The ecology of parental care in the burying beetle *Nicrophorus vespilloides* Herbst

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Declaration

I hereby declare that this thesis was composed by myself, and the work is my own except where acknowledged in the text.

'Should I stay or should I go now?
If I go there will be trouble,
if I stay there will be double.
So you gotta let me know,
should I stay or should I go?'

The Clash

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Abstract

Nicrophorus vespilloides Herbst (Coleoptera; Silphidae) bury the carcasses of small vertebrates which provide food for their developing larvae. The use of such a valuable, yet rare and ephemeral resource has led to the evolution of a complex and variable social system that ranges from parental care by a single female, through monogamy and biparental care to co-operative breeding. Concentrating on broods raised by either one or two parents, I used laboratory and field populations to study the benefits of parental care in *N. vespilloides*.

A decline in the apparent clutch size of *N. vespilloides* with successive generations of laboratory culture was correlated with an increase in numbers of the phoretic mite *Poecilochirus davydovae* Hyatt. Beetles with their mites removed had significantly larger apparent clutch sizes than beetles whose cargoes were left intact. Observations of mite behaviour suggested that the mite eats the eggs of its host. A comparison of the apparent clutch sizes of beetles in the presence or absence of carrion fly eggs implied that *P. davydovae* is predatory on burying beetle eggs in the field.

Adult beetles eclosing from larvae raised on small carcasses (where brood size is regulated by the parents killing a proportion of the first instar larvae) were at least as big as beetles that successfully secured, and raised broods on carcasses placed in the field. There was no difference in the degree of filial cannibalism in broods raised by a single female or a male and female.

In the laboratory, broods tended by a single female were vulnerable to being taken over by conspecifics resulting in the death of the larvae and the production of a smaller replacement brood. The additional presence of a caring male completely eliminated this risk. The probability of take-over of uniparental broods diminished as the carrion resource was depleted and yet, in biparental broods, males consistently stayed for longer than necessary to defend the brood and carcass. There was no difference in the success of broods raised in the field by one or two parents, in the absence of a risk of take-over by other burying beetles.

When they were provided with two carcasses sequentially, females with male assistance in their first brood only, produced larger second broods than did females who raised both broods alone. It is argued that the parental effort of the female is reduced by the presence of the male who benefits by fathering a proportion of his mate's subsequent brood by sperm competition.

Chapter 1

General introduction

1.1. THE ECOLOGY OF PARENTAL CARE

To maximise lifetime reproductive success, an organism must make trade-offs between life history traits. The distribution of an organism's resources between its offspring and its own continued growth and survival is one such trade-off, and is crucial to the understanding of the ecology and evolution of parental care.

As theory predicts (Williams 1966; Trivers 1972), parental care has frequently been demonstrated to increase the survival (eg. Townsend 1986; Diesel 1989) and the reproductive success (Albon & Clutton-Brock 1988; Huck *et al.* 1987) of offspring, and to reduce the future reproductive success of the parents (eg. Hairston 1983; Gross & Sargent 1985; Smith 1995).

Care may be provided by one or both parents. Generally, one parent should desert unless the success of broods is much greater when tended by two parents (Maynard Smith 1977), and the decision to care or to desert will be decided by the relative costs and benefits to each parent, which may be different for males and females.

Trivers (1972) suggested that females should invest more than males in parental care because the unequal costs of producing eggs and sperm mean that females waste a greater reproductive effort, should a breeding attempt be unsuccessful. Dawkins & Carlisle (1976) criticised the theory for its over-emphasis on past investment (the 'Concorde fallacy'), and it is now generally accepted that both sexes should base a decision to provide care on the likely future benefits, relative to costs (Dawkins & Carlisle 1976; Maynard Smith 1977).

Anisogamy may, however, be pertinent to explanations of differences in care provided by males and females, if future reproductive success is limited by gamete production. The low cost of sperm relative to eggs predicts that males have more to gain from inseminating large numbers of females, leading to males incurring greater costs if parental care reduces access to other mating opportunities. This constraint may be expected to favour the evolution of female parental care (Emlen & Oring 1977). However, if parental care is not costly in terms of lost mating opportunities, male care may also be selected. For example, paternal care predominates in fish species whose egg survival rate is increased by parental guarding or fanning. Several clutches may be tended simultaneously at sites suitable for oviposition, and males compete for these sites in order to attract females and gain inseminations (Baylis 1981).

It should be considered that the evolution of parental care is itself likely to alter the balance of costs and benefits of care to parents, and the outcome may be that a female has as much to gain as a male from deserting and seeking further reproductive opportunities (Maynard Smith 1977). Additionally, a decision by a parent on whether or not to provide care should take into account the strategy adopted by its partner (Maynard Smith 1977; Lazarus 1990; Houston & Davies 1985). It follows that generalisations about which sex should provide care cannot be made (Clutton-Brock 1991). General models of parental care, therefore, tend not to include assumptions about differences in the costs and benefits of caring to males and females (eg. Maynard Smith 1977; Lazarus 1990).

The model of Maynard Smith (1977) used game theory to predict the conditions under which no care, uniparental care or biparental care could be expected. If care by one parent is almost as effective as biparental care then the evolutionarily stable strategy is that either the male or female will care alone (Maynard Smith 1977). Which sex deserts will depend on the ecology of the animal under consideration. Male care is predicted if, for example, the female's investment in producing a large clutch leaves her with few resources to care effectively, or if there is an operational sex ratio in favour of males. Alternatively, if the male has a greater chance than the female of remating, then the female will care (Maynard Smith 1977).

The same model predicts that biparental care is favoured if two parents can raise twice as many offspring as one, or if the prospects of a deserting parent gaining further matings are low (Maynard Smith 1977).

Monogamy and biparental care is the most frequent arrangement found in birds. Reproduction in birds is usually limited by the rate at which food can be brought to the nest or by the number of eggs that can be incubated effectively (Lack 1968). The presence of two parents can, therefore, greatly enhance brood success. In mammals, polygyny and care by the female is the norm. A long gestation period, and lactation by females but not males, are characteristic of this group, so males have more to gain than females from access to other matings (Maynard Smith 1977; Clutton-Brock 1991).

Parental care after oviposition is rare in invertebrates, possibly as a consequence of their small size rendering parents incapable of providing adequate protection for offspring, and the tendency toward the production of large numbers of eggs (Zeh & Smith 1985; Tallamy & Wood 1986). Where care has evolved, it is usually provided by the female, a situation that likely reflects the prevalence of internal fertilisation (Clutton-Brock 1991), which allows the male to desert after insemination; the so-called 'cruel bind' (Trivers 1972).

Parental care in invertebrates is associated with the exploitation of physically harsh or biotically dangerous habitats (Wilson 1971). For example, females of the intertidal beetle *Bledius spectabilis* are required to remain with their eggs in a burrow to prevent both flooding by the incoming tide and anoxia within the burrow (Wyatt 1986).

Biparental care is particularly unusual among invertebrates, and appears, in the main, to be restricted to species that utilise bonanza resources such as dung or carrion (Wilson 1971). Exceptions are found in species such as the desert isopod

Hemilepistus reamuri, where high male mortality during pair formation means that subsequent mating opportunities are restricted (Schachak *et al.* 1976).

The spectacular social system of *Nicrophorus* can, broadly, be attributed to their exploitation of carrion as a reproductive resource. The biparental care displayed by burying beetles is a peculiarity among invertebrates but, nevertheless, these organisms lend themselves well to experimental analysis of the costs and benefits of parental strategies. Their reproductive cycles are shorter than those of most vertebrates, and they are amenable to laboratory culture where conditions can be controlled and manipulated.

1.2. THE GENUS *NICROPHORUS*

The genus *Nicrophorus* (Coleoptera; Silphidae) comprises 85 species world-wide, all of which use the carcasses of small vertebrates as a reproductive resource. They are commonly known as burying beetles, sexton beetles or grave diggers, because of their habit of interring the carrion in an underground chamber called the crypt.

Carrion is a rare, yet valuable resource, and is, therefore, the subject of intense competition from diverse taxa such as scavenging vertebrates, carrion flies, ants, fungi and bacteria (Putnam 1983; Scott *et al.* 1987; Trumbo 1990d). There is also fierce competition within the genus *Nicrophorus*, which is exemplified by the observation that often many burying beetles, of several species, will locate a carcass that will eventually support the brood of only a pair of beetles (Pukowski 1933). For example, within $3^1/_2$ hours of placing a freshly killed mouse in a birch woodland in Ontario, Canada, nine burying beetles, representing two species had located the carcass (Milne & Milne 1944). The high level of competition has led to segregation of species by temperature (Wilson *et al.* 1984; Trumbo 1990d), season (Anderson 1982; Wilson *et* *al.* 1984) or carcass size (Anderson 1982; Trumbo 1990b) allowing several species to co-exist within a single habitat.

In the absence of any other beetles at a carcass, a female will bury it and raise a brood alone using sperm stored from previous matings, an option that is not open to a male. Pukowski (1933) first described the way that male beetles, having arrived at a carcass and there being no female present, climb a nearby twig or the carcass itself, and take up the 'sterzeln' position: head pointing down and the tip of the abdomen pushed into the air. Pheromone release was the suggested function of this behaviour (Pukowski 1933) and evidence that females are attracted to signalling males (Mosenbach 1936) and, that signalling males do, indeed, release a pheromone (Bartlett 1987b; Eggert & Müller 1989a), has since been provided.

In the event of several beetles discovering a carcass, ownership is decided by the outcome of fights. Large species displace small ones (Wilson *et al.* 1984) and, within species, intrasexual fighting leads to all but the largest male and female being expelled from the carcass (Bartlett & Ashworth 1988; Otronen 1988). Individuals of the smaller species, such as *N. defodiens*, may delay intraspecific aggression until they have co-operated in the burial of the carcass, so as to reduce the chance of displacement by larger congeners (Fabre 1919; Wilson & Fudge 1984).

A remarkable feature of the reproductive biology of *Nicrophorus* is the level of care provided for the young. Parental care is uncommon among invertebrates, with the notable exception of the eusocial insects, and burying beetles are particularly unusual in that both the female and the male care for offspring. The complexity of their social structure has led to burying beetles being described as having the most developed system of parental care amongst the coleoptera (Wilson 1971; Tallamy & Wood 1986; Zeh & Smith 1985).

Parental duties commence with the carcass being buried by the victorious pair. If the substrate directly beneath the carcass is not amenable to excavation, it may be transported a short distance to a more suitable site (Fabre 1919; Pukowski 1933). *N.*

orbicollis prefers to bury in soil that contains a bulk structural component large enough to facilitate easy burial, but not so great as to prevent stable crypt construction (Muths 1991). During burial, the fur or feathers are stripped from the carcass and used to reinforce the walls of the crypt. The carcass is rolled into a ball, to the surface of which the beetles apply secretions which retard its decay (Halffter *et al.* 1983).

Eggs are laid in the soil surrounding the crypt, and, in *N. vespilloides*, at 20°C, these hatch 56h later (Müller 1987). On hatching, the larvae are attracted to the crypt by stridulatory vibrations produced by the parents (Niemitz & Krampe 1972), who eat a depression into the top of the carcass in which the larvae congregate. Burying beetles use two methods to regulate brood size, resulting in a consistency in the mass of individual larvae dispersing across the range of carcass sizes. Clutch size is adjusted on very small and very large carcasses (Bartlett & Ashworth 1988; Müller *et al.* 1990b; Trumbo 1990c). On carcasses of intermediate size, adults selectively cull a proportion of first instar larvae (Bartlett 1987c).

The larvae feed directly from the carcass and are also fed partially digested carrion which is regurgitated by the parents. After about a week, and having moulted twice, the fully grown larvae disperse from the crypt to pupate in the surrounding soil. The female parent generally remains with the larvae until they disperse but the duration of male care is more variable. In *N. vespilloides* the male deserts 1 or 2 days before the female but, in contrast, female *N. vespillo* are reported to drive the male away after egg laying (Pukowski 1933). Two parents are better than one at defending the brood and carcass against conspecifics (Scott 1990; Trumbo 1990a, 1991; Robertson 1993) and congeners (Trumbo 1990b) attempting to usurp the carcass in order to raise their own brood.

Wilson & Fudge (1984) frequently found beetles in the leaf litter surrounding an occupied carcass. These peripheral individuals were usually smaller than the resource-holders, suggesting that they had lost a contest for the resource, but had not immediately dispersed to seek alternative reproductive opportunities elsewhere.

A contest-losing female may benefit from remaining at a carcass if she is able to lay a clutch of eggs which, after hatching, are cared for by the residents. In 60% of laboratory broods of *N. vespilloides* in which two females were placed on a carcass, some of the loser's offspring were cared for by the winner and survived to maturity (Müller *et al.* 1990a). There is a cost of caring for unrelated young in that resources are diverted away from the residents' own larvae. Burying beetles are unable to recognise their own young directly (Bartlett 1987c; Müller & Eggert 1989; Trumbo 1990c) but, by killing larvae that arrive at the crypt outside of a time window during which larvae are expected to hatch, residents increase the probability that they care only for their own offspring (Müller & Eggert 1990). This mechanism will be ineffective if the resident female and the parasite oviposit simultaneously. The broods of large species may also be parasitised by smaller congeners (Trumbo 1994).

A degree of reproductive success may be salvaged by a contest-losing male if he can gain copulations with the resident female. Bartlett (1988) found that a proportion of larvae in broods raised by a pair of resident beetles were, indeed, fathered by a peripheral male. However, only limited rewards can be accrued by this sneaky strategy as caring males achieve a high degree of paternity (92%) of broods by frequent inseminations of the caring female (Müller & Eggert 1989).

There are other phenotype-limited strategies (Parker 1982) by which individuals who otherwise could expect few reproductive opportunities may gain a degree of success. Firstly, males may release pheromones when not in possession of a carcass in order to inseminate females (Müller & Eggert 1987). Since caring males ensure a high degree of paternity by multiple copulations with their mates (Müller & Eggert 1989), carrion-independent pheromone emission is not as profitable a strategy as searching for carcasses (Eggert 1992). In *N. vespilloides* all males use both tactics but pheromone emission is favoured towards the end of the day when female activity is high but carcass availability may be lowest (Eggert 1992).

Small individuals of both sexes adopt strategies that increase their fitness by avoiding agonistic encounters. Bartlett (1987a) found that the first beetles to arrive at carcasses placed in the field were smaller than those caught in pitfall traps over the same period of time. By spending a greater proportion of time foraging, small individuals increase the chance that they can find and bury a carcass before it is discovered by a larger beetle, although they will likely also incur increased energetic and predation costs (Bartlett 1987a). Similarly, smaller individuals emerge earlier in the season which facilitates foraging in the absence of competition from larger beetles (Dressel & Müller 1988) a strategy that is also likely to have associated costs making it profitable only for individuals who would otherwise have little reproductive potential.

On large carcasses, monogamy and biparental care give way to co-operative breeding (Eggert & Müller 1992; Trumbo 1992) where the number of beetles of each sex is variable (Trumbo 1992) and adults care for unrelated larvae (Eggert & Müller 1992; Trumbo 1992; Trumbo & Wilson 1993). This reproductive system may be described as facultative quasisociality (Trumbo 1992) which is characterised by co-operative brood care without reproductive castes or overlapping generations (Michener 1969). The benefits of communal breeding to the participants is a matter for debate.

The patchy distribution of carrion means that individuals co-operating to utilise a carcass are unlikely to be related, so no increase in inclusive fitness (Hamilton 1964) will be conferred on co-operating individuals (Eggert & Müller 1992; Scott & Williams 1993; Trumbo & Eggert 1994; Trumbo & Wilson 1993).

Communal groups of burying beetles frequently contain consexuals of different sizes (Eggert & Müller 1992; Trumbo 1992; Scott 1994a). On smaller carcasses, diminutive beetles would normally be evicted by larger consexuals (Bartlett & Ashworth 1988; Otronen 1988). There will be a net benefit to smaller individuals of breeding co-operatively if the number of offspring they produce is greater than the product of the probability that they will find and bury a carcass and raise a brood monogamously, over the same time period, and the number of resulting offspring

(Scott 1994a). Since the availability of carcasses is probably low enough to be the limiting factor in burying beetle reproduction (Springett 1967; Scott & Gladstein 1993), the presence of more than one breeding beetle of the same sex at a carcass requires an explanation from the point of view of the larger, potentially dominant individuals (Scott 1994a).

The brood mass that can be sustained by a large carcass exceeds that which can be raised by a single female (Eggert & Müller 1992; Trumbo 1992; Trumbo & Wilson 1993; Scott 1994a) because there is an upper limit to clutch size (Bartlett & Ashworth 1988; Müller *et al.* 1990b). This is likely to reduce the costs to a female of tolerating the presence of another consexual (Trumbo 1992) although the reproductive success of each female is reduced, compared to that when breeding alone on a carcass of the same weight, by the presence of another (Eggert & Müller 1992; Scott 1994a). Males are not limited by clutch size and co-operative associations are less common between males than between females (Scott 1994a).

It may be more difficult for a potentially dominant female to exclude a smaller individual from a large carcass, allowing the latter greater opportunity to lay a clutch of eggs (Eggert & Müller 1992). Once eggs have been laid, there is little to be gained from excluding a second female, particularly if the larger broods raised on large carcasses require a greater parental effort in terms of feeding larvae and maintaining the carcass, and if the presence of a second caring female allows earlier desertion of the larger female (Eggert & Müller 1992).

The difficulty of efficient burial and maintenance of large carcasses leads to another possible benefit of the additional parental care provided in a co-operative system. Larger carcasses have a larger surface area and, often are not rolled into a brood ball by pairs (Bartlett 1988), making microbial activity more difficult to control which leads to the attraction of more competitors (Trumbo 1992). Scott (1994a) found that competition with carrion flies promoted communal breeding in *N. tomentosus* and hypothesised that smaller individuals are tolerated on large carcasses because of the increased efficiency in the elimination of fly eggs and maggots which may otherwise consume the entire resource (Trumbo 1994).

Burying beetles are less likely to see a reproductive attempt through to completion on larger carcasses (Trumbo 1995) due to the elevated degree of interspecific competition (Trumbo 1994). This effectively reduces the value of the resource to resident beetles (Trumbo 1995). Contests for resources of low value are predicted to be brief and of low-intensity (Davies 1978; Parker & Rubenstein 1981). By contrast, fights between burying beetles for possession of a carcass often result in injury to the participants (Pukowski 1933; Otronen 1988). It has been proposed that, on large carcasses, consexuals tolerate each other's presence rather than engage in costly fights because the expected reproductive rewards are small (Trumbo 1995; Trumbo & Wilson 1993).

Given that helpers are tolerated by the largest consexual, adaptive explanations for the care provided by helping females may not be necessary. Burial of a carcass stimulates ovarian development which, in turn, induces brood-care behaviour (Scott & Traniello 1987). Thus, parental care may simply be a product of a physiological constraint on behaviour (Eggert & Müller 1992; Scott & Williams 1993). A similar argument has been proposed to explain the behaviour of helpers in co-operatively breeding birds (Jamieson 1991).

1.3. OUTLINE OF CHAPTERS

The last 20 years have seen an explosion of interest in the field of animal breeding systems (Clutton-Brock 1991). Given their complex social system and variable reproductive strategies, it is not surprising that burying beetles have likewise been the attention of a growing volume of work over a similar time period.

Much of the recent work on *Nicrophorus* has focused on the system of parental care in the genus and, particularly, on the reproductive rewards of biparental over uniparental care, and the benefits of communal breeding.

In this thesis, I concentrate on the ecology of parental care in monogamous pairs of *Nicrophorus vespilloides*.

After an account of the methods used in the laboratory and field (chapter 2), chapter 3 describes work that investigated the cause of a decline in apparent beetle clutch size over successive generations of laboratory culture, and whether it is due to the presence of a mite that increased in numbers over the same period of time.

In chapter 4 I look at some aspects of the ecology of brood regulation in *N. vespilloides*. In particular, I address two questions. The first is whether the reduction regime implemented by the parents results in the dispersal of larvae that eclose into adults of a size that enables them to compete for reproductive opportunities in the field. The second is whether the brood is culled to the same degree if it is tended by one or two parents.

Chapters 5 and 6 are concerned with the benefits of paternal care in biparental reproductive attempts. Chapter 5 looks at the role of the male in defence against take-overs of the carcass by conspecifics. Whilst several studies have demonstrated the importance of biparental care in brood and carcass defence in other *Nicrophorus* species (Scott 1990, 1994b; Trumbo 1990a, 1990b, 1991; Robertson 1993), this is the first to attempt to compare the duration of male care with the period of vulnerability to take-overs.

Chapter 6 tests the hypothesis that parental care provided by a male reduces the parental effort of his mate who may achieve greater reproductive success in a subsequent brood. The possible benefits accrued by males are discussed.

Chapter 2

General methods

2.1. THE STUDY SITE

The primary site used for trapping *N. vespilloides* and for many of the field experiments was Penicuik Estates, Penicuik, Midlothian (NGR NT217594) (fig.2.1). Burying beetles were found in the areas of open deciduous woodland which forms much of the vegetation to the south of the River North Esk (fig. 2.1). Beech (*Fagus sylvatica* L.) was the commonest tree, with the occasional sycamore (*Acer pseudoplatanus* L.), oak (*Quercus robur* L.) and birch (*Betula splendens* L.). Bracken (*Pteridium aquilinum* L.) provided the major ground cover, and there were patches of rhododendron (*Rhododendron* sp.), bilberry (*Vaccinium myrtillus* L.) and bramble (*Rubus* sp.).

Unfortunately, the habitat is under threat as the deciduous woodland is being felled gradually to make way for commercial conifer plantations. Efforts to trap *Nicrophorus* in the plantations were unsuccessful.

2.2. TRAPPING

Trapping was mainly carried out in the beech woodland South of the North Esk (fig.2.1) from late May through to the end of September. Baited pitfall traps were used which consisted of lidless baked bean tins or similar, sunk into the earth until the top was flush with ground level. Small holes were punched into the base of the tins to allow drainage. Traps were placed at roughly 40m intervals along an established path through the woods, and baited with ox liver which was renewed every week. Traps were checked daily for beetles.

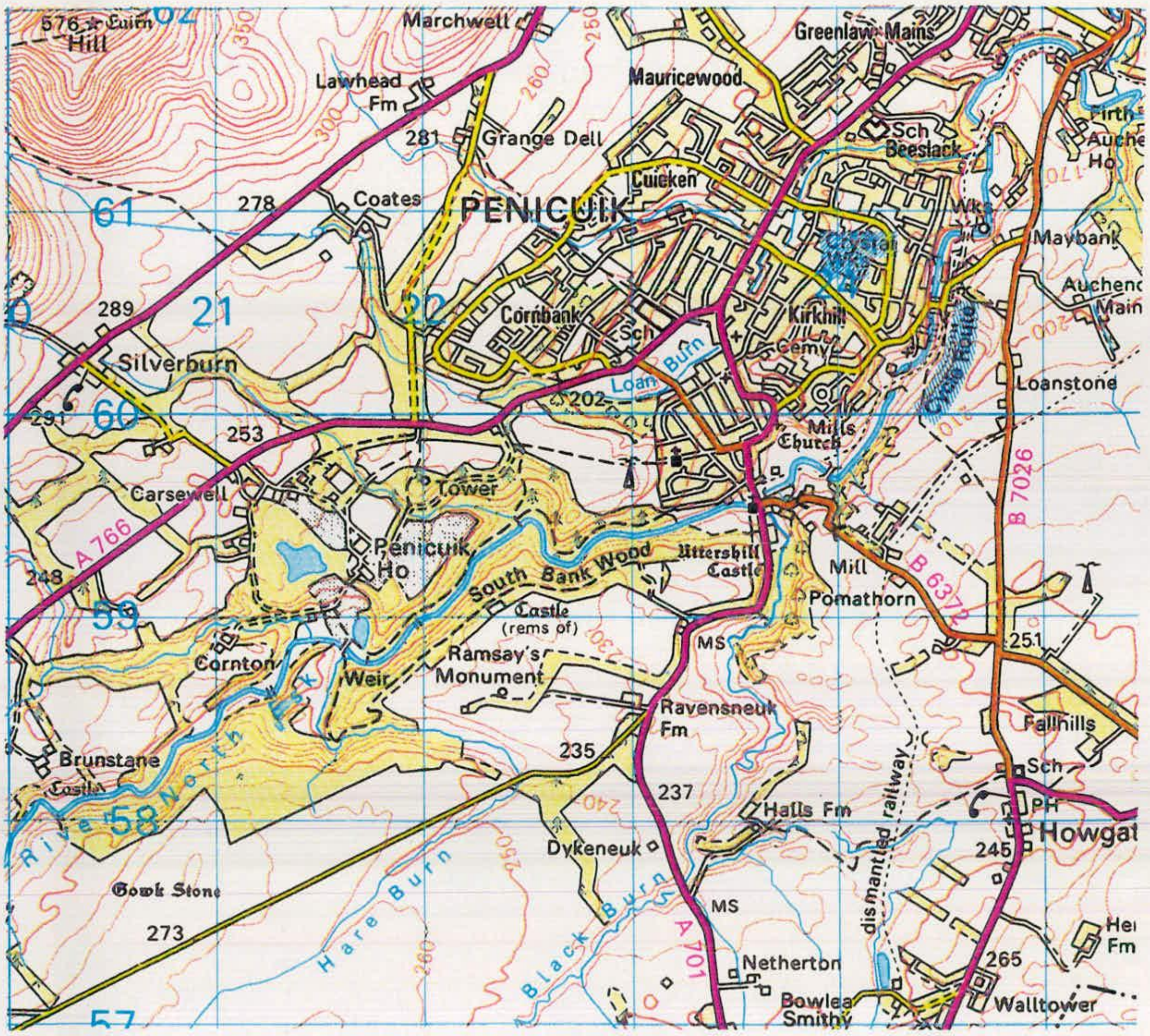


Figure 2.1. A map of Penicuik showing Penicuik Estates. Trapping, and most of the field experiments, were carried out in the woodland south of the weir.

