since the deuteronymphs avoid losing contact with the beetle, transfer between beetles was restricted to situations in which the beetles came into direct contact. 24 h after the start of the experiment, the beetles were taken out of the arena and the adhering mites counted. Similar choice experiments were performed with two beetles of the same sex where the younger was 3 and the older was 9 weeks old. Hence, the age difference of the beetles was still 6 weeks, but now both were sexually mature.

To test whether the deuteronymphs have a preference for one sex, we performed choice experiments using 2 beetles of different sex but of the same age (4 weeks). At the start of each experiment, 10 deuteronymphs were put on one of the two beetles. In half of the experiments the mites were placed on the male beetle and in the other half on the female.

Mite loads of field-caught beetles

The field study was run from 4 April to 28 October 1986 at Lohmannshof, Bielefeld. Three pitfall traps baited with pigs' lung were placed in a row 10 m apart in a wood, while three other traps were placed in an adjoining meadow. The traps were opened for 24 h at weekly intervals. Trapped beetles were taken to the laboratory, anaesthetized with CO₂ and their mites counted. Beetles were classified as "young", if their pronotum was still weak and flexible. Previous experiments proved that the pronotum becomes rigid 3–4 weeks after the beetle emerges from the pupal chamber.

Results

Duration of brood care, and mite loads of beetles dispersing from the crypt

The male beetle terminated brood care on average 3 days earlier than the female (Table 1). Despite its early departure, the male carried more deuteronymphs than the female (Wilcoxon test, $P < 0.05$) – on average 50% of all deuteronymphs emerging from the crypt (Table 2). Only a small proportion of deuteronymphs appeared on the beetles' offspring when they emerged from their pupal chambers, resulting in a median density of 2 deuteronymphs per young beetle (range 0–18). The proportion of deuteronymphs leaving on the male correlated with its resident time: the later it left, the higher

Table 1. Adult dispersal from the crypt and emergence of offspring from the pupal chambers in *N. vespilloides* ($n=37$ beetle pairs; measured in days since the burial of the mouse)

	Day of dispersal		Day of offspring emergence	Number of offspring
	Male	Female		
Median	8	11	31	28
Quartiles (25%–75%)	7–9	10–12	29–33	26–34

Table 2. Mean proportion of deuteronymphs on adult beetles dispersing from the crypt and on beetle offspring emerging from the pupal chambers ($n=37$)

	Proportion of deuteronymphs on			Number of deuteronymphs per crypt
	male	female	offspring	
Median	50%	36%	14%	203
Quartiles (25%–75%)	40%–60%	25%–48%	8%–21%	145–262

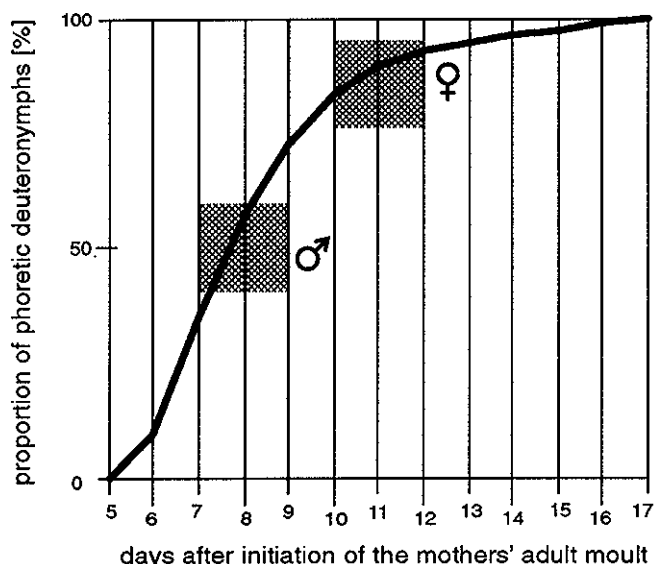


Fig. 1. Time required for deuteronymph development in absence of the beetles. The diagram shows the mean proportion of mites that have reached the phoretic deuteronymphal stage at a given day after the initiation of their mothers' adult moult ($n=31$ mite females, $\bar{x}=114$ deuteronymphs per female, range 20–232). For comparison, the residence times of male and female beetles in the crypt (Table 1) are indicated by shading (inter-quartile range)

the proportion of deuteronymphs it carried (Spearman rank coefficient, $r_s=0.40$, $P < 0.05$, $n=37$).

