

# Adaptive indirect effects: the fitness of burying beetles with and without their phoretic mites

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## Summary

Any behavior that equally affects a group of organisms cannot be selected by the evolutionary forces operating within that group. The evolution of such behaviors requires a population structure consisting of many groups that vary in their genetic and/or species composition. In this paper we present evidence for the evolution of behaviors with shared consequences in phoretic mites that utilize *Nicrophorus* beetles (Silphidae) for transport. Eighteen experiments, totalling over 1500 beetle broods, demonstrate that the mites (1) have no negative effects on the beetles at normal densities, (2) occasionally have short-term beneficial effects, (3) appear to have long-term beneficial effects that require a period of time to manifest themselves, and (4) themselves have negative effects at abnormal densities. A survey of other phoretic associations indicates a similar mix of commensalism and mutualism. We conclude that most phoretic associations have evolved to eliminate their own negative effects on the carrier, and also have evolved positive effects when the ecological situation permits.

*Keywords:* *Nicrophorus*; Silphidae; group selection; mutualism; commensalism; burying beetles; phoresy.

## Introduction

One of Darwin's most famous quotes describes the cascading effects that a species can have on its community.

Hence, I have very little doubt, that if the whole genus of humble-bees became extinct or very rare in England, the heartsease and red clover would become very rare, or wholly disappear. The number of humble-bees in any district depends in a great degree on the number of field-mice, which destroy their combs and nests; and Mr. H. Newman, who has long attended to the habits of humble-bees, believes that 'more than two thirds of them are thus destroyed all over England.' Now the number of mice is largely dependent, as everyone knows, on the number of cats; and Mr. Newman says 'Near villages and small towns I have found the nests of humble-bees more numerous than elsewhere, which I attribute to the number of cats that destroy the mice.' Hence it is quite credible that the presence of a feline animal in large numbers in a district might determine, through the intervention first of mice and then of bees, the frequency of certain flowers in that district! (p. 125, first edition)

Cascading effects such as these, which now usually are termed indirect effects, have become a major focus of ecological research. Part of the interest stems from the theoretical literature; indirect effects become important in any mathematical model involving more than two species (Levins, 1974, 1975; Levene, 1976; Holt, 1977; Lawlor, 1979; Schaffer, 1981; Vandermeer *et al.*, 1985). Much of the interest, however, also stems from empirical studies that clearly demonstrate the importance of indirect effects in nature. Darwin's example was hypothetical, but today there

is no doubt that species often have strong effects on other species that can ramify throughout the entire community (e.g. Estes and Palmisano, 1974; Brown *et al.*, 1986; Lubchenco, 1986).

The importance of indirect effects raises questions for evolutionary ecologists that are only beginning to be explored. For example, consider a predator that accepts some prey and ignores others in a way that maximizes energy gained per unit time. Assume that this pattern of prey choice has numerous indirect effects on the community, which on balance are negative for the predator. Perhaps consumption of the favored prey species causes them to be replaced by less favored prey species. The foraging behavior is adaptive from the standpoint of direct caloric gain, but maladaptive from the standpoint of indirect effects. How should an evolutionary ecologist weigh the direct and indirect consequences of the behavior, to predict whether it will be favored by natural selection?

As discussed in detail elsewhere (Wilson, 1980, 1983a,b), this question cannot be answered without an appreciation of population structure. Indirect effects frequently are diffuse in their action; they alter the fitness not only of the individuals that cause them, but also others in their vicinity. The number and genotypic composition of these neighbors must be known before the total effect of the behavior on allele frequency change can be calculated. Evolutionists that study intraspecific social behaviors (such as warning cries, whose effects also are shared by a group of neighbors) are familiar with this problem, and have devoted much attention to it (reviewed by Wilson 1983b). This literature becomes relevant to community ecologists to the extent that indirect effects, shared by neighbors, are important in nature.

Wilson (1980, pp. 114–26) argued that phoretic associations are elegant communities for studying the evolutionary consequences of indirect effects. Phoresy refers to the use of one animal for transport by another. This form of dispersal is especially common in mites and other wingless creatures that specialize on patchy ephemeral resources such as dung, carrion, and rotting wood. These creatures are adapted to attach to insects that themselves are specialized on the same resource. When the insects colonize a fresh resource patch, they carry with them an entire multispecies community of phoretic associates, which disembarks to pursue a free-living existence. The density and diversity of phoretic communities can reach spectacular proportions. For example, at one of our study sites, over 14 species of mites from four families are associated with the carrion beetle genus *Nicrophorus* (Silphidae). Over 95% of the beetles carry mites, at average densities that can exceed 500 mites per beetle (depending on the beetle species and time of year). With few exceptions the mites are found exclusively on carrion and arrive exclusively on the bodies of carrion beetles. Comparable examples could be listed for dung beetles (Costa, 1969), wood-feeding insects (Moser and Roton, 1971), and other insects that specialize on patchy ephemeral resources. The phoretic associates include not only mites but nematodes (Kinn, 1984), fungus (Batra, 1979), microbes (Gilbert, 1980), and even other insects (Monteith and Storey, 1981). These are some of the most spectacular and neglected symbioses that exist in nature.

Adaptive indirect effects can effectively be studied in phoretic associations for two reasons. First, the global community consists of many discrete local communities for which the parameters of population structure can be measured. Second, all phoretic associates have a shared dependency on the carrier for transport, which makes adaptive indirect effects fairly easy to recognize, when and if they occur. To see this, consider the following version of the foraging example described above. A phoretic mite behaves in ways that maximize fecundity on the resource patch. These behaviors have numerous indirect effects, some of which decrease the number of insects – and therefore phoretic associates – that will disperse from the patch. The direct effects increase the fitness of mites performing the behaviors, but the indirect effects decrease the fitness of all phoretic associates on the resource patch, regardless of their genotype or species. Because this is a shared cost, it cannot change the relative frequencies of genotypes or species within the

resource patch. Considering only the relative fitness of genotypes on a single patch, we would predict such behaviors to evolve, despite the negative indirect effects. Conversely, we would predict that mutualistic behaviors that increase insect survival (positive indirect effect) at some cost to the mutualist (negative direct effect) would not evolve. In sociobiological terms, the mutualistic behaviors are 'altruistic' because the indirect effects increase the fitness of the entire community, while the direct effects decrease the fitness of the mutualists relative to other phoretic associates on the same patch.

This is not the entire story, however, because the indirect effects are shared only by members of a single local community. Many local communities exist that vary in the relative proportion of species and genotypes within species. If some of these communities promote the survival of the carrier more than others, with corresponding differences in dispersal to new patches, then the differential productivity of communities can select for the very mutualistic behaviors that are selected against within each community. What actually evolves is a balance between the opposing forces of within and between-community selection. See Wilson (1976, 1980, 1983a, 1986) for a fuller treatment.

To summarize, activities of phoretic associates which benefit the insect carriers are adaptive indirect effects. Their evolution depends critically upon population structure – variation and differential productivity of isolated local communities. Phoretic associations are elegant for the study of adaptive indirect effects because their population structure can be rigorously measured and then correlated with the degree of mutualism that has evolved.

In this paper we examine the effects of phoretic mites on the fitness of *Nicrophorus* beetles. We also survey the literature on other phoretic associations. We conclude that most phoretic associations have evolved to eliminate their own negative effects, and either are commensal or mutualistic towards their carriers. The degree of mutualism appears to depend primarily on the ecological situation, i.e., the degree to which the carrier is faced with problems that the phoretic associate can solve.