As well as *N. vespilloides*, two other burying beetles, *N. investigator* and *N. humator*, were trapped at the site. The relative proportions in which the three species were trapped can be found in Bartlett (1987a).

2.3. LABORATORY CULTURE

Cultures of *N. vespilloides* were set up in the laboratory using an initial population trapped at Penicuik Estates. They were maintained at 20°C and on a 16:8h light:dark cycle so that they would reproduce year round (Bartlett 1987a). Cultures of *N.investigator* and *N.vespillo* were housed in the same laboratory for much of the time.

The beetles will breed readily in the laboratory. Pairs or single females were placed, with the carcass of a previously frozen laboratory mouse *Mus musculus*, in a clear plastic box measuring 225x120x90mm three-quarters filled with potting compost. Larvae would disperse from the crypt in about 10 days. At this time larvae were transferred to a box of fresh compost to pupate, as the pupal stage is particularly susceptible to mould (Bartlett 1987a) which is more virulent in compost that contained the carcass. Adults eclosed after about three weeks.

At eclosion the ovaries of female burying beetles are immature (pre-vitellogenic) (Bartlett 1987a; Springett 1967; Wilson & Knollenberg 1984) which renders the female incapable of breeding if presented with a carcass (Wilson & Knollenberg 1984). Female *N. vespilloides* are able to breed 21 days after eclosion, at which time there is one mature egg in each ovariole (Christie 1981; Easton 1979). Adults were kept at a density of about 15 beetles per box (dimensions as above) in mixed sex and mixed familial groups and fed decapitated mealworms *ad libitum* until ready to breed. Experimental beetles were provided with a carcass 21-28 days after eclosion.

Bartlett (1987a) reported a decline in reproductive success of laboratory-maintained *N. vespilloides* in the spring, the founders of the population having been trapped in the Autumn of the previous year, and he attributed the decline to inbreeding depression.

Several precautions were taken to minimise inbreeding in my laboratory population:

1. Cultures were propagated from an initial population of at least 50 pairs.

2. It was ensured that the most recent common ancestor shared by a pair of beetles was a great grandparent. This was achieved by individually marking each beetle at eclosion using a hot needle to score, on an orange band of the elytra, a number which identified its ancestry. This procedure also facilitated the individual identification of beetles if this was required.

3. In spring, when beetles emerged from hibernation in Penicuik, the laboratory culture was discarded and replaced with newly trapped beetles. The culture was similarly renewed in the autumn prior to the field population entering hibernation.

Inbreeding depression, which, in Bartlett's (1987a) study, was apparent as a high brood failure rate (J. Bartlett, pers. comm.), was not evident in my population, so the measures taken to prevent inbreeding were effective.

2.4. REMOVAL OF MITES

Burying beetles carry a cargo of phoretic mites *Poecilochirus* spp. which also use the carcass as a reproductive resource, and these may increase in numbers in the laboratory due to the beetles' inability to shed them by flying or burrowing into fresh earth (Pers. obs.; Wilson & Knollenberg 1987). This artificially high mite load has detrimental effects on brood success: second broods raised in the laboratory by females with their mite cargoes intact were smaller than those raised by females whose mites had been removed (Wilson & Knollenberg 1987). This was attributed to the mites attacking beetle eggs and larvae (Wilson & Knollenberg 1987). Indeed, one mite species (*Poecilochirus davydovae* Hyatt) that is phoretic on *N. vespilloides* has been observed, in the laboratory, to eat the eggs of its carrier (chapter 3; Blackman & Evans 1994). Post-reproductive beetles were particularly affected and were, therefore, brushed with a stiff paintbrush to remove the excess. This process apparently reduced the numbers of mites to that found on individuals trapped in the field (Pers. obs.).

Some experiments required beetles to be completely free of mites. Beetles were anaesthetised by placing them in a stream of CO_2 gas which took about 30s to immobilise them. Without removing the beetles from the CO_2, the mites, which were also anaesthetised, could be removed with a stiff paintbrush, any that escaped the brushing being picked off with forceps. The major mite aggregations were on the femurs of the third pair of legs, beneath the elytra and on the ventral side of the prothorax. Removing the mites took about 60s after which time the beetles were allowed to recover with no obvious ill effects. Unwanted mites were brushed off directly into 70% alcohol.

Chapter 3

***Poecilochirus davydovae* (Hyatt): a mite predatory on the eggs of *N. vespilloides*.**

3.1. INTRODUCTION

Mite-*Nicrophorus* associations are common. For example, in North America at least 14 mite species, representing four families, reproduce on carrion and disperse on one or more of five sympatric *Nicrophorus* species (Wilson & Knollenberg 1987). One such association, between *Nicrophorus* species and mites of the genus *Poecilochirus* (Parasitidae), has been described as mutualistic (Wilson 1983), although the degree to which the mite benefits the beetle is a matter of debate. A species of the *Poecilochirus carabi* complex (hereafter referred to as "*P. carabi*") destroys fly eggs (Springett 1968) and it has been shown that the presence of this species has a beneficial effect on the breeding success of *Nicrophorus* spp. in the laboratory (Springett 1968) and in the field (Wilson 1983). Wilson & Knollenberg (1987), however, found that "*P. carabi* " only benefited the beetles in the field under extreme conditions. For instance, if the depth of carcass burial was shallow, it might permit flies to lay eggs throughout the duration of development of the beetle larvae, in which case the mites may be of assistance (Wilson & Knollenberg 1987).

The presence of a cargo of various mite species has been found not to have any harmful effects on the breeding success of *Nicrophorus* spp. in the field (Wilson & Knollenberg 1987). However, laboratory-maintained *Nicrophorus* spp. accumulated large numbers of mites after reproductive attempts, as they were unable to lose them by flying or burrowing into fresh earth (Wilson & Knollenberg 1987). Such abnormal loads had a detrimental effect on beetle breeding success, and this was attributed to the mites attacking beetle eggs and larvae (Wilson & Knollenberg 1987).

This chapter describes observations on the mite *Poecilochirus davydovae* Hyatt (1980) which suggest that it feeds on the eggs of its carrier species *N. vespilloides* and that its presence accounts for a decline in apparent clutch size of its host over 6 generations of laboratory culture. To investigate further the feeding behaviour of *P. davydovae*, the clutch sizes of beetles with or without their mite cargoes are compared. The hypothesis that predation by the mite on beetle eggs is a product of the laboratory situation, there being no carrion fly eggs to eat, is tested by comparing the clutch sizes of beetles burying carcasses in the presence or absence of carrion flies.

3.2. METHODS

3.2.1. Observations on the feeding behaviour of *P. davydovae*

P. davydovae was first seen during clutch counts of third generation laboratory-bred *N. vespilloides* being carried out as part of another experiment. To count clutch size, broods were checked every 4 hours and as soon as beetle larvae started to arrive on the carcass the count was made, the number of larvae being added to the number of unhatched eggs in the surrounding soil. This method is likely to give the most accurate assessment of clutch size, as oviposition is likely to be complete but culling of the brood by the adults (Bartlett 1987c) will not have commenced.

For sixth generation broods, a count was also made of the number of physogastric (physogastry: an enlargement of the body allowing the mite to gorge on a discrete resource such as eggs) *P. davydovae* females present at the time of the clutch size count.

3.2.2. Clutch sizes of beetles with and without mites

In order to test whether the decline in clutch size was brought about by the activities of the phoretic mite population clutch sizes were compared for beetles with and without their mite cargoes.

Mice weighing 12g were given to 46 pairs of 9th and 10th generation laboratory-bred *N. vespilloides*. Twenty three of these pairs had their mites removed (method described in ch.2). To control for any effects of the CO_2 all beetles were anaesthetised and any mites that fell off those beetles whose cargoes were to be left unaltered would be seen to climb back onto their host soon after they were removed from the CO_2. Clutches were counted as described in section 3.2.1 as were the number of physogastric female *P. davydovae*.

3.2.3. Does *P. davydovae* prefer beetle or fly eggs?

Fifty pairs of 10th and 11th generation, laboratory-bred *N. vespilloides* were each provided with a 12g mouse carcass to bury. To half of the boxes four female blowflies *Calliphora vicina* were also added. Half of the beetles with *Calliphora*, and half of those without, had their mite cargoes removed giving a total of four treatments. All carcasses in replicates which included *Calliphora* were seen to be infected with fly eggs before the mouse was completely buried. Clutch size and the number of physogastric *P. davydovae* were counted when larvae first arrived on the carcass.

3.3. RESULTS

3.3.1. Feeding behaviour of *P. davydovae*

A single physogastric female would typically be found adjacent to the remains of a beetle egg. However, egg remains were not always associated with a mite, and physogastric *P. davydovae* were not exclusively found with a *Nicrophorus* egg. Direct observations of feeding were not made. In several instances a number of *P. davydovae* larvae and eggs were also found with the *Nicrophorus* egg remains. Non-physogastric (unfed) female *P. davydovae* were found in Tullgren funnel samples of the crypt and surrounding soil 24h after beetle oviposition but not after 48h implying that all females had fed by this time.

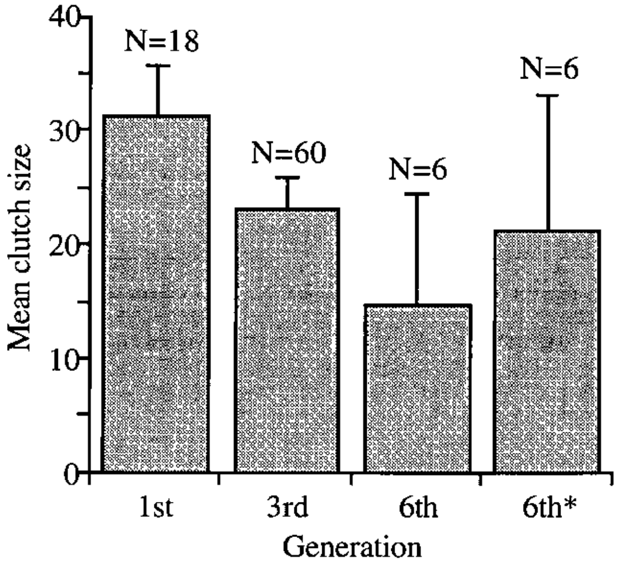


Figure 3.1. Mean apparent clutch size of 1st, 3rd and 6th generation beetles. * denotes where clutch size has been estimated by summing the number of eggs and physogastric female mites. Bars indicate 95% confidence limits.

Figure 3.1 shows the mean apparent clutch sizes produced by pairs of first, third and sixth generation *N. vespilloides*. Only whole eggs were counted; it was not possible to obtain a reliable count of the true clutch size by additionally counting partially eaten eggs because these egg remains were easily mistaken for lightly coloured particles in the soil unless a mite was found with them. Mouse carcasses varied from 10g to 30g and *N. vespilloides* does not adjust clutch size over this range (Bartlett & Ashworth 1988; Müller *et al.* 1990b). First generation clutches were significantly larger than those of both third and sixth generation. Third and sixth generation clutches were not significantly different in size. For sixth generation broods the clutch size and the number of mites were summed and the mean was not significantly different from first generation clutch sizes, suggesting that the reduction in clutch size between generations could have been due to the effects of *P. davydovae*, assuming that each female consumes one egg.

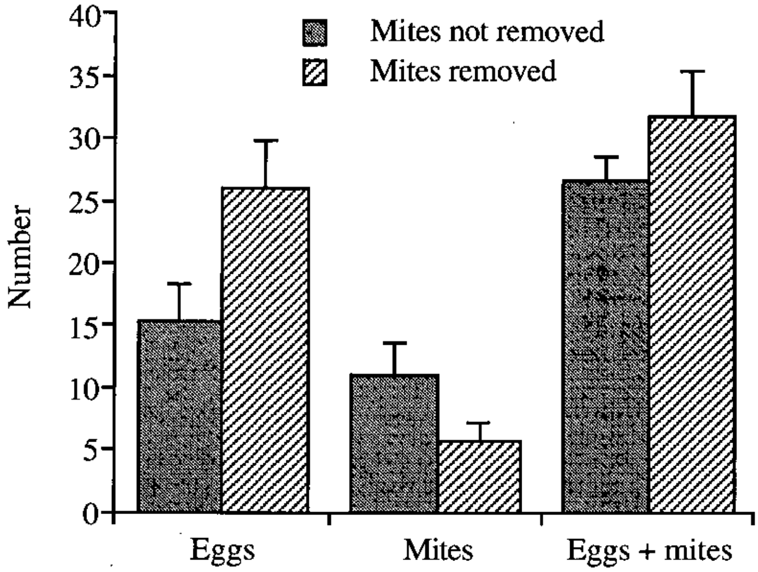


Figure 3.2. Mean apparent clutch size and number of physogastric female *P. davydovae* found in clutches of *N. vespilloides* with (n=19) and without (n=19) their mite cargoes (4 females from each treatment failed to produce any eggs). Bars show 95% confidence limits.

3.3.2. Clutch sizes of beetles with and without mites

The mean apparent clutch size of beetles with their mites removed was significantly larger than that of beetles whose cargoes were left intact (t=4.29, 36df, $p<0.001$) (fig. 3.2). Physogastric female *P. davydovae* were found during clutch size counts for both treatments indicating that the method of mite removal employed was not completely effective. However, significantly fewer *P. davydovae* were found when counting the clutches of 'de-mited' beetles (t=3.58, 36df, $p<0.01$) (fig. 3.2). If, as assumed above, each female *P. davydovae* eats one beetle egg, it could be expected that the sum of clutch size and number of physogastric mites would not be different between treatments. This was not found to be the case (fig. 3.2) as de-mited beetles had a significantly greater total than those with unaltered cargoes (t=2.34, 36df, p=0.025).

3.3.3. Does *P. davydovae* prefer beetle or fly eggs?

No effect of presence or absence of carrion fly eggs was found on apparent beetle clutch size (table 3.1). In contrast to the findings in section 3.3.2, there was no effect of mite removal on apparent clutch size (table 3.1). Furthermore, there was no significant effect of the interaction between mites and flies on apparent clutch size (table 3.1).

Dependent var. **clutch** N=46 Multiple R=0.300 Squared multiple R=0.090

Source	Sum-of-squares	Degrees of freedom	Mean-square	F-ratio	p
Mites	325.858	1	325.858	3.278	0.077
Flies	7.908	1	7.908	0.080	0.779
Mites*Flies	68.294	1	68.294	0.687	0.412
Error	4175.613	42	99.419		

Table 3.1. ANOVA table showing the effects of mite removal and the presence of carrion fly eggs on apparent beetle clutch size.

3.4. DISCUSSION

It would appear, at least in the laboratory situation, that *P. davydovae* eats the eggs of *Nicrophorus vespilloides*. The observational evidence and the data on clutch sizes laid by beetles with or without mites are supported by the presence of morphological features, namely adaptations for physogastry and for piercing the chorion of eggs (Blackman & Evans 1994).

It is unlikely that the high proportion of 6th generation beetles' clutches taken by *P. davydovae* (fig.3.1) is representative of the proportion taken in the field, since physogastric females were not noticed during either the first breeding attempts of wild-caught laboratory beetles (despite rigorous clutch size counts) or natural broods in the field (pers. obs.). Furthermore, the observation from figure 3.1 that clutch size drops in later generations implies that *P. davydovae* undergoes a population increase under laboratory conditions.

An alternative explanation for the decline in clutch size is inbreeding depression in the *N. vespilloides* stock. Bartlett (1987a) reported a decline in breeding success of laboratory-bred *N. vespilloides* in the spring, the founders of the population having been trapped in August of the previous year. This reduction in success was apparent as a high brood failure rate; successful pairs produced broods not significantly different in size from those of previous generations (J. Bartlett, pers. comm.). The decline in success of the population used in the present study is not likely to be due to inbreeding depression as it differed from the decline reported by Bartlett in two ways. Firstly, my beetles showed a reduction in clutch size after only three generations (about 16 weeks), and secondly, this reduction was apparent as a decline in clutch size in all successful broods; an increased brood failure rate was not apparent.

It may be that the *N. vespilloides* stocks were infected with *P. davydovae* from the populations of *N. investigator* or *N. vespillo* housed in the same laboratory. However, no *P. davydovae* were found on either species. *P. davydovae* occurs on *N. vespilloides* in the field (Hyatt 1980) and it is more likely that mite numbers increased in the laboratory because of the inability of the beetles to shed them by flying or by burrowing in fresh earth, and that the resulting large numbers of mites attack the eggs of *N. vespilloides* (Wilson & Knollenberg 1987). Despite *P. davydovae* being outnumbered by "*P. carabi*" on *N. vespilloides*, all the mites found adjacent to the remains of a beetle egg were identified as *P. davydovae*. This may be explained by the laboratory procedure of brushing excess mites from beetles with an unnaturally heavy cargo: the deuteronymph of *P. davydovae* is significantly smaller than that of "*P. carabi*" and this could enable the former to shelter beneath a beetle's elytra, or in other body recesses, and escape removal. The numbers of *P. davydovae* would, therefore, be artificially high, whereas "*P. carabi*" would be nearer to a natural population density. Alternatively, there could be a difference in the natural histories of *P. davydovae* and "*P. carabi*". It is likely that members of the *P. carabi* complex have a different mite-host relationship from that of *P. davydovae*. This has been established for *Poecilochirus subterraneus* Müller, a closely related species to *P. davydovae*. According to Korn (1983), the successful reproduction of "*P. carabi*" is not dependent on the breeding of the beetle whereas the reproduction of *P. subterraneus* "presumes coincidence with the breeding of *Nicrophorus*". Such a difference in mite-host relationship could be explained if *P. subterraneus* is a specialist predator on the eggs of *Nicrophorus*.

The idea that *P. davydovae* is a specialist predator of beetle eggs is given credence by the finding that the apparent clutch sizes of *N. vespilloides* were not affected by the presence or absence of carrion fly eggs on carcasses. If, in the field, *P. davydovae* is a predator of carrion fly eggs and only takes beetle eggs due to the lack of such a resource and/or the artificially high mite population in the laboratory, it would be expected that if fly eggs were provided then a greater proportion of each beetle clutch would survive to hatching.

Fly larvae did not disperse from any of the carcasses which suggests, at least at the densities of fly eggs used here, that the beetles are themselves capable of preventing a portion of the carrion resource being lost to developing fly larvae. This is probably effected by the beetles eating fly eggs and larvae (Trumbo 1994). The experiment could be criticised for not including the appropriate control to check that the fly eggs would produce larvae in the absence of beetles and mites. Whilst the possibility that the fly eggs were non-viable cannot be completely discounted, the *Calliphora* females laid them concurrently with females from the same population, that laid eggs which did produce larvae (S. Grant, pers. comm.). Another interpretation of these findings is that fly eggs were present in too low numbers for their presence to dilute noticeably the effects of predation by the mites on the beetle clutches. Fly eggs were seen on carcasses in all replicates where *Calliphora* was introduced. Since the mean number of *P. davydovae* found during clutch counts was only just into double figures (fig.3.2), it is not expected that many fly eggs would be required to divert the attentions of the mites such that apparent beetle clutch size would be measurably altered.

It is difficult to explain the failure to find an effect of mite removal on apparent beetle clutch size in the latter experiment (despite the inclusion of treatments in which beetles were bred with and without mites in the absence of fly eggs) whilst such an effect was shown in fig.3.2. The sample sizes for the two experiments were similar as were the sizes of the carcasses provided. The only difference was that the beetles used in the *Calliphora* experiment were from a later laboratory generation than those used to collect the data for fig.3.2. In the time between the two experiments the mite population may have suffered a population drop due, for example, to inbreeding or a density dependent effect.

If predation on beetle clutches by *P. davydovae* does occur in the field, it may shed light on the observation that *N. vespilloides* parents cull a proportion of first instar larvae on 15g carcasses (Bartlett 1987c): if an unpredictable number of eggs are lost from each brood, then the laying of excess eggs may be an insurance against poor larval recruitment to the crypt (Bartlett 1987c; see ch.4 for a more detailed discussion of these issues).

Using mite-*Nicrophorus* associations as a model, Wilson & Knollenberg (1987) argue that most phoretic associations (phoresy is the use of one animal for transport by another) evolve to eliminate negative effects on the carrier. However, predation by phoretic mesostigmatic mites on the eggs of the carrier species is not uncommon and occurs, for example, in the association between *Macrocheles muscaedomesticae* (Macrochelidae) and house flies in manure (Filipponi 1955) and between *Arctoseius cetratus* and sciarid flies in mushroom compost (Binns 1972). The cost to the beetles of the behaviour of *P. davydovae* may actually be negligible, particularly if only a small proportion of a clutch is taken due to the low natural densities of *P. davydovae*.

Also, the costs of producing a large number of eggs may be very low because of the beetles' high protein diet (Trumbo 1990c).

It is perhaps significant that *P. davydovae* occurred only on *N. vespilloides* whereas *P. subterraneus* was limited to *N. vespillo* and *N. investigator*. This observation, and the morphological similarities between *P. davydovae* and *P. subterraneus* (Blackman & Evans 1994), imply that these two species occupy a similar niche, specialist oophagous predator, on their respective hosts. "*P. carabi* ", a generalist feeder, was found on all 3 *Nicrophorus* species in the laboratory (Blackman & Evans 1994) but Müller & Schwarz (1990) have demonstrated differences in carrier preference and evidence for reproductive isolation between "*P. carabi*" from *N. vespilloides* and *N. vespillo*. *N. vespilloides* and *N. investigator* are sympatric but there are differences in their reproductive seasonality and development time which could have acted as an ecological barrier and led to speciation within the two feeding niches (see Müller & Schwarz 1990).

Chapter 4

Brood reduction

4.1. INTRODUCTION

N. vespilloides parents kill and eat a proportion of their first instar offspring when reproducing on small carcasses and it has been suggested that this method of brood reduction serves to optimise the ratio of larvae to the amount of food available (Bartlett 1987c). In birds, where reproduction is often limited by the rate of food provisioning to the young (Lack 1968) brood reduction is common (O'Connor 1978), but is normally brought about by siblicide or starvation rather than direct infanticide. Unlike bird chicks, burying beetle larvae are not totally dependent on their parents for food as they can feed directly from the carcass. It is therefore to the parents' advantage to actively reduce the brood size at an early stage so that more of the limited food resource is available for those larvae that survive (Bartlett 1987c) instead of allowing scramble competition which would result in the production of a larger number of underfed larvae (Trumbo 1990c). Brood regulation results in a smaller number of larger third instars dispersing from the crypt than if all larvae were allowed to survive (Bartlett 1987c) implying an advantage of large body size and, therefore, that brood size is the result of a trade-off between the number and size of the dispersing larvae. Indeed, the outcome of fights over carcasses is largely determined by body size, small beetles gaining fewer reproductive opportunities (Wilson & Fudge 1984; Bartlett & Ashworth 1988; Otronen 1988). Furthermore, both the size of a single clutch on very large carcasses (75g) and total lifetime egg production are positively correlated with female pronotum width (Bartlett & Ashworth 1988).