In one case, which was excluded from the above analysis, the female left before the male (female after 9 d, male after 13 d). Here, the female carried 62% of the deuteronymphs, 28% were found on the male, and 10% on the offspring ($n=147$ deuteronymphs).

Mite reproduction and development

In the absence of carriers, the adult moult of *P. carabi* occurred within 9–15 h of contact with carrion. In 14 isolated pairs of mites checked at 3-h intervals, copulation occurred within the same 3-h interval as the adult moult of the female; egg-laying began either within the same interval (64%) or in the following 3 h (36%). The first larvae hatched 37.9 h (SD = 2.5 h) after egg laying.

The first deuteronymphs appeared 6 days after the adult moult of their parents ($n=31$) had been triggered (Fig. 1). Most of the mites (90%) had reached the phoret-

Table 3. Median proportion of deuteronymphs found on the male in brood-caring pairs of *N. vespilloides* ($n = 19$ beetle pairs)

	Days after burial of the carcass				
	6	7	8	9	10
% Deuteronymphs on the male beetle (median)	100	98	95	81	61
Quartiles (25–75%)	71–100	95–100	70–98	39–95	51–87
Average number of deuteronymphs per beetle pair	23.0	68.4	119.3	165.6	190.6
Probability ¹	<0.01	<0.001	<0.001	<0.01	<0.01

¹ Wilcoxon test, H_0 : the deuteronymphs are evenly distributed between male and female beetles

Table 4. Median proportion of deuteronymphs found on the peripheral *Necrophorus vespilloides* in brood caring beetle pairs

	Days after burial of the carcass				
	6	7	8	9	10
A:					
% Deuteronymphs on the peripheral beetle (median)	92	91	81	36	–
Quartiles (25%–75%)	82–97	77–95	60–88	12–61	
Average number of deuteronymphs per beetle pair	26.7	69.3	122.2	162.5	
Probability ¹	<0.01	<0.01	<0.05	ns	
B:					
% Deuteronymphs on the peripheral beetle (median)	53	89	96	93	78
Quartiles (25%–75%)	0–71	87–97	89–99	54–97	43–88
Average number of deuteronymphs per beetle pair	22.8	68.6	156.7	218.4	273.9
Probability ¹	ns	<0.01	<0.01	<0.05	ns

¹ Wilcoxon-test, H_0 : the deuteronymphs are distributed equally on both beetles

A: one male and one female present; the female is forced to the peripheral position by caging ($n = 12$)

B: no male, two females present ($n = 10$)

ic deuteronymphal stage at day 11. By day 8 a mean proportion of 57% of the deuteronymphs had developed. This proportion corresponds to the proportion of mites that were shown to leave on the male beetle, if *P. carabi* reproduces in the crypt of *N. vespilloides* (Table 2).

The average number of eggs laid per day after the initiation of the adult moult was ($n = 7$ females): day 1: 8.3 (SD = 4.9); day 2: 54.2 (SD = 16.9); day 3: 44.4 (SD = 29.9); day 4: 33.9 (SD = 22.9); day 5: 22.2 (SD = 19.3); day 6: 10.3 (SD = 14.7); day 7: 3.1 (SD = 8.3). The deuteronymphs produced by the females in average hatched 5.9 days (SD = 0.9 d, $n = 1235$) after egg-laying.