#### *Natural history of the Nicrophorus phoretic association*

Before proceeding to the experiments, it is important to understand the basic ecology of the species involved. *Nicrophorus* beetles are specialized to reproduce upon small carcasses, such as dead mice, which they bury in the ground to raise their brood upon. Their common name of burying beetle is thus well chosen. A given carcass frequently is found by numerous beetles, but usually is monopolized by a single male and female, who remain in the underground chamber throughout most of their brood's development. The pair shaves the carcass and molds it into a spherical shape, spreads an anal secretion over the surface of the carcass, and regurgitates a highly proteolytic oral secretion into one or more 'feeding pits' (Pukowski, 1933). The female tunnels into the soil to oviposit, and her first instar larvae are guided to the burial chamber both by olfactory and acoustic cues, the latter produced by stridulating adults. The larvae congregate next to a feeding pit, and initially are fed trophylactically (by regurgitation) by the parents. Eventually the larvae feed directly on the carcass, but trophylaxis continues throughout development (unpublished data). Burying beetles represent the highest level of sociality attained by the Coleoptera (Wilson, 1971).

As many as five species of *Nicrophorus* can coexist in a single habitat. Their niches are defined primarily by seasonal phenology and short-term temperature fluctuations (Wilson *et al.*, 1984). In addition, *Nicrophorus pustulatus* departs from the other species by reproducing on large carcasses that cannot be buried (S. Trumbo, unpublished). Despite the fact that coexisting species have well defined niches, individuals of different species frequently encounter each other, both on small carcasses and on large carcasses where adults congregate to feed themselves.

At least fourteen species of mites from four families also specialize on carrion at our study sites, and disperse phoretically on *Nicrophorus* beetles (Parasitidae, Macrochelidae, Uropodiidae, Histiostomatidae). Patterns of association between beetles and mites range from complete specificity (mite species restricted to a single beetle species), to the parasitid mite *Poecilochirus necrophori* Vitzthum, which is found on four of the five sympatric *Nicrophorus* in addition to other genera of silphid beetles (e.g., *Necrophila americana* Linnaeus). This generalist species is genetically polymorphic, however, and each morph has more specific associations (Wilson, 1982). In general these mites are highly adapted to life in association with their insect carriers.

The mites attach to the beetles at only a single stage of their life cycle (macrochelid females attach as adults, the other species as deutonymphs). The mites typically disembark after a small carcass has been found and buried, and reproduce near the beetle larvae. The next generation of mites either attach to the parent beetles or accompany the beetle larvae to their pupal chambers.

Other phoretic associates of *Nicrophorus* beetles include nematodes (*Rhabditis* sp.) and microbes. These definitely are transmitted from carcass to carcass by burying beetles (thus qualifying as phoretic associates), but their degree of specificity and adaptation to life in association with *Nicrophorus* is not known.

## Materials and methods

The research was conducted at two sites in Michigan; the University of Michigan Biological Station (UMBS; lat. 45°34') and Michigan State University's Kellogg Biological Station (KBS; lat. 42°34'). Five species coexist in deciduous forests at UMBS (*Nicrophorus orbicollis* (Say), *N. tomentosus* (Weber), *N. defodiens* (Mannerheim), *N. sayi* (Laporte) and *N. pustulatus* (Herschel)). All except *N. defodiens* coexist at KBS, although *N. orbicollis* and *N. tomentosus* are by far the most numerous. Salient differences between these sites are described in Wilson (1982), Wilson *et al.* (1984), Wilson and Fudge (1982), and Wilson and Knollenberg (1984).

Beetles were collected in baited pitfall traps, and either were used immediately in experiments or else bred to create cohorts of same-aged offspring to be used in experiments (see below).

### *Generating beetles with and without mites*

Large parasitid mites were removed by blowing a stream of CO<sub>2</sub> over the beetles, and brushing the mites off with a fine camel's-hair brush. This procedure anesthetized both the beetles and mites for less than thirty seconds.

Two methods exist for removing all species of phoretic mites from *N. orbicollis*. The first is to allow beetle pairs to bury mice in plastic shoeboxes (31 × 17 × 9 cm) filled with potting soil, and retrieve them after 36 h. In this time approximately 98% of the mites have disembarked (unpublished data) but the beetles have not yet oviposited (Wilson and Knollenberg, 1984). The second method is to allow the beetles to oviposit, and transfer the late first or early second instar larvae to fresh dead mice (*N. orbicollis* larvae do not survive if transferred as eggs or early first instars; unpublished data). This method creates a cohort of same-aged adults, 100% free of mites, but it must be initiated about eight weeks prior to the actual experiments.

All methods for removing mites could themselves alter beetle fitness, which would confound the interpretation of results. To circumvent this problem, we removed mites from all beetles used in the experiments, and then replaced mites on half the beetles. In this fashion all beetles experienced the de-miting procedure, and differed only in the presence or absence of mites. For experiments involving removal of only *Poecilochirus* sp., the mites were anesthetized, counted, and introduced directly onto the beetles. For experiments involving removal of all phoretic mites, a beetle with mites was decapitated and placed in a small tub with a single miteless beetle.

Virtually all mites transfer from the decapitated to the live beetle within 24 h (unpublished data). Because the live beetle often eats the decapitated beetle, beetles scheduled to remain miteless were provided either a beetle killed by freezing (which also kills the mites), or a piece of fish of comparable size.

#### *Short term experiments in laboratory and field*

In deciduous forest, dead mice (*Mus musculus*, killed and frozen until 12 h before use) were placed 20 m apart in transects on the morning of day 0. On the afternoon of day 0, small plastic tubs containing beetle pairs were placed tightly over the mice for at least 15 min. During this time the beetles commenced their normal sequence of behaviors with the carcass, after which the tub was removed. A plastic shoebox was then placed over the carcass for the first night, which allowed room for burial and helped to prevent free-flying burying beetles from discovering the carcass. Beetles with and without mites alternated positions along the transects. A length (50 cm) of dental floss tied to a hind leg of the mouse allowed us to find the burial chamber. Parents and their maturing brood were retrieved on day 10–12 of the experiment (depending on weather) and preserved in 70% glycerine alcohol. Depth of burial chamber (in cm, from the floor of the chamber to the soil surface), number and size of offspring, and number of mites on adults and larvae were recorded. A small notch was cut on the elytrum of each parent, allowing us to detect whether they had been replaced by free-flying burying beetles during the course of the experiment. Such takeovers were infrequent.

In the laboratory, beetles were allowed to raise broods in plastic shoeboxes filled with soil to a depth of about 7 cm. An effort was made to simulate natural conditions in different ways, depending on the experiment. In some cases mice were first placed in deciduous forest to allow natural fly oviposition, and in other cases soil blocks were cut from the forest floor and fit into the shoeboxes. The laboratory experiments permitted retrieval of the offspring as emerging adults, thus yielding estimates of pupal mortality and better estimates of offspring size.

#### *Long-term experiments in laboratory and field*

Burying beetles are multivoltine and capable of raising as many as five broods in the laboratory (see below). To measure long-term fitness of beetles with and without their mites, we conducted three field experiments lasting two broods, and one laboratory experiment lasting five broods of the original parents and two generations of their offspring.