Clutch size is adjusted by *N. vespilloides* on carcasses up to about 10g (Easton 1979; Bartlett 1987c; Müller *et al.* 1990b) and *N. tomentosus* (Trumbo 1990c) but not enough to account for the large differences in the numbers of larvae dispersing from various sized carcasses (Trumbo 1990c). Clutch size is not adjusted on carcasses in the range 10-30g in *N. vespilloides* (Bartlett 1987c; Müller *et al.* 1990b) and filial cannibalism does not occur on carcasses at the larger end of this spectrum (Bartlett 1987c). Brood regulation after the egg stage also occurs in *N. orbicollis* (Wilson & Fudge 1984) and *N. tomentosus* (Trumbo 1990c) whilst cannibalism has only been implied in these instances. It is still not clear why burying beetles lay an excessively large clutch that needs to be reduced after hatching.

Asynchronous hatching in birds is thought in some cases to be a response to uncertain food availability, the last chick to hatch starving when food is scarce (O'Connor 1978), and it has been argued (Wilson & Fudge 1984) that, similarly, brood reduction in *Nicrophorus* is an adaptation to an unpredictable amount of the carcass being ruined by fungal infection. If this were the case there should be no need for brood reduction in ideal conditions, but brood reduction is still practised when the larvae subsequently consume the entire carcass (Trumbo 1990c).

An alternative explanation for asynchronous hatching in birds is the insurance hypothesis (Clark & Wilson 1981) where only a single chick is ever raised, and any additional eggs serve as an insurance against failure of the first. Bartlett (1987c) proposes that too many eggs are laid by female burying beetles as an insurance against poor larval recruitment to the crypt. However, brood reduction does not occur on 30g carcasses and there is no reason to suppose that larval recruitment to small carcasses is lower than to large ones (Trumbo 1990c). Furthermore, excess larvae consistently arrived at small carcasses in the field (Trumbo 1990b) indicating that poor recruitment is rare. The idea may stand up, however, if poor recruitment is rare but future reproductive opportunities are very limited so that each reproductive attempt must be maximised (Trumbo 1990c). But the reproductive effort on 30g corpses is not maximised since on 75g mice *N. vespilloides* lays a larger clutch than on 30g mice (Bartlett 1987c). This last observation also casts doubt on the claim made by Müller *et* *al.* (1990b) that no adaptive explanation is needed to explain why an excess of eggs are not laid by *N. vespilloides* on large carcasses if this species is prevented from utilising such carcasses due to competition with larger congeners.

Beetles that successfully secure a carcass for reproduction are liable to have their broods parasitised by defeated female conspecifics (Müller *et al.* 1990a) and congeners (Trumbo 1994) resulting in impaired reproductive success for the resident beetles. A further possible explanation for the laying of excess eggs on smaller carcasses is to dilute the effects of brood parasitism (Trumbo 1990c) which, due to the smaller broods raised, would be more detrimental to reproductive success on small rather than large carcasses.

Even once a carcass has been interred by burying beetles it is still in danger of being taken over by aggressive conspecifics (Scott 1990; Robertson 1993; see ch.5) and congeners (Trumbo 1990b) wishing to secure the resource for their own reproduction. It is, therefore, in the interests of the parents to reduce the period that the carcass is vulnerable to take-over by minimising the time taken for the larvae to develop (Trumbo 1991). This could be achieved in part by ovipositing at the earliest opportunity to facilitate earlier hatching. If oviposition occurs before the size of the carcass has been accurately assessed, a female would benefit from producing an excessively large clutch which could be reduced when more information about the size of the carrion resource was available. There may be little energetic cost to the female of such over-production due to the high protein diet of burying beetles (Trumbo 1990c). Assessment of carcass size probably takes place during burial and eggs are laid before this process is complete (pers. obs.). It may be that at oviposition the female has some knowledge of carcass size which accounts for the adjusted clutch sizes laid on very large (75g) and very small (<10g) carcasses. If resource size is assessed by means of linear dimensions rather than mass then the ability to adjust clutch size on very small carcasses may in part be an effect of allometry: a given change in linear dimensions will have less effect on the mass of the resource on a small, as opposed to a large, carcass.

A brood will be of optimal size if the reproductive rewards to the parents, in terms of numbers of grandchildren, are maximised. To establish what constitutes an optimal brood, the success of the offspring of carers should, therefore, be studied. The first part of this chapter is concerned with how a beetle's reproductive success is affected by the culling regime implemented by the parents. To this end, the size of beetles reared in culled broods and the size of beetles successfully securing carcasses for reproduction in the field are compared.

The size and number of larvae dispersing from culled broods is established for both the lab and the field situation. Bartlett & Ashworth (1988) found, for laboratory broods, that even after culling and a disproportionate allocation of resources by small larvae into adult size, adults produced by broods raised on 10g mice were smaller than those from broods raised on 30g mice. These data could be explained in either of two ways. Firstly, too few eggs may be laid on 30g carcasses in that the extra weight of each larva confers no significant increase in breeding success over larvae from smaller mice (Bartlett & Ashworth 1988). If, for example, a large carcass cannot be rolled up and buried as neatly as a small one, control of mould may be more difficult in the field resulting in a reduced availability of carrion to the larvae (Bartlett & Ashworth 1988). Secondly, the parents may allow too many larvae to survive culling on 10g carcasses in that the subsequent low weight of the larvae is a disadvantage in terms of breeding success (Bartlett & Ashworth 1988). This may be true if the parents cull to a total that allows for further larval mortality that happens in the field but not the laboratory (Bartlett & Ashworth 1988), a hypothesis that I test by comparing broods from 10g carcasses in the field and the laboratory.

A major obstacle to designing an experiment to assess the sizes of successful beetles is that it must not significantly raise the natural carcass availability. This problem is compounded by the fact that virtually no information exists as to what the natural carcass availability may be as the potential difficulties involved in its assessment are considerable. The obvious solution is to use only naturally occurring carcasses but this option is not practical because of the difficulties of locating them, so carcasses must be placed experimentally and efforts made to minimise their impact on the local ecology. Two field studies (Springett 1967; Easton 1979) have been criticised (Wilson & Fudge 1984) for not adequately overcoming this problem. Both studies used island beetle populations and, as Wilson & Fudge (1984) pointed out, a burying beetle was never further than 50m and 20m from an experimental mouse carcass in Easton's (1979) and Springett's (1967) studies respectively. In their own work, Wilson & Fudge (1984) raised carcass density by only one mouse per 8000m^2 but, if carcass availability is limiting to burying beetle reproduction, even this value could in theory affect the number and, therefore, the size of successful beetles. In this investigation I have attempted to keep the experimental augmentation of carcass availability to a minimum by placing carcasses singly in discrete areas of woodland.

The second part of the chapter investigates whether the degree of culling is the same in broods tended by a single female and those reared biparentally. Scott (1989) proposed that a difference in the degree of culling by one or two parents accounted for the difference in success of laboratory broods raised uni- or biparentally. In *N. vespilloides* both parents cull the brood (Bartlett 1987c) so if no differences in larval size or number are found between the two parental treatments here, the implication is that a beetle compensates for the presence or absence of a mate when culling the brood.

4.2. METHODS

4.2.1. Brood reduction and offspring success

a) The size and number of larvae dispersing from culled broods

Each of 84 pairs of *N. vespilloides* were allowed, in the laboratory, to bury and rear a brood on a mouse carcass weighing 6-26g. Forty-eight hours after burial the soil above the crypts was replaced with a piece of damp paper towel to allow easy observation of the carcass. Checks were made every 4h and when larvae appeared in the crypt the brood size was manipulated to 25 larvae. If fewer than 25 larvae had arrived on the carcass the brood was augmented with first instar larvae taken from a pool of 50 additional broods not otherwise used in the experiment; *N. vespilloides* are unable to distinguish unrelated larvae from their own offspring (Müller & Eggert 1990). The brood, carcass and adults were transferred to an artificial crypt in fresh compost to ensure that no further larvae arrived on the carcass and decapitated mealworms were placed on the soil surface as food for males so that they were not motivated by hunger to attack their own larvae and reduce the apparent brood size if they dispersed before the brood. The broods were then left undisturbed until dispersal when larvae were weighed and counted.

To establish the size and number of larvae dispersing from culled broods in the field 20 beetle pairs were each provided with a 10g mouse to bury within the confines of a plastic flowerpot covered with a muslin lid and sunk into the ground at 20m intervals along an established route through the wood. Holes 3mm in diameter were made in the flowerpots at and below ground level to allow the passage of most soil organisms (including the staphylinid *Philonthus* which is known to attack *Nicrophorus* larvae [Easton 1979; Bartlett 1987a]), but not burying beetles or their third instar larvae (see fig.5.1 for details of the apparatus design). Since the parents were unable to escape from the flowerpot, decapitated mealworms were placed on the soil surface to provide a food source for dispersed males. Towards the end of larval development broods were checked twice daily and on dispersal larvae were counted and weighed. These broods were set up on 11/8/94.

To compare the size of beetles successfully securing carcasses in the field with that of beetles produced on small carcasses, it is necessary to know the size of beetles eclosing from larvae of known weight. To establish the relationship between larval weight and adult size, larvae dispersing from broods raised in the laboratory were weighed and placed individually in a plastic tube 3/4 filled with compost to pupate. At eclosion each beetle was measured across the widest part of the pronotum.

b) Size of beetles securing carcasses in the field

Six sites in or around Penicuik were chosen for this study (fig.4.1). Each site was beech woodland and they were separated from each other and from the trapping site at Penicuik Estates by farmland or conifer plantations. No information on the distances travelled by foraging burying beetles is available, and presumably some migration does occur between sites, but a lack of suitable areas of beech woodland meant that greater spacing between experimental sites was not possible. No beetles were caught in traps placed in the coniferous woodland for the duration of the 1994 field season which implies that these areas were obstacles to beetle movement.

A single mouse carcass was placed in each site and, so that it could be located after burial, it was tied by its back leg to a 2m length of dental floss which in turn was tied to a wooden stake pushed into the ground. Carcasses were checked daily and, if buried, they were carefully exhumed, any beetles present being measured across the pronotum and individually marked by scoring the elytra with a hot needle before being replaced in the crypt. Subsequent daily checks were made to check which beetles were present in the crypt, new arrivals also being marked and measured. If a carcass was found to have disappeared from the end of the dental floss it was assumed to have been taken by a vertebrate. To minimise the degree to which the natural carcass density

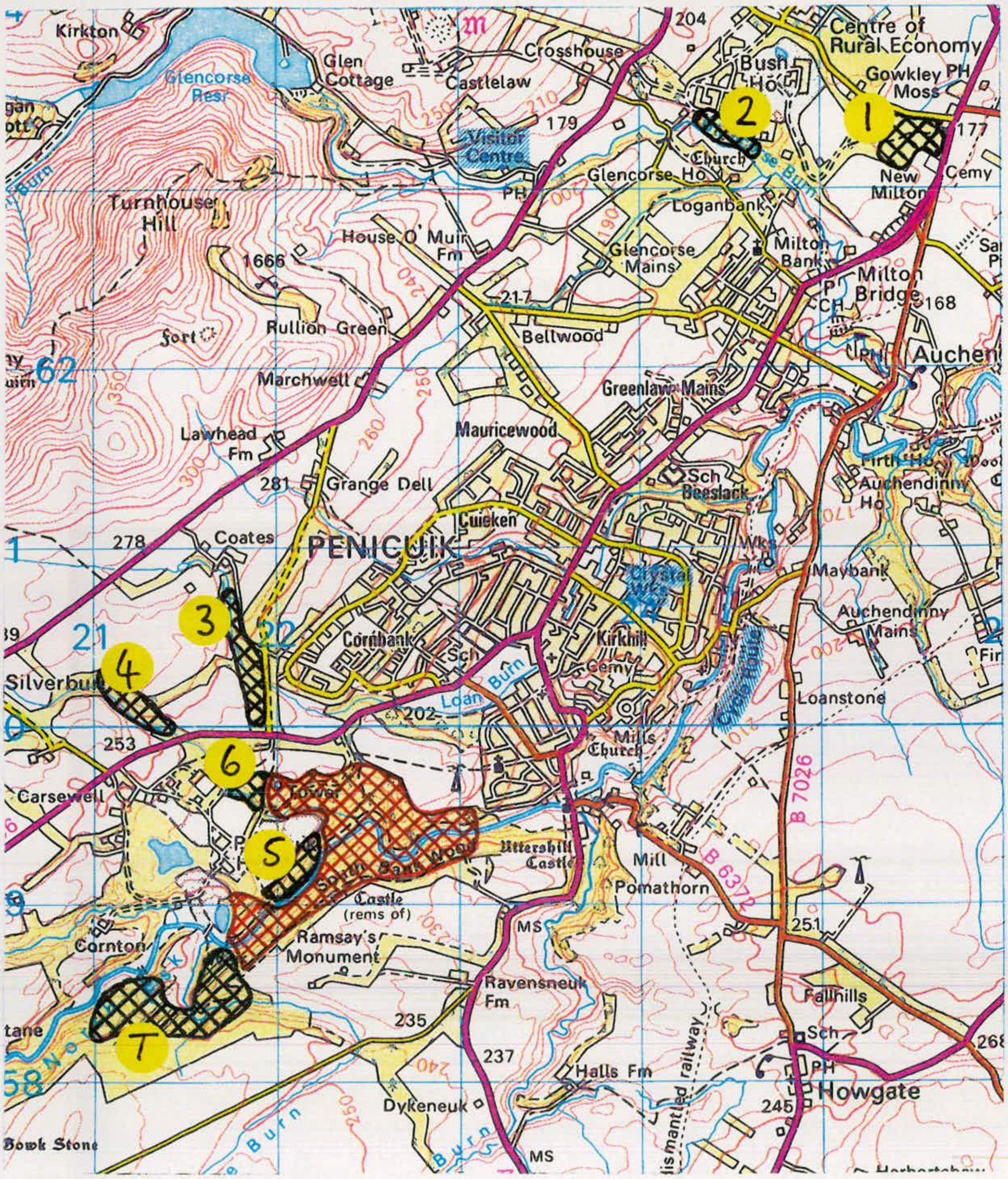


Fig.4.1. A map of Penicuik, Midlothian and the surrounding area showing sites (marked 1 to 6) in which mouse carcasses were placed to establish the size of successful beetles in the field. The strip of woodland between sites 3 and 4 had been felled before the experiment was started.

T = trapping site ▨ = beech woodland ▨ = coniferous woodland was raised artificially, fresh mice were only placed at a site once the previous one had been completely consumed. This was taken to be when a *Nicrophorus* brood had dispersed, a carcass had been taken by a vertebrate or, if eaten by blowflies, wasps or other scavenging insects, when only bones remained. To eliminate the possibility of vertebrates learning the position at which a carcass could be found, a replacement carcass was placed 20m from where its predecessor had been. Two mouse sizes (9g or 22g) were used and, at each site, the size class was alternated. The first carcasses were put out on 29/5/94, the last on 30/8/94.

In addition, a single baited pitfall trap was placed in each site, 50m from the location of the carcass, for the duration of the experiment.

4.2.2. Brood reduction in uni- and biparental broods

A mouse carcass weighing 9.60-11.40g was given to each of 10 pairs and 10 single female *N. vespilloides*. Forty-eight hours later the soil above the crypt was replaced with a piece of damp paper towel. Crypts were checked every four hours and, when larvae first arrived on the carcass, broods were manipulated to 25 and, along with the mouse and parents, transferred to an artificial crypt in fresh compost. Decapitated mealworms were provided as food for dispersed males. Twenty-four hours after larval arrival the number of larvae still present was counted and at dispersal they were counted and weighed.

4.3. RESULTS

4.3.1. Brood reduction and offspring success

a) The size and number of larvae dispersing from culled broods

All three measures of brood size at dispersal increase with carcass size in the laboratory (fig.4.2). The number of larvae dispersing increases up to a carcass mass of 16g and does not increase further. Mean mass of dispersing larvae does not vary significantly between carcass weights of 8-20g although it drops off below, and rises above, these weights. Brood mass appears to increase steadily but does not change significantly between 12-26g carcasses.

There were no differences in any measures of size between broods raised in the field or in the laboratory (fig. 4.2).

b) Size of adults eclosing from larvae raised in culled broods

To establish the size of adults that disperse from different sized carcasses (fig.4.4), the data on mean mass of dispersing larvae (fig.4.2b) have been converted into adult pronotum width using the relationship illustrated in fig. 4.3a. A stepwise regression analysis shows that log. larval weight accounts for a significant amount of the variance of log. adult size ($F_{1,169}$=0.30E+04, $p<0.001$). When this variance is excluded there is no significant effect of the sex of beetles on log. adult size ($F_{1,169}$=0.115, $p=0.735$). There is an effect of the interaction between log. larval weight and sex ($t=1.97$, $p=0.051$) but this translates into a maximum difference in predicted adult body size between the sexes of only 2%. It was, therefore, ignored and fig.4.3a includes both male and female data. Pronotum width does not vary significantly up to a carcass mass of 18g but does increase above this (fig.4.4).

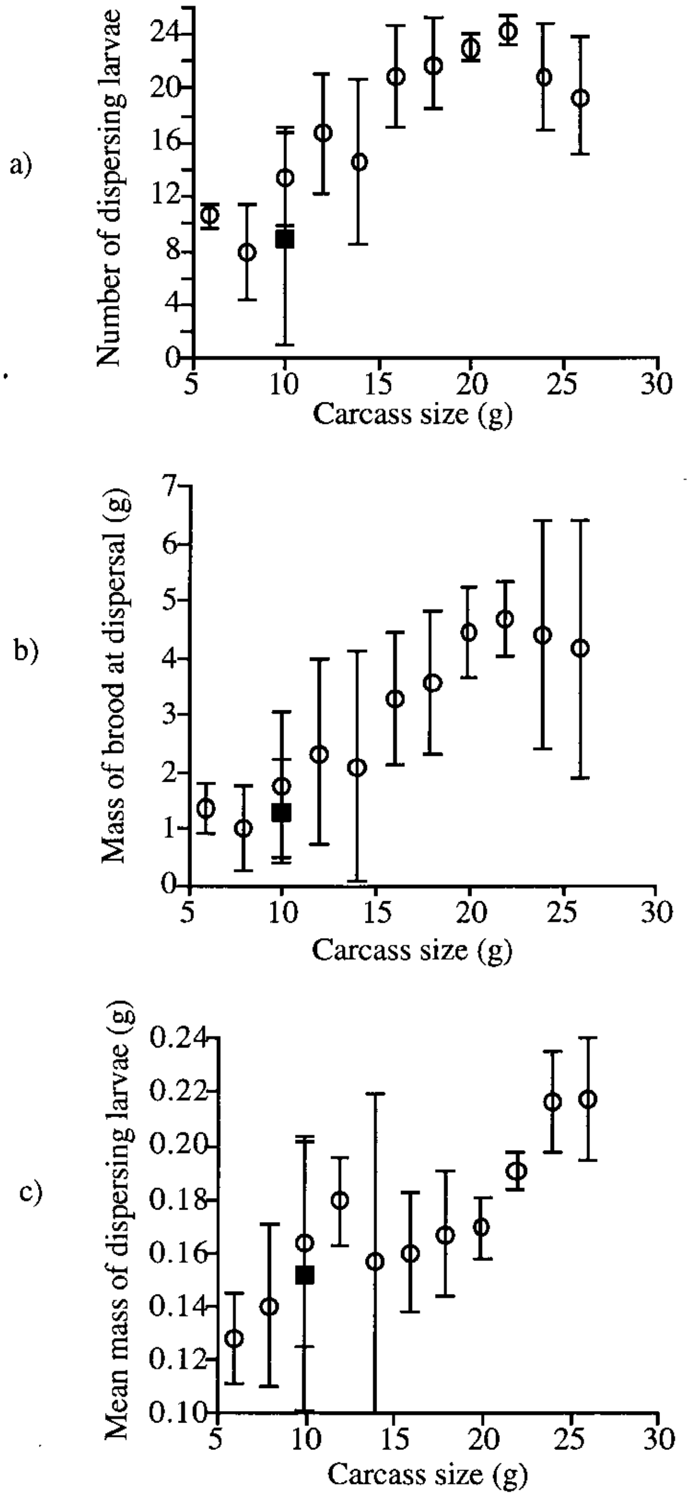
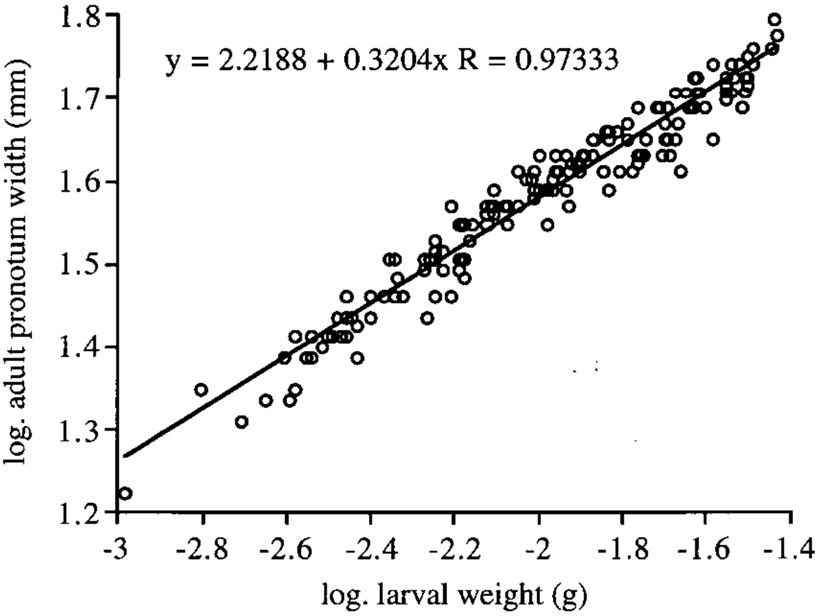


Fig.4.2. Measures of the size of broods dispersing from carcasses of different weight. Circles = lab data; squares = field data. Bars show 95% confidence limits.

a)



b)

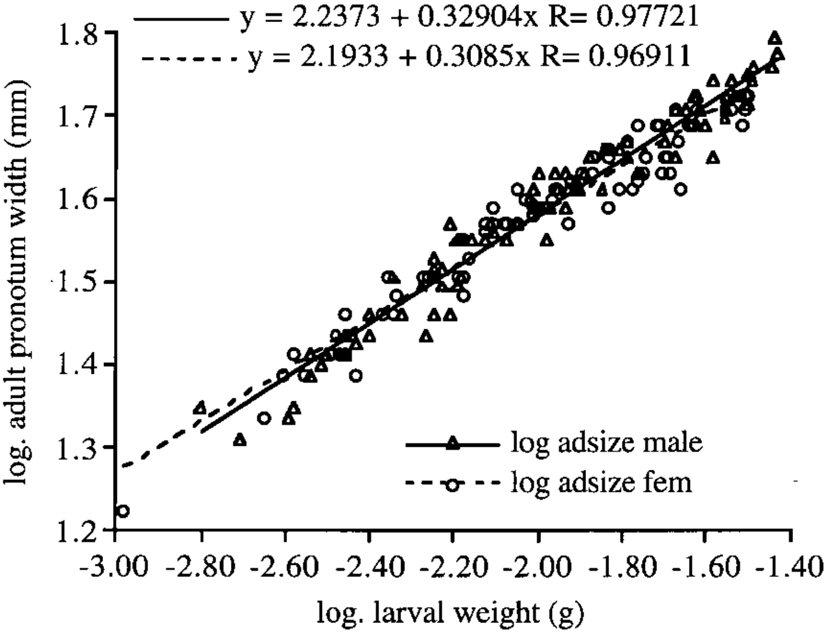


Fig.4.3. The relationship between larval weight at dispersal and adult pronotum width. a) Log. transformed data for all beetles b) A comparison of the regression lines fitted separately to log. transformed data for males and females.

