The behavioural ecology of the burying beetle *Nicrophorus vespilloides* (Coleoptera: Silphidae).

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Abstract.

A population of burying beetles (*Nicrophorus vespilloides* Herbst. Coleoptera: Silphidae) was kept in the laboratory for almost three years. All aspects of the life cycle were studied by breeding beetles on the corpses of mice. The beetles were also studied in the field.

In the laboratory, females became sexually mature 15-17 days after eclosion, but the final period of egg formation was delayed until a corpse had been buried. Adults fought for corpses, females as soon as they found a corpse, males only if a female was present at the corpse. If there was no female present, males buried the corpse together and signalled for a female, probably through release of a pheromone. The outcome of a fight depended on size; the larger individual always winning regardless of which arrived first at the corpse. The length of a fight increased with the size of a matched pair.

Eggs were scattered around the burial crypt, not laid in a side chamber as was previously believed. Clutch size varied with corpse weight; on the most common corpse weight of 10-30g it was about 25-30. On corpses weighing 10-15g more larvae hatched than the corpse could support and up to half the brood was killed and eaten by the parents. However, adults from broods raised on 10-15g corpses were still smaller than adults from broods on 25-30g corpses. Larvae which were light at dispersal from the corpse had a relatively high size:weight ratio at eclosion.

Both parents cared for the young. They drove off staphylinid predators and other burying beetles and the female was able to recognise her own mate. Larvae were fed as all three instars, but soon after moulting to the third were hardly fed at all. Males usually stayed until this time, but on 5g corpses they left the crypt soon after egg-laying and may have been driven away by the females. Parental care reduced lifetime egg production, but no effect was found on lifespan.

Chapter 1.

General introduction.

'This is the Burying-beetle, the Necrophorus, so different from the cadaveric mob in dress and habits. In honour of his exalted functions he exhales an odour of musk; he bears a red tuft at the end of his antennae; his breast is covered with nankeen; and across his wing cases he wears a double-scalloped scarf of vermillion.'

J.H. Fabre: 'The Glow-Worm and other Beetles', 1919.

1.1. Historical background.

Burying beetles (*Nicrophorus*, Coleoptera: Silphidae) are amongst the most remarkable of insects and some aspects of their behaviour have been known for many years. According to Pukowski (1933) recorded interest begins with Gleditsch (1752) who provided different species with small animal corpses, observing burial and the subsequent raising of broods, and with Melm (1755), who independently described the same events on the carcass of a mole. It was Gleditsch who first reported that a burying beetle could bury a corpse suspended from a stake by undermining the stake and causing the arrangement to fall. Results such as this convinced Lacordaire (L'intervation de la raison, 1834-1838) that in *Nicrophorus* he had found an insect with the ability to reason. The experiments of Fabre (1919) were designed to refute this view, and showed that the complex behaviour surrounding burial (a burying beetle can move a corpse several yards from unsuitable ground to soft soil, or can free it from tethering by chewing through the threads) needed no assumption of reasoning for its explanation.

The standard reference for the genus remains that of Pukowski (1933) who studied six species in the area around Frankfurt and produced an account based mainly on the behaviour of *N.vespilla*. Since then, most work has been concerned either with questions of population ecology and distribution (Easton 1979; Anderson 1982; Wilson et al 1984) or with specific aspects of behaviour (e.g. the detection of corpses (Shubeck 1968; Ernst 1972a,b) the production of sound (Niemitz & Krampe 1972) and the association with mites, particularly *Poecilochirus necrophori* (Springett 1968; Christie 1981; Wilson 1983; Korn 1983)). The literature is reviewed thoroughly by Easton (1979).

Some recent studies have also dealt with life history and behaviour, and it is in this category of work that the present study belongs. *N. vespilloides* and *N. investigator* were bred by Easton (1979), *N. mexicanus*, which can be found on dead rats in Mexico City, by Halffter et al (1983). Two North American species, *N. defodiens* and *N. orbicollis* were studied in the field and the laboratory by Wilson & Fudge (1984) and Wilson & Knollenberg (1984), adding to the earlier work on the latter species and on *N. tomentosus* by Milne & Milne (1944).

There are two patterns in the sequence of work I have described. The first is that of changing technique and interpretation with time. Lacordaire read reports of the behaviour of *Nicrophorus* and drew conclusions without experiments of his own. For this he was scorned by Fabre (1919), who proved his point with careful experimentation but provided no numerical data. The first quantitative results appear with Pukowski's (1933) work. Since then almost all published work has been based on experimental data, and yet the genus remains little enough known that description alone can still be valuable. To illustrate the point, the work of Ling (1957) is almost entirely descriptive but is still a valuable reference for any new study of *Nicrophorus*. In this study I report mainly the results of experiments but also observations that were not acted upon but which I believe show significant differences from reports on other *Nicrophorus* species and could be the basis of future work. This is discussed further in chapter 7.

The second pattern is that of addition and modification to what had gone before. The small number of published studies makes it easy to see how each led to the next. I have already described how Fabre (1919) set out specifically to destroy the claim for reasoning powers. In turn Pukowski (1933) reported that she began work with the intention of answering a single point described by Fabre (1919): that of how the several burying beetles which might find a corpse were reduced to a single pair. She went far beyond this first aim, describing field distribution, burial and egg-laying, and her work has been the inspiration for almost all subsequent studies. It is interesting to find that at the end she returned to Lacordaire and noted that though the claim for reason had been disproved, still the behaviour of *Nicrophorus* was such that she found it easy to understand why it had been made.

Thereafter, studies on burying beetles begin increasingly to lead on not only from previous work on the genus, but from predictions produced in response to results from other animals. The aims of this study were based on both kinds of source. I hoped to compare the breeding biology of *N. vespilloides* with that of *N. vespillo* as reported by Pukowski (1933) and since taken as applying to all species of burying beetle. One aspect to be compared was that of pair formation. This was an opportunity to compare two species (if indirectly) but also to extend Pukowski's (1933) work to include discussion in terms of recent theory on fighting and assessment of opponents. In the same way, I hoped to study clutch size and sex allocation, comparing with earlier work (Pukowski 1933; Easton 1979; Wilson & Fudge 1984) and putting the results in the context of theories of optimal egg number and sex ratio. Differences in behaviour between the sexes were also to be studied. Ultimately, the aim was to develop a picture of the life-history of *N. vespilloides* by studying each aspect of the life cycle and trying to identify the key 'decision-points' at which alternative strategies were available, partly defined by what had already happened and partly by the conditions prevailing at the time. I hoped to outline the alternatives and to examine their effects. Of course, to do this completely is far beyond the capacity of a single study, but what follows is the skeleton of such an attempt. It runs through the life cycle of *N. vespilloides*, and is organised according to the main events of that cycle.

1.2 The genus *Nicrophorus*.

A summary of the nomenclature, systematics and distribution of *Nicrophorus* is given by Easton (1979). In Britain there are said to be seven species of burying beetle (Kloet & Hinks 1945). Three of these are now found in Scotland: *N. humator*, *N. investigator* and *N. vespilloides*. The most common is the smallest of the three, *N. vespilloides*, and this was the species chosen for this study.

The life cycle is outlined in Figure 1.1. Overwintering occurs as the adult stage. The first beetles are trapped in the spring, in late April or May. They bury the corpses of small mammals or of birds and create an underground chamber, termed the crypt, around the corpse. Larvae develop on the corpse, feeding on the carrion themselves and being fed regurgitated carrion by their parents. In *N. vespilloides* both parents seem to care for the brood, although this may be unusual amongst *Nicrophorus* (Pukowski 1933). The larvae pupate in chambers in the soil around the site of the crypt and eclose about a month after hatching. These give rise to the adults which survive in diapause over the winter.