Deuteronymph behaviour in the crypt

In the crypt of *N. vespilloides*, the first deuteronymphs appeared on the beetles 6 days after burial of the mouse: 71–100% of them were attached to the male beetle (Table 3). The male bias remained high until day 9, when the

proportion of deuteronymphs congregating on the male began to decline until it reached a median percentage of 61% on day 10. On day 6 in all replicates both beetles were directly on the carcass. However, whereas the females were either on top of the carcass or in the cavity that contained the larvae, the males were always on the underside or attached to the side of the carcass. From day 7 onwards, more and more males were found some distance from the carcass, indicating that they had terminated brood care and would leave the crypt under natural conditions.

When the female beetle was put into a cage, the male took over feeding the larvae. In this situation the deuteronymphs congregated on the female beetle (Table 4A). On day 9 we had to stop this experiment, since the male beetles attacked the females through the wire mesh of the cage, indicating that they treated them as intruders (Otronen 1988). Two females were killed, and several had legs or antennae amputated.

The fact that the deuteronymphs' preference for the male switches to the female if she is prevented from

brood care suggests that the deuteronymphs discriminate between the beetles in the crypt by behavioural cues. To test this without preventing one beetle from caring for the brood, we performed an experiment in which two females cared for the brood. If two females cooperate in brood care, one female will reduce its care after some days and finally leave the crypt. In our experiments the female that continued brood care was recognizable because of its central position on top of the carcass (central female). The other female was found either attached to the carcass wall or hidden in the soil (peripheral female). The peripheral female carried significantly more deuteronymphs than the central female at days 7, 8 and 9 after the burial of the carcass (Table 4B). Only on day 6, when the first deuteronymphs appeared, did they show no preference for either female.

Choice experiments: Do deuteronymphs discriminate between beetles outside the crypts?

If the deuteronymphs were given the choice between two beetles of the same sex but different age, one of which was newly hatched and immature, the other 6 weeks old and sexually mature, the deuteronymphs clearly preferred the older beetle (Table 5A). The preference for the older beetle was absent if both the younger and the older beetle were sexually mature (Table 5B).

Table 5. Average proportion of deuteronymphs choosing the older beetle in the choice experiments

	<i>n</i> replicates	Mean proportion of deuteronymphs on older beetle	Probability (sign-test)
A: younger beetle newly emerged	36	81.7	<0.001
B: younger beetle 4 weeks old	24	52.1	ns

The beetles differed in age by 6 weeks. At the start of each replicate 5 deuteronymphs were placed on each of the two test beetles

Table 6. Average proportion of deuteronymphs choosing the male beetle in choice experiments between one male and one female beetle of the same age

	<i>n</i> replicates	Mean proportion of deuteronymphs on male beetle	Probability (sign-test)
A: start on male beetle	19	48.9	ns
B: start on female beetle	20	43.3	ns

At the start of each replicate 10 deuteronymphs were placed on one of the test beetles

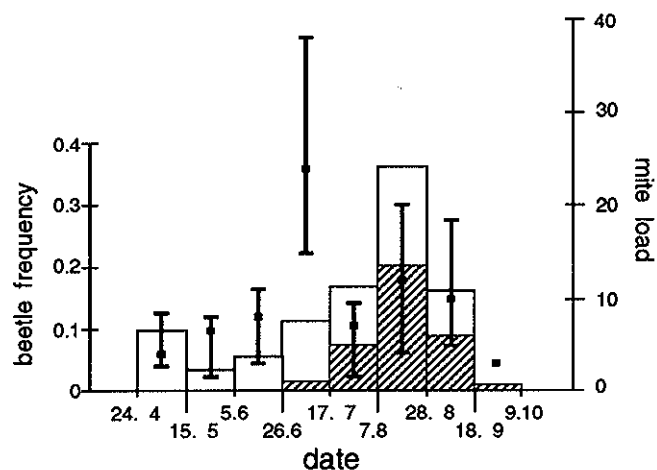


Fig. 2. Seasonal fluctuation in beetle frequency and mean mite load. The columns indicate the proportion of beetles trapped ($n=185$ beetles). Shaded areas represent the proportion of young beetles. The mean mite loads per time interval is represented by the median (■) and the inter-quartile range (bars)

Choice experiments using beetles of the same age revealed that deuteronymphs do not discriminate between male and female *N. vespilloides* outside the crypt (Table 6). The deuteronymphs evened out the differences in mite numbers by transferring between the test beetles.