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c) Size of beetles securing carcasses in the field

Of 34 carcasses placed in the field only 13 (38.2%) were discovered by *Nicrophorus* spp. and larvae dispersed from only 5 carcasses (14.7%), all of which were buried by *N. vespilloides* (table 4.1). This low rate of carcass discovery by burying beetles contrasts with the high rates, between 65-94% (Wilson & Fudge 1984) and 86% (Eggert 1992) found in other studies.

Total number of carcasses	34
Number buried by *N. vespilloides*	12 (35.3%)
of which produced brood	5 (14.7%)
Mean pronotum width of beetles producing brood (±SE)	4.96 (0.24)mm
Number buried by *N. investigator*	1 (2.9%)
of which produced brood	0

Table 4.1. The utilisation by *Nicrophorus* spp. of mouse carcasses placed in the field.

The mean pronotum width of *N. vespilloides* successfully producing a brood was 4.96(±0.236SE)mm (table 4.1). Unfortunately, due to the low success rate of *Nicrophorus* in this study, this figure is derived from a sample of only nine beetles. Fig.4.4 shows that adults eclosing from larvae raised on all carcass sizes are equal in size to, or larger than, the mean size of successful beetles.

N. vespilloides both buried carcasses and were trapped at all experimental sites with the exception of Site 3. This site is an area commonly used by ramblers and for exercising dogs and it could be that this disturbance has affected the ecology of the site so as to exclude its utilisation by *Nicrophorus*. Site 3 was, therefore, excluded from the analysis.

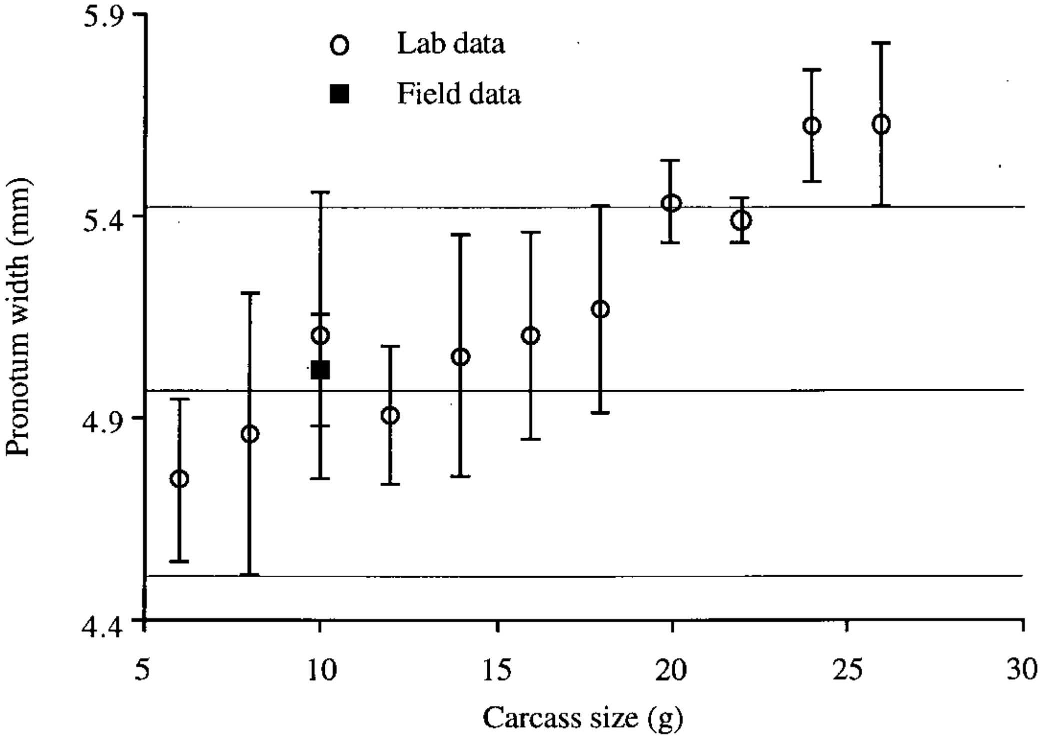

Fig.4.4. The mean size (±95% CL) of adults eclosing from larvae raised on different sized carcasses. The horizontal lines represent the mean size (±95% CL) of beetles that successfully found, and raised broods on, carcasses placed in the field.

4.3.2. Brood reduction in uni- and biparental broods

No significant differences between broods raised biparentally or by a single female were found for any measures of brood size (table 4.2).

Parents	Female + Male (n=10)	Female (n=10)	Independent t-test
Number of second instars	12.80±2.33	12.80±3.05	t<0.001, 18df, p>0.9
Number of dispersing larvae	11.70±2.26	11.10±2.23	t=0.370, 18df, p=0.716
Mean larval weight at dispersal (g)	0.153±0.012	0.162±0.016	t=0.922, 18df, p=0.369

Table 4.2. The number and size of larvae (±95% CL) in broods tended either by a single female or a pair of beetles.

4.4. DISCUSSION

4.4.1. Brood reduction and carcass size

All three measures of brood success increase with the size of the carrion resource (fig.4.2). Since the number of dispersing larvae increases up to a carcass mass of 16g above which there is no further change, it is tempting to assume that culling of the brood by the parents occurs only on carcasses weighing up to 16g. However, it should be remembered that the initial number of 25 larvae on the carcass places an upper limit on the number of larvae that can be raised. If this ceiling was elevated then culling may occur on larger carcasses. The upper limit on larval number may also explain the rise in the mean mass of dispersing larvae above a carcass weight of 20g: if more larvae were present then fewer resources would be available to individual larvae.

It is perhaps surprising that the total brood mass does not increase significantly above a resource mass of 12g. Although there is an upward trend in brood mass, there is overlap in error bars. This may in part be due to the difficulty of managing a large carcass compared to a small one. If a bigger carcass cannot be rolled up properly, the resulting large surface area could mean that a greater proportion of the resource is lost to mould (Bartlett & Ashworth 1988) and is, therefore, not available to the developing larvae. Similarly, a large carcass presumably requires the parents to apply more antibacterial secretions to prevent decay and, if the demand cannot be met, again a proportion of the resource will be lost to mould.

4.4.2. Success of laboratory and field broods

In an attempt to explain why larvae were smaller when dispersing from small (10g) rather than from large (30g) carcasses, Bartlett & Ashworth (1988) postulated that parents cull their brood on small carcasses to a total that allows for subsequent mortality which occurs in the field but not in the laboratory. My results (fig.4.2) suggest that this is not the case as there is no difference in any measure of brood size between those raised on 10g carcasses in the field and in the laboratory. The alternative hypothesis must, therefore, be considered, that on a large carcass the female lays a smaller clutch than can be supported in the laboratory because the difficulties of neatly burying and rolling up a large carcass mean that a proportion of it is lost to fungal infection in the field (Bartlett & Ashworth 1988).

4.4.3. Success of beetles reared on small carcasses

A comparison of the size of adults eclosing from larvae reared on small carcasses and the size of beetles successfully raising broods in the field (fig.4.4) is limited in this study by the small sample size for successful beetles (n=9) (table 4.1). The paucity of data prevents a comparison of the sizes of beetles that successfully reproduce on small and large carcasses and of the relative sizes of successful males and females. The difference in success rates of *Nicrophorus* between this and other studies (Wilson & Fudge 1984; Eggert 1992) needs to be addressed, as does the high failure rate of broods after carcass discovery.

Carcass availability is thought to limit the reproduction of *Nicrophorus* (Springett 1967) and so the difference may reflect variation, spatial or temporal, in the populations of small mammals between the studies.

Small mammal populations can fluctuate drastically from year to year, either cyclically (Krebs & Myers 1974), or chaotically (Hanski *et al* 1993), and these fluctuations can have knock-on effects on the populations of other groups such as predators (Korpimäki 1984). It may be that my own study and those of Wilson & Fudge (1984) and Eggert (1992) were carried out at different stages of the natural population fluctuations of the indigenous small mammals. The field work for all three studies was done in a single field season and so no information on population cycles can be gleaned from the data.

Wilson & Fudge (1984) found differences in the number of carcasses taken by vertebrates between two sites in North America. They found that where vertebrate success was high, beetle success was low and vice versa, suggesting an interaction between vertebrate and beetle populations. However, in my study the proportion of carcasses taken by vertebrates (5.9%) was identical to that found by Wilson & Fudge (1984) at one of their sites where the proportion of carcasses secured by beetles was 94.1% compared to my own 14.7%.

Of the thirteen carcasses buried by *Nicrophorus* only 5 (41.7%) were successful in raising larvae to dispersal. This is a very low proportion as is highlighted by a comparison with the field data in fig.4.2 where larvae were raised on 16 out of 20 (80%) carcasses.

Since it is possible that *N. vespilloides* has greater difficulty in manipulating large carcasses (Bartlett & Ashworth 1988), the high brood failure rate may be explained by the use of 22g carcasses as opposed to the smaller 10g mice used to obtain the field data in fig.4.2. Whilst *N. vespilloides* buried more 22g than 9g carcasses (9 and 3 respectively), the subsequent failure rates (5 and 2) were not significantly different (χ^2=0.0476, 1 df, p>0.9) implying that carcass size did not influence failure rate.

A further possibility is that the method of exhuming the buried carcasses daily to record which beetles were present disturbed the residents causing them to desert. Neither Wilson & Fudge (1984) nor Eggert (1992) performed exhumations on such a regular basis and, whilst this factor cannot be ruled out as a cause of failure, frequent exhumations (every 4h) in the laboratory do not promote desertion by the residents (pers. obs.). It may also be argued that the intense competition for carrion means a carcass is unlikely to be deserted due to its great value to the residents.

The low discovery rate by *Nicrophorus* and the subsequent high failure rate of broods may reflect more general differences in the ecology of the sites used by myself and Wilson & Fudge (1984) and Eggert (1992). For example, in my own study most (73.5%) of the carcasses were ultimately eaten by invertebrates other than burying beetles, notably carrion flies and wasps. Flies are particularly numerous at Penicuik Estates and are often present in unbearable numbers during the summer months. This is perhaps a product of the use of the estates for pheasant shooting, as the rearing pens seem to be the focus of the flies' attentions. If, for whatever reason, the populations of small mammals or the relative abundance of competitors for their carcasses varies between sites, it could be expected that the relative success of *Nicrophorus* will also vary.

The finding that beetles eclosing from carcasses are at least as large as the size of beetles successfully reproducing in the field (fig.4.4) is evidence that parents cull the brood to a total whereby the offspring that are produced stand a chance of gaining reproductive access to a carcass and, therefore, that the parents' success, in terms of number of grandchildren, is maximised. But the small sample size destines that the error about this mean is large and, consequently, that the finding is less conclusive than if a larger sample had been obtained.

4.4.4. Brood reduction in bi- and uniparental broods

The finding that the degree of culling is similar in broods raised by a single female and by a pair of beetles raises the question of how a parent compensates for the presence or absence of a mate. Single male and single female *N. orbicollis* provisioned larvae and maintained the carcass more frequently than did paired males and females (Fetherston *et al.* 1994), showing that behavioural compensation is a possibility for *Nicrophorus*. With regard to culling behaviour, a parent would need to compensate for presence or absence of a partner only if s/he assesses the number of larvae that the carcass can support and the number of larvae present prior to culling and 'decides' to cull a number of larvae that represents the difference between these amounts. If, however, the parents assess the number of larvae that the carcass can support and cull until this number has been reached, then compensation does not have to be invoked to explain why the same number of larvae are culled in bi- and uniparental broods. For the latter system to work the parents must each frequently assess the number of larvae that are present during the period that culling takes place. Whichever of the two strategies is true, the way in which a parent makes such an assessment of larval numbers is undetermined. Presumably a parent is unable directly to count larval numbers but may respond to a correlate of brood size such as the frequency with which the parent is approached by larvae begging for food or the degree to which the depression where larvae congregate on the carcass is full of larvae. The former possibility is made more plausible by the observation that frequently a culling incident punctuates a bout of regurgitation behaviour by a parent (pers. obs.).

My data provide no support for Scott's (1989) hypothesis that the larger broods raised by single females than those raised by two parents in the laboratory are a product of over-culling of the brood by two parents. It is possible that fewer larvae were raised by two parents in Scott's (1989) experiment because males were left in the boxes containing the broods until the larvae dispersed. This was done despite the fact that males of the species used (*N. orbicollis*) desert the brood between 9 and 3 days before larval dispersal (Scott 1989). A deserting male is, if not provided with an alternative food source or allowed to escape from the container, likely to kill and eat his own larvae as can be seen by the presence of mutilated larvae at dispersal (pers. obs.). This scenario provides a more reasonable interpretation of Scott's (1989) data because it accounts for both the smaller number of larvae and the lower total brood mass of biparental, compared with uniparental broods, at dispersal. If two parents over-cull a brood then it would be expected that the total brood mass would be the same between the treatments but that fewer, heavier larvae would disperse from biparental broods.

4.4.5. Parent-offspring conflict

I have addressed the issue of optimal brood size from the perspective of the parents. It should be considered that a different size of brood may be optimal from the point of view of the larvae, introducing a possible source of parent-offspring conflict (Trivers 1974). Parent-offspring conflict (POC) is, perhaps, particularly relevant to parental care in *Nicrophorus*, due the parents' practice of culling a proportion of first instar larvae (Bartlett 1987c). A larva may, therefore, be expected to behave so as reduce the chances of being eaten itself. The validity of POC theory is currently being questioned on the grounds that the wealth of theoretical models (eg. Trivers 1974; Parker & Macnair 1978, 1979; Macnair & Parker 1978, 1979; Parker 1985) are supported by little empiricle evidence and, that the interests of parents and offspring may often coincide, despite behavioural observations (eg. chicks begging for food) that imply the contrary (Mock & Forbes 1992; Bateson 1994). There is no information to date on whether *Nicrophorus* parents allow the most valuable (eg. largest, or genetically superior) larvae to survive. This could be investigated by comparing the success of broods that are reduced naturally and experimentally. If the former are more successful, a larvae may benefit, through inclusive fitness, by being culled and POC need not be invoked. On the hand, if artificially reduced broods are more successful, any larval behaviour that improves its chances of survival to second instar may be shaped by POC selection pressures.

Chapter 5

Biparental care and brood defence

5.1. INTRODUCTION

A consequence of the rich, and yet rare and ephemeral nature of carrion is that it is the subject of intense competition from a wide variety of taxa (Putnam 1983). Furthermore, as it is found in discrete packages, carrion is relatively easily monopolised, a property that *Nicrophorus* exploits by burying the resource to remove it from the attention of competitors. However, interring the carcass does not ensure its exclusive use by burying beetles, whose reproductive success can subsequently be diminished by ruination of a part, or all, of the carcass by ants (Scott *et al.* 1987; Scott 1994b), carrion flies (Scott 1994a, 1994b; Trumbo 1994) or fungal infection (Wilson & Fudge 1984). It is also still liable to be taken over by conspecifics and congeners wishing to use the resource for their own reproduction (eg. Scott 1990; Trumbo 1990b).

An intraspecific take-over typically entails an intruding beetle entering the crypt, driving off or killing the same-sexed resident, killing the eggs or larvae and raising a brood with the resident of the opposite sex (Scott 1990; Trumbo 1990a; Robertson 1993). The intruder may also expel or kill the opposite-sexed resident (Trumbo 1990b) in which case a female intruder will be able to raise a brood on her own, an option that is not open to a male who will, therefore, signal for another female by pheromone emission (Pukowski 1933; Mosenbach 1936; Bartlett 1987b; Eggert & Müller 1989a). Interspecific take-overs result in the death or expulsion of both residents (Trumbo 1990b).

The frequency of take-overs of natural broods is variable. Intruders replaced at least one resident at 19% and 44% of carcasses buried by *N.orbicollis* (Trumbo 1990a and Robertson 1993 respectively). Scott (1990) found that take-overs only occurred when competition for carcasses was augmented by releasing conspecifics near to established broods. Such inconsistency may reflect geographical or temporal variation in burying beetle populations and carcass availability (Scott 1994b).

Take-overs are costly to both residents. The same-sexed resident will forfeit any reproductive success from the current attempt and, although the opposite-sexed resident may remain with the intruder, broods raised following a take-over are smaller than successful first broods (Robertson 1993). This is largely because some of the carcass will have been depleted by the original residents' brood prior to the take-over event. Also, the extra time required to raise a second brood means that, firstly, more of the carcass is likely to be spoiled by, for example, fungal infection and, secondly, opportunities for further reproductive attempts will be sacrificed (Scott 1990). Selection could, therefore, be expected to favour parental behaviours that reduce the vulnerability of the brood to potential usurpers.

Several studies of burying beetles have found an advantage of biparental over uniparental care in defending the brood and carcass against take-overs by conspecifics (Scott 1990; Scott & Gladstein 1993; Trumbo 1991; Robertson 1993) and congeners (Scott 1994b; Trumbo 1990b). In *N. orbicollis* the presence of two parents, compared to a single female, dramatically reduced the probability of the carcass being usurped by experimentally-introduced conspecifics (Scott 1990). A similar effect has been found for the same species at natural population densities (Trumbo 1990a, 1991).

The intruder:resident size ratio is important in determining the outcome of a take-over attempt: larger male and female *N. orbicollis* defend carcasses more successfully against same-sexed, conspecific intruders, suggesting active defence (Trumbo 1990a; 1991) and, indeed, fights between residents and intruders have been observed (Trumbo 1990a). The idea is further supported by the finding that single female *N. orbicollis* are as successful as pairs at repelling female intruders smaller than themselves, but are less successful than pairs when threatened by a larger female intruder (Scott 1990). Male intruders that take over broods tended by a single female are not significantly bigger than the resident (Trumbo 1990a).

In *N. defodiens*, two parents are more likely than single females to prevent take-overs by the larger *N. orbicollis* (Trumbo 1990b). The large size difference between the participants in this instance suggests that the residents cannot rely on active defence to deter the intruder. It is more likely that two parents can bury and prepare a carcass more efficiently than can a single parent. Consequently, a carcass buried by a pair will be less susceptible to decay and attract fewer free-flying congeners (Trumbo 1990b, 1994).

As Scott (1994b) pointed out, the focus of studies to date has been on intraspecific competition for the large species (Scott 1990; Trumbo 1991; Scott & Gladstein 1993) and intrageneric competition for the smaller *N. defodiens* (Trumbo 1990). In this chapter I investigate the importance of biparental care in defence against conspecific intruders in *N. vespilloides*, the smallest British species, by comparing the success of single females and pairs in preventing take-overs by experimentally-introduced competitors of both sexes and varying relative size.

The probability of take-over diminishes as the carcass is depleted by the developing brood (Scott & Gladstein 1993). This is to be expected: as the brood develops, the value of the carrion resource is reduced from the standpoint of a potential intruder, who should, therefore, fight harder for access to carcasses with younger broods. Conversely, parents are predicted to defend an older brood more vigorously as less investment is required to see the reproductive attempt through to completion. I test whether the duration of male care is related to the period that the buried carcass is vulnerable to take-overs. This could be expected if defence against intruders is the major function of paternal care, as stated by Scott (1994b). By recording the success of intruders added to broods at different stages of the reproductive cycle, it can be established whether caring males desert the brood when the risk of take-over has passed.

The larger the carcass the more larvae it can support. In addition, at any given stage during larval development there will be more of a large, rather than a small, carcass remaining that could be utilised by an intruder to raise their own brood. It may be expected then, that large carcasses are vulnerable to take-overs for longer than are small ones. Male *N. orbicollis* care for longer on larger carcasses (Trumbo 1991) perhaps in response to the longer duration of vulnerability to takeovers compared to smaller carcasses. I compare the change in take-over vulnerability with time for small and large carcasses and relate these data to the duration of paternal on the respective carcass sizes.

Finally, to test whether there are benefits of paternal care to broods in addition to defence against take-overs, I compare the success of uni- and biparental broods raised in the field in the absence of any competition from other burying beetles.

5.2. METHODS

5.2.1. Take-overs of broods tended by one or two parents

79 matched pairs of biparental and uniparental broods were allowed to bury a mouse carcass (12.70-14.29g) and raise a brood. Within each matched pair the resident beetles had the same pronotum width (to the nearest 0.1mm). Extreme size classes of beetle (<4.6mm and >5.7mm) were not used due to the low incidence of these sizes in the laboratory population. 48h after burial the soil above the crypts was replaced with a piece of damp paper towel. Crypts were then checked every four hours for the arrival of larvae. Four hours after larval arrival a third beetle was added to the box containing the broods. Half of the matched pairs received a male, and half a female intruder. Within each matched pair intruders were of equal pronotum width, but were different in size to the residents. The intruder was encouraged to bury into the soil away from the crypt, by gently prodding it with a finger, to ensure that it did not enter the crypt accidentally before being motivated to do so. Decapitated

mealworms were scattered on the soil surface so that neither the intruder nor a dispersed resident male would be driven, through hunger, to attack the brood. Subsequently, broods were checked every 24h to establish which beetles were resident in the crypt and whether or not larvae were present. Towards the end of larval development, checks were made every 4h and, at larval dispersal, larvae were weighed and counted.

5.2.2. Vulnerability to take-over and the duration of paternal care

Since only broods tended by a single female were susceptible to being taken over, and because single females are largely successful at defending against female intruders (see section 5.3.1), subsequent experiments focus on the vulnerability of uniparental broods to male intruders.

a) A mouse carcass (14.00-15.09g) was given to each of 60 single females and 18 pairs of beetles. After burial, broods were checked every 4h for the appearance of eggs which could be seen through the transparent sides and base of each box. Crypts were displayed as before and 4h checks continued until larvae were seen in the crypt. Male intruders were introduced to uniparental broods at the times specified in table 5.1a. No intruders were added to the biparental broods. Since there was no significant effect of intruder: resident size ratio on the probability of intrusion in the last experiment (see section 5.3.1), the sizes of intruders and residents were matched. As before, intruders were encouraged to bury away from the crypt and decapitated mealworms were provided as a food source.

To establish the duration of parental care biparental broods were checked every 4h from when larvae arrived in the crypt until brood dispersal and the presence of any beetles in the crypt was recorded.

b) A second experiment was set up in order to home in on the vulnerability of the carcass to take-over during the first 24h after larval arrival (see table 5.1b). Due to a shortage of mice of the size used above, carcasses used in this experiment weighed 16.00-16.99g. Otherwise the procedure was identical to that described in 5.2.2a.

a)

Treatment	Residents	Male intruder added	n
1	F	4h after eggs	12
2	F	4h after larvae	12
3	F	28h after larvae	12
4	F	52h after larvae	12
5	F	76 h after larvae	12
6	M + F	No intruder	18

b)

Treatment	Residents	Male intruder added	n
1	F	4h after eggs	14
2	F	4h after larvae	14
3	F	8h after larvae	14
4	F	12h after larvae	14
5	F	16h after larvae	14
6	F	20h after larvae	14
7	F	24h after larvae	14
8	F + M	No intruder	14

Table 5.1. The treatments used in the experiment to establish the period of vulnerability of a carcass tended by a single female to take-over by a male intruder (see section 5.2.2). F = Female, M = Male. a) Intruders added at intervals throughout larval development. b) Intruders added at intervals during the first 24h after the appearance of larvae in the crypt.

5.2.3. Carcass size and vulnerability to take-over

To test whether the size, and hence the value, of the carrion resource affects its vulnerability to take-over, the experiment described in section 5.2.2b was repeated using two sizes of carcass (5.00-5.99g and 20.00-20.99g). The intervals between intruder addition times were greater than before in order to increase sample sizes within treatments (see table 5.2 for details of the treatments used). In this experiment the sizes of the residents and intruders were not matched, but, within each biparental brood, the male and female were the same size.

Treatment	Carcass size (g)	Residents	Intruder added	Treatment	Carcass size (g)	Residents	Intruder added
1	5	F	4h after eggs	6	20	F	4h after eggs
2	5	F	4h after larvae	7	20	F	4h after larvae
3	5	F	12h after larvae	8	20	F	12h after larvae
4	5	F	20h after larvae	9	20	F	20h after larvae
5	5	F	28h after larvae	10	20	F	28h after larvae
11	5	F + M	No intruder	12	20	F + M	No intruder

Table 5.2. The treatments used to compare the period of vulnerability of small and large carcasses tended by a single female to take-over by a male intruder (see section 5.2.3). F = Female, M = Male. Each treatment contained 13 replicates except treatments 11 and 12 which were contained 14 and 15 respectively.