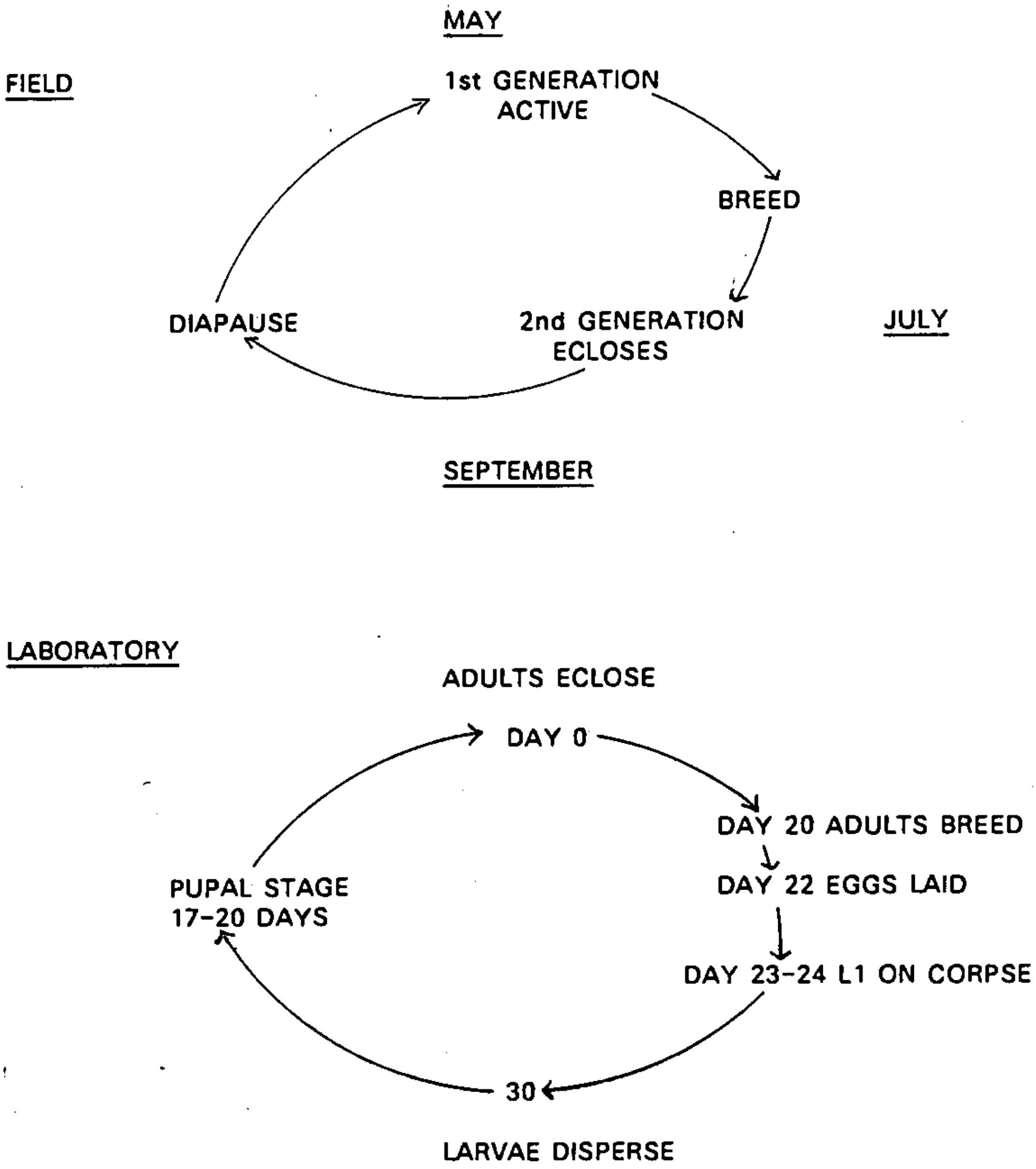


Figure 1.1

The life cycle of *N. vespilloides*.

1.3. Outline of chapters.

Chapter 2 describes the methods used to study *N. vespilloides* in the field and the laboratory and summarises some features of the field population: time at which adults occur in the field; the size and weight of trapped adults and their sex ratio at different times of year. These features are compared in the laboratory population in chapter 3, which also describes maturation, the period from eclosion to sexual maturity. It discusses ovary development, the possible abundance and availability of carrion in the field, and some aspects of competition for carrion. The next stage in the life cycle is that of finding and winning a corpse. Chapter 4 describes signalling for a mate and the fights by which pair formation is settled. The corpse is then buried and eggs laid. In chapter 5 I discuss some of the factors affecting clutch size, how adults may adjust the clutch they lay and some of the effects of brood size on the members of the brood. After hatching, the brood is cared for by its parents. Chapter 6 describes defence of the brood, feeding of larvae and the costs and benefits of parental care to the adults and to their brood. The role of the male in parental care is examined.

Chapter 2.

General methods and the field population.

'What a spectacle, in the spring, beneath a dead Mole! The horror of this laboratory is a beautiful sight for one who is able to observe and to meditate.'

J.H. Fabre: 'The Glow-Worm and other Beetles' 1919.

2.1 Introduction.

Although the outline of burying beetle biology has been known for more than two hundred years (Pukowski 1933), *Nicrophorus* has been infrequently studied and this is probably the first time that a population has been kept in the laboratory over several generations. This chapter describes the trapping of *N. vespilloides* in the field and subsequent maintenance and breeding in the laboratory between field seasons.

In 1985 field work was concentrated on reproductive biology and traps were set out only during some periods of the field season (which lasted from April to September). In the following year traps were left out continuously and a record of beetles caught was obtained for the whole season. Attempts were also made to trap, in the south of England, species of *Nicrophorus* other than those which occur in Scotland. I hoped to keep these species in the laboratory (particularly *N. vespillo*, since this is the species about which most is known [Pukowski 1933]) and compare their breeding biology with that of *N. vespilloides*.

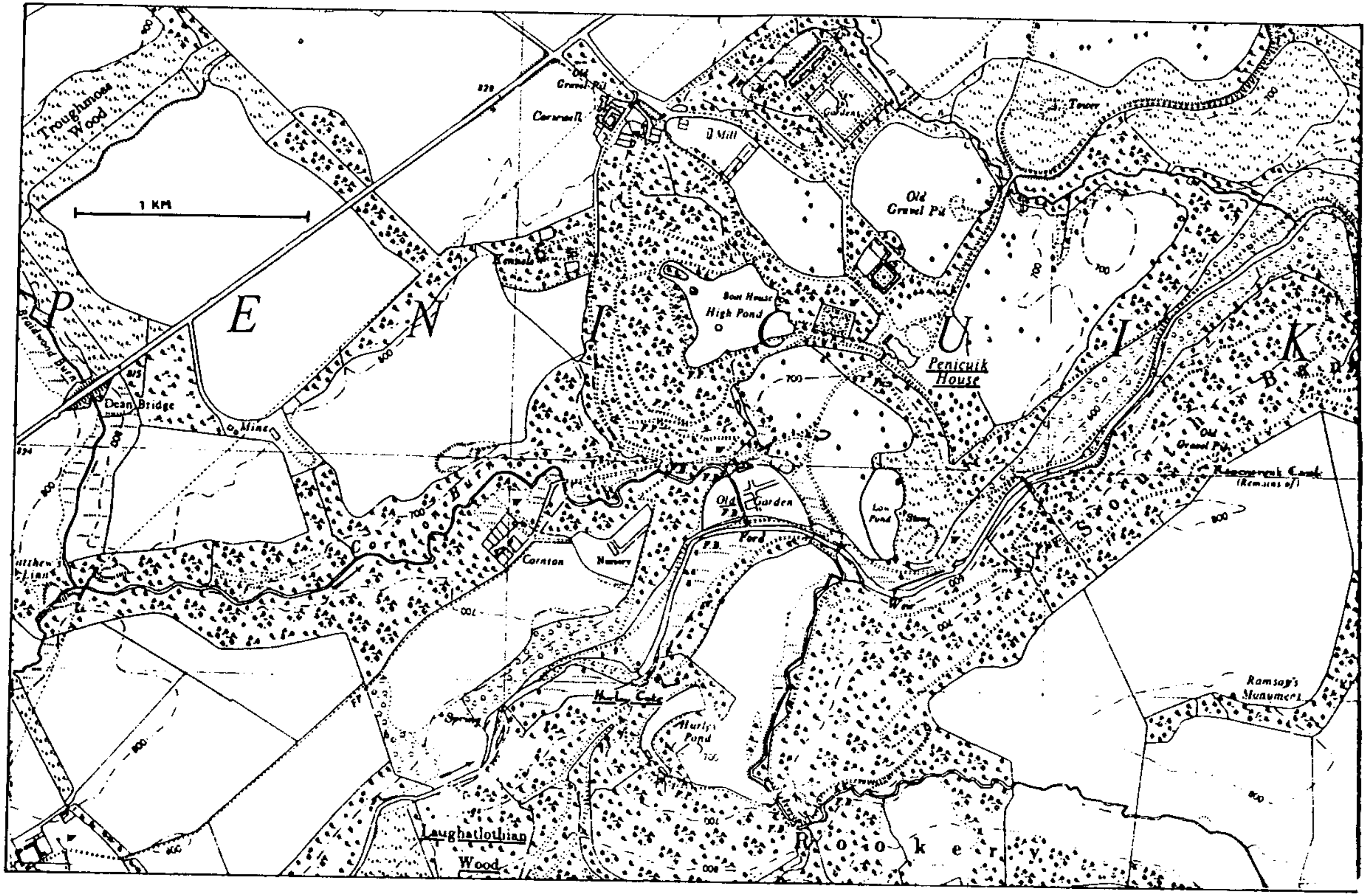
2.2 Study site and field methods.