For each field experiment, cores (19 cm deep and 22 cm dia.) from deciduous forest floor were taken 20 m apart along transects. The cores were placed in 7-liter styrofoam buckets with drainage ports. Care was taken to minimize disturbance of the soil profile. Buckets were then placed in the holes from which the soil cores were taken. Beetles were placed on mice inside the buckets in the same fashion as the short term experiments. On day 7, the buckets were transferred to an enclosed, shaded porch and fitted with insect traps consisting of a screen cone leading into an inverted canning jar. All insects emerging from the soil, including the parent beetles and their offspring, were collected nightly. The parent beetles were maintained individually for 3 to 7 days with ample food, and then placed in another set of buckets (as described above) to rear a second brood. The first of these two-brood experiments used mixed-aged beetles caught from pitfall traps and de-mited with the 36-h method described above. The second and third experiment used the 8-week method that generates a same-aged cohort.

In the laboratory, a cohort of same-aged beetles were provided mice in shoeboxes filled with forest soil, and retrieved as they emerged. They were maintained individually for 10 days with ample food, provided another mouse, and so forth until their death. 'Widowed' males and females were re-paired when possible. Offspring emergence usually occurs over a period of 2–4

days (unpublished data). To prevent cannibalism, boxes were dismantled when the first offspring appeared on the surface. Some offspring were preserved for analysis, while others were maintained and bred as a continuation of the experiment.

For all of the above experiments, the components of beetle fitness are defined in the following way: (1) the proportion of successful broods (yielding one or more offspring), (2) the average number of offspring from successful broods that survive to late third instar, (3) the average number of offspring from successful broods that emerge as adults, and (4) the average size of offspring, measured either as blotted wet weight (for larvae) or pronotum width (for adults). Wet weights should be compared only within and not between experiments, for two reasons. First, some broods had not completed growth at the end of the experiment, and the proportion of these broods varied across experiments. Second, wet weight is partially a function of the length of time spent in alcohol, which was not controlled across experiments.

#### *The effect of fly eggs on mite fecundity*

In one laboratory experiment we placed pairs of *N. tomentosus* on mice, half of which had been exposed to natural fly oviposition. Each beetle pair carried 10 *P. necrophori*. Offspring mites were collected 10 days later, at the completion of larval beetle development.

To count nematodes on the bodies of beetles, we placed preserved beetles in a centrifuge tube with 20 ml of 70% ethanol (wings and elytra detached), and spun them for 30 sec with a vortex mixer. We counted the nematodes in three 0.2-ml aliquots of the alcohol under a dissecting microscope.

## Results

Our results can very briefly be summarized with four statements:

- (1) Occasional short-term benefits. *Poecilochirus* sp. may increase the fitness of burying beetles by reducing fly competition. Under many circumstances, however, the beetles themselves eliminate fly larvae, and then *Poecilochirus* has no effect on beetle fitness.
- (2) Neutral short-term effects at normal densities. The removal of all phoretic mites from *N. orbicollis* appears to have no effect on beetle fitness, at least over the short term.
- (3) Long-term positive effects. The removal of all phoretic mites appears to decrease the fitness of *N. orbicollis* over the long term (second and third broods), suggesting that the mites' activities have positive indirect effects that require a period of time to manifest themselves.
- (4) Negative effects at abnormal densities. At least some of the phoretic mite species are capable of preying on beetle eggs or larvae, and do so when mite density becomes sufficiently high (approx. 2-9 times higher than observed in the field).

These results will now be presented in greater detail.

#### *Occasional short term benefits*

Springett (1968) reported that *P. necrophori* behaved mutualistically toward the European species *N. investigator* by piercing fly eggs which, if allowed to hatch, would outcompete the beetle larvae. Our own studies confirm that the mites pierce fly eggs (Wilson, 1983, Table 2), but also show that the beetles themselves can eliminate fly competition under many circumstances. Our current understanding is portrayed in Fig. 1 and Table 1, which includes the data reported in Wilson (1983a, 1986).

Figure 1 shows the results of three experiments on *N. tomentosus* at UMBS, in which all parasitid mites were removed (experiments 5-7 in Table 1). This includes primarily *P. necrophori*

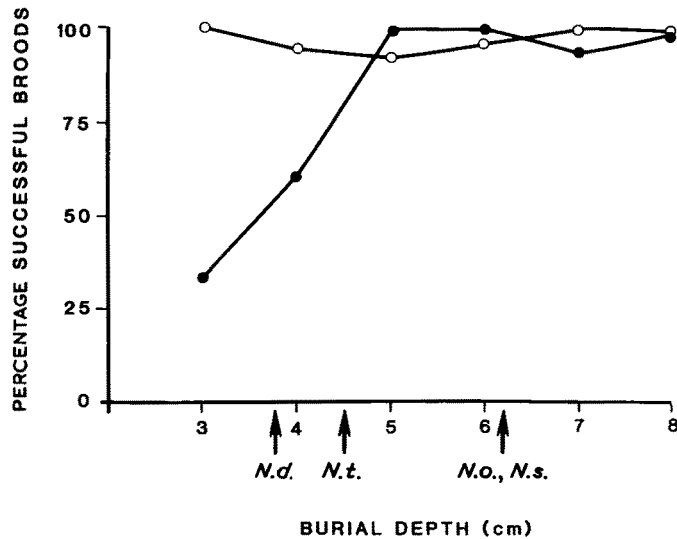


Figure 1. Combined results of three experiments (experiments 5–7 in Table 1), showing the relationship between burial depth and the proportion of broods that were successful for *Nicrophorus tomentosus*. Open and solid dots refer to the presence and absence, respectively, of *Poecilochirus* sp. Arrows on the X-axis indicate the average burial depth for *N. defodiens* (*N.d.*), *N. tomentosus* (*N.t.*), *N. orbicollis* (*N.o.*) and *N. sayi* (*N.s.*).

plus a minority of an unnamed species. When the carcass can be deeply buried, the mites have no effect on beetle fitness. When the carcass is shallowly buried, however, the mites dramatically increase the proportion of broods that succeed. Number and size of offspring from successful broods are uninfluenced by *P. necrophori*.

It is important to stress that all carcasses were deeply buried for experiments 6 and 7, yielding no treatment effect (Table 1). Thus, Fig. 1 shows the combined results of three experiments, but only experiment 5 yielded a significant result. Nevertheless, two lines of evidence indicate that the results are caused by the presence and absence of mites, and are not simply an improbable event. First, the relationship between brood survival and burial depth exists for experiment 5 alone. Second, several initially miteless broods acquired *P. necrophori* during the course of the experiment, presumably from free-flying burying beetles. These broods were uniformly successful, despite being shallowly buried (Wilson 1983a).

Based on these results, we hypothesized that the beetles themselves eliminate fly eggs oviposited prior to burial (perhaps during their extensive modification of the carcass), and that flies cannot gain access to deeply buried carcasses. Shallowly buried carcasses may experience continuous fly oviposition, however, in which case the egg-piercing mites enhance beetle fitness.