5.2.4. Other benefits of biparental care

To establish whether there are benefits of biparental over uniparental care in addition to brood defence, an experiment was set up to compare the success of broods raised by one and two parents in the field in the absence of a risk of take-over.

35 matched pairs of uniparental and biparental broods were set up during the 1992 and 1993 field seasons. Within each matched pair adults were the same size (to the nearest 0.1mm across the width of the pronotum). All mouse carcasses weighed between 14.50 and 15.49g. To eliminate the risk of broods being taken over by other burying beetles, the adults were forced to bury within the confines of a plastic

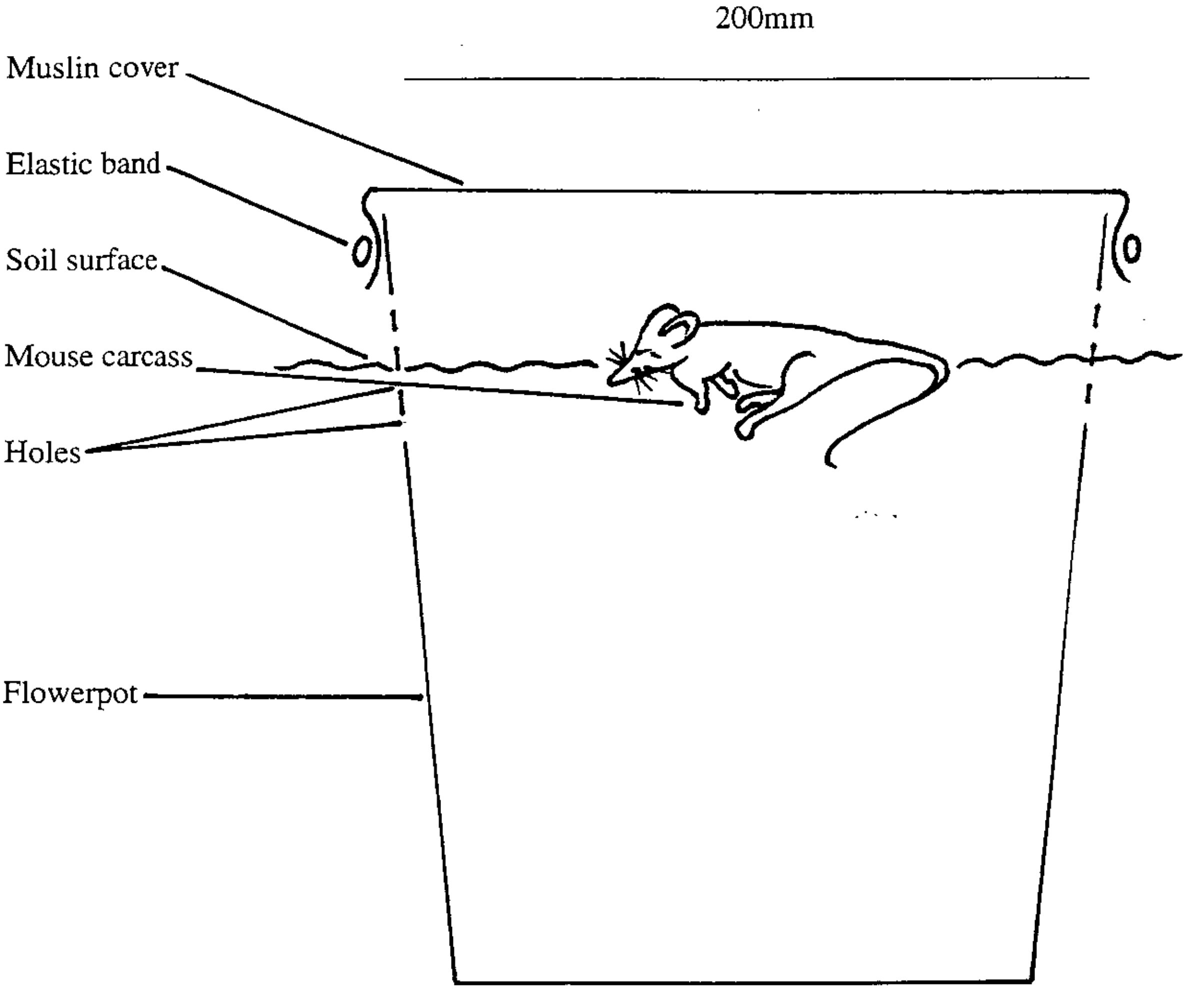

Figure 5.1. The apparatus used to compare the success of broods raised by one or two parents in the field, in the absence of competition from other burying beetles.

flowerpot (diameter 200mm) that had been sunk into the ground, the earth that was displaced being used to fill the flowerpot (see fig.5.1). Potential intruders and residents were prevented from entering and leaving the flowerpot respectively by placing a muslin lid over the top and securing it with a strong elastic band. Holes 3mm in diameter were punched into the sides of the pot. These allowed the passage of many soil arthropods, including the staphylinid *Philonthus* which is known to attack burying beetle larvae (Easton 1979; Bartlett 1987a), but were not large enough for either *Nicrophorus* adults or their dispersing 3rd instar larvae to pass through. Paired flowerpots were placed 2m apart and replicates were spaced every 20m along an established route through the field site. Decapitated mealworms were provided as a food source for dispersed males. Towards the end of larval development, broods were checked twice daily and, at dispersal, larvae were counted and weighed. Any uneaten carcass that remained at larval dispersal was weighed.

5.3. RESULTS

5.3.1. Take-overs of broods tended by one or two parents

A take-over was judged to have occurred if the intruder was seen in the crypt *and* the larvae disappeared from the carcass before completing development, presumably as a result of being eaten by the intruder (Trumbo 1990a). Examination of the mouse carcass following a take-over frequently revealed the presence of dead larvae sealed inside. These larvae had no visible external injuries and had apparently suffocated.

Uniparental broods were vulnerable to being taken over whereas the additional presence of a male completely eliminated this risk ($\chi^2 = 22.08$, df = 1, $p < 0.001$) (table 5.3). When added to uniparental broods, male intruders were more successful than female intruders ($\chi^2 = 14.19$, df = 1, $p < 0.001$). In many of the boxes where female intruders were added, larvae were seen wandering on the surface of the soil several days after intruder addition. It is likely that they had hatched from eggs laid parasitically by the intruder (Müller *et al.* 1990a). There was no difference in the number of take-overs of bi- and uniparental broods by female intruders ($\chi^2 = 2.30$, df = 1, $p > 0.1$). Subsequent analysis, therefore, concentrates on take-overs of uniparental broods by male intruders.

Residents	Intruder	Take-overs	n
F + M	F	0	38
F + M	M	0	36
F	F	2	34
F	M	16	35

Table 5.3. The effects of number of parents and sex of intruder on the frequency of brood take-over. F = Female, M = Male. Broods that failed to produce larvae are omitted.

The intruder: resident size ratio was not significantly different between broods that were taken over (mean±SE = 1.02±0.02) and those that were not (mean±SE = 0.98±0.02) (t = 1.91, df = 32, p = 0.065).

	Take-over	No take-over	
Total larval mass	1.63±0.13g	2.36±0.17g	t=-3.027, 28df, p=0.005
Number of larvae	10.18±0.87	15.95±1.51	t=-2.75, 28df, p=0.01
Mean larval weight	0.16±0.01g	0.16±0.01g	t=0.784, 28df, p=0.440
Development time	291.9±9.2h	208.6±8.8h	t=6.15, 28df, p<0.001

Table 5.4. A comparison of measures of success of uniparental broods that were, and were not taken over by a male intruder. Only successful (ie. produced at least one larva) broods are included. Values are means (±SE).

Broods produced following a take-over were smaller in terms of total larval mass and larval number than were broods not taken over. Additionally, development time was longer for broods that were taken over (table 5.4).

5.3.2. Vulnerability to take-overs and the duration of paternal care

a) Takeovers only occurred when the intruder was added at an early stage of brood development (table 5.5a). There were no take-overs when the intruder was added 28h or more after the larvae appeared in the crypt. The distribution of take-overs is significantly different from that which would be expected if they were randomly scattered between treatments ($\chi^2 = 21.49$, 4df, $p < 0.01$). For treatment 1 only, a take-over was judged to have occurred if the intruder was regularly seen in the crypt. Intruding *N. orbicollis* will kill unhatched eggs (Robertson 1993) and this may be why in only 2 of the 8 take-overs that took place in treatment 1 (fig. 5.5a) did larvae disappear from the crypt.

In the biparental broods males stayed for a mean (±SE) of 50.2±5.0h, only one male deserting within 24h after larval arrival (fig.5.2a). Males were judged to have deserted if they were absent from the crypt for 6 consecutive 4h checks, the time of desertion being taken as the first of those checks. This is a slight overestimate as, in reality, desertion will have taken place at some point during the 4 hours between the last time a male was seen in the crypt and the following check. The duration of care provided by the male was taken as the last time he was observed in the crypt which will be a slight underestimate for the reason given before.

b) When intruders were added at intervals during the first 24h after larval arrival at the carcass, take-overs only occurred up to 20h after this time (table 5.5b). Again, this distribution is significantly different from random ($\chi^2 = 14.64$, 6df, $p < 0.05$). Males in biparental broods stayed for a mean (±SE) of 75.0±17.9h, none deserting within the period of vulnerability (fig.5.2b).

a)

Treatment	Intruder added	No. of take-overs	n	Proportion taken over
1	4h after eggs	8	10	0.80
2	4h after larvae	4	11	0.36
3	28h after larvae	0	10	0.00
4	52h after larvae	0	9	0.00
5	76h after larvae	0	11	0.00

b)

Treatment	Intruder added	No. of take-overs	n	Proportion taken over
1	4h after eggs	6	11	0.64
2	4h after larvae	3	12	0.17
3	8h after larvae	1	11	0.09
4	12h after larvae	1	10	0.10
5	16h after larvae	1	12	0.08
6	20h after larvae	1	13	0.08
7	24h after larvae	0	13	0.00

Table 5.5. The numbers of successful take-overs when intruders were added at different times a) throughout the duration of brood development and b) during the first 24h after larval arrival at the crypt. Broods that failed to produce larvae are omitted.

5.3.3. Carcass size and vulnerability to take-overs

There is a non-significant tendency for take-over risk to diminish with time for both carcass sizes (fig.5.3) (5g: $\chi^2 = 6.76$, 4df, $p > 0.05$. 20g: $\chi^2 = 8.44$, 4df, $p > 0.05$). There is no difference in the probabilities of small and large carcasses being taken over ($\chi^2 = 0.99$, 1df, $p > 0.05$).

All males in biparental broods on 20g carcasses cared for longer than the risk of take-over to uniparental broods persisted, but, on 5g carcasses, 5 of 9 males deserted during the period of vulnerability (fig.5.4). Males provided care for significantly longer on 20g carcasses (median = 84h after larval arrival) than on 5g carcasses (median = 28h after larval arrival) (Mann-Whitney U = 3.5, $p < 0.001$).

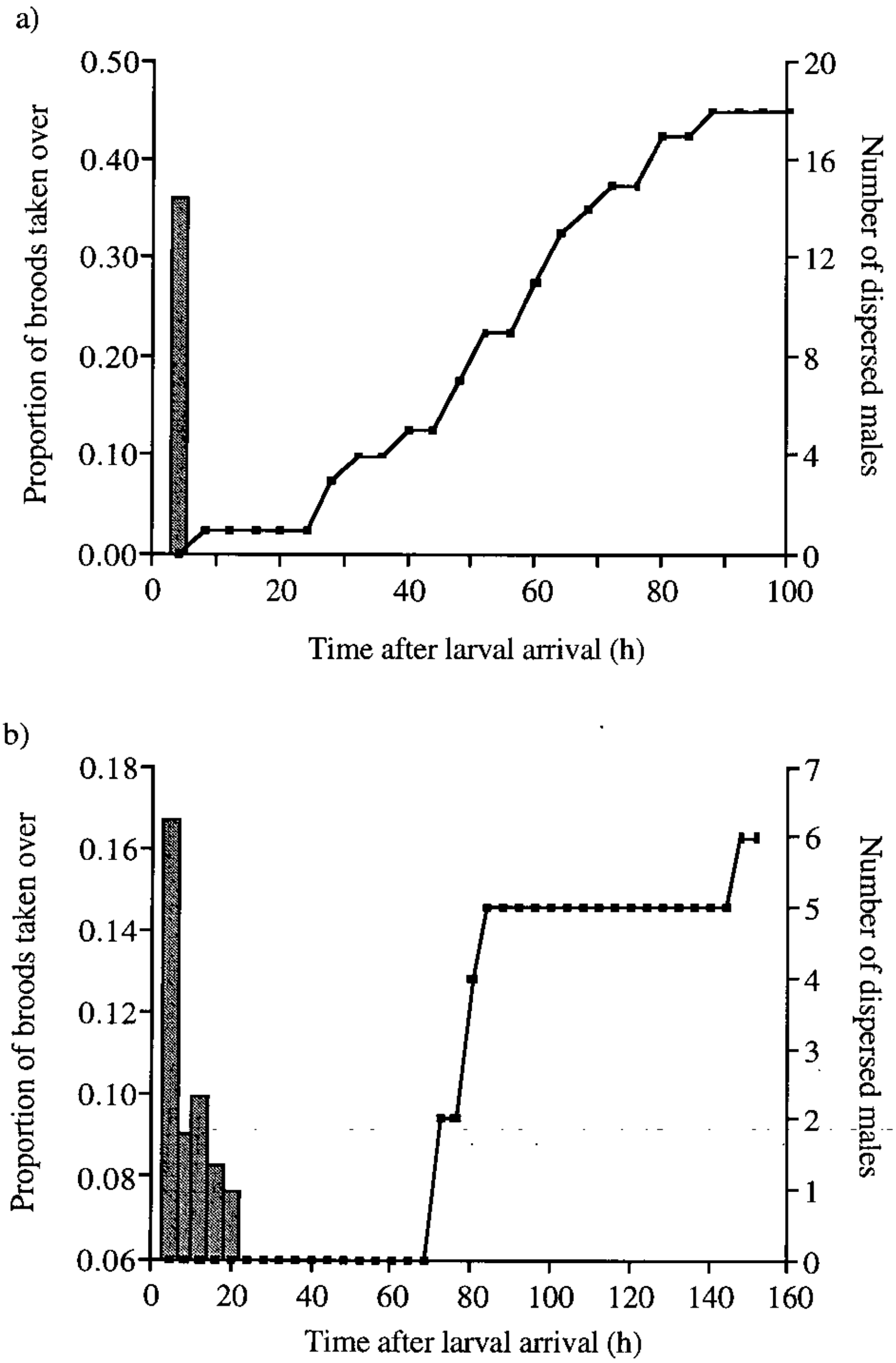

Figure 5.2. The proportion of uniparental broods taken over by male intruders introduced at different times after larval arrival (bars) and the cumulative number of males dispersing from biparental broods (points). The figure does not include take-overs by intruders added 4h after the appearance of eggs. a) Intruders added at 4h, 28h, 52h and 76h after larval arrival. b) Intruders added at 4h, 8h, 12h, 16h, 20h and 24h after larval arrival.

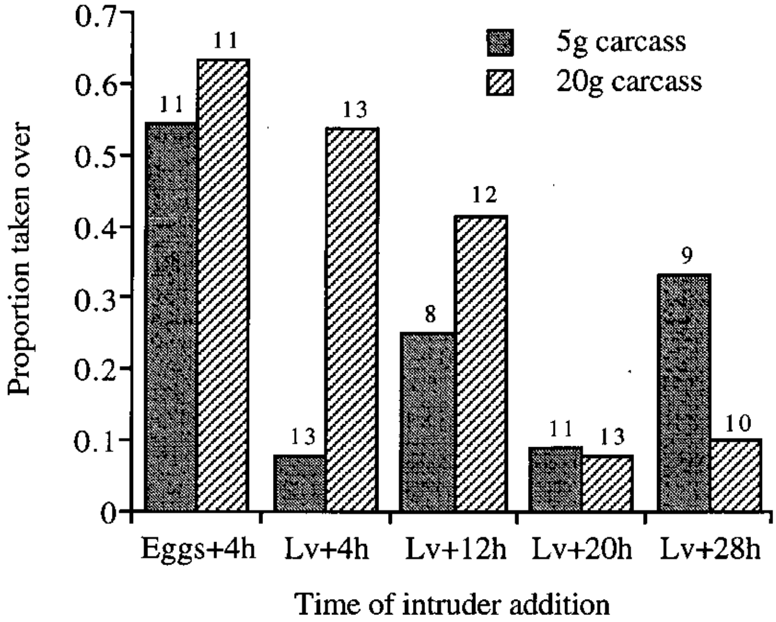

Figure 5.3. The proportion of small and large carcasses tended by a single female that were taken over by male intruders added at different times with respect to the appearance of either eggs or larvae (lv). The number of broods to which intruders were added is given at the top of each bar.

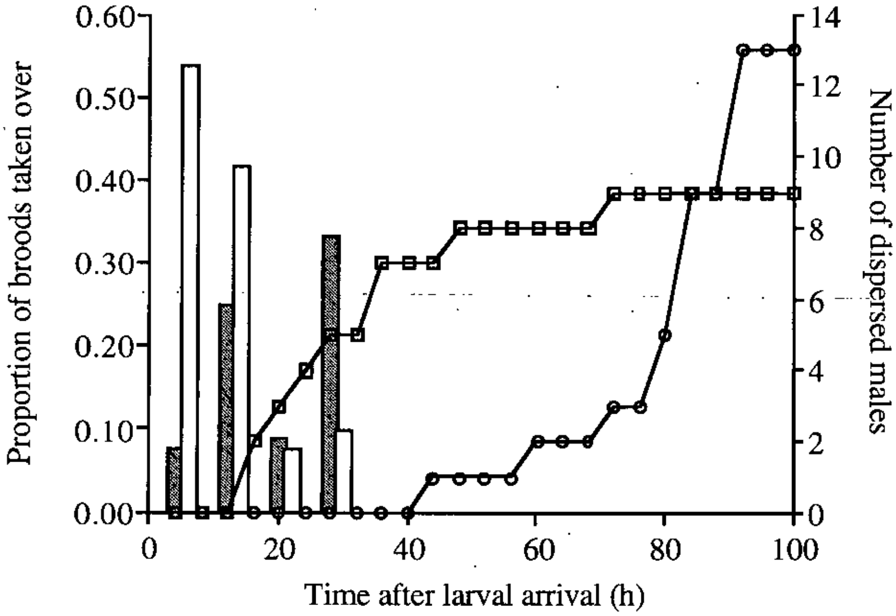

Figure 5.4. The proportion of uniparental broods raised on 5g (solid bars) and 20g (open bars) that were taken over by male intruders introduced at 4h, 12h, 20h and 28h after the appearance of larvae in the crypt. The cumulative number of males dispersed from biparental controls where no intruder was added is shown for 5g (open squares) and 20g (open circles) carcasses. The figure does not include take-overs by intruders added 4h after the appearance of eggs.

There was no significant effect of intruder:resident pronotum width ratio on the probability of take-over either on 5g (broods taken over - mean = 1.017±0.010SE; broods not taken over - mean = 0.995±0.006SE; t = 1.79, 52df, p = 0.080) or 20g carcasses (broods taken over - mean = 1.007±0.008SE; broods not taken over - mean = 0.992±0.007SE; t = 1.345, 57df, p = 0.184).

On 20g carcasses, broods that dispersed following a take-over were smaller, in terms of brood mass and number of larvae, than those dispersing from carcasses that had not been usurped (table 5.6a). No such difference was found for broods dispersing from 5g carcasses (table 5.6b) but this is likely to be, in part, due to the small number (n=2) of broods produced following a take-over. 11 out of 13 5g carcasses that were taken over failed to produce a second brood, compared to only 6 of 21 on 20g carcasses. This difference is significant ($\chi^2 = 5.04$, 1df, $p < 0.05$).

a)

	Taken over	Not taken over	
Number of larvae	16.13±1.71	21.38±1.17	t=2.46, 50df, p=0.017
Total mass of larvae	2.63±0.30g	3.45±0.16g	t=2.62, 51df, p=0.012
Mean larval mass	0.163±0.005g	0.167±0.004g	t=0.56, 50df, p=0.577

b)

	Taken over	Not taken over	
Number of larvae	4.50±2.51	7.29±0.46	t=1.31, 41df, p=0.196
Total mass of larvae	0.54±0.15g	0.93±0.05g	t=1.867, 41df, p=0.069
Mean larval mass	0.150±0.050g	0.133±0.004	t=-0.794, 41df, p=0.432

Table 5.6. A comparison of measures of success of broods raised on a) 20g carcasses and b) 5g carcasses that were, and were not taken over by a male intruder. The table only includes successful broods (ie. produced at least one larva). Values are means (±SE). For one brood raised on a 20g carcass only the total mass of dispersing larvae was recorded.

5.3.4. Other benefits of biparental care

There were no significant differences in any measure of size of broods raised by a single female or a pair of beetles in the field, in the absence of competition from other burying beetles (table 5.7). Furthermore there was no difference in the frequency of failed broods raised by one (n=17) and two (n=11) parents (χ^2=1.29, 1df, p>0.05). No difference was found between treatments for either the time taken from burial to larval dispersal or the amount of carcass remaining at dispersal (table 5.8).

a)

	Biparental	Uniparental	Wilcoxon rank sum analysis
Number of larvae	8 (0-13.75)	4 (0-13.75)	z=-0.84, n=33, p=0.402
Total larval weight	1.23 (0-2.26)g	0.28 (0-2.29)g	z=-0.79, n=32, p=0.427
Mean larval weight	0.14 (0-0.17)g	0.04 (0-0.16)g	z=-1.56, n=32, p=0.118

b)

	Biparental	Uniparental	Paired t-test
Number of larvae	12.08±1.94	13.25±1.97	t=-0.45, 11df, p=0.659
Total larval weight	1.97±0.27g	2.23±0.36g	t=-0.60, 11df, p=0.562
Mean larval weight	0.17±0.01g	0.16±0.01g	t=0.72, 11df, p=0.486

c)

	Biparental	Uniparental	Independent t-test
Number of larvae	12.73±1.33	13.24±1.45	t=-0.26, 37df, p=0.799
Total larval weight	2.08±0.20g	2.21±0.29g	t=-0.41, 35df, p=0.688
Mean larval weight	0.17±0.01g	0.16±0.01g	t=0.72, 35df, p=0.471

Table 5.7. The success of broods raised in the field by one or two parents in the absence of a risk of being taken over. a) Median (interquartile range) including broods where no larvae were produced. b) Analysis of matched pairs where both broods were successful (ie. produced at least one larva). c) Analysis of all successful broods. Two matched pairs for which brood data was not collected have been omitted from the analysis. For one matched pair the number of larvae only was recorded.

a)

	Biparental	Uniparental	Wilcoxon rank sum analysis
Time to dispersal	409 (402-574)h	402 (379-581)h	z=-0.30, n=13, p=0.767
Carcass remaining	9.9 (0-15.0)g	5.0 (0-13.2)g	z=-0.77, n=12, p=0.441

b)

	Biparental	Uniparental	Mann-Whitney U-test
Time to dispersal	482 (402-599)h	478 (379-615)h	U=448, 37df, p=0.144
Carcass remaining	9.9 (0-13.4)g	9.9 (0-13.2)g	U=430, 37df, p=0.252

Table 5.8. The median (interquartile range) time taken from burial to larval dispersal, and median (interquartile range) mass of carcass remaining at larval dispersal for broods raised by one and two parents in the field in the absence of competition from other burying beetles. a) Includes matched pairs in which both broods were successful (ie. produced at least one larva). b) Includes all successful broods.

5.4. DISCUSSION

The importance of biparental care in defence of the brood and the carrion resource against take-overs has been well documented for *N. orbicollis* (Scott 1990; Scott & Gladstein 1993; Trumbo 1991; Robertson 1993) and *N. defodiens* (Trumbo 1990b; Scott 1994b). In these species take-overs of biparental broods did happen but at lower rates than take-overs of uniparental broods. My results confirm that the residence of two caring parents has similar benefits in *N. vespilloides*. In my study the additional presence of a male completely eliminated the occurrence of take-overs, so the benefits of paternal care may be greater for *N. vespilloides* than for either *N. orbicollis* or *N. defodiens*. The small size of *N. vespilloides* creates the potential for it to be vulnerable to take-over by larger congeners. In this respect it is perhaps similar to *N. defodiens* but, even for the latter species, a proportion of biparental broods were lost to conspecific intruders in the field (Trumbo 1990b; Scott 1994b). My data were obtained from experiments in the laboratory where conditions are rather different, but the confinement of intruders to the boxes containing established broods would, perhaps, be expected to increase, rather than diminish, the probability of successful intrusion.