The field site (Figure 2.1) was in the grounds of Penicuik House, 16 km south of Edinburgh (NGR NT217594). Occasionally, nearby areas of woodland were also used. All areas were open beechwood (*Fagus sylvatica* L.) with occasional oak (*Quercus robur* L.) birch (*Betula pendulans* L.) and sycamore (*Acer pseudoplatanus* L.). The ground vegetation was mainly bracken (*Pteridium aquilinum* L.), with patches of bilberry (*Vaccinium myrtillus* L.), bramble (*Rubus sp.*) and rhododendron (*Rhododendron sp.*). A study based near Frankfurt concluded that *N. vespilloides* was a woodland species and found it to be absent in 'meadow' where there was no forest nearby; in such open habitat, *N. vespillo* was the species usually trapped (Pukowski 1933). The only major field study on *N. vespilloides*, that of Easton (1979), was also done in deciduous or mixed woodland, on the shore of Loch Lomond and on Inchcailloch, an island in the loch.

The study areas were used in two ways. On some occasions traps were set out and the beetles caught were taken back to the laboratory for measurement and sometimes to be bred. At other times corpses of laboratory mice (*Mus musculus*) were laid on the ground and reproduction was studied in the field. In the latter case a line of 15 bamboo canes 100m apart was set out and a corpse was tethered to each cane with a metre of nylon thread so that it could be found again after burial. Canes were also used to mark the position of traps if beetles were to be brought to the laboratory. The traps (Figure 2:2) were glass jars 80mm deep and 90mm in diameter with plastic lids. A hole 1.5cm in diameter was drilled in the lid. The corpse bait was placed inside beneath a strainer so that its smell could still escape but flies and beetles could not reach it. The base of the jar was lined with small stones so that captured beetles could stand above collected rainwater and in some measure

Figure 2.1

The study site in the grounds of Penicuik House. Most field work was done in South Bank Wood, Hurley Cote and Laughatlothian Wood.


PENICUIK
Penicuik House
High Pond
Boat House
Low Pond
Stone
Old Garden
Ford
F.B.
Weir
Old Gravel Pit
Kennels
Mill
Caravan
Cornton
Nursery
Corn Burn
Mine
Dean Bridge
Troughmoss Wood
1 KM
Hurley Cove
Hurly's Pond
Spring
Laughatlothian Wood
Rookery
Ramsay's Monument
Ravensneuk Castle (Remains of)
Tower
Esk
700
800

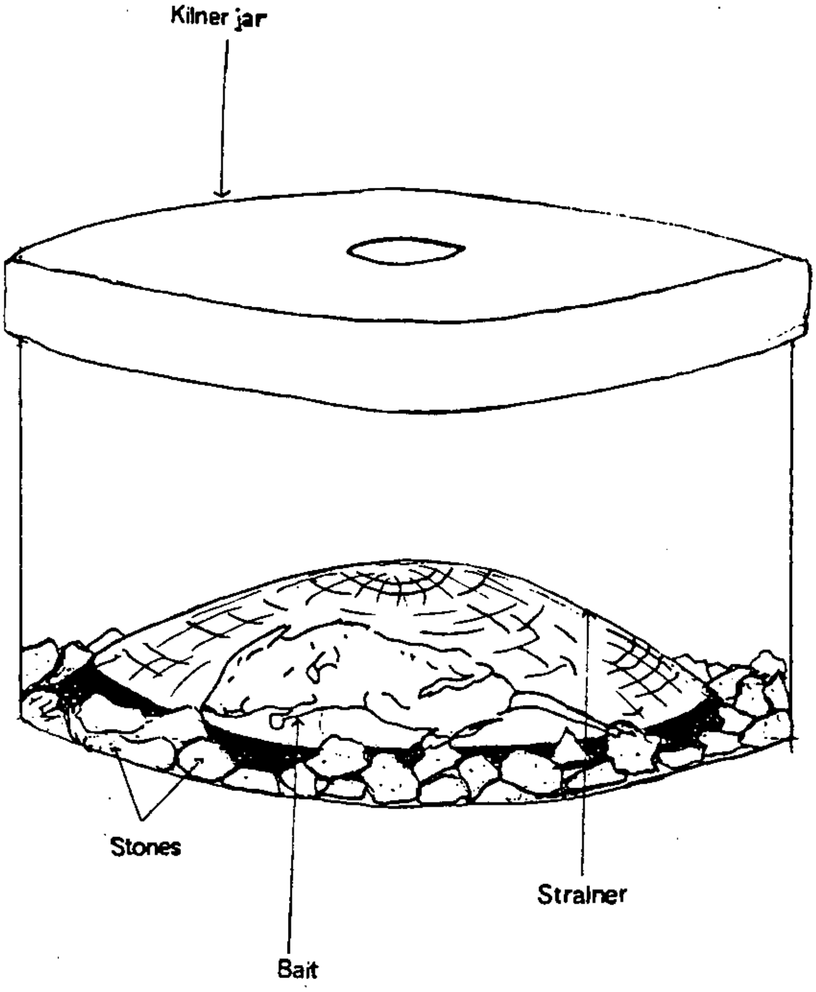


Figure 2.2

hide from one another.

In all cases the bait were laboratory mice. These were frozen within half an hour of being killed and thawed overnight before use. Burying beetles are attracted to a wide range of baits (Fabre 1919) lumps of meat apparently working as well as whole corpses (Christie 1981). Fish is said to be particularly effective (J.Parry pers.comm.) and cat food can be of limited use. The corpses of small rodents may be preferred to those of birds (Ling 1957). Pitfall traps of the type used in this study, which are baited with small corpses normally used by *N. vespilloides* for breeding, may capture a biased sample of the female population. A study on North American species of *Nicrophorus* found that small corpses in pitfall traps attracted a large proportion of mature females relative to that attracted by large carrion items which were intended to mimic carrion of the type used for feeding rather than breeding (Wilson & Knollenberg 1984). My traps would therefore have attracted mainly *N. vespilloides* ready to breed on the bait. The founding generation in each new laboratory population was used only to create the population and not for laboratory experiments. The reproductive status of females caught in my traps would therefore not have affected any of the data collected in this study.

2.3 The field population.

On the field site at Penicuik 15 traps were set out 100m apart through Lower South Bank Wood, Hurley Cote and Laughatlothian Wood (Figure 2.1). The traps were usually visited every two days. The species and sex of any *Nicrophorus* caught were noted. Beetles were usually taken to the laboratory and bred there, but some were marked and released. The three species found at Penicuik were easily distinguished. *N. humator* is the largest of the three and is completely black except for the orange clubs of its antennae. *N. investigator* and *N. vespilloides* both have the orange markings on their elytra typical of burying beetles, but the former is a larger beetle and has orange-clubbed antennae, while the antennae of the latter species are completely black. Sexing was done using the method of Easton (1979). He noticed that one more abdominal segment was visible in females compared with males and that the tip of the female abdomen was more rounded than that of the male. Dissection of beetles showed that the method was a reliable indicator of sex (Easton 1979).