We attempted to measure the direct effect of egg piercing on mite fitness in two ways. First, we reasoned that if fly eggs are an important food source, and if shallowly buried mice are more accessible to fly oviposition, then mite fecundity should correlate inversely with burial depth. This prediction is not confirmed, even with a large data base (Wilson 1983a). Second, we experimentally compared the fecundity of *P. necrophori* on carcasses with and without fly eggs (see Methods section). No differences exist (15 broods in each treatment; average mite fecundity = 115 offspring without fly eggs and 111 offspring with fly eggs). Thus, the only measurable

Table 1. Summary of experiments involving the removal of *Poecilochirus* sp. from different species of *Nicrophorus*. The table shows the proportion of broods that successfully raised offspring (% success), average number of offspring raised from successful broods, and the size of the average offspring.

Ex- peri- ment	Species	Location	Lab/field	Mouse weight (g)	Place date	With mites				Without mites			
						Number of pairs	Success (%)	Number of pupae ± SD	Size† ± SD (g)	Number of pairs	Success (%)	Number of pupae ± SD	Size† ± SD (g)
1	<i>N. orbicollis</i>	KBS	Field	25-35	08/10/80	20	80	18.8±6.5	0.11±0.04	21	71	15.6±6.0	0.11±0.05
2	<i>N. orbicollis</i>	KBS	Lab	30-35	08/13/80	22	81	19.4±4.4	0.11±0.03	30	70	18.2±4.9	0.13±0.02
3	<i>N. orbicollis</i>	KBS	Lab	30-35	8/29/80	20	85	19.3±7.0	0.12±0.02	20	80	19.9±4.9	0.12±0.02
4	<i>N. orbicollis</i>	KBS	Lab	30-35	09/01/80	20	55	15.5±4.0	0.11±0.02	19	47	18.2±4.4	0.12±0.02
5	<i>N. tomentosus</i>	UMBS	Field	25-30	08/14/81	30	90*	15.7±7.7	0.08±0.04	28	53	14.5±6.8	0.08±0.03
6	<i>N. tomentosus</i>	UMBS	Field	25-30	08/21/82	30	86	14.7±4.9	0.12±0.12	30	80	14.0±4.2	0.09±0.05
7	<i>N. tomentosus</i>	UMBS	Field	25-30	08/28/82	14	86	16.5±5.6	0.06±0.03	14	93	18.7±6.0	0.08±0.02
8	<i>N. defodiens</i>	UMBS	Field	25-30	06/19/84	30	76	27.7±6.7	0.14±0.03	30	73	25.6±9.6	0.14±0.04
9	<i>N. defodiens</i>	UMBS	Field	25-30	07/11/84	14	64	22.6±12.0	0.18±0.12	14	85	29.8±9.6	0.15±0.03

\* Indicates a significant difference between treatments at the 0.05 level

† Average size was measured as blotted wet weight of preserved larvae. Average size varies markedly across experiments for two reasons. First, some broods had not completed growth at the end of the experiment, and the proportion of these broods varied across experiments. Second, wet weight is partially a function at the length of time spent in alcohol, which was not controlled across experiments.



benefit of egg piercing for the mites appears to be the shared benefit of enhancing the survival of the dispersal agent.

At this point, a very interesting interspecific pattern began to emerge. The coexisting *Nicrophorus* species at UMBS differ in their body size, and therefore, in the average depth to which they can bury a carcass (arrows in Fig. 1; see also Wilson and Fudge, 1984; Wilson, 1986). Based on the results for *N. tomentosus*, we predicted that *N. orbicollis* and *N. sayi* would rarely benefit from egg-piercing mites, while *N. defodiens* would frequently benefit. In addition, we found that *P. necrophori* is primarily associated with the two smaller species at UMBS, and in fact is genetically polymorphic, with two morphs that prefer *N. tomentosus* and *N. defodiens* respectively, and no morphs that prefer the two larger species (Wilson 1982, 1985, and unpublished data). The few *P. necrophori* found on the large species 'jump ship' when offered the choice. Thus, this mite appears to associate primarily with the beetle species that they most benefit.

Our expectation of no benefit for the larger species agrees with the data we had collected from *N. orbicollis* in four experiments conducted prior to our work with *N. tomentosus* (Table 1, experiments 1–4). In every case, the mites had no effect on *N. orbicollis*'s fitness. Unfortunately, our expectation of benefit for *N. defodiens*, the small species, was not confirmed (Table 1, experiments 8–9).

To summarize, experiments involving the removal of *Poecilochirus* sp. usually resulted in no treatment effect. Occasionally, however, these mites dramatically increased the probability of brood survival, at least for *N. tomentosus*. The conditions that cause the mites to become beneficial are poorly understood at present. Possibilities are reviewed in the discussion section.

#### *Neutral short-term effects*

Because the removal of *Poecilochirus* sp. usually had no effect on beetle fitness, we initiated another set of experiments in which the entire phoretic community was removed from *N. orbicollis*. This includes three species of histiostomatid mites, one species of macrochelid, at least one species of uropodid and two species of parasitids. Depending on the season and locality, the total mite community exists at an average density of 43–193 mites per beetle (unpublished data).

The results of nine experiments, totalling over 500 broods, are shown in Table 2. No significant differences exist between treatments for any single experiment. Beetles with mites had more larvae surviving to pupation in five of the nine experiments, more emerging adults in three of the four experiments for which this parameter was measured, and larger or equal sized offspring in four of the nine experiments. The phoretic mites appear to have no effect whatsoever on these parameters, even when the results of all experiments are combined.

The proportion of successful broods normally would be analyzed with a  $\chi$ -square test, comparing the number of successes and failures for each treatment. The number of failures is so low in both treatments, however, that the expected value always is less than 5, which renders the  $\chi$ -square test inapplicable. Nevertheless, beetles with mites have a greater success rate in only two of the nine experiments, suggesting a slight negative effect of the mites on brood survival. Judged by itself, this result is not statistically significant (Wilcoxon matched-pair signed-ranks test,  $P=0.078$ ). Furthermore, even this probability level is misleading, because the probability that one of four comparisons differs by this amount by chance alone is much greater than for a single comparison (Sokal and Rohlf, 1981, pp. 242–3).

To summarize, the entire phoretic mite community has a remarkably neutral effect on the fitness of *N. orbicollis*. This result can be interpreted in two ways. The mites could have a genuinely neutral effect, or they could have a mixture of positive and negative effects that balance out to zero. It seems unlikely to us that a mixture of effects would exactly balance in nine separate experiments conducted at different times, different localities, and under different

Table 2. Summary of experiments involving the removal of all phoretic mites from *N. orbicollis*; first broods. Column headings are the same as in Table 1, with the addition of the number of offspring in a brood that emerge as adults.