Males were more successful than females at taking over a carcass defended by a single female resident. There are two possible interpretations of this finding: the female resident may have more to lose, and, therefore, be less willing to accept a female intruder or, a female intruder has less to gain, than a male, from taking over a carcass and, therefore does not fight as hard for it.

In the first case, the forfeit of the carcass to a female intruder results in the loss of all reproductive success apart from that which can be salvaged by parasitising the brood of the new resident (Müller *et al.* 1990a). Take-over by a male will result in the death of the current larvae followed by the production of a smaller replacement brood. This drop in reproductive success may not be as large as that which will result from a costly, and potentially fatal, fight with the intruder. There may even be a net gain to a single female in accepting a male intruder as she will subsequently be at no risk of a more costly take-over by a female intruder.

The second possibility, that the benefits of take-over to a male intruder outweigh those to a female, is given credence when it is considered that in order to gain any reproductive success from an already occupied carcass, a male must take it over, whereas a female can acheive a degree of success, without a potentially costly fight, by parasitising the clutch of the resident female (Müller *et al.* 1990a). Evidence that this strategy is adopted by would-be female intruders was provided in this study by the appearance of first instar larvae on the soil surface several days after intruder addition.

These explanations are not mutually exclusive and, in reality, there is likely to be an interaction between the two: the greater costs to a female resident of take-over by a female, as opposed to a male, intruder lead to the resident fighting harder against a female which, in turn, leads to reduced benefits for a female intruder.

Successful intruders were not significantly bigger than those that were unsuccessful. Trumbo (1990a) also found no effect of size ratio on the outcome of intrusions by males into broods guarded by a single female, although successful male and female intruders were significantly bigger than same-sexed residents. The lack of a size ratio effect suggests that single females do not actively defend the carcass against male intruders and reinforces the idea that a female is more willing to accept an intruding male than an intruding female.

A carcass with a single female resident was vulnerable to being taken over for only about a day after larvae first appeared in the crypt and, in biparental broods, with the exception of those raised on very small (5g) carcasses, every male, bar one, remained with the brood for long enough to remove this risk. Males on 14g carcasses stayed for 50.2±5.0h despite there being no take-overs by intruders added to uniparental broods at 28h or later, on 16g carcasses the latest take-over occurred at 20h but males stayed for 75.0±17.9h, and a similar excess duration of care was provided on 20g carcasses. If defence against intruders is the main benefit of the extended duration of paternal care then the surplus care provided by these males could be spent more profitably by deserting the current brood to seek reproductive opportunities elsewhere. It may be the case that later take-overs do, rarely, occur, the high cost of which pay the male to remain for longer. This is especially credible if future reproductive opportunities are very limited in which case a male will benefit from maximising the current attempt. Against this is the finding that on very small (5g) carcasses, 5 out of 9 males deserted during the period of vulnerability to take-over. The reproductive rewards are less on small carcasses and, consequently, so are the costs of take-over to the residents. However, the fact that males do not stay for long enough to prevent take-overs implies that there are reproductive opportunities to be found elsewhere. Alternatively, caring male *N. vespilloides* may be driven off by their mates on 5g carcasses (Bartlett 1988) so the males may not be leaving to gain other reproductive opportunities, but rather because their presence is detrimental to the success of the current brood to a greater extent than is the risk of take-over. This may be due to, for example, a male's consumption of a portion of the carcass that that would otherwise be available to the developing larvae (Bartlett 1988; Scott & Gladstein 1993).

Trumbo (1990a) observed conspecific take-overs in *N. orbicollis* and noted how an intruding male would opportunistically kill the resident's larvae one by one whilst inspecting the carcass over a period of several hours. In contrast, intruding *N. vespilloides* would appear to seal the larvae inside the carcass, thus killing them all in one fell swoop. Whether this method of infanticide is the norm (intruding *N. vespilloides* have also been seen to kill individual larvae [pers. obs.] in the manner of *N. orbicollis*) or, maybe, a side effect of the vigorous activity in the crypt during a take-over attempt, requires further investigation. It would seem, however, to be an efficient method of dispatching a large number of larvae, as the sooner that infanticide is carried out, the more of the carrion resource will remain for the intruder's own brood.

It is, perhaps, surprising that so few intruders took over a brood, particularly when it is considered that the variation in take-over success is not explained by the size ratio of intruder to resident. The beetles in this study had no previous experience of reproduction and were used shortly after reaching sexual maturity. They may, therefore, have been able to afford to wait for a more profitable breeding opportunity, given the lower success of broods raised on carcasses following a take-over and, the potentially high cost of a fight to gain ownership of an occupied carcass. Had older beetles, who could expect lower future reproductive success, been used, a higher frequency of take-overs might have been observed.

In all the experiments where the aim was to establish the period of vulnerability of broods to take-overs, intruders were added at a time relative to a point in the reproductive cycle of the residents. It follows that intruders were added at different times of the day (0000h, 0400h, 0800h, 1200h, 1600h or 2000h). When not raising a brood, beetles from my laboratory population are most active from about 1600h to 0000h each day (pers. obs.), so it may be that intruders added between these times are more likely to successfully take over a brood than those added at other times. However, an analysis of all broods to which intruders were added (ie. experiments described in 5.2.2a, 5.2.2b and 5.2.3) shows there is no effect of time of day of intruder addition on the probability of take-over ($\chi^2 = 4.60$, 5df, $p > 0.05$).

The field experiment found no evidence for advantages of biparental over uniparental care to the brood in the absence of competition from other burying beetles. Admittedly, the design of this experiment prevented access to the brood by large invertebrate predators such as carabid beetles whose attentions may have detrimental effects on brood success. However, the results suggest that, at least on the carcass size used (15g), a single female is as capable as a pair at controlling the effects of bacterial and fungal infection, and at defending the brood against smaller invertebrate predators.

My experiments did not take into account the threat of interspecific take-over and so the importance of biparental care in preventing these can only be speculated upon. One replacement of a single female on a carcass in the field by a pair of the larger *N. investigator* has been witnessed (pers. obs.) so the potential is there for the presence of a male to reduce vulnerability. However, it seems unlikely that competition from congeners is a driving force behind the maintenance of the extended duration of male care. This is because the value of the carcass to congeneric intruders will diminish with time, as it does to conspecifics. However, the effect is likely to be greater in the case of congeners as larger species of burying beetle specialise in the use of larger carcasses for reproduction (Trumbo 1990b).

In conclusion, biparental care has been demonstrated to prevent conspecific take-overs of the carcass. However, defence against such take-overs does not fully explain the duration of paternal care as males stayed for longer than was required to see the reproductive attempt through to completion. As no further benefits of male care were conferred on the brood in the field, in the absence of take-overs, it is perhaps necessary to look for advantages of paternal care outside the effects on the current brood.

Chapter 6.

Biparental care and female reproductive success

6.1. INTRODUCTION

In biparental species the experimental removal of males has frequently demonstrated the rewards of biparental over uniparental care (eg. Lyon *et al* 1987), but some studies, using bird species, have failed to find a detrimental effect of male removal on the success of the current brood (Gowaty 1983; Richmond 1978). Similarly, the rewards of biparental over uniparental care in burying beetles are unclear.

Bartlett (1988) found no difference in the number and size of dispersing *N. vespilloides* larvae raised biparentally or by a single male or female. A laboratory study of *N. orbicollis* actually found a detrimental effect of biparental care (Scott 1989). However, the presence of both parents reduces the likelihood of the carcass being taken over by aggressive conspecifics in *N. vespilloides* (chapter 5) and *N. orbicollis* (Scott 1990; Robertson 1993), and by congeners in *N. defodiens* (Trumbo 1990), attempting to secure the resource for their own reproduction.

Two characteristics of the males' behaviour imply that defence against take-overs does not fully explain paternal care in burying beetles. Firstly, when intruders were added to boxes containing established uniparental broods at different stages of development, take-overs only occurred in broods of larvae up to 28h old (Chapter 5). This is perhaps to be expected: as the carcass is consumed by the developing larvae its value to a potential intruder diminishes, whilst its value to the resident increases as progressively less investment is required to see the reproductive attempt through to completion. However, in biparental controls the male stayed, on average, for much longer (50h and 75h in two experiments), only one of the 37 males (with the exception of those breeding on very small carcasses) deserting within the period of vulnerability (chapter 5). If there are no benefits of paternal care outwith defence against takeovers then, by remaining at the carcass long after the risk of take-over has passed, a male is needlessly depriving himself of the chance to desert and gain reproductive opportunities elsewhere, although it should also be considered that later takeovers may occasionally occur, and the high cost to the brood's father may then outweigh any benefits he may incur from earlier desertion.

Secondly, male burying beetles perform care behaviours apparently unconnected with brood defence. Males and females show the same repertoire of care behaviours although females of the American species *N. orbicollis* spent a greater proportion of time than males regurgitating to larvae, and males were engaged in guarding behaviour more often than were females (Fetherston *et al.* 1990). Male and female *N. vespilloides* showed no difference in feeding effort (Bartlett 1988). Presumably regurgitating food to the larvae and assisting in carcass burial and maintenance are costly to the male and it could be expected that they would not be performed without a payoff in terms of improved reproductive success. It could be that the male performs these non-defence behaviours as an insurance against the death of his mate (Fetherston *et al.* 1994). It should also be considered that these behaviours do serve a brood defence function, two parents controlling the escape of odours more efficiently by each contributing antibacterial secretions, making it more difficult for intruders to locate the carcass (Trumbo 1990; 1994). The additional presence of a male speeded up the rate of larval development on large carcasses so reducing the period of vulnerability to takeover (Trumbo 1991). This may be facilitated by the additional proteolytic secretions provided by the male speeding up the rate of carcass utilisation or, paternal feeding of the larvae increasing the rate of larval development.

A further advantage of biparental care is that the presence of two parents reduces the failure rate of broods on carcasses buried by *N. defodiens* when in direct competition with carrion flies (Trumbo 1994). Since the reason for the greater success rate of biparental broods is, in this instance, probably a result of two parents more efficiently killing fly eggs and larvae already present on the carcass, it is unlikely to provide an explanation for the duration of male care.

I found that no benefits of biparental care are conferred on the current brood other than a reduced risk of take-over (chapter 5) so it is necessary to look elsewhere for such advantages. Specifically, this chapter examines the effect of biparental care on the success of the caring female raising subsequent broods.

There is evidence that parental care entails physiological costs for female burying beetles. When *N. tomentosus* were bred sequentially on two carcasses, fewer larvae were raised per unit mass of carcass in the second attempt (Trumbo 1990b). Similarly, second and third broods of *N. orbicollis* were significantly lighter than first broods (Scott & Traniello 1990). Neither of these experiments had non-breeding, same aged controls, but the ages of the beetles used were such that age alone should not have affected reproductive success as burying beetles are typically able to raise four or five broods (Bartlett 1988).

If parental care is costly for females then there is scope for these costs to be reduced if parental assistance is received from the male parent. Few attempts have been made to examine the effect of paternal care on subsequent reproductive success of females in biparental species although it has been implied that male care reduces female parental effort in lesser snow geese *Anser caerulescens* (Martin *et al.* 1985) and cardinals *Cardinalis cardinalis* (Richmond 1978). Wolf *et al.* (1991) suggest that the paucity of data from bird studies on the benefits of male care on subsequent brood success is at least in part due to male removal experiments necessarily preventing a female from renesting with her original mate. This restriction does not apply to *Nicrophorus;* the patchy distribution of carrion means that a female is unlikely to re-pair with the same male, so burying beetles are ideal subjects for such an investigation. If a caring male is not present at subsequent broods brought up by his mate, the question of how he gains from reducing the female's parental effort is raised. It has been stated (Wolf *et al.* 1991) that '...obviously [the reduced parental effort of the female] is relevant to male fitness only if females tend to remate with the same males for subsequent attempts'. But female birds, like insects, are capable of storing sperm (Birkhead & Møller 1992) a characteristic that theoretically removes Wolf's restriction as the male could achieve a degree of reproductive success in subsequent broods, at which he is not present, by sperm competition.

To assess the effect of male care on the subsequent reproductive success of their mate, I bred females sequentially on two carcasses. Half the females raised the first brood alone and half had male assistance. The success of these females raising a second brood alone was compared. In an attempt to quantify the reduced parental effort of females with male help I observed female beetles with and without assistance and compared the rates of regurgitation of carrion to larvae.

6.2. METHODS

6.2.1. Paternal care and female reproductive success

Each of 74 laboratory-bred female *N. vespilloides* was provided with a mouse carcass (12.70-14.19g) and a male beetle was added to half the broods. The beetles were weighed before and after the reproductive attempt and at dispersal the larvae were weighed and counted. To ensure that males deserting before larval dispersal were not motivated to attack the brood through hunger, decapitated mealworms were scattered on the surface of the compost as a food source. After larval dispersal the adult females were kept individually and fed mealworms *ad libitum* until all broods had dispersed when they were presented with a second carcass (12.35-14.99g) on which to breed (13 days after the provision of the first carcass). Second broods were started simultaneously to avoid the introduction of confounding variables such as the age of the compost and humidity. All second broods were uniparental. Once again, the beetles were weighed before and after reproduction and dispersing larvae weighed and counted.

When breeding on large carcasses, biparental broods of *N. orbicollis* dispersed sooner than those raised uniparentally (Trumbo 1991). To test whether any differences in second brood success were due to a longer recovery period between broods for assisted females the times from burial to larval dispersal for each treatment were compared.

Any difference between treatments in female weight change over a reproductive attempt may reflect a difference in the size of the cargo of phoretic mites which disperse with the parent beetles. As it is usually the male beetle who deserts first, most of the mites disperse with him (Schwarz & Müller 1992) leaving the female relatively free of passengers. In a uniparental brood, however, all the mites must disperse with the female thus increasing her apparent weight.

To estabish a more realistic measure of weight change over a reproductive attempt it is necessary to remove the mite population. To this end 72 females, half of which had male assistance, were bred on carcasses weighing 17.00-17.99g. Prior to being presented with a carcass each beetle had its mite cargo removed as described in chapter 2. The removal process was repeated after larval dispersal to remove the progeny of any mites that escaped removal first time round. The beetles were weighed after having their mites removed both before and after reproduction.

6.2.2. Longevity of stored sperm

Since females had no access to males between reproductive attempts, any difference in reproductive success of second broods may be due to the fact that females who received male assistance in their first broods had fresher sperm in their spermathecae than did females who cared alone. Eggert (1992) showed that sperm stored in a female's spermatheca start to become infertile 3 weeks after insemination. This was the case even if no eggs had been laid since insemination (Eggert 1992). In my experiment the second carcass was presented to females 13 days after the last opportunity for insemination and eggs would have been laid about 24h after this which means that stored sperm should not have started to become infertile. However, a clutch of eggs had already been produced so, if the number of viable stored sperm was limiting, assisted females would be expected to lay a greater number of fertile eggs. To test whether the more recent access to fresh sperm by assisted females affected the success of second broods 36 single females were allowed to raise 2 broods consecutively. Between broods females were fed decapitated mealworms *ad libitum* and half the females were provided with a male beetles for 24h prior to provision of the second carcass. The mice used (17.00-17.99g for both broods) were larger than those in the above experiment and were, therefore, more likely to show up any difference in success due to the greater number of larvae that they can sustain. Mice on which to raise second broods were presented 24h after all first broods had dispersed (14 days after provision of the first). At dispersal of the second broods the larvae were weighed and counted.

6.2.3. Female parental effort with and without male assistance

Thirteen pairs and thirteen single female *N. vespilloides* were provided with a mouse carcass to bury. Broods were checked every four hours and, when larvae were seen in the crypt, the soil forming the roof was replaced with a piece of damp paper towel which could be removed with minimum disturbance to facilitate observations into the crypt. Twelve hours after larval appearance the brood was watched for ten minutes under red light. The observation period was subdivided into 30s intervals during which the presence or absence of regurgitation to the larvae by the female was recorded. After uncovering the crypt the brood was left undisturbed for 5 minutes to allow the beetles to resettle before observations commenced. Observations were carried out every 12h after this. To allow easy identification of the sex of the parents, females were marked with a hot needle on their left elytron, males on their right.

6.3. RESULTS

6.3.1. Paternal care and female reproductive success

There were no significant differences between the treatments for any of the measurements of reproductive success in brood 1 (table 6.1). However, females who raised first broods biparentally produced heavier second broods containing more larvae than did females without prior male assistance implying that male assistance in the first brood reduced the parental effort of the female leaving her with more reserves with which to raise the second. Mean larval weight at dispersal was not significantly different between the treatments.

The difference in second brood success between treatments is explained neither by the distribution of failed broods nor a difference in success when brood failures are ignored. Fifteen second broods failed to produce any larvae. Of these, six had raised first broods biparentally, and nine uniparentally. This difference in failure rate between treatments is not significant (χ^2=0.6, 1df, p>0.25). If failed broods are omitted from the analysis (which normalises the data), no difference is found in total brood mass between treatments (treatment 1±SE = 2.67±1.05g, treatment 2±SE = 2.16±0.97g, t=1.92, 55df, p=0.06). Treatment 1 females are still found to produce significantly more larvae (treatment 1±SE = 20.20±10.18, treatment 2±SE = 14.89±9.23, t=2.06, 55df, p=0.045) but these are significantly smaller than larvae raised in treatment 2 (treatment 1±SE = 0.147±0.035g, treatment 2±SE = 0.167±0.042g, t=2.03, 55df, p=0.048).

Total brood mass was considered the best measure of reproductive success (Scott 1989) due to the trade-off between mean larval weight and larval number (Bartlett & Ashworth 1988). Since the difference in total brood mass between the treatments in table 1 is explained by neither of the above analyses it is, therefore, likely to be due to a combination of the two effects.

No significant difference was found in time to dispersal between treatments (biparental ±SE = 236.9±19.9h; uniparental ±SE = 245.7±26.8h independent t=1.493, 72df, p=0.140) so the difference in success between the treatments is not attributable to a greater recovery period between broods for assisted females.

FIRST BROOD			
Treatment	1 (n=37)	2 (n=37)	Mann-Whitney U stat.
Number	19 (17-25)	21 (13.5-25)	U=679.0 p=0.953
Total mass	2.96 (2.50-3.29)g	2.97 (2.23-3.37)g	U=712.5 p=0.762
Mean mass	0.15 (0.13-0.16)g	0.14 (0.13-0.17)g	U=760.5 p=0.406
SECOND BROOD			
Treatment	1 (n=36)	2 (n=36)	Mann-Whitney U stat.
Number	18 (5.25-26)	10 (0.25-18)	U=827.0 p=0.043
Total mass	2.78 (1.00-3.31)g	1.94 (0.05-2.71)g	U=807.5 p=0.031
Mean mass	0.13 (0.10-0.17)g	0.14 (0.02-0.20)g	U=570.5 p=0.414

Table 6.1. The medians (interquartile range) of number, total mass and mean mass of larvae dispersing from two broods raised consecutively by a female *N. vespilloides*. The analysis includes replicates where the carcass was buried but no larvae were produced. In treatment 1 the first brood was raised biparentally, the second uniparentally. Both broods in treatment 2 were uniparental. Two females, one from each treatment, died between reproductive attempts.

Within treatments, second broods were less successful than first broods (Mann-Witney U tests): number of larvae (treatment 1 U=743.0, p<0.001; treatment 2 U=984.0, p<0.001); total brood mass (treatment 1 U=810.5, p<0,001; treatment 2 U=1008.0, p<0.001); mean larval weight at dispersal (treatment 1 U=852.5, p<0.01; treatment 2 U=680, p<0.001) suggesting a cost of reproduction to subsequent reproductive success.

If the difference in second brood success between treatments is due to presence of the male reducing the reproductive effort of the female, it is predicted that during the rearing of the first brood uniparental females suffer a greater weight loss than those with male help. In fact, uniparental females' weight increased during brood one (weight after/weight before x 100 ± SE = 101.06±6.74%) whereas biparental females actually lost weight (96.22±8.24%), the difference between treatments being significant (Mann-Whitney U=408.5, p=0.006). This difference may be due to a greater number of mites dispersing with single, rather than paired, females.

Analysis of the weight changes of the 34 single and 34 paired females who produced a brood in the absence of a mite population reveals no significant difference (Mann-Whitney U=1202.5, p=0.72).

6.3.2. Longevity of stored sperm

No difference in any measure of second brood success was found between broods raised by a single female with or without access to fresh sperm prior to burying the second carcass (table 2).

Treatment	1 (n=17)	2 (n=17)	Mann-Whitney U stat.
Number	25 (20-28.5)	25 (23.5-27)	U=285 p=0.678
Total mass	3.7 (3.07-4.14)g	3.89 (3.64-4.14)g	U=271 p=0.370
Mean mass	0.146 (0.135-0.165)g	0.156 (0.143-0.164)g	U=273.5 p=0.418

Table 6.2. The median (interquartile range) number, total mass and mean mass of larvae dispersing from second broods raised by single female *N. vespilloides*. The analysis includes replicates (one in each treatment) where the carcass was buried but no larvae were produced. First broods were raised without male assistance. In treatment 1 the female was provided with a male for 24h prior to provision of the second carcass. Treatment 2 females had no such access to a male.

6.3.3. Female parental effort with and without male assistance

Figure 6.1 shows the mean number of 30s intervals during 10 minute observation periods in which larvae were seen to receive regurgitated carrion from their mother in uni- and biparental broods. None of the differences in feeding rate are significant.

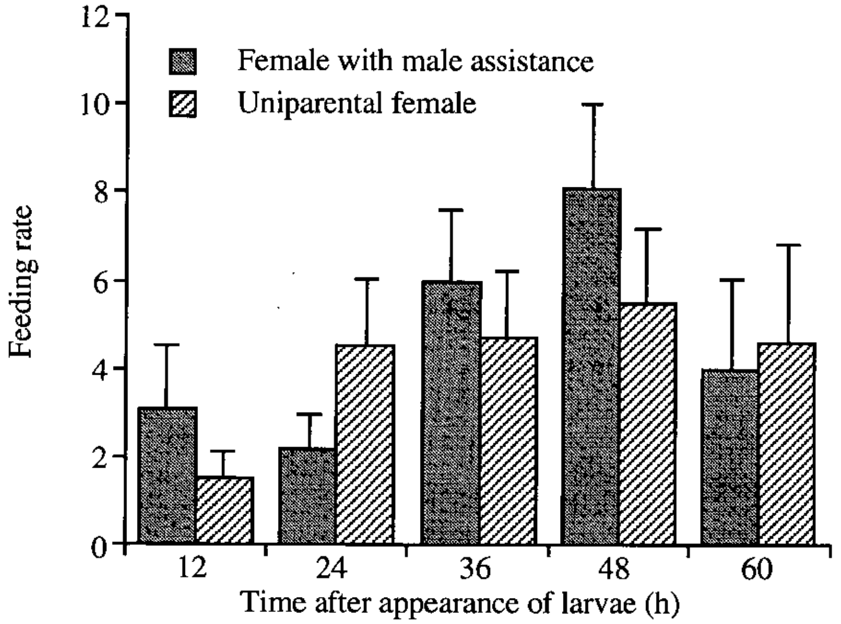

Fig.6.1. Mean rates of regurgitation by females with/without male parental assistance. Feeding rate is the number of 30s intervals within a 10 minute period (max. 20) in which the behaviour was observed. Bars show standard errors.

6.4. DISCUSSION

There are at least two possible interpretations of the greater second brood success achieved by females receiving male assistance in their first brood compared with females caring alone in both broods.