A sample of the *N. vespilloides* found in the traps was taken back to the laboratory for measurements. Wet weight was measured to the nearest 0.01g. The measure of linear size used was that of the width of the pronotum at its widest point (following Christie 1981). This was found to be quicker and more convenient than measuring total body length and more accurate than measuring head width. The measurement was made with calipers reading to 0.05mm.

I chose the areas in the south of England in which to search for *N. vespillo* on the basis of past records. Forty years ago it and other species of burying beetle were common in Kent and East Sussex (J.Parry pers.comm.) and *N. vespillo* had also been trapped in the grounds of Bishops Stortford School (Ling 1957). I made three attempts to find *N. vespillo*, in May, July and August of 1986. In May I set traps around Tenterden and the north-west of Kent, in July in Ashdown Forest in East Sussex and in August in Hatfield Forest, a nature reserve near Bishops Stortford. In July 1987, a further attempt was made on a 20 mile circuit from Amberley in West Sussex.

Results.

Species trapped and life cycles.

At Penicuik the three species of burying beetle described above were found, the same three species as were trapped in a study at Loch Lomond (Easton 1979) and in North Yorkshire (Christie 1981). They found *N. vespilloides* throughout the field season but the population showed two peaks, one in May and one towards the end of the season, in July/August. My sample shows a similar bimodal distribution (Figure 2.3) with peaks in May and July. The record for *N. vespilloides* can be interpreted in terms of the life cycle outlined in chapter 1. Appearance of the overwintering generation in May causes the first population peak; the second peak in late summer is made up of surviving adults of the first-generation and young adults of the second generation, which eclose at this time (Easton 1979; Christie 1981). Between the two is a period when the first generation is breeding and therefore a proportion of the population is underground and not available to be trapped. Beyond this outline, the details of *N. vespilloides* field biology are not clear: the proportion of the first generation which survives to the second generation and then to the following year, for example, or how many breeding attempts are possible in this time are both unknown.

N. humator was found in large numbers at the beginning of the season and was then absent from traps until the end (Figure 2.4). *N. investigator* appeared in traps in July but few were caught: 25 in 1985 and 16 in 1986. These results also agree well with those of Easton (1979). The record for *N. humator* is not as easily interpreted as that for *N. vespilloides*. It has the same life cycle as *N. vespilloides*, but disappears from traps almost completely between the end of May and the end of August. *N. humator* is a larger beetle than *N. vespilloides* and is thought to breed on much larger corpses, those of

Figure 2.3

The weekly totals of *N.vespilloides* caught in 15 traps set 100m apart at the Penicuik study site between April and September, 1986.

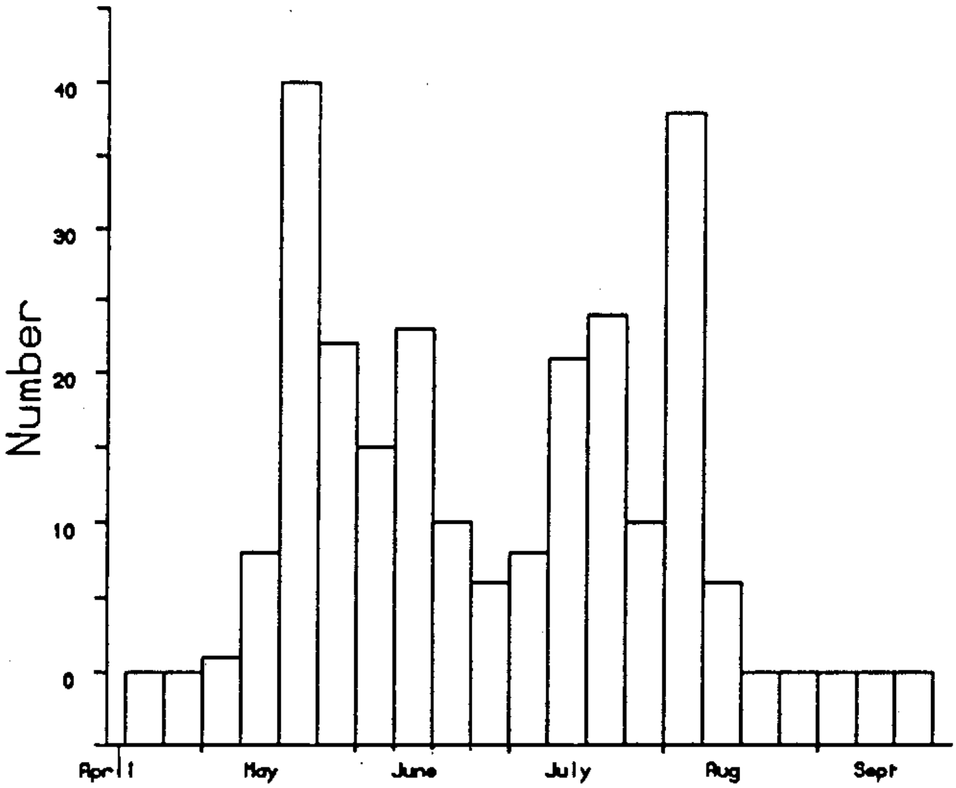
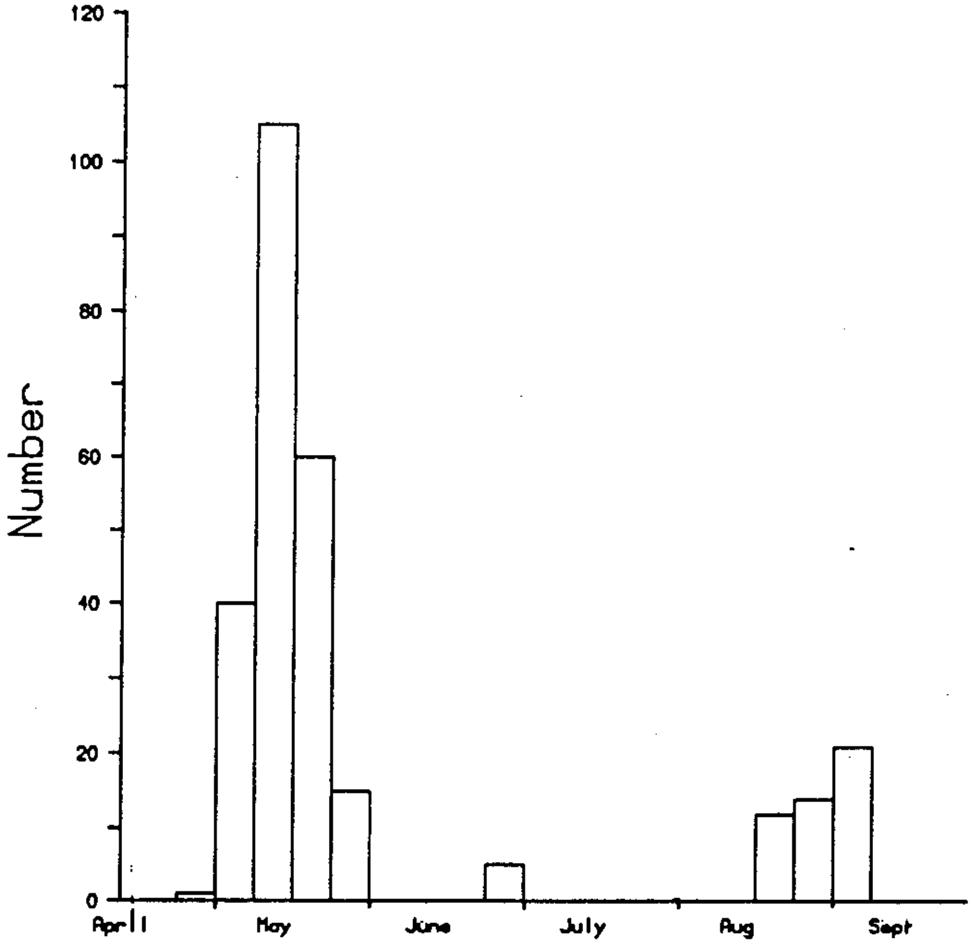


Figure 2.4

The weekly totals of *N.humator* trapped in 1986 at the same site.



sheep or deer, for example, or large birds. I have tried to breed it on mice in the laboratory but only once succeeded. It may be attracted to mouse-baited traps just after eclosion at the beginning and end of the season in order to eat the bait whilst developing to maturity, and then only respond to carrion suitable for breeding. This implies that differences in carrion type can be detected by smell. Some support for this is given by experiments on *N. orbicollis* (Wilson & Knollenberg 1984). As explained above, they found that small, fresh corpses in pitfall traps attracted a different sample of the female population from that attracted by large, decayed pieces of carrion, the former attracting a larger proportion of sexually mature individuals.