Ex- peri- ment	Location	Lab/field	Mouse weight (g)	Place date	With mites					Without mites				
					Number of pairs	Success (%)	Number of pupae ± SD	Number of adults ± SD	Size* ± SD	Number of pairs	Success (%)	Number of pupae ± SD	Number of adults ± SD	Size* ± SD
10	KBS	Lab	25-30	08/05/81	25	88	16.32±6.0	13.68±5.4	0.12±0.02	25	96	15.08±5.1	11.79±4.6	0.13±0.03
11	UMBS	Field	25-30	07/23/82	21	86	11.78±3.7	—	0.38±0.16	21	95	12.50±5.0	—	0.33±0.11
12	UMBS	Field	25-30	08/06/82	25	88	9.05±3.8	—	0.08±0.05	25	92	10.91±5.3	—	0.08±0.06
13a	UMBS	Field	25-30	07/01/83	30	100	—	12.17±4.8	7.43±0.59	30	97	—	11.97±4.2	7.32±0.59
14a	UMBS	Field	20-25	08/16/84	40	90	12.44±3.3	11.83±3.9	7.59±0.48	40	100	12.00±2.8	11.40±3.3	7.64±0.32
15a	UMBS	Field	35-40	08/16/84	40	97.5	16.92±4.9	16.08±5.5	7.66±0.66	40	100	15.95±4.3	14.55±5.7	7.57±0.40
16a	KBS	Lab	25-30	08/06/84	37	100	21.11±4.4	20.78±4.3	6.95±0.45	37	100	22.46±3.6	21.57±3.9	7.01±0.27
17	KBS	Field	25-30	06/13/85	29	82	9.17±6.3	—	0.29±0.11	36	76	8.79±5.6	—	0.31±0.12
18	KBS	Field	25-30	07/12/85	20	64	5.00±2.0	—	0.28±0.12	16	81	8.10±4.9	—	0.36±0.11

\* Size measured as body weight (g) for experiments 10-12 and 17-18, and as pronotum width (mm) for experiments 13-16.

conditions. It also seems unlikely that a mixture of effects would balance for each and every component of fitness listed in Table 2. Thus, we conclude that the entire community of phoretic mites has a genuinely neutral short-term effect on beetle fitness.

#### *Long-term beneficial effects, and negative effects at abnormal densities*

The remarkable neutrality demonstrated in Table 2 made us wonder if the phoretic mites have any ecological impact on the carrion community at all. In an effort to answer this question, we inspected the number of nematodes on the bodies of the parent *N. orbicollis*, as they emerged from the burial chambers. The results were dramatic: beetles without mites had an average of 18,522 nematodes clinging to their bodies while beetles with mites had an average of only 3,134 ( $N = 6$  and  $15$ , respectively; Mann–Whitney,  $P < 0.001$ ). Thus, the mites appear to have a six-fold effect on the number of nematodes that are carried to the next carcass. A more general analysis of the mites' ecological impact on the carrion community is in preparation.

This result caused us to frame the following hypothesis: the carrion community includes numerous minute organisms such as nematodes, bacteria, and fungi, that grow explosively during the period of brood development. The parent and offspring beetles become coated with these organisms, which they transport to future carcasses. If these minute organisms influence the survival and fecundity of *Nicrophorus*, and if phoretic mites alter their transmission to future carcasses, the indirect effects of the mites on the beetles may not be neutral after all. To demonstrate these indirect effects, however, the experiments must be extended beyond a single brood. We therefore conducted three field experiments (13–15) that lasted for two broods, and a laboratory experiment (16) that lasted for five broods of a cohort and three broods of their offspring.

The results of the field experiments are shown in Tables 2 (first broods) and 3 (second broods). For experiment 13, the beetles were captured in pitfall traps and de-mited using the 3-day procedure (see Methods section). They therefore comprise an unknown mixture of ages and reproductive histories. Virtually all of the beetles successfully raised their first brood, and the number of offspring from successful broods was comparable to the other single-brood experiments (Table 2, experiment 13a). As expected, the presence of phoretic mites had no effect on beetle fitness.

The beetles were much less successful at raising their second brood, and differences between treatments emerged. Without the phoretic mites, fewer beetles survived to have a second brood, fewer of their broods survived, and successful broods had a smaller number of offspring (Table 3, experiment 13b). Only the latter difference is statistically significant (Mann–Whitney,  $P < 0.05$ ).

For experiments 14 and 15, the beetles were de-mited using the 8-week procedure, and therefore comprised a cohort of newly emerged adults. These two experiments were conducted simultaneously, and differ only in size of carcass. We hypothesized that more nematodes, etc., would grow on the larger carcasses, and that the control of these organisms by the mites would be correspondingly more important for beetle fitness. As before, no differences between treatments exist for the first brood (Table 2). Mutualistic effects again emerged during the second brood, but only for experiment 15 (the larger carcasses). More offspring from successful broods survive to emerge in the presence of mites (Table 3; Mann–Whitney,  $P < 0.05$ ).

Thus, the mites appear to have no direct negative effects on their beetle carrier, and indirect effects that are positive on balance but which take a period of time to manifest themselves.

The results of the laboratory experiment (16) are presented in Figs 2 and 3. For both figures, the top row of five boxes represent five successive broods of the original cohort (labelled a–e). The offspring of the original parent's first brood (16a) were themselves allowed to raise two

Table 3. Summary of experiments involving the removal of all phoretic mites from *N. orbicollis*; second broods. See Table 2 for first broods and Table 1 for column headings and abbreviations.

Ex- peri- ment	Mousc weight (g)	Place date	With mites					Without mites					
			Adult survivors (%)	Number of pairs	Success (%)	Number of pupae ± SD	Number of adults ± SD	Size ± SD	Adult survivors (%)	Number of pairs	Success (%)	Number of pupae ± SD	Number of adults ± SD
13b	25-30	07/21/83	77	23	43	—	<sup>†</sup> 7.8±4.4	65	18	28	—	4.60±2.3	0.48±0.15
14b	20-25	09/02/84	90	32	84	12.81±4.6	6.75±0.34	98	37	94	12.60±4.9	12.20±5.0	6.81±0.44
15b	35-40	09/02/84	90	33	75	16.56±6.7	<sup>†</sup> 16.36±6.7	93	34	82	14.57±6.3	12.50±6.5	6.66±0.23

<sup>†</sup> Indicates a significant difference between treatments at 0.5 level.

Size measured as body weight (g) in experiment 13 and as pronotum width (mm) in experiments 14-15.

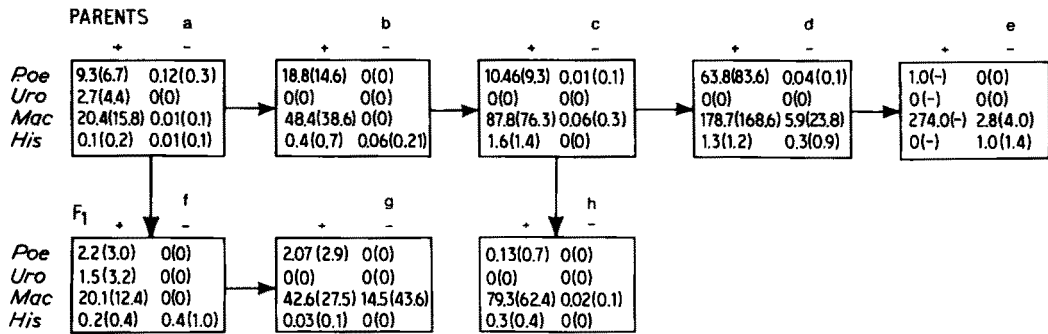


Figure 2. Average density (with standard deviation in parentheses) of mites on a single offspring beetle as it emerges from its pupal chamber in experiment 16. Each box represents a set of broods, including a treatment with mites (+) and without mites (-). The top five boxes (a-e) represent five successive broods of the original parental cohort. The progeny of their first brood were themselves allowed to raise two broods, shown in boxes f and g. The progeny of the original parent's third brood also was allowed to raise a single brood, shown in box h. Poe=*Poecilochirus* sp., Uro=*uropodid* sp., Mac=*macrochelid* sp., and His=*histiostamatid* sp. Numbers for histiostomatids are an average score, where 0=none, 1=1-10, 2=11-30, and 3=>30.