The first hypothesis is that females unassisted in their first brood carry greater numbers of mites than do assisted females into their second brood attempt due to there being no male present to dilute their cargo and that this larger mite load has detrimental effects on brood success. Second broods raised in the laboratory (where mite numbers may become artificially high) by females with their mite cargoes intact were smaller than those raised by females whose mites had been removed (Wilson & Knollenberg 1987). This was attributed to the mites attacking beetle eggs and larvae (Wilson & Knollenberg 1987). Indeed, one mite species (*Poecilochirus davydovae* Hyatt) that is phoretic on *N. vespilloides* has been observed, in the laboratory, to eat the eggs of its carrier (chapter 3; Blackman & Evans 1994). However, the practice of brushing off the excess mites from post-reproductive beetles maintains the laboratory mite population at a density that is apparently similar to that found on beetles in the field (pers. obs.). It is felt, therefore, that no detrimental effects of mite infection will be conferred on the broods of unassisted females and that consequently, differences in the numbers of mites carried by females in the two treatments do not account for the greater second brood success of assisted females. If such an effect does exist it is likely also to be important in the field, given the similarity of the mite numbers found on beetles in the field and in my laboratory population, and may be interpreted as a benefit of male care to females' future reproductive success.

Secondly, male assistance in the first brood may reduce the parental effort of the female leaving her with more reserves with which to raise a second brood. Single female *N. orbicollis* regurgitated to larvae and maintained the carcass significantly more frequently than did paired females but guarded the carcass significantly less (Fetherston *et al.* 1994). Since guarding behaviour entailed simply standing on top of the carrion (Fetherston *et al.* 1994) it is unlikely to be as energetically, or physiologically, expensive as regurgitation or carcass manipulation, suggesting that paternal care could indeed reduce the efforts of the female. The hypothesis is not supported by the data on the comparative weight change of assisted and unassisted females in that no difference was found between the treatments. It should be considered, however, that the costs of care are manifested in physiological processes that cannot be elucidated by the measure of weight change. This argument is perhaps particularly relevant with regard to *Nicrophorus*, who, throughout a reproductive attempt, have a supply of meat from which to feed.

The predicted reduced regurgitation rate by assisted females was not found (figure 6.1). This contrasts with the finding that single female *N. orbicollis* regurgitated to larvae and maintained the carcass significantly more frequently than did paired females but guarded the carcass significantly less (Fetherston *et al.* 1994). The hypothesis that paternal care reduces female parental effort may stand up, however, if a male's presence reduces the effort of his mate in an aspect of parental care other than feeding behaviour in *N. vespilloides*. Alternatively, the absence of a significant difference in feeding rate may be due to a failing in the method of observation: whilst making the observations it was noticed that single females were generally more unsettled than assisted females. I suggest that, in the absence of males, females are forced to assume a guarding role if the brood is considered to be under threat, which it may be when under observation, despite the precautions of a red light source and the resettling period after uncovering the crypt, whereas assisted females are able to leave defence duties to their mate. This problem could be overcome by the use of a video camera to record female behaviour so as to reduce disturbance further.

If the duration and quality of paternal care is to some extent evolutionarily determined by its effects on female reproductive success, then there must be an advantage to the caring male of his mate's larger subsequent brood. For instance, he might father a proportion of the second brood. In the current study it is likely that most or all of the second brood was fathered by the caring male since the female had no access to other males between broods. In the field, however, females may receive sperm from pheromone-emitting males (Müller & Eggert 1987) which will dilute the paternity of the caring male. Furthermore, females may often raise a second brood with a different male who will achieve a high degree of paternity (92%) by multiple copulations (Müller & Eggert 1989) allowing a brood 1 male only a low genetic payoff by sperm competition. But brood 1 males may gain a high degree of paternity of subsequent broods in the field if a significant proportion of natural broods are raised by single females. Of 258 mouse carcasses buried in the field by *N. vespilloides*, 100 (39%) were tended by a single female the day after burial (Eggert 1992), suggesting that the rewards to a caring male are, indeed, potentially high.

Prolonged paternal care is a striking feature of burying beetle reproduction. Both parents continue to regurgitate to larvae (considered the most important measure of parental care [Fetherston *et al.* 1990]) in *N. vespilloides*, into the fourth day after larval arrival in the crypt (Bartlett 1988). This provides potential for the male to reduce the costs of care to the female late in the reproductive cycle and, consequently, a possible explanation for the extended duration of male care. The time at which the male reduces the female's costs is amenable to experimental analysis.

The greater second brood success of assisted females is not explained by their more recent access, compared with unassisted females, to fresh sperm. If, in the field, the time interval between the burial of the first and second carcasses exceeds the 14 days allowed in this study, then a male's sperm may start to become infertile and he will achieve reduced paternity in his mate's subsequent brood. The male may, therefore, be staying with the brood in part to gain copulations which are traded by the female for help with parental duties. The female is unlikely to benefit from copulations alone as she will be able to replenish her sperm reserves through copulations with carrion-independent pheromone emitting males (Müller & Eggert 1987). Fetherston *et al.* (1990) observed that male *N. orbicollis* attempted to gain copulations after larval arrival at the crypt but none of these attempts were successful as he was always pushed away by the female. Bartlett (1988) states that, for *N. vespilloides*, if either of a pair goes outside the crypt they copulate as soon as they next meet, but he does not specify whether this behaviour continues after larval arrival when copulations could only raise his paternity in the female's subsequent broods. If gaining copulations is a selection pressure causing the male to remain with the brood then a conflict situation will arise if the male stays after ceasing to be of assistance to the female and, if there is some disadvantage of the male's presence as there may be if he feeds from the carcass or distracts her with his attempts at copulation. When pairs of *N. vespilloides* were bred on very small carcasses (5g) males deserted earlier, and sustained more injuries, than those on large carcasses (Bartlett 1988) implying that the duration of paternal care is being determined by the female (Bartlett 1988; Fetherston *et al* 1990; Pukowski 1933). If she needs to make less effort to raise a brood on a small carcass, the presence of the male may be costly to her if he cannot reduce her parental effort in return for copulations. Female *N. vespillo* were also reported to drive the male off after egg laying and care for the brood alone in 80% of cases (Pukowski 1933).

An implication of this study is that, contrary to expectation, in certain cases the benefits of paternal care may be greater to the male than to the female. In these instances the most important issue is not perhaps why the the male stays but rather why his presence is tolerated by the female.

The obvious next step would be to look at the paternity of second broods raised uni- and biparentally in order to see whether a caring male does benefit from the improved future reproductive success of his mate. On very large carcasses monogamy gives way to communal breeding and the mating system is variable (Eggert & Müller 1992; Trumbo 1992). This further complicates the relative costs and benefits of care to the male. It will be necessary to investigate the frequency of different mating systems in natural populations. In part this could be done by placing carcasses of varying sizes in the field and recording the mating system of beetles utilising the resource. Information about the natural availability of different sized carcasses will also be required and this data is very difficult to collect. However, comparative studies could be made at locations with different vertebrate populations (pheasant shooting estates, for example, will have a high proportion of very large carcasses) and the relative costs and benefits of males caring in order to increase the reproductive success of their mates could be established.

Chapter 7

General discussion

The benefits of parental care highlighted in this study of *N. vespilloides* can be broken down into 3 categories. Firstly, parental care can be regarded as an adaptation to increase the reproductive success of offspring (chapter 4). By regulating brood size, parents ensure that dispersing larvae are of a size that enables them to compete for carcasses and, hence, gain reproductive opportunities. Secondly, the parental care provided by males raises the survival of offspring by reducing the vulnerability of carcasses to take-overs (chapter 5). Finally, a component of paternal care increases the size of brood that a male's mate can raise in a subsequent breeding attempt and, consequently, improves his own reproductive success if he can father a proportion of the second brood by sperm competition (chapter 6).

I have made little attempt in this work to measure the costs of care to burying beetle parents. Fitness costs are notoriously difficult to quantify (Clutton-Brock 1991), and in burying beetles they are, perhaps, even more so. This is due to the almost complete lack of information about the availability of carcasses in the field and, therefore, the chances of gaining a further breeding opportunity that a parent sacrifices by caring for a current brood.

Though the idea is not a new one (Wolf *et al.* 1990), this is the first study to demonstrate empirically an effect of male parental care on future female reproductive success in a biparental species. It is feasible that similar selection pressures act on paternal care in other taxa, such as birds, where 90% of species are socially monogamous and display biparental care (Lack 1968). A difference in the reproduction of burying beetles and birds is that, while the former likely pair with different mates for each reproductive attempt, the latter frequently pair monogamously until separated by the death of one partner. Consequently, a caring male bird will probably be present during the rearing of his mate's second brood, and he will see a more direct improvement in his own fitness than will a male burying beetle who must rely on sperm competition to achieve paternity in the female's subsequent brood. Testing the hypothesis in bird species may be complicated by the removal of males necessarily preventing a female from renesting with the same male (Wolf *et al.* 1990).

Birds that raise successive broods with different mates would provide a model closer to the *Nicrophorus* system. Such mate switching between broods is rare in birds (Mock and Fujioka 1990), but it may occur when there is a high rate of male mortality which can be found, for example, in species where the male's parental role is in brood defence (Kendeigh 1952). Mate switching may also be common in species which, like burying beetles, utilise rich but widely spaced resources for breeding, making pairing with the same male logistically difficult. An example is the Quelea *Quelea quelea* which may travel hundreds of miles between breeding attempts in order to follow heavy rains which create local conditions ideal for breeding (Bruggers & Elliott 1989). A drawback is that the very reasons that prevent a female pairing with the same male over reproductive attempts also make measurements of the success of females across reproductive attempts very difficult.

Following Trivers' (1972) prediction that males should make adjustments in their level of parental care according to their certainty of paternity of their putative young, much of the current research in parental care is focused on that which is provided by the male in biparental species. The few studies which have found a clear adjustment of the amount of care with variations in the degree of paternity have been confined to species where the level of paternity is unpredictable from one breeding attempt to the next (Davies & Houston 1986; Dixon *et al* 1994). Many studies using birds have failed to find the predicted adjustment of levels of parental care by males in response to variation in their certainty of paternity (eg. Gavin & Bollinger 1985; Frederick 1987; Westneat & Sherman 1988; Whittingham *et al* 1993) and several theoretical models have been proposed to account for these negative results (Westneat

& Sherman 1993; Whittingham *et al.* 1992). So far no studies have been made on invertebrate species.

Burying beetle mating systems are variable and are governed at least in part by the size of the carrion resource on which they reproduce. On very small carcasses little or no care is provided by the male (Bartlett 1988), broods raised on larger carcasses receive biparental care and, as the resource increases further in value, monogamy gives way to communal breeding where the number of beetles of each sex is variable (Eggert & Müller 1992; Trumbo 1992). This variation reflects differences in the costs and benefits of caring for offspring on different sized resources. It will pay a male to remain with the brood if the expected reproductive benefits of doing so outweigh those provided by missed opportunities elsewhere, and this is more likely on a large carcass where the potential reproductive success is greater than on a small one. Like dunnocks *Prunella modularis* (Davies 1992) the variable mating system of burying beetles makes them an ideal study animal in which to examine the reproductive consequences of individuals' decisions (Trumbo & Eggert 1994).

To date, studies on burying beetle parental care have concentrated on the benefits of parental care to the developing brood (eg. Scott 1989, 1990; Trumbo 1990). The duration of parental care, and especially paternal care, is variable both within (Bartlett 1988) and between (Pukowski 1933) species of burying beetles but little attempt has been made to explain this variation (but see Bartlett 1988; Scott & Williams 1993; Scott & Traniello 1990; Trumbo 1991).

Following intra-sexual contests for medium sized carcasses which almost always result in burial of the resource by the largest male and female present (Bartlett & Ashworth 1988; Otronen 1988), defeated males often stay near the corpse to gain copulations with the resident female resulting in paternity of a proportion of the brood (Bartlett 1988). Monogamous males are, therefore, susceptible to reduced paternity and may adjust their provision of care accordingly although they achieve a high degree of paternity by frequent copulations with their mate before and during oviposition

(Müller & Eggert 1989). The unpredictable paternity of broods tended by caring males raises several questions. Do males facultatively adjust the level of care they provide to offspring in response to their perceived level of paternity in the current brood? A male may predict his paternity by assessing the number of other males that fought for the carcass and/or the time the female spends away from the carcass before and during oviposition. Do males increase their copulation frequency and/or ejaculate size in response to a perceived threat to their paternity? Is the level of care provided by the male correlated with his degree of paternity of the brood? Paternity may be established by PCR with randomly amplified polymorphic DNA. This method has been successfully used by Scott & Williams (1993) to assess paternity in *N.tomentosus*.

When reproducing on large carcasses burying beetle breeding systems are variable; they may be monogamous, polygynous, polyandrous or polygynandrous (Eggert & Müller 1992; Trumbo 1992). Factors other than resource size are likely to affect mating system and hence levels of parental care. Trumbo & Eggert (1994) found that when reproducing communally on large carcasses, polygynous males had greater reproductive success than when in either monogamous or polyandrous systems. Furthermore, males provided with a large carcass and access to a single female spent more time releasing pheromones to attract additional females than did males provided with a large carcass and four females (Trumbo & Eggert 1994). By altering the potential reproductive benefits to the male, the operational sex ratio induced a facultative adjustment of his signalling behaviour. Does a male similarly adjust his level of parental care in response to such variation in operational sex ratio? A polygynous male may be expected to provide more care, in terms of quality or duration, than one that breeds monogamously or polyandrously, due to the differences in his expected reproductive pay-offs between the mating systems.

The breadth and complexity of *Nicrophorus* social systems makes them a behavioural ecologist's Heaven on Earth. The increase in research on the genus over the last decade has uncovered as many new aspects of their ecology and behaviour as it has explained. This is a trend that will likely continue, given the comparative lack of understanding of the reproductive biology of burying beetles compared to vertebrates. It would be nice to think that some aspects of *Nicrophorus* biology have a wider relevance, and that they may shed light on the ecology of other social animals.

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Appendix

Blackman, S.W. & Evans, G.O. (1994) Observations on a mite (*Poecilochirus davydovae* Hyatt) predatory on the eggs of burying beetles (*Nicrophorus vespilloides* Herbst) with a review of its taxonomic status. *J. Zool. Lond.* 234:217-227.

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Observations on a mite (*Poecilochirus davydovae*) predatory on the eggs of burying beetles (*Nicrophorus vespilloides*) with a review of its taxonomic status

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Observational evidence is presented suggesting that the mite *Poecilochirus davydovae* Hyatt (Mesostigmata: Parasitidae) is predatory on the eggs of the burying beetle *Nicrophorus vespilloides* Herbst and that an increase in numbers of the mite in the laboratory accounts for a reduction in apparent beetle-clutch size over successive generations. Morphological adaptations for oophagy are described and physogastry is reported for the first time in the genus *Poecilochirus*. A new sub-genus *Physoparasitus* is proposed for the reception of *P. davydovae* and *P. subterraneus* and the female of *P. davydovae* is redescribed. The implications of the oophagous behaviour of *P. davydovae* on the mite-*Nicrophorus* relationship are discussed.

Contents

Introduction

Members of the genus *Nicrophorus* (Coleoptera: Silphidae) bury the carcasses of small mammals and birds on which they raise their broods. After carcass burial, eggs are scattered in the soil around the corpse where, for *N. vespilloides* at 20 °C, they develop for 56 h before hatching (Müller, 1987). The larvae then return to the corpse where one or both parents remain and regurgitate carrion to the brood and defend it and the carcass. The larvae disperse as third instars and pupate in the surrounding soil.

Mite-*Nicrophorus* associations are common. For example, in North America at least 14 mite species, representing four families, reproduce on carrion and disperse on one or more of five sympatric *Nicrophorus* species (Wilson & Knollenberg, 1987). One such association, between *Nicrophorus* species and mites of the genus *Poecilochirus* (Parasitidae), has been described as mutualistic (Wilson, 1983), although the degree to which the mite benefits the beetle is a matter of debate. A species of the *Poecilochirus carabi* complex destroys fly eggs (Springett, 1968) and it has been shown that the presence of this species has a beneficial effect on the breeding success of *Nicrophorus* spp. in the laboratory (Springett, 1968) and in the field (Wilson, 1983). Wilson & Knollenberg (1987), however, found that "*P. carabi*" only benefited the beetles in the field under extreme conditions, such as when the depth of carcass burial was shallow, allowing flies to lay eggs throughout the duration of development of the beetle larvae.

The presence of a cargo of various mite species has been found not to have any harmful effects on the breeding success of *Nicrophorus* spp. in the field (Wilson & Knollenberg, 1987). However, laboratory-maintained *Nicrophorus* spp. accumulated large numbers of mites after reproductive attempts, as they were unable to lose them by flying or burrowing into fresh earth (Wilson & Knollenberg, 1987). Such abnormal loads had a detrimental effect on beetle breeding success, and this was attributed to the mites attacking beetle eggs and larvae (Wilson & Knollenberg, 1987).

This study describes observations (by SWB) on the mite *Poecilochirus davydovae* Hyatt 1980, a species that associates with *N. vespilloides*, and investigates the possibility that its presence was linked to the decline in mean apparent clutch size of *N. vespilloides* over successive generations of laboratory culture, suggesting a detrimental effect of *P. davydovae* on the reproductive success of *N. vespilloides*. The review of the taxonomic status of *P. davydovae* and the redescription of the female is the work of GOE.

Observations on the feeding behaviour of *P. davydovae*

Materials and methods

A laboratory population of *N. vespilloides* was established from beetles caught at Penicuik, Midlothian for studies on their system of parental care. They were maintained at 20 °C with a 16 h : 8 h light : dark cycle and fed mealworms (larval *Tenebrio* sp.) *ad libitum*. Broods were raised on the carcasses of laboratory mice (*Mus musculus*) which were frozen soon after death and thawed before use. Each pair of beetles was allowed to breed in a clear plastic box measuring 225 mm × 120 mm × 90 mm depth, 3/4 filled with potting compost. Two other species, *N. investigator* caught at Penicuik, and *N. vespillo* from South Wales, were kept in the same laboratory.

To count clutch size, broods were checked every 4 hours and as soon as beetle larvae started to arrive on the carcass the count was made; the number of larvae being added to the number of unhatched eggs in the surrounding soil. This method is thought to give the most accurate assessment of clutch size, as oviposition is likely to be complete but culling of the brood by the adults (Bartlett, 1987*b*) will not have commenced.

If it was seen that a cargo of mites had accumulated that was large enough to hamper a beetle's movements, the excess was removed using a stiff paintbrush. This procedure usually only had to be applied to post-reproductive beetles, but newly eclosed individuals were sometimes treated.

Results and discussion

Poecilochirus davydovae was first seen during the reproduction of third generation *N. vespilloides*. A single physogastric female would typically be found adjacent to the remains of a beetle egg. However, egg remains were not always associated with a mite, and physogastric *P. davydovae* were not exclusively found with a *Nicrophorus* egg. Direct observations of feeding were not made. In several instances a number of *P. davydovae* larvae and eggs were also found with the *Nicrophorus* egg remains. Non-physogastric (unfed) female *P. davydovae* were found in Tullgren funnel samples of the chamber containing the carcass (crypt) and surrounding soil 24 h after beetle oviposition but not after 48 h.

Figure 1 shows the mean apparent clutch sizes produced by pairs of first, third and sixth generation *N. vespilloides*. Only whole eggs were counted; it was not possible to obtain a reliable count of the true clutch size by additionally counting partially eaten eggs because these egg remains were easily mistaken for lightly coloured particles in the soil unless a mite was found with them. Mouse carcasses varied from 10 to 30 g and *N. vespilloides* do not adjust clutch size over this range (Bartlett & Ashworth, 1988; Müller, Eggert & Furlkroger, 1990). First generation clutches were significantly larger than those of both third and sixth generation. Third and sixth generation clutches were not significantly different in size. For sixth generation broods, a count was also made of the number of physogastric *P. davydovae* females present at the time of the clutch size count. The clutch size and the number of mites were summed and the mean was not significantly different from first generation clutch sizes, suggesting that the reduction in clutch size between generations could have been due to the effects of *P. davydovae*, assuming that each female consumes one egg. Making this assumption, *P. davydovae* would have been taking about 1/3 of each sixth generation clutch. It would seem unlikely that this proportion of a beetle's clutch is taken in the field, since physogastric females were not noticed during either the first breeding attempts of wild-caught laboratory beetles (despite rigorous clutch size counts) or natural broods in the field (S. W. Blackman, unpubl. obs.). Furthermore, the observation from Fig. 1 that clutch size drops in later generations implies that *P. davydovae* undergoes a population increase under laboratory conditions. Alternatively, the decline in clutch size may be due to inbreeding depression in the *N. vespilloides* stock. Bartlett (1987*a*) reported a decline in breeding success of laboratory-bred *N. vespilloides* in the spring, the founders of the population having been trapped in August of the previous year. This reduction in success was apparent as a high brood failure rate; successful pairs produced broods not significantly different in size from those of previous generations (J. Bartlett, pers. comm.). The decline in success of the population used in the present study differed from the decline reported by Bartlett in two ways. First, it showed a reduction in clutch size after only three generations (about 16 weeks), and secondly, this was apparent as a decline in clutch size in all successful broods. An increased brood failure rate was not apparent. Furthermore, to reduce inbreeding in our population, it was ensured that the nearest common ancestor of a pair of beetles was a great-grandparent. It is unlikely, therefore, that the observed decline in breeding success was attributable to inbreeding depression.

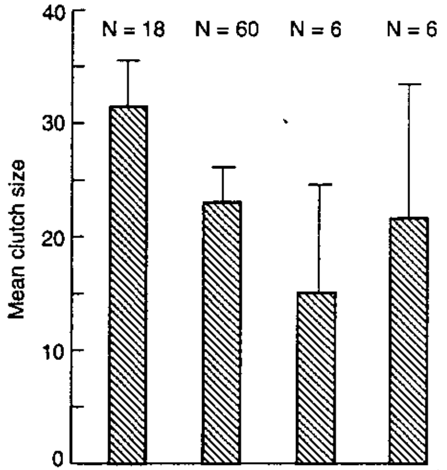


FIG. 1. Mean apparent clutch size of 1st, 3rd and 6th generation *N. vespilloides*. * Denotes where clutch size has been estimated by summing the number of eggs and the number of physogastric female *P. davydovae*. Bars indicate 95% confidence limits.

It may be that the *N. vespilloides* stocks were infected with *P. davydovae* from the populations of *N. investigator* or *N. vespillo* housed in the same laboratory. However, no *P. davydovae* were found on either species. *Poecilochirus davydovae* occurs on *N. vespilloides* in the field (Hyatt, 1980) and it is more likely that mite numbers increased in the laboratory because of the inability of the beetles to shed them by flying or by burrowing in fresh earth, and that the resulting large numbers of mites attack the eggs of *N. vespilloides* (Wilson & Knollenberg, 1987). Despite *P. davydovae* being outnumbered by "*P. carabi*" on *N. vespilloides*, all the mites found adjacent to the remains of a beetle egg were identified as *P. davydovae*. This may be explained by the laboratory procedure of brushing excess mites from beetles with an unnaturally heavy cargo: the deuteronymph of *P. davydovae* is significantly smaller than that of "*P. carabi*" and this could enable the former to shelter beneath a beetle's elytra, or in other body recesses, and escape removal. The numbers of *P. davydovae* would, therefore, be artificially high, whereas "*P. carabi*" would be nearer to a natural population density. Alternatively, there could be a difference in the natural histories of *P. davydovae* and "*P. carabi*". It is likely that members of the *P. carabi* complex have a different mite-host relationship from that of *P. davydovae*. This has been established for *Poecilochirus subterraneus* Müller, a closely related species to *P. davydovae*. According to Korn (1983), the successful reproduction of "*P. carabi*" is not dependent on the breeding of the beetle, whereas the reproduction of *P. subterraneus* "presumes coincidence with the breeding of *Nicrophorus*". Such a difference in mite-host relationship could be explained if *P. subterraneus* is in fact a specialist predator on the eggs of *Nicrophorus*.

It is also possible that the observed feeding behaviour is a product of some other aspect of the laboratory set up: for example, *P. davydovae* may consume the eggs of carrion flies in the field but in their absence is forced to take *Nicrophorus* eggs. This could be tested by presenting *P. davydovae* with a choice between the eggs of *Nicrophorus* and those of carrion flies.

A review of the taxonomic status of *Poecilochirus davydovae* with a redescription of the female

Poecilochirus davydovae was described by Hyatt (1980) from deuteronymphs collected from the silphids *Nicrophorus vespilloides* in S. England and *Thanatophilus rugosus* in Scotland. He considered his specimens to be conspecific with those from Western Siberia described and illustrated by Davydova (1969, 1976) as *Poecilochirus subterraneus* (Müller). Adults of *P. davydovae* were not seen by K. H. Hyatt who reproduced the illustrations of both sexes from Davydova (1976). The present material of unfed and physogastric females and of deuteronymphs of *P. davydovae* affords an opportunity to redescribe the female and to reappraise the taxonomic status of the species within the genus *Poecilochirus*.