In laboratory experiments Easton (1979) found that *N. investigator* was able to displace *N. vespilloides* from corpses, and on the basis of these results and the observation that the appearance of *N. investigator* in his traps seemed to coincide with the disappearance of *N. vespilloides,* he argued that interspecific competition may occur in the field, with *N. vespilloides* being displaced. I found no evidence of *N. vespilloides* disappearing when *N. investigator* was first found in traps. The appearance of *N. investigator* in fact coincided with the second peak of the *N. vespilloides* population (Figure 2.3). However, I found so few *N. investigator* that any effect on the population of *N. vespilloides* would have been surprising.

The attempts to find *N. vespillo* were unsuccessful. In May, *N. humator* was found, and in July and August, *N. vespilloides*, though both in fewer numbers than at Penicuik. Only three *N. vespillo* were caught and these were all males. Two were found in Ashdown Forest, the other in Hatfield Forest. In 1987 no *Nicrophorus* at all were caught.

Characteristics of the field population of *N. vespilloides.*

The distribution of pronotum widths for *N. vespilloides* caught in the field is shown (Figure 2.5). There was considerable variation and pronotum width did not differ significantly between males and females in 1986 or 1985 (Table 2.1). The distribution of weights is shown in Figure 2.6. Wet weight of females was significantly greater than that of males in both seasons (Table 2.1). The relationship between pronotum width and the cube root of weight was plotted for both sexes (Figure 2.7). The greater relative weight of females might reflect a need for higher fat reserves in readiness for egg production.

The sex ratio of trapped beetles in 1985 and 1986 was compared for two periods, mid-May to mid-June, when a slight excess of males was recorded at Loch Lomond (Easton 1979), and mid-July to mid-August. In both years I found a significant male bias from 1:1 in the earlier period but not in the latter. There was no significant male bias between the two periods in either year (Table 2.2). This is discussed further in chapter 3 when the sex ratio of laboratory populations is presented.

2.4. Keeping *Nicrophorus.*

A population of *N. vespilloides* was kept in the laboratory between field breeding seasons. Throughout the winter, when adults would normally be in diapause, a temperature of 21°C and a light:dark cycle of 16h:8h were maintained and the beetles remained active and able to breed.

They were kept in plastic food boxes, 225mm x 120mm x 90mm, threequarters filled with Levington's potting compost. This was found the most suitable of the varieties of soil and compost tried, but still humidity had often to be adjusted by adding water or leaving the compost to dry for a day or two before use. If the soil is too dry adult survival seems to be reduced and the burial chamber is not properly formed; if too wet egg hatching and success of

Figure 2.5

The pronotum widths of 120 *N.vespilloides* trapped at Penicuik in 1986.

mean = 4.91mm

95% CL = 0.09.

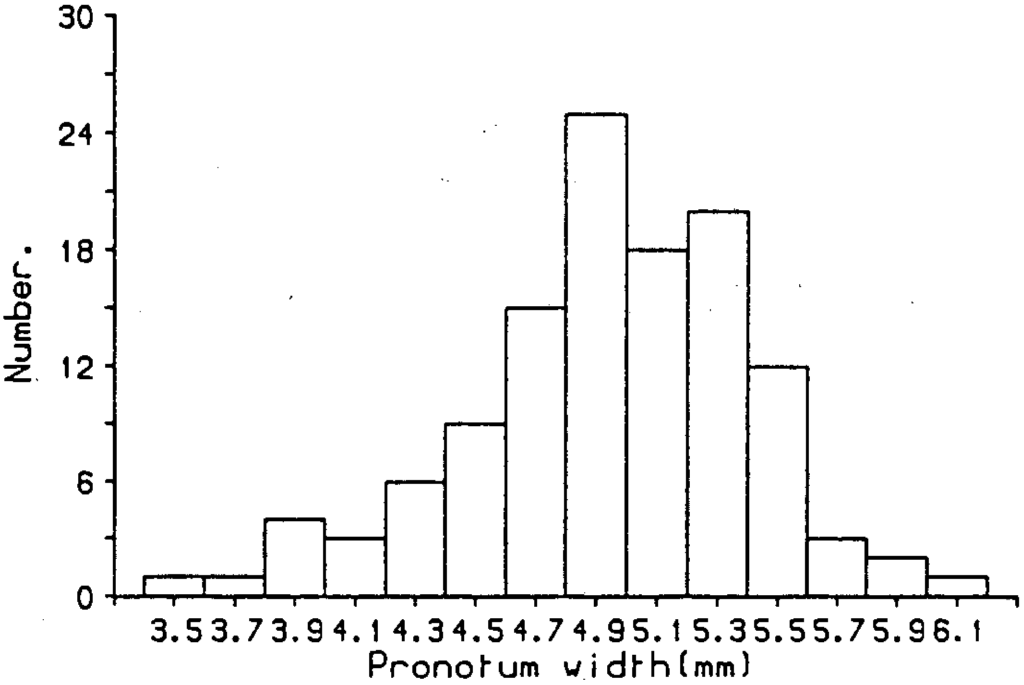


Table 2.1

a. 1985.

	Females	Males	t test
n	25	27	
Width(95% CL)	4.90 (0.18)	4.78 (0.14)	n.s.
Weight(95% CL)	0.23 (0.01)	0.20 (0.02)	P<0.05

b. 1986.

	Females	Males	t test
n	49	71	
Width(95% CL)	4.99 (0.13)	4.85 (0.11)	n.s.
Weight(95% CL)	0.22 (0.02)	0.19 (0.01)	P<0.05

Weights(g) and pronotum widths(mm) for a sample of *N. vespilloides* trapped in 1985 and a sample from 1986. In both years females were significantly heavier than males, but the pronotum widths of the two sexes were not significantly different.

Figure 2.6

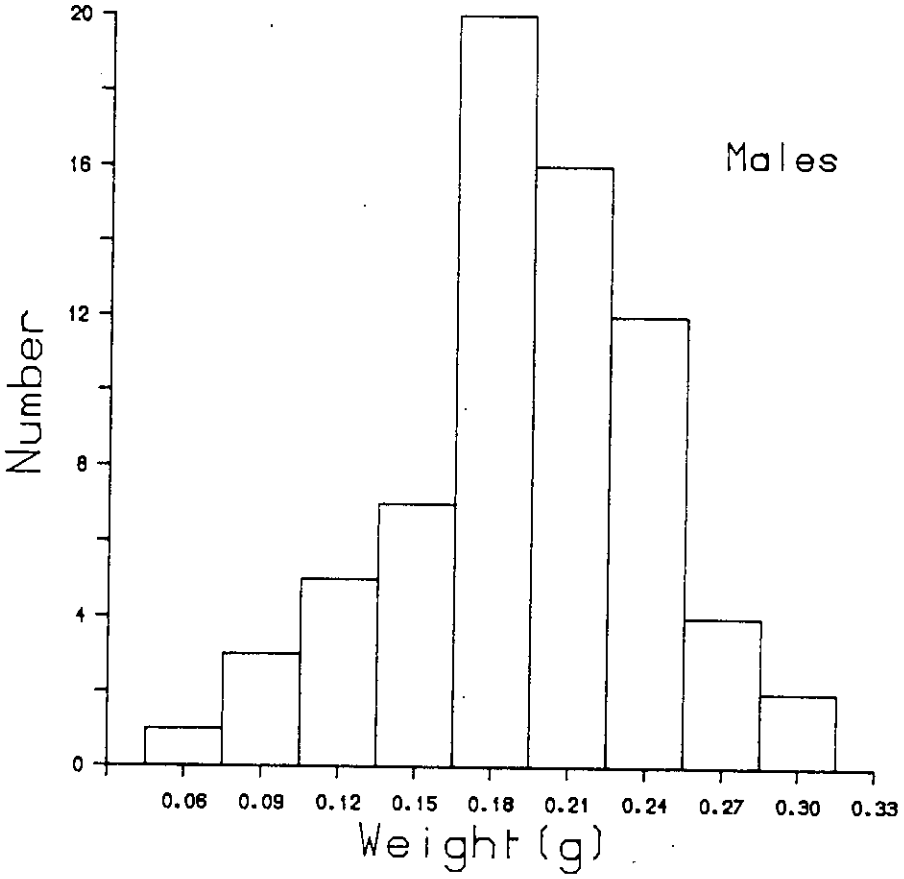
The wet weight of 49 female *N.vespilloides* and 71 male *N.vespilloides* trapped at Penicuik, 1986.