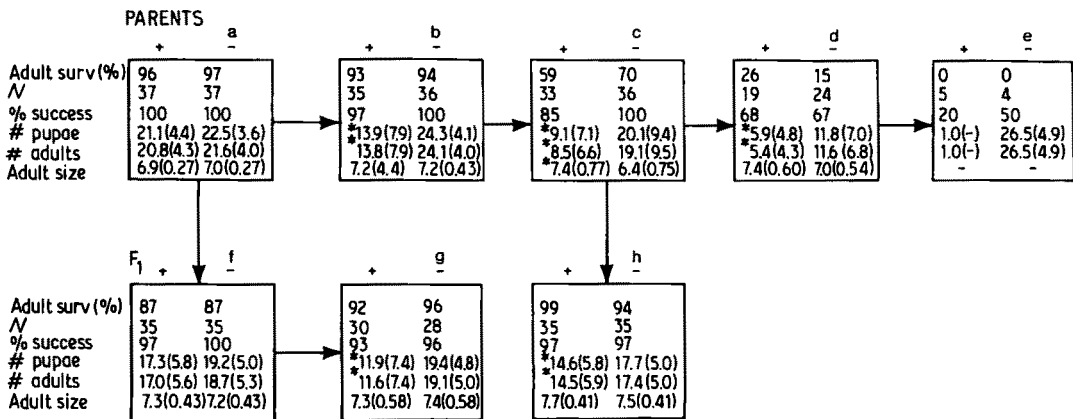


Figure 3. Adult survivorship, number of broods in the treatments, and the components of fitness for the broods of experiment 16. See text and captions to Table 1 and Fig. 2 for details. Asterisks indicate significance at or below the 0.05 level.

broods, which are represented in boxes f and g. In addition, the offspring of the original parent's third brood (16c) were allowed to raise a single brood (h).

Experiment 16 is complicated by the fact that the phoretic mite community destabilized during the course of the experiment, with some mite species going extinct and others reaching densities far greater than observed for field-caught beetles. In nature, the mites usually reproduce prolifically within the burial chamber, attach to the parent beetles in excessive numbers and to the larvae in considerably smaller numbers (adults are preferable to larvae from the standpoint of the mites, because they will immediately begin searching for another carcass). Since parents emerging from the burial chamber carry far more mites than beetles captured in pitfall traps, they

must have means of reducing their mite load, possibly by flying or by tunnelling through compact soil. Neither of these means were available in the laboratory experiment. We were able to remove excess numbers of *Poecilochirus* sp. with a stream of CO<sub>2</sub> (see Methods section), but could not remove macrochelids or anoetids without damaging the beetles. As a result, excessive numbers of phoretic mites were transmitted to subsequent broods, to initiate another phase of exponential growth. The consequences are shown in Fig. 2, which gives the number of mites carried by offspring beetles as they emerge from their pupal chambers. Macrochelid numbers increase from 20.4 in brood a to 178.7 in brood d. Far greater numbers of macrochelids probably existed on the original parents, but could not be counted without damaging the beetles. By contrast, the average density for field-caught beetles ranges from 9 to 22 (unpublished data for seven sampling dates).

The parasitid, macrochelid and histiostomatid mites develop rapidly, and reach their phoretic stages in time to attach to the original parents. Uropodids develop more slowly and leave only with the larvae, which explains their absence from broods b–e, g, and h. Other changes in the phoretic mite community are unexplained, but perhaps are caused by interactions among the species themselves. In any case, with the exception of broods a and f, experiment 16 compares one treatment containing virtually no mites with another treatment containing abnormal densities of the phoretic mites.

Fig. 3 shows the survival of the parents (proportion of adults initiating a brood that survive to initiate the next brood), the number of broods in each treatment, and the various measures of reproductive success. Beetles with mites have many fewer offspring for all broods except a and f. Thus, the phoretic mites themselves have negative effects on the beetles, probably in the form of direct mortality on eggs and small larvae, but only at abnormal mite densities.

In addition, the absence of mites appears to have different negative effects on the beetles, which is reflected in the offspring sizes of c-broods. Fig. 4 shows the relationship in a brood between the number of offspring that form pupal chambers and their average size as emerging adults, measured as pronotum width. The slope typically is linear and negative; the fewer the offspring, the larger they are. For a-broods, the presence or absence of mites have no effect on the number of offspring or the number–size relationship (Figs 3 and 4a; analysis of covariance,  $P=0.12$ ). For b-broods, mites decrease the average number of beetle offspring, but the treatments still do not differ in their number–size relationship (Figs 3 and 4b;  $P=0.81$ ). For c-broods, the mites again decrease the average number of beetle offspring, but the absence of mites now appears to change the number–size relationship (figs 3 and 4c). Most strikingly, five miteless broods produced very small numbers of very small adult offspring.

Observationally, miteless c-broods were disrupted by a variety of species that we have rarely observed in association with burying beetles. White molds grew over many of the carcasses, which were incompletely consumed by the beetle larvae. Larvae grew slowly and seemed to reach maturity at a small size. In some broods the larvae were so small that most failed to create pupal chambers, and died in the vicinity of the carcass. These broods therefore produced small numbers of very small pupae, as shown in Fig. 4c. In addition, in many broods a soil mite (*Sancassania* sp.) grew prolifically, accompanied the larvae into the pupal chambers, and remained attached to the emerging adults.

Statistical analysis of the c-broods of Fig. 4 is made complex by the fact that there is a positive slope to the number–size relationship over small brood sizes for the miteless treatment, rendering an analysis of covariance inapplicable. If the comparison is restricted to small brood sizes, the difference between treatments is highly significant (e.g.,  $P<0.001$  for brood sizes 1–10; Mann–Whitney). In addition, if the three most extreme data points are removed (pupal number less than five and pronotum widths less than 6 mm), the slopes of the two treatments are not