Mite loads of field-caught beetles

The first individuals of *N. vespilloides* were caught in April and May (Fig. 2). Since *N. vespilloides* hibernate as adults, these were beetles of the previous year. Beetle abundance was constant until the beginning of July, when the first beetles of the summer generation were trapped. The highest abundance was found in the interval from 8 to 28 August. In this interval more than half of the beetles were young beetles, indicating that most beetles of the summer generation do not emerge before the beginning of August. Since *N. vespilloides* reaches sexual maturity about 2 weeks after emerging from the pupal chambers and may reproduce until late August (Pukowski 1933), it is likely that the first beetles of the summer generation managed to reproduce before the end of the season.

Beetles caught from April to June carried 4–8 *P. carabi* deuteronymphs. In July, the mean mite load per beetle showed a considerable increase, preceding the increase in beetle abundance. Some beetles carried more than 40 deuteronymphs (maximum: 94), indicating that they were post-reproductive beetles that had just left their crypts (Springett 1968). From August onwards, the average mite load decreased again. This decrease was due to the increasing number of newly hatched beetles carrying low numbers of mites; young beetles carried fewer deuteronymphs than older beetles (Mann-Whitney *U*-test, $P < 0.001$, calculated for animals caught after 26 June). There was no significant sex bias in mean mite load (*U*-test, $P > 0.05$).

Discussion

For the phoretic mite *P. carabi*, which reproduces in the subterranean crypts of *Necrophorus* beetles, maintaining contact with its carrier is vital. Therefore, the deuteronymphs of the new mite generation have to leave the crypt by attaching to a beetle. The deuteronymphs do not disperse equally on the beetles in the crypt: as long as both parent beetles are present, the deuteronymphs attach to the male. Deuteronymphs that develop after the male has left congregate on the female. Only those deuteronymphs that miss the female's departure disperse on the larvae. In summary, the distribution of deuteronymphs on beetles departing from the crypt is determined by the preferences of the deuteronymphs, and by the proportion of mites in the phoretic stage at the time the preferred beetles depart. This proportion largely depends on the egg-laying behaviour of the female mites, which lay their eggs over a period of several days.

Our experiments demonstrate that the deuteronymphs do not use sex-specific traits to discriminate between the parent beetles in the crypt, but rather traits that are related to the behaviour of the beetles: they prefer the non-feeding peripheral beetle to the central one which feeds the brood. Since *P. carabi* deuteronymphs are known to identify their carriers by a chemical organ on tarsus I (Neumann 1943; Korn 1983), it is likely that they use differences in scent to discriminate between the central and the peripheral beetle. These may either be differences in beetle pheromones, as Trumbo (1991) reports that at the time of dispersal male beetles undergo rapid physiological changes, or differences that are due to external factors: the central beetle regurgitates carrion to feed the larvae and is often in direct contact with the liquefied meat inside the carcass ball, which may provide it with a scent that distinguishes it from the peripheral beetle.

The advantage of preferring the peripheral beetle, which is the male in most cases, seems obvious: it is the beetle that is most likely to leave first and thus represents the fastest way out of the crypt. However, since both parent beetles carry high loads of mites when departing, the preference for the peripheral beetle may also represent a mechanism to facilitate the distribution of a high proportion of mites on both parents. Assuming the deuteronymphs displayed no preference and dispersed equally on male and female, it would only be possible for 50% of all the deuteronymphs raised in the crypt to attach to the male if all the deuteronymphs had completed their development when the male departs. This would require either the mite female to lay all its eggs during the first 2 days after the burial of the carcass, and/or the offspring to shorten their developmental time. Since *P. carabi* already has a high egg-laying rate and the period required for reproduction and development is short in comparison to a sympatric sibling species (Müller and Schwarz 1990; Schwarz and Müller 1990) and to other mesostigmatic mites (Rapp 1959; Karg 1971, 1989; Lindquist 1975; Hunter and Rosario 1988; Wise et al. 1988), the evolution of a preference for the peripheral