mean female weight = 0.22g

95% CL = 0.02

mean male weight = 0.19g

95% CL = 0.01


Males
Number
0
4
8
12
16
20
0.06
0.09
0.12
0.15
0.18
0.21
0.24
0.27
0.30
0.33
Weight (g)

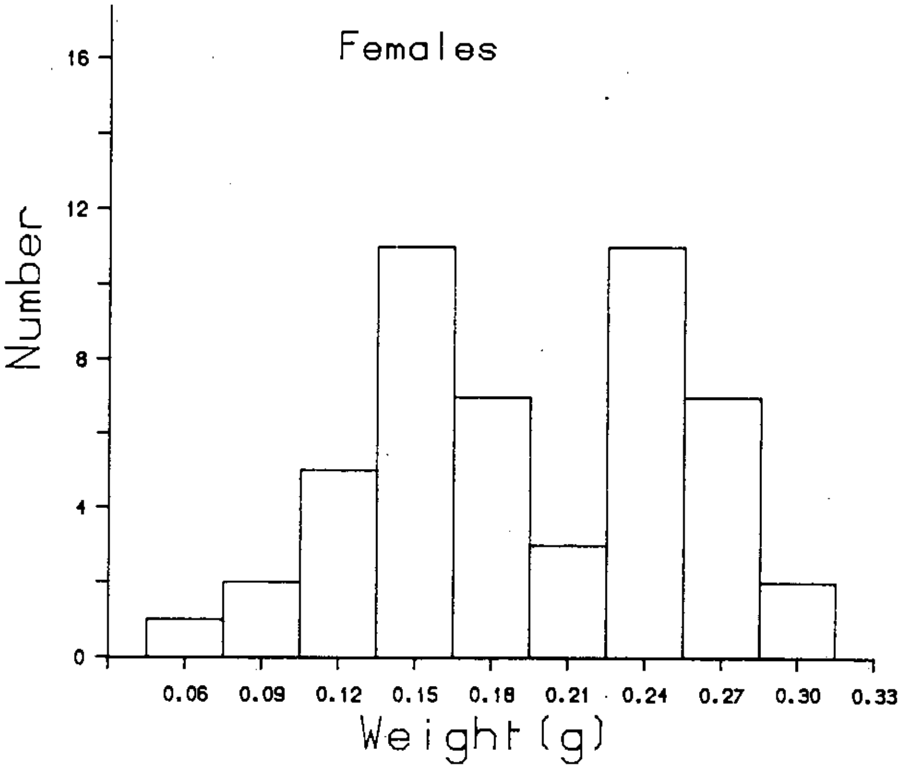

Females
Number
0
4
8
12
16
0.06
0.09
0.12
0.15
0.18
0.21
0.24
0.27
0.30
0.33
Weight (g)

Figure 2.7

Cube root of wet weight plotted against pronotum width(mm) for 49 female and 71 male *N.vespilloides* trapped at Penicuik in 1986.

regression equation for females:$y = 0.11x + 0.048$

$r^2 = 0.86$

regression equation for males: $y = 0.11x + 0.05$

$r^2 = 0.88$

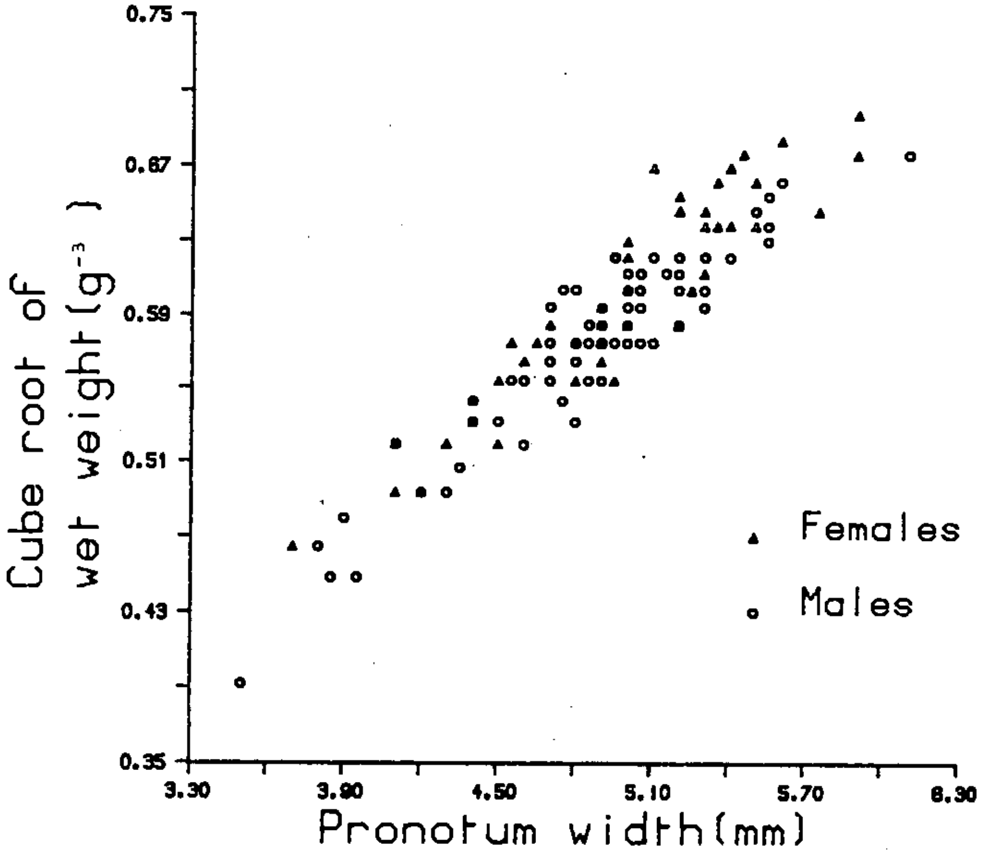

0.75
0.67
0.59
0.51
0.43
0.35
3.30
3.90
4.50
5.10
5.70
6.30
Pronotum width(mm)
Cube root of
wet weight(g⁻³)
▲ Females
○ Males

Table 2.2.

	a. 15.5.85–5.6.85	b. 15.7.85–10.8.85
	n	n
Female	23	20
Male	39	27
χ^2 for deviation from 1:1		
	$P<0.01$	$P>0.05$
2 x 2 χ^2	$P>0.05$	

	c. 10.5.86.–15.6.86	d. 20.7.86.–1.9.86.
	n	n
Female	43	36
Male	75	42
χ^2 for deviation from 1:1		
	$P<0.01$	$P>0.05$
2 x 2 χ^2	$P>0.05$	

The sex ratio of samples of *N. vespilloides* trapped at Penicuik over the two periods shown in each of two field seasons. In both seasons the sex ratio is significantly male-biased in the earlier period but not significantly different from 1:1 in the later. The sex ratio is not significantly biased between the two periods in either season.

pupation are poor.