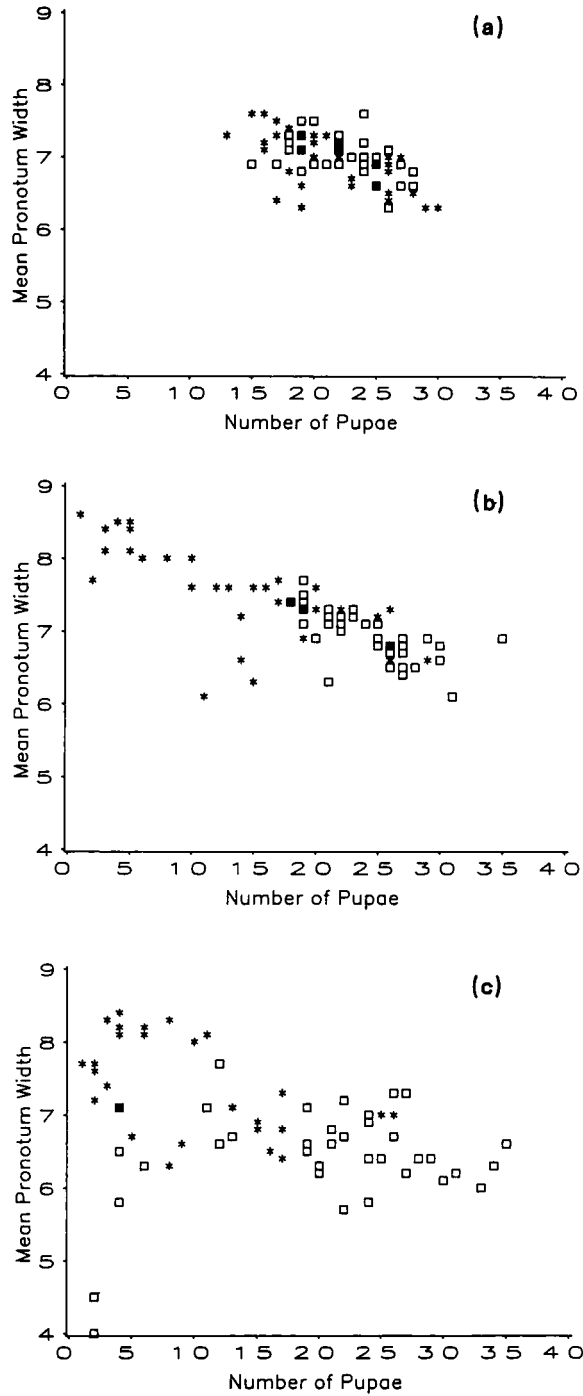


Figure 4. The relationship between number of offspring that survive to pupation and the size of individual offspring for broods a–c of experiment 16. Stars and squares represent broods with and without mites respectively.

significantly different, permitting an analysis of covariance for the remaining data. Adjusting group means for pronotum widths are 7.21 with mites and 6.76 without mites ( $P < 0.01$ ). Thus, the two treatments appear to have diverged in their number–size relationship, even when the most extreme data points are removed.

Our interpretation of these results and observations are as follows. When present in abnormal numbers, at least some of the phoretic mites (possibly the macrochelids) prey on beetle eggs and first instar larvae. Beetle larvae that survive grow well, however, and conform to the number–size relationship shown in Fig. 4. Egg and first instar survival is high when the phoretic mites are absent, but other species – derived from the surrounding soil and perhaps carried by the parent beetles from previous broods – grow and decrease the quality of the carcass as a resource for the beetles. As a result, the offspring complete development at a smaller size, which changes the number–size relationship in Fig. 3c. In some cases growth is so retarded that many of the offspring die before pupating, resulting in few offspring of very small size.

If harmful species are carried by parents and offspring to subsequent broods, we would predict the above scenario to apply for d-, e-, and h-broods. This prediction was not confirmed. Adjusted mean pronotum widths are indeed smaller for miteless beetles from d- and h-broods, but the differences are not significant (analysis of covariance,  $P = 0.19$  for d-broods,  $P = 0.06$  for h-broods). Statistical analysis could not be performed on e-broods, because of insufficient sample sizes. Observationally, the *Sancassania* mites that attached to the emerging c-brood offspring disembarked during the 3-week beetle maturation period, and were not transitted to the h-broods. Neither were the molds so highly visible on carcasses of the c-broods apparent on carcasses of the subsequent broods.

## Discussion

The relationship between burying beetles and their phoretic mites appears to be an interesting blend of commensalism and mutualism. In most experiments the mites have a neutral effect on beetle fitness, but in four cases the effect becomes positive (experiments 5, 13, 15, 16). Negative effects are remarkably absent, except when the mites exist at densities rarely observed in nature.

Although our experiments have demonstrated occasional mutualism, the mutualistic behaviors and the conditions that elicit them remain poorly understood. We have considered two hypotheses, and both have been partially falsified by our data.

### *P. necrophori*, fly competition, and burial depth

Springett (1968) appeared to show that *N. investigator* cannot survive without *P. necrophori* in the presence of fly competition. Wilson (1983a, 1986) appeared to show that *N. tomentosus* could itself eliminate fly competition under some conditions but not others. Specifically, *P. necrophori* was mutualistic only when the carcass was shallowly buried. To explain this context dependent mutualism, Wilson (1983a) formed the following hypothesis; (i) fly eggs deposited on a carcass prior to discovery by beetles are destroyed during modification of the carcass, (ii) deeply buried carcasses are protected from subsequent fly oviposition, and (iii) shallowly buried carcasses receive a continuing influx of fly eggs, which hatch in the absence of *P. necrophori* and outcompete the beetles.

Two experiments utilizing *N. defodiens* (experiments 8 and 9) falsify this specific hypothesis. The burial chamber of *N. defodiens* usually is only a shallow depression in the soil covered by leaf litter. Nevertheless, the removal of *P. necrophori* had no effect on beetle fitness.

We can think of two ways to revise the hypothesis. First, we have observed that many flies are reluctant to walk under leaves, which perhaps prevents their rapid escape from spiders and other



ambush predators. A thick layer of leaves might be as effective a barrier to flies as a layer of soil. If so, then burial depth might correlate with exposure to flies for *N. tomentosus* (who attempt to completely bury the carcass), but not for *N. defodiens* (who cover the carcass with leaves rather than attempting to completely bury it). The important variable for *N. defodiens* would then be leaf cover and not burial depth. Second, the beetles might preserve the carcass from flies and other competitors in a very different way than we originally envisioned. By forming the carcass into a ball and spreading an anal secretion over it, the beetles might cause the interior of the ball to become anaerobic. If so, then vulnerability to flies might depend on the amount of time required to complete the modification of the carcass. Perhaps the correlation between burial depth and mutualism in experiments 5–7 is caused not by post-modification fly oviposition, but by the amount of time required for modification. Soft soil could allow fast deep burial and rapid modification, while hard soil could prolong the burial process, limit the burial depth, and delay modification of the carcass, allowing the initial input of flies to hatch and consume the carcass in the absence of *P. necrophori*. These revised hypotheses must be tested with future experiments.

#### *The evolved phoretic community, the non-evolved phoretic community, and time*

Our research clearly shows that phoretic mites of *N. orbicollis* reduce the number of nematodes carried to future carcasses. Generalizing from this observation, we formed the following specific hypothesis: (i) carrion is an easily utilized, undefended resource that is abundantly inoculated by soil organisms during the burial process; (ii) in the absence of phoretic mites, many of these organisms grow prolifically; (iii) the parent beetles and their offspring become covered with these organisms, which constitutes a ‘non-evolved’ phoretic community (by definition, the species that compose this community can successfully grow on and around the carcass, but they are not specifically adapted to life in association with burying beetles); (iv) future carcasses are inoculated by the non-evolved phoretic community, which grow to even greater numbers; (v) eventually the non-evolved phoretic community negatively effects the beetles, either directly via predation/parasitism or indirectly via consumption or alteration of the carcass; and (vi) the evolved phoretic community itself has no negative effects on the beetles, and has an indirect positive effect by suppressing the non-evolved phoretic community.

This hypothesis caused us to conduct multi-brood and multi-generational experiments (experiments 13–16), which did demonstrate mutualistic effects. It also caused us to predict successfully that mutualism would be more likely in experiment 16 than 15. Nevertheless, we have no knowledge of the factors that reduce beetle fitness in second and third broods and no evidence that they were transmitted from earlier broods by beetles without mites. In addition, the factors reducing the fitness of c-broods in experiment 16 apparently were not transmitted to subsequent broods. These results will remain confusing until the actual factors that reduce beetle fitness are better understood.