beetle may be a more economical way to distribute large numbers of deuteronymphs more evenly between both parent beetles: only those deuteronymphs leaving on the male have to be in the phoretic stage at male departure. Those dispersing on the female may develop later.

There are several reasons that may explain why most of the mites leave the crypt on the parent beetles and not on their offspring. Firstly, the parents leave the crypt and start to search for a carcass only a few days after the first mites have reached the phoretic stage, whereas their offspring remain another 20 days in their pupal chambers. Secondly, adult beetles not only represent the fastest way of dispersal from the crypt, but also the safest. A parent beetle that is still alive at the end of brood care will soon leave the crypt, and the chances that it will die before departure are low. Its offspring, in contrast, have to disperse in the soil, build their pupal chambers, and pupate before they emerge. During this period they are exposed to attacks by predators and parasites (Pukowski 1933). Finally, parent beetles leaving the crypt begin to search for small carcasses in order to reproduce again, whereas teneral beetles prefer big carcasses, which are used for feeding only (Wilson et al. 1984). Thus, deuteronymphs on the parent beetles may reach the next crypt a short time after dispersal, whereas the deuteronymphs on the offspring have to wait until their carriers have reached sexual maturity and start to search for small carcasses.

Leaving the crypts on the parent beetles, however, also involves severe problems. Most of the mites raised in a crypt disperse on the two parents, which generates extraordinarily high mite loads that handicap the beetle (200 mites weigh about half as much as their carrier). If the carrier reproduces again, the high mite density in the crypt increases intraspecific competition (Korn 1982). In addition, the mites that disperse on the parent beetles risk losing contact with the next carrier generation. *P. carabi* can avoid these problems because the deuteronymphs are not compelled to stay on their old and overlaid carrier. They can transfer between burying beetles which meet at carcasses and pheromone-emitting males (Wilson and Knollenberg 1984; Müller and Eggert 1987; Otronen 1988). In *N. vespilloides*, a bivoltine species with overlapping generations, beetles of both generations may meet at these places (Korn 1983). Since *P. carabi* deuteronymphs tend to even out density differences and avoid immature beetles, carrier transfer at the meeting places results in a reduction of mite loads on post-reproductive beetles and a dispersal onto the sexually mature beetles of the population. Early in the year these are exclusively beetles of the spring generation. Later on, more and more beetles of the summer generation reach sexual maturity and become attractive to the deuteronymphs. Since the deuteronymphs tend to abandon very old beetles (Korn 1983), carrier transfer will eventually result in the accumulation of deuteronymphs on beetles of the summer generation, thus assuring the continuity of the phoretic association.

Other stenoxenous mites follow the generation cycles of their carriers more closely (Hunter and Rosario 1988); they reproduce in the carrier's nests and disperse on the

carrier's progeny. They do not reproduce until their juvenile carriers have completed their development and built a nest of their own, although development of the mites may be completed within a few days. *P. carabi* has become independent of its carrier's generation cycle. The mites leave the crypt at the earliest opportunity and switch between carriers, thus increasing their chances of arriving early in the next crypt. Several reports of extraordinarily high mite numbers on departing parent beetles (Pukowski 1933; Springett 1968; Korn 1983; Wilson and Knollenberg 1987; Bartlett 1988) and field-caught burying beetles carrying record numbers of several hundred deuteronymphs (Starzyk 1967; Costa 1969; Hyatt 1980) indicate that this dispersal behaviour is not restricted to the association between *P. carabi* and *N. vespilloides*, but also occurs in associations with other species of burying beetles.

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