The beetles were fed on mealworms (larvae of *Tenebrio*); they also ate carrion during breeding and readily fed on one another. They are willing to eat a wide variety of food, from dipteran larvae (Steele 1927) to earthworms (Easton 1979) and even catfood. Another carrion beetle, *Necrodes surinamensis*, was found to take lettuce, hamburgers and peanut butter in addition to more predictable items (Ratcliffe 1972) and probably *Nicrophorus* could be kept on an equally varied diet.

The population was kept in this way with only occasional difficulties. Adults sometimes died in large numbers if kept for long in the same compost; boxes were therefore cleaned out every ten days or so and uneaten pieces of food removed whenever the beetles were fed. Breeding success declined suddenly towards the end of the spring following the year in which the founders of the population were trapped (see section 2.6); the stock was therefore replaced early in the summer by beetles caught in the field and replaced again towards the end of August.

2.5. Laboratory breeding.

Breeding took place in the plastic boxes already described. The corpses used were those of laboratory mice. Normally one female and one male was placed with each corpse. After the corpse had been buried and the burial chamber or crypt formed, the soil above the corpse was removed and replaced with a fallen beech leaf. This marked the position of the corpse and could be lifted away to allow the crypt to be watched. Pukowski (1933) let her beetles bury between two glass sheets and was able to see into the crypt from the side, but I found that the beetles never left the glass without a layer of compost on the inside, even if light was kept out during burial. The leaf covering, if lifted away with care, allowed observations to be made without any noticeable disturbance of the adults.

Larvae were easily handled without ill-effects. Eggs, however, had to be treated with great care if they were afterwards to hatch. The most successful technique was not to touch the eggs directly at all but to lift away with forceps the lump of compost on which each lay. A similar difficulty and solution were afterwards reported by Cameron Easton (pers. comm.).

Larvae were counted as first, second or third instars and replaced in the crypt without difficulty. They were handled with forceps and loose earth removed with a paintbrush. They could be transferred from crypt to crypt without the foster-parents rejecting them (also found by Easton (1979)); parents could also be transferred between mice without harm to their new brood. Larvae could not, however, be given to parents which had not already hatched a brood of their own: in these cases the transferred larvae would be eaten.

Once the larvae had dispersed from the corpse they were placed in new compost. The pupal stage is that of highest mortality in lab and field (Easton 1979) and fragments of mouse or mouse hair in the old compost can be the innoculation site for mould to which the pupae are extremely susceptible. The humidity of the compost was also found to be important in this respect: there must be enough moisture to allow the larvae to form a chamber in which to pupate, but pupae easily rot if the compost is too damp. Pupae were checked every few days and any mould on the soil surface removed.

All burying beetles carry mites (Neumann 1943; Christie 1981); these are of arguable value in beetle reproduction (see chapter 3). They breed on the corpse buried by their hosts and large numbers gather on the *Nicrophorus* adults when these are about to leave the corpse. In flight a beetle is said to lose most of them (Springett 1967), but in the laboratory they stay in such numbers as to hinder the beetle in movement and feeding. The majority were therefore brushed away until only ten or so remained visible on the host, this being the situation usually seen in the field.

2.6. Laboratory measurements.

As in the field, the size of adult beetles was measured with calipers reading to 0.05mm. The measurement was made across the pronotum at the widest point. After eclosion the sexes were kept apart until their use in experiments.

Beetles were marked by warming a mounted needle at a flame and scorching a number on to the orange markings on the elytra. The metal need not be heated strongly and the process seems to do the animal no harm. No paint or varnish that was tried would stick to any part of the cuticle for more than a day. Easton (1979) used a coded mutilation of the cuticle but in the laboratory scorching was found easier to do and the result more readable. In the field the technique involved using a gas stove to warm the needle and was therefore awkward.

Beetles of the same brood were usually given the same number and this was then recorded alongside the numbers of the parents of the brood (assuming complete paternity by the male). To reduce inbreeding, beetles were not paired if any of these four parental numbers was the same, resulting in the nearest common ancestor being a great-grandparent.

Even with these precautions the viability of the stock declined towards the end of the overwinter season as described in section 2.4. This may have been due to inbreeding depression, a nutritional problem or parasite load accumulating over several crowded generations. Nematode parasites of burying beetles can cause sterility or reduced fertility (Nickle 1972) and under laboratory conditions such parasites might have accumulated over the year to a significant level. For almost the whole season, however, beetles bred predictably and produced offspring which appeared healthy and behaved normally. As far as I am aware, the conditions under which the population was cultured introduced no important distortion into the results which were found. *Nicrophorus* is suitable for long-term and fairly large-scale experimental work. Manipulations of the sort needed for experiments on clutch size and parental care can, with experience, easily be done.

Chapter 3.

Eclosion to reproduction.

'The four winds of heaven bore forth in all directions the odour of the carrion; and the undertakers hurried up...'

J.H. Fabre: 'The Glow-Worm and other Beetles' 1919.

3.1 Introduction.

The behaviour of *Nicrophorus* has hardly been studied except in the context of reproduction. However, for at least two weeks after eclosion (Springett 1967) and for an unknown period after each breeding attempt, burying beetles may hold a place in a community quite different from that in which they breed. It has been suggested that they behave as generalist predators at this time and are ecologically closer to predatory staphylinids or carabids than to obligate carrion feeders (Easton 1979). Corpses too large or too far decayed to be useful for breeding may be one type of feeding site; immature beetles may be attracted to these whilst mature individuals are attracted to small carrion suitable for breeding (Wilson & Knollenberg 1984). Females caught in traps baited with small carrion are usually inseminated (Christie 1981) and insemination may occur during aggregation at food sites. This pre-reproductive period may affect eventual reproductive success through its effects on nutritional status. This chapter describes some characteristics of a laboratory population of *N. vespilloides* at eclosion and maturity and compares the results with the field data summarised in the previous chapter. The abundance and availability of carrion and some of the factors affecting the success of *N. vespilloides* in obtaining a corpse on which to breed are also discussed.

I first discuss size and weight at eclosion. The size of adult burying beetles has an important effect on their ability to win a corpse for breeding in fights with other *Nicrophorus* (chapter 4) and on subsequent reproductive ability (chapter 5). Size is partly established during larval development and data at eclosion can provide some information on future success.

Sex ratio at eclosion is then examined. No study has reported a biased sex ratio for *Nicrophorus* raised in the laboratory although Easton (1979) recorded an excess of males in the early part of one field season and I found the same result in the field in 1985 and 1986 (chapter 2). I compared sex ratio at eclosion in the laboratory of a population raised on 25g mice and of one raised on 10g mice. Brood reduction is practised on 10g mice (see chapter 5) and the 10g population was used to test whether larvae of one sex were more likely than the other to be culled.

Ovary development in laboratory females is then investigated. Immediately following eclosion, burying beetles are incapable of breeding even if provided with a corpse (Wilson & Knollenberg 1984). Females are said to become sexually mature two weeks after eclosion Springett (1967). In the laboratory I found that females could breed 16 or 17 days after eclosion. The ovaries of *Nicrophorus* are of the acrotrophic type (Anderson 1982), each ovariole having at its apex nutritive cells which provide for the development of the eggs. A description of the development of this type of ovary was given by Suzzoni (1973) for another silphid, *Phosphuga atrata*.

Ovaries from trapped *Nicrophorus* have typically been divided into categories of development from immature (no sign of developing eggs) to post-reproductive (see Christie 1981). This classification, and the technique by which beetles were obtained for dissection, were criticised by Wilson & Knollenberg (1984). Working with laboratory-reared *N. orbicollis*, a North American species, they found that ovary weights increased slowly from eclosion until the beetles were given a corpse (20 days from eclosion) and then rose within 48 hours to levels never seen in females found in the field. They concluded that the final phase of egg development was delayed until the female was in possession of a corpse, interpreting this as an adaptation to breeding on a scattered and uncommon resource. The discovery of mature females in traps during earlier studies (Springett 1967; Easton 1979; Christie 1981) was explained by Wilson & Knollenberg as being caused by a delay in collection that allowed females to develop eggs and so mature their ovaries within the traps. In support of their conclusions, no females with mature ovaries were found in a study in which several species of *Nicrophorus* in Ontario were caught using traps which killed the animals at the time of capture (Anderson 1982).