Although the hypothesis outlined above may not explain our experimental results, something akin to it must operate over long time periods. It is remarkable that within months after the removal of the phoretic mites, a *Sancassania* mite not normally associated with burying beetles grew in large numbers and accompanied the beetle larvae into their pupal chambers. These mites did not remain attached to the emerging adults long enough to be transmitted to the h-broods. Nevertheless, it seems likely that within a relatively small number of generations, mite populations could become established that accompany the beetles from brood to brood. Of course, the phoretic mites themselves must have arisen by such a process. It would be fascinating to conduct such a multi-generational experiment, perhaps by introducing onto islands populations of insects with their phoretic associates removed.

### Other phoretic associations

Before interpreting our results, it will be useful to review the literature on other phoretic associations. Because of their status as economic pests, wood-feeding insects have been studied extensively, and their mutualisms with phoretic fungi are well known (Graham, 1967; Francke-Grossman, 1967; Batra, 1979). The fungi benefit their carriers in at least two ways; by killing or weakening the tree, and by serving as food for the carrier. Frequently these activities are accomplished by different fungal species. For example, the southern pine bark beetle (*Dendroctonus frontalis*) carries the debilitating bluestain fungus (*Ceratocystis minor*) as spores adhering to its surface, and the nutritious fungi in a specialized structure called a mycangium. The bluestain fungus actually is detrimental to the beetle if it grows close to the developing larvae, but in the normal course of events it is inhibited by the nutritious fungi (Barras, 1970). The nutritious fungi themselves are usually not a single species, but rather a multi-species community (Haanstad and Norris, 1985). The degree to which they are differentiated in their beneficial effects is unknown, but in some cases it appears that they provide vitamins and other specific nutrients to the beetles (Kok, 1979).

Wood-feeding insects also carry mites, which appear to be either mutualistic or commensal, but rarely detrimental to their carriers. Kinn (1980) showed that the mite *Dendrolaelaps neodisetus* reduced the density of endoparasitic nematodes, which themselves have been shown to reduce the fitness of *D. frontalis* (MacGuidwin, 1979). In the actual experiments conducted by Kinn, however, removing the mites did not decrease beetle fitness. Bridges and Moser (1983) demonstrated that *Tarsonemus* mites themselves carry spores of the bluestain fungus on specific regions of their bodies. Beetles with mites transmitted significantly more fungal spores, but the effect on beetle fitness was not directly measured.

Extensive searches for predatory phoretic mites as biological control agents so far have turned up only a single species, *Pyemotes parviscolyti*, which does feed voraciously on its carrier species *Pityophthorus bisulcatus* (Moser *et al.*, 1971). *Dendrolaelaps neodisetus* and *Macrocheilus boudreauxi* are fully capable of feeding on their carrier *D. frontalis*, but prefer nematodes when given a choice (Kinn and Witcosky, 1977; Kinn, 1980). The genus *Tarsonemoides* preys on the eggs of its carrier species, but a single female mite raises her entire progeny from a single egg (Lindquist, 1964). Finally, J. Moser and his colleagues provide compelling evidence that mites phoretic on *D. frontalis* are less virulent than other mite species from the same habitat, that encounter *D. frontalis* but do not depend upon it for transport (analyzed in Wilson 1980, pp. 119–24).

Another phoretic association involves yeasts and bacteria transmitted by flies (Gilbert, 1980). Starmer (1982) has conclusively demonstrated that microbial associates of cactophilic *Drosophila* detoxify free fatty acids, allowing the insects to develop faster and to a larger size. On the other hand, Howard *et al.* (1985) could find no beneficial effect of microbial associates on *Rhagoletis* flies.

Finally, many insect species are phoretic as larvae on other insects, but as adults are themselves capable of dispersing from the local resource patch. Meloid beetles, for example, oviposit on flowers. First instar larvae attach to bees and are carried into their nests, where they develop and disperse on their own. These phoretic associations are interesting because benefiting the carrier does not result in positive indirect effects for the associate. As might be expected, the associates usually are highly detrimental to their carrier (Clausen, 1976). A similar situation might exist for the mite *Macrocheles muscaedomesticae*, which is phoretic on flies and pierces fly eggs (Farish and Axtell, 1971). The mites develop very fast and disperse on adult flies visiting the habitat. Thus, they depend on flies for transport, but not on the individual flies with which they develop on the resource patch.

*Adaptive indirect effects in phoretic associations*

Based on this review of the literature and our own research, we provisionally offer three generalizations about phoretic associations. First, when harming the carrier results in no negative indirect effects, phoretic associates frequently are detrimental to their carriers. Second, when harming the carrier reduces the probability of dispersal from the resource patch, phoretic associations exhibit a remarkable absence of negative effects on their carriers. Third, when benefiting the carrier increases the probability of dispersal from the resource patch, phoretic associations are only sometimes mutualistic. Sometimes they are largely or even entirely commensal.

These three generalizations represent something of a paradox. Countless species of bacteria, fungi, mites, etc., have been shown to be pathogenic towards insects. Their absence among phoretic associates that depend on their carriers for transport must represent the outcome of a selection process that eliminates the virulent species and/or genotypes within species. But if this selection process has eliminated the negative effects, why has it not more consistently produced positive effects that even further insure transport to new resource patches?

We suggest that the presence and absence of mutualism is governed primarily by the ecological situation. Very simply, a phoretic associate cannot be mutualistic unless its carrier is faced with a problem that the associate can solve. Wood-feeding insects feed on a truly formidable resource; living trees that are both nutritionally poor and capable of fighting back by producing resins. Apparently the activities of phoretic associates (especially fungi) can solve these problems better than the insects themselves, and the result is an elaborate multi-species mutualism. By contrast, burying beetles are faced with a much less formidable resource; a nutritionally rich carcass with no defenses against being eaten. Under normal circumstances the beetles apparently can utilize this resource quite well by themselves, with or without the phoretic associates. In certain circumstances, however, the beetles do appear to be faced with formidable problems, and the status of the associates changes from commensal to mutualistic. By extension, it is easy to imagine other insects that never encounter problems which phoretic associates can solve, but which nevertheless carry elaborate phoretic associations. A similar argument might explain why catophilic *Drosophila* microbes are mutualistic whereas *Rhagoletis* microbes are not.

The idea that mutualisms are most common in biotically and abiotically stressful environments (e.g., lichens, gut biota of wood-eating insects) is a part of ecological conventional wisdom that our research supports. Another part of conventional wisdom, however, is that commensalism is evolutionarily unstable, a saddle point dividing mutualism from parasitism. For example, Whitney (1982, p. 185) states that 'commensalism . . . might better be considered as a lack of our ability to perceive effects.' Our research suggests that commensalism might often be evolutionarily stable, simply because many environments provide no opportunity for commensals to become mutualistic.

*Population structure and adaptive indirect effects*

Finally, what can we conclude from our research about the evolutionary consequences of indirect effects? By definition, any behavior that equally affects a group of organisms cannot change the frequencies of genotypes and/or species within that group. If the group is an entire breeding population, then natural selection is insensitive to the shared consequences of indirect effects, no matter how beneficial or detrimental they might be. If the group is only one of many such groups in the breeding population, however, natural selection can favor genotypes and species that increase the productivity of their group via indirect effects. This process of between-group

selection appears to have been important in the evolution of phoretic associations, and thus may also be important for other species and communities with similar forms of population structure.

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