Among the described species of *Poecilochirus*, two species, *P. davydovae* and *P. subterraneus*, exhibit a number of morphological features which clearly distinguish them from the remaining species. These features comprise, in the female, the presence of a digitiform anterior extension of the fixed digit of the chelicera, no increase in the number of setae on the opisthonotal shield from the deuteronymphal complement, a marked increase (about four-fold) in the length of the setae lateral and posterior to the opisthonotal shield in comparison with the condition in the deuteronymph and the presence of a spur on the femur (both species) and on the genu and tibia (*P. davydovae*) of the second pair of legs. Further, setae J3 are lacking in the deuteronymph and female, probably also in the male. The characteristics of the female of *P. subterraneus* are taken from Korn (1982) and Màca (1989). The deuteronymphs of both *P. davydovae* and *P. subterraneus* are also characterized by having the dark band of the sternitogenital shield extending posteriorly around the lateral and posterior margins of the shield (see figs 60B and 62A in Hyatt (1980)—a condition which does not occur in other described species of the genus.

The presence of a relatively small opisthonotal shield and the increased length of the posterior setae on the expansive area of corrugated flexible cuticle of the opisthonotal region are clearly adaptations for physogastry (Figs 2–4), a condition which is not known to occur in other species of *Poecilochirus* whose females show an increase in the relative size of, and in the number of, setae on the opisthonotal shield in comparison with their deuteronymphs. Reduction in opisthosomatic sclerotization is common in forms which engorge on fluids, such as many haematophagous species of the Macronyssidae, and allows for the distension of the idiosoma while the increased length of the mechanosensory setae compensates for the increased distance between their setal bases resulting from the stretching of the unsclerotized cuticle during engorgement. The deuteronymphs of *P. davydovae* and *subterraneus*, like other members or the genus, have a hyaline, membranous extension of the fixed digit of the chelicera (Fig. 8). However, the occurrence of a well-sclerotized anterior appendage of the fixed digit in females occurs only in *davydovae* (Figs 9, 10) and *subterraneus*. This structure, together with the strong dentition of the relatively shorter, stouter digits, suggests a specialized method of feeding in which the terminal hook of the movable digit is capable of penetrating unsclerotized body cuticle or the chorion of eggs. It is possible that the appendage of the fixed digit may also play a role in penetration or in effecting a hold on a smooth surface. Other species of *Poecilochirus* may include the eggs and first-instar larvae of flies in a diet consisting of other mites, insects and free-living nematodes, but lack such a cheliceral appendage (Wise, Henessy & Axtell, 1988). Could it be that *davydovae* and *subterraneus* are more selective in their feeding, for example, preying mainly on the eggs and instars of *Nicrophorus*, and that this is reflected in the form of the cheliceral digits? Some support for this may be seen in the closer association between *P. subterraneus* and *Nicrophorus* in the crypts than obtains in either the *P. carabi*-complex or *P. austroasiaticus*, to the extent that the reproduction of *P. subterraneus* is restricted to the crypts of *Nicrophorus* (Korn, 1983).

The form of the second pair of legs in the female resembles that of the male in the presence of spurs on one or more podomeres of a somewhat crassate appendage (Fig. 12). This condition also occurs in the female and deuteronymphs of the genus *Gamasodes*. Deuteronymphs of *Gamasodes* have been found clinging to the bristles of the abdomen of sciarid flies by the second pair of legs and the spurs play a part in attachment. There is no evidence, at present, that the females of *davydovae* are phoretic or that the second pair of legs are used for clasping during mating.

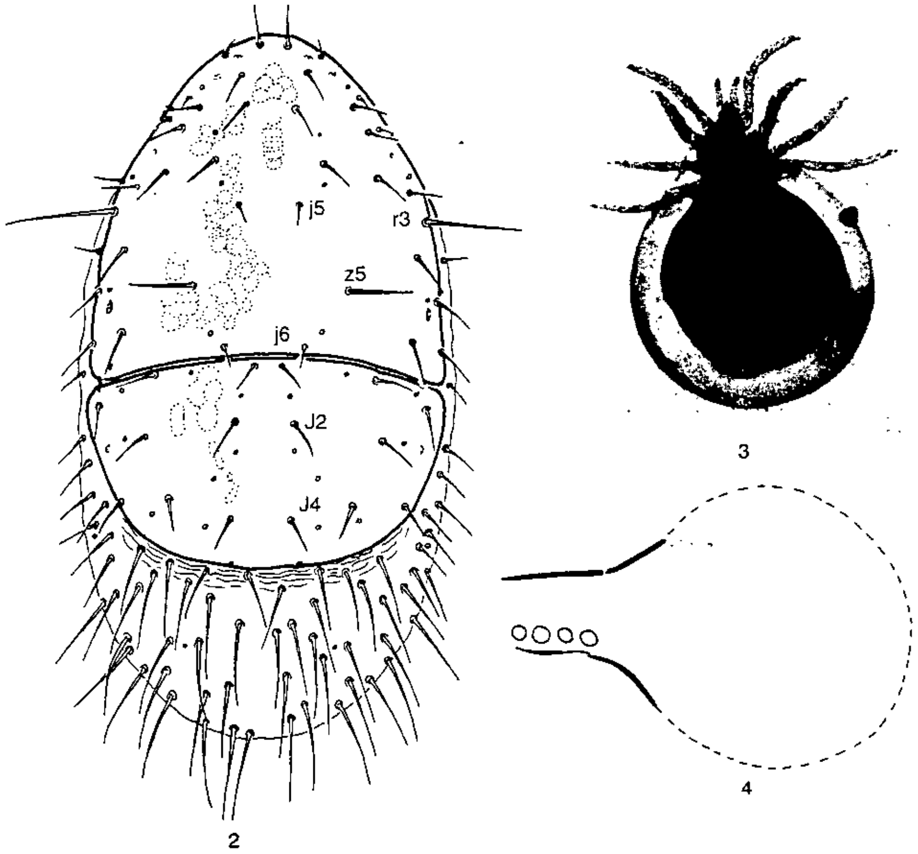
The *davydovae-subterraneus* group of species forms a distinct bio-morphological group which can be distinguished from the *carabi-austroasiaticus* group by a combination of morphological characters, discussed above. We propose to recognize the existence of the two groups by erecting a new subgenus, *Physoparasitus* (type: *Poecilochirus davydovae* Hyatt 1980) for the *davydovae-subterraneus* group. Thus, the genus *Poecilochirus* s. lat. consists of two subgenera, namely, *Physoparasitus* and *Poecilochirus* s. str.

The measurements given in microns in the following description of the female of *P. (P.)davydovae* are taken from specimens macerated in lactic acid or Vitzthum's fluid.

Poecilochirus (*Physoparasitus*) *davydovae* Hyatt

Poecilochirus davydovae Hyatt, K. H. (1980). *Bull. Br. Mus. Nat. Hist.* (*Zool.*) 30(5): 358–361.
Poecilochirus subterraneus: Davydova, M. S. (1969). *Akad. Nauk SSSR, Novosibirsk*: 27–28.
Poecilochirus subterraneus: Davydova, M. S. (1976). *Akad. Nauk SSSR, Novosibirsk*: 106–109.

Female: The idiosoma of non-physogastric females measures 660–700 μm in length and 320–335 μm in width at the level of setae j3. A physogastric female (Figs 3, 4) was approximately 1600 μm in length and 1300 μm at its widest point.



FIGS (2–4). *Poecilochirus (Physoparasitus) davydovae* Hyatt, female. Fig. 2, dorsum of the idiosoma of an unfed female; Fig. 3, physogastric female after partial maceration in Vitzthum's fluid; Fig. 4, schematic illustration of the inflated idiosoma of a physogastric female in lateral view.

The pronotal shield, 300–315 μm in length and lacking distinct ornamentation, typically carries 20 pairs of setae but in one specimen r2 was lacking on one side of the body. The humeral setae (r3) are the longest (92–98 μm) while setae z5 measure 60–65 μm in length and setae j5 and j6 are approximately 20 μm (Fig. 2). Gland pores gd4 lying near setae s5 are conspicuous. The distribution of other gland pores and poroids, which show some intraspecific variability, and the sigillotaxy are indicated in Fig. 2. The opisthonotal shield, 220–230 μm in length, bears only eight pairs of subequal setae measuring about 34 μm. Two pairs of setae (J5 and Z4) situated on the posterior margin of the shield in the deuteronymph, which has a complement of 10 pairs, are situated on unsclerotized cuticle in the female. Setae J3 are considered to be lacking on the basis of the presence of two pairs of pores and the atypically long distance between the second and third setae of the J series. The area of corrugated unsclerotized cuticle posterior to the opisthonotal shield is extensive and bears numerous setae of which the longest are 85–93 μm in length. It is the posterior of this region of the opisthosoma which swells so markedly during feeding. No eggs were found in the "unfed" females but a single egg was present in the physogastric females.

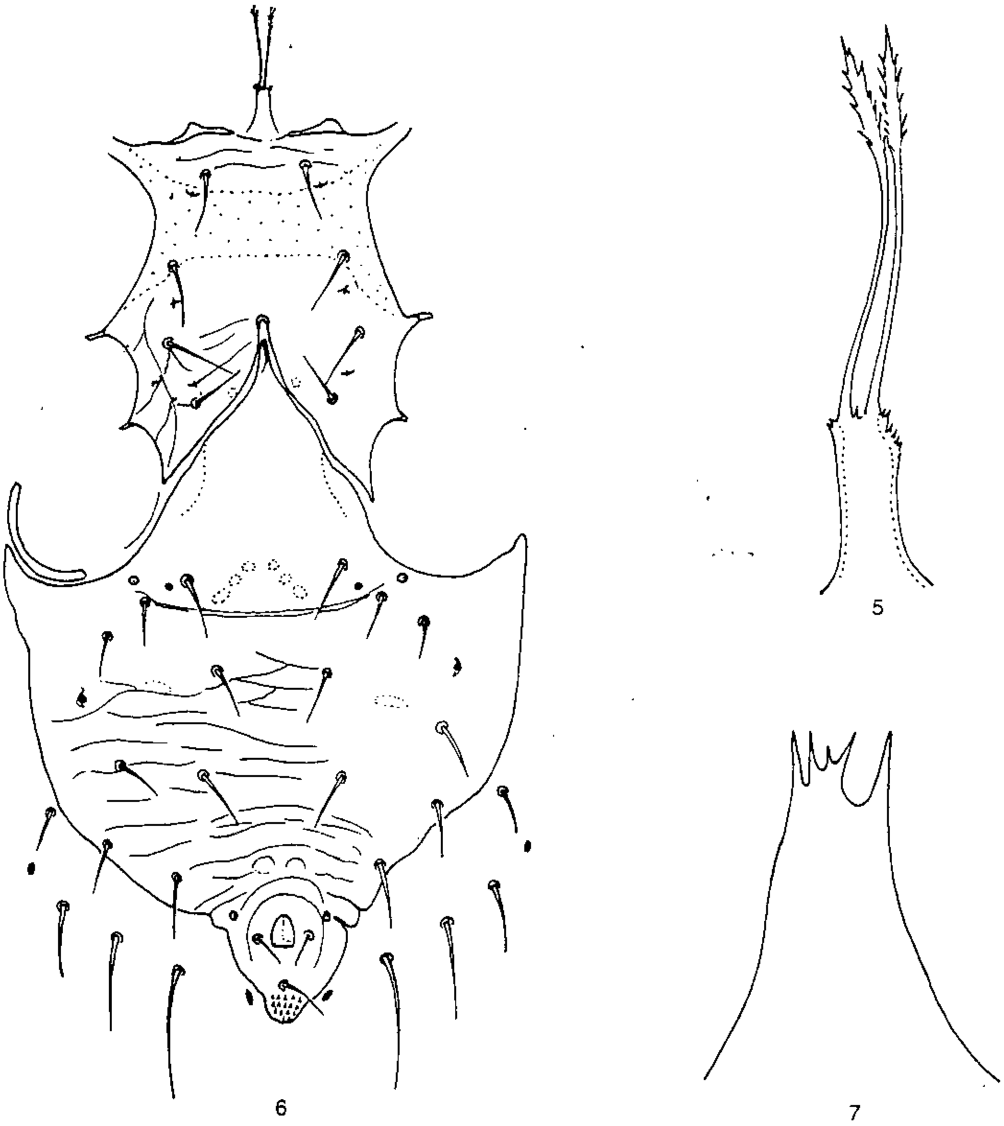
The biramous tritosternum has a narrow base and a pair of lacinae which are thickened and spiculate in their distal third (Fig. 5). The sterno-metasternal shield bears four pairs of setae and three pairs of slit organs. There is no division between the sternal and metasternal elements. In phase-contrast microscopy, a weak transverse dark band can be defined in the region between the first two pairs of sternal setae and is similar in position to that of the deuteronymph (Fig. 6). However, the extensive lateral extension of the band which is characteristic of the deuteronymphs of *Physoparasitus* is not apparent in the female. A pair of small presternal shields is present. The triangular genital shield is fused postero-laterally with the opisthogastric shield which bears seven pairs of preanal setae and the three setae (paired adanal and a postanal) normally associated with the anus. The cribrum is well developed. The peritrematal shield is weakly developed and free while the peritreme extends to about the level of the posterior margin of coxae I.

The gnathosoma is compact with the chelicerae differing in the shape and dentition of the digits from that of the deuteronymph (Figs 8, 9, 10). The terminal hook of the movable digit is particularly well developed and two or three denticles on its internal face gives it a serrated appearance. The dentition of the fixed digit shows some variation in the development of the smaller teeth and the illustrations of the digit in paraxial and antiaxial views are from different specimens. The anterior appendage of the fixed digit is well sclerotized dorsally and forms a finger-like process but is membranous ventrally. The *pilus dentilis* is minute. The normal two slit organs and a dorsal seta are present. The gnathotectum (Fig. 7) is produced into a relatively narrow gnathotectal process terminating in basically three prongs which may show secondary divisions. The chaetotaxy of the five free articles of the pedipalp is normal (2–5–6–14–15) and the apotele is three-tined. Seta al on the femur and al_1 and al_2 on the genu are spatulate distally. The corniculi are short and horn-like and do not accommodate the salivary styli dorsally while the hypostomatic processes (internal malae) are fimbriate (Fig. 11). Eleven transverse rows of denticles are present in the subcapitular groove and the distribution and form of the three pairs of hypostomatic and the pair of palpcoxal setae are shown in the figure.

The chaetotaxy of the podomeres is typical for the Parasitidae (Evans, 1963) although some unilateral variability has been observed, such as, the presence of 12 setae on femur I (a ventral seta lacking) and four or five, instead of the normal six, dorsal setae on tibia I. Leg II (Fig. 12) has seta av of the femur in the form of a hooked spur and setae av of the genu and tibia and av_3 of the tarsus inflated. Setae av_1, av_2, pv_1, pv_2, pl_1 and pl_2 on the tarsus are thickened with blunt or pointed apices. All ambulacra have strong claws and a lobate pulvillus. The pulvillar lobes are considerably smaller and the ambulacral stalk less sclerotized than in the deuteronymph in which the ambulacrum probably acts as a sucker and facilitates movement over, and attachment to, the cuticle of the host (Fig. 13).

Material: Three non-physogastric females from crypt contents and surrounding soil of laboratory-housed *Nicrophorus vespilloides* in the University of Edinburgh, Scotland. The physogastric females were associated with egg remains of *N. vespilloides* also under laboratory conditions. Specimens are deposited in the Collections of The Natural History Museum, London [formerly the British Museum (Nat. Hist.)].

Deuteronymphs of *P.* (*P.*) *davydovae* were collected from post-reproductive *N. vespilloides* and in crypts containing third instar larvae. No deuteronymphs of this species were found on *Nicrophorus vespillo* and *N. investigator* but these beetles carried deuteronymphs of *P.*(*P*) *subterraneus* and *P. carabi*-complex. Pale (teneral) deuteronymphs of these species have the dark bands of the sternitogenital shield less well defined than in the phoretic phase.

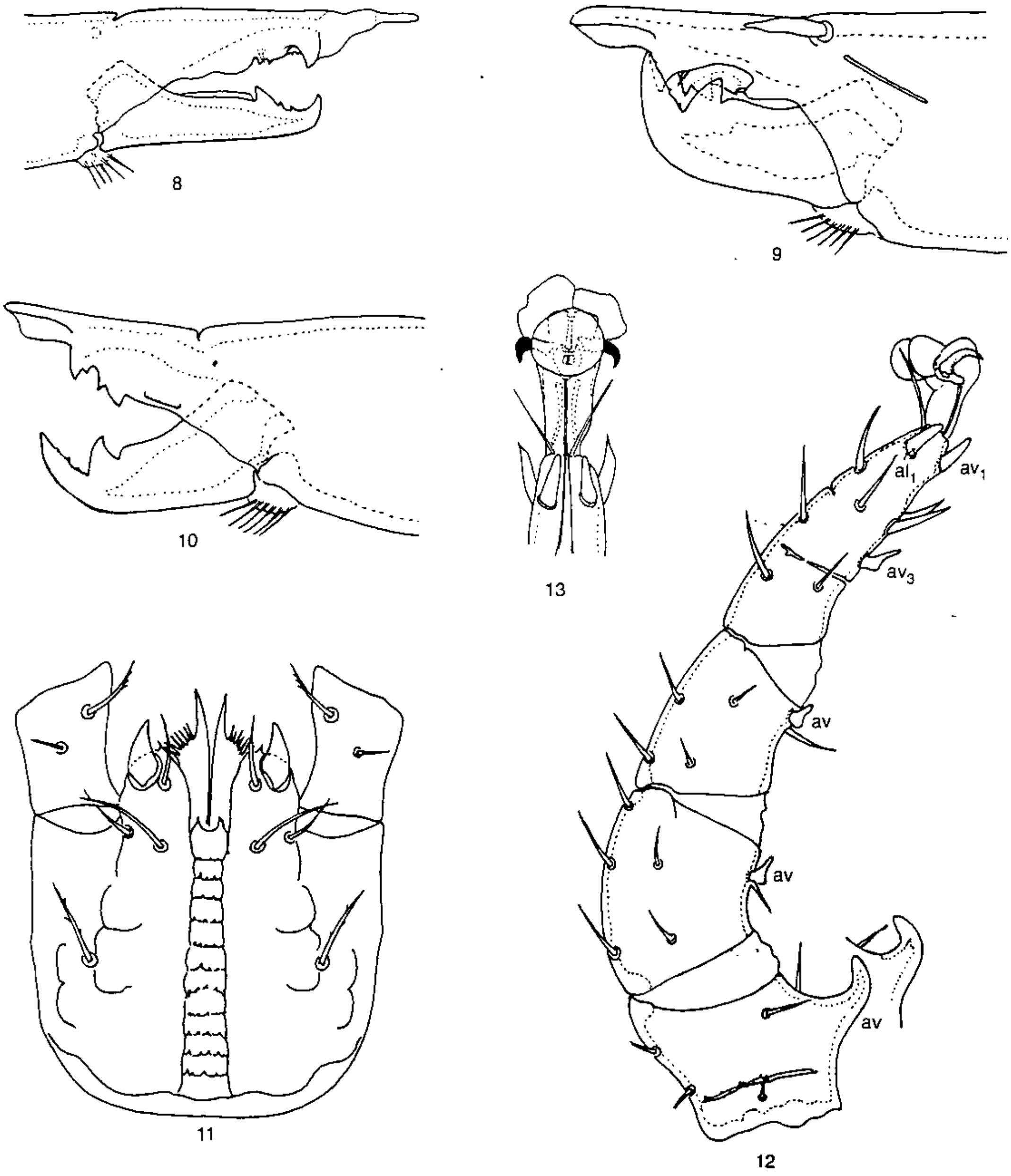


FIGS (5–7). *Poecilochirus (Physoparasitus) davydovae* Hyatt, female. Fig. 5, tritosternum; Fig. 6, ventral sclerotization and chaetotaxy of the idiosoma; Fig. 7, gnathotectum.

Hypopodes of *Pelzneria crenulata* (Anoetidae) were attached to the idiosoma and legs of many of the deuteronymphs of *P.(P.) davydovae* and *subterraneus* collected from adult beetles.

General discussion

It would appear, at least in the laboratory situation, that *P. davydovae* does take the eggs of *Nicrophorus vespilloides*. The observational evidence and the data on beetle clutch sizes are



FIGS (8–13). *Poecilochirus (Physoparasitus) davydovae* Hyatt, female. Fig. 8, chelicera of deuteronymph in antaxial view; Figs 9, 10, chelicerae of the female in antaxial (Fig. 9) and paraxial (Fig. 10) views; Fig. 11, venter of subcapitulum of female; Fig. 12, femur to tarsus of leg II of female; Fig. 13, ambulacrum of leg II of female. al, anterolateral seta; av, anteroventral seta.

supported by the presence of morphological features, namely adaptations for physogastry (an enlargement of the body allowing the mite to gorge on a discrete resource such as eggs) and for piercing the chorion of eggs. Evidence is still needed to show whether these adaptations actually enable *P. davydovae* to take fly eggs, which are not present on carcasses buried in the laboratory.

If predation on beetle clutches by *P. davydovae* does occur in the field, it may shed light on the observation that *N. vespilloides* parents cull a proportion of first instar larvae on 15 g carcasses (Bartlett, 1987*b*): if an unpredictable number of eggs are lost from each brood, then the laying of excess eggs may be an insurance against poor larval recruitment to the crypt (Bartlett, 1987*b*).

However, excess eggs are not laid on 30 g carcasses (Bartlett, 1987*b*) and there is no reason to suppose that recruitment is lower on smaller carcasses (Trumbo, 1990*a*). Furthermore, for the N. American species *N. defodiens* and *N. orbicollis*, parents consistently produced excess larvae on small carcasses in the field (Trumbo, 1990*b*), indicating that poor recruitment is rare. The theory may stand up if poor recruitment is rare but future reproductive opportunities are very limited so that success at each reproductive attempt must be maximized (Trumbo, 1990*a*). However, the reproductive effort on 30 g carcasses is not maximized since, on 75 g carcasses, *N. vespilloides* lays a larger clutch than on one weighing 30 g (Bartlett, 1987*a*). Trumbo (1990*a*) gives a more detailed discussion of these issues.

Using mite-*Nicrophorus* associations as a model, Wilson & Knollenberg (1987) argue that most phoretic associations (phoresy is the use of one animal for transport by another) evolve to eliminate negative effects on the carrier. However, predation by phoretic mesostigmatic mites on the eggs of the carrier species is not uncommon and occurs, for example, in the association between *Macrocheles muscaedomesticae* (Macrochelidae) and house flies in manure (Filipponi, 1955) and between *Arctoseius cetratus* and sciarid flies in mushroom compost (Binns, 1972). The cost to the beetles of the behaviour of *P.*(*P.*) *davydovae* may actually be negligible, particularly if only a small proportion of a clutch is taken owing to the low natural densities of *P. davydovae*. Also, the costs of producing a large number of eggs may be very low because of the beetles' high protein diet (Trumbo, 1990*a*). Furthermore, it should be remembered that the observed behaviour of *P. davydovae* could simply be a product of laboratory culture. If, for example, *P. davydovae* does in fact feed on the eggs of carrion flies in the field, it is likely to be beneficial to the reproductive success of *Nicrophorus* and the relationship will be one of mutualism.

It is perhaps significant that *P. davydovae* occurred only on *N. vespilloides*, whereas *P. subterraneus* was limited to *N. vespillo* and *N. investigator*. This observation, and the morphological similarities between *P. davydovae* and *P. subterraneus*, imply that these two species occupy a similar niche, specialist oophagous predator, on their respective hosts. The generalist feeder "*P. carabi*" was found on all three *Nicrophorus* species in the laboratory but Müller & Schwarz (1990) have demonstrated differences in carrier preferences and evidence for reproductive isolation between "*P. carabi*" from *N. vespilloides* and *N. vespillo*. *Nicrophorus vespilloides* and *N. investigator* are sympatric and there are differences in their reproductive seasonality and development time which could have acted as an ecological barrier and led to speciation within the two feeding niches (see Müller & Schwarz, 1990).

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