Experiments were done in this study to try to resolve the following points: whether the European classification of burying beetle ovaries (Springett 1967; Easton 1979; Christie 1981) is invalid; if so, whether the authors who used it were misled by an artifact of trapping technique, as suggested by Wilson & Knollenberg (1984); whether *N. vespilloides* is similar to *N. orbicollis* in showing a burst of ovary development after burial of a corpse.

Finally, the abundance and availability of carrion are discussed. Some experiments on the success of *N.vespilloides* in winning corpses are described. Carrion is used in two ways. *Nicrophorus* adults both feed on it (Steele 1927; Wilson & Knollenberg 1984) and use it for reproduction. There may be some discrimination between carrion types before arrival so that different species of burying beetle are more likely to arrive at different types of carrion (Ling 1957), and mature and immature beetles distinguish between carrion suitable for breeding and carrion suitable for feeding before arrival (Wilson & Knollenberg 1984).

Carrion types.

Nicrophorus is capable of breeding on a wide range of corpses. '...the Burying-beetle refuses no sort of cadaveric putrescence...He accepts without hesitation extraordinary finds, probably unknown to his race...' (Fabre 1919). The burial of moles, mice, reptiles and fish has been recorded (Fabre 1919); and that of birds, kittens and a snake (Ling 1957). Any small vertebrate may be suitable, only shrews seem to lie for some time without being buried. If the corpse is not buried, large numbers of burying beetles may still collect on it and feed on the meat or on the maggots there (Steele 1927). I found a pigeon and a stoat which had each accumulated twenty or thirty *N. vespilloides* without being buried, and the beetles showed no aggression towards one another as they do on corpses which are to be buried (chapter 4).

Carrion abundance.

The abundance and availability of the types of carrion likely to be used by *Nicrophorus* has rarely been directly studied. A summary was given for his study site at Loch Lomond by Easton (1979), his main conclusion being that carrion fell into two general categories. Between July and August carrion would mostly be small (less than about 20g) consisting of shrews and fledgling birds. From April to July Easton (1979) claimed that carrion was likely to be more variable in size (5-30g) and possibly more abundant.

Another source of data for carrion abundance is work dealing directly with the population biology of the animals which will form the carrion. Such data as has been published deals mainly with the wood mouse *Apodemus sylvaticus* and the bank vole *Clethrionomys glareolus.* Published data show great variation between sites in densities of both voles and mice but are in some agreement on the main features of population dynamics during the year (see e.g. Crawley 1970; Smal & Fairley 1982). Overwintering individuals become active again in March, breeding starts around the end of April (at which time *Nicrophorus* becomes active) and the first juveniles appear in mid-June. Mean weight seems to fall from August onward due to recruitment of juveniles into the population; in general corpses might be estimated in the range 10-30g (Bobek 1969; Smal & Fairley 1982). Corpses of this size range were used in laboratory experiments.

Life expectancy of voles and mice may be only a few months (Bobek 1969), with adult mortality rate increasing once the breeding season starts (Crawley 1970). The rate of juvenile recruitment can exceed that of adult mortality (Crawley 1970; Nabaglo 1973) and a population may be completely replaced each year. Potentially, then, there are many corpses suitable for burial by *Nicrophorus* but only a limited number of these may actually be available to be buried.

Carrion availability.

Carrion is an important resource for a wide range of taxa (Putman 1983), many of which will compete with *Nicrophorus.* Putman (1976) argued that vertebrate scavenging of small corpses represented a fairly constant background whose apparent effects were modified according to season by the very much more variable activity of invertebrate users. In winter and spring, when invertebrate activity is low, vertebrates will eventually remove virtually 100% of corpses laid out in an experiment. In summer and autumn a proportion is used by invertebrates before vertebrate scavengers can find them. This proportion is highly variable. In woodland around Oxford Putman recorded a loss of 90% of small carcasses to vertebrates. He suggested that Wytham Wood might be deficient in *Nicrophorus* (R.J.Putman pers.comm.) although large numbers were noted by Elton (1966). In the same year at Loch Lomond Easton (1979) found that scavengers removed only 13% of his corpses. On two

Michigan sites 315km apart vertebrate removal was recorded as 35% in one and 6% in the other (Wilson & Fudge 1984). Other studies in the Soviet Union and Britain reported 67% removal by vertebrates (Akopyan 1953) and 100% removal (Collins 1970) but the latter warned that carrion placed on the surface for experiments might give a biased picture of the importance of vertebrate scavengers. Voles, for example, might normally die in grass runs and be less obvious to a scavenger.

There are very few cases where it is possible to find any corpses in a natural situation and it is therefore usually necessary to study burying beetles in the field by using laboratory corpses. Sometimes, however, it may be possible to use naturally occurring carrion. For example, in rook colonies, fledgling rooks sometimes fall from the nests in spring (P.Green pers.comm.). Ten rookeries in East Lothian were used to study the breeding of *Nicrophorus* on natural corpses.

Competition with invertebrates.

A carcass attracts many invertebrate species (see e.g. Elton 1966; Nabaglo 1973). The most serious competitors faced by *Nicrophorus* are likely to be Diptera such as *Calliphora* and *Lucilia.* A study on pig carcasses exposed to insects found that they were were reduced in 7 days to 10% of their original weight, whilst buried animals took 6-8 weeks to drop to 20% of their original weight (Payne 1965). Micro-organism activity is far less important: in one study on smaller corpses only 3% of carrion material was used after 85 days whilst blowfly colonisation accounted for 75% of the original weight in 7-8 days (Putman 1978).

Blowflies and burying beetles illustrate two broad categories of life history. Flies typically produce large numbers of rapidly developing young which quickly consume a corpse where it lies. The young of *Nicrophorus* are few in any one brood by comparison with the offspring of a fly, and they develop more slowly. Direct competition between fly larvae and *Nicrophorus* larvae could be expected, therefore, to end with a corpse being eaten by maggots; however, the behaviour of adult burying beetles, which allows exclusive use of a corpse by their own brood, can give the beetle larvae the advantage. This is discussed further in chapters 5 & 6. The interaction of *Nicrophorus* with blowflies, particularly with respect to the mites carried by burying beetles (Neumann 1943) has been examined several times. It was shown that laboratory breeding of *N. vespilloides* in competition with Diptera was successful only if the beetles carried mites. Without mites, fly eggs placed on a corpse hatched to maggots and the corpse became unusable by *N. vespilloides*. If the beetles carried mites, these ate the fly eggs and the beetle larvae faced no competition from maggots (Springett 1968). In later studies, however (Korn 1983; Wilson 1983) the laboratory results could not be repeated; *Nicrophorus* bred successfully whether it carried mites or not. In the field, a need for mites was shown (Wilson 1983). The difference in laboratory results may arise from the different techniques used. Wilson allowed blowflies to lay eggs naturally and these would have been laid on the surface of the mouse and removed when the beetles stripped the hair from the corpse and buried it, making the presence of mites to remove the eggs unnecessary. In contrast Springett placed the fly eggs by hand in the eviscerated bodies of mice, where hair removal alone would have no effect. This, however, would not explain the difference between Wilson's laboratory and field results. Wilson argued that in the field the importance of the mites results from the longer time it takes beetles to bury a corpse. In this time, if the fly eggs are not destroyed by mites, they might hatch before the corpse is buried and the hair removed.

The extent of competition from flies therefore seems to be determined both by the time a corpse lies exposed to flies before beetles reach it and by the time taken by beetles to bury the corpse and strip the hair (and in the process destroy any eggs already laid). As with vertebrates, the activity of the flies can be seen as a background against which the beetles act. Laboratory and field experiments were done in this study to investigate the competition between the two groups of carrion user.

Competition with other *Nicrophorus* species.

Several studies have recorded more than one species of *Nicrophorus* in an area and have speculated on competition for carrion between these species. In some cases different species were found to predominate in different habitat types (Pukowski 1933; Anderson 1982). An interesting example is that of the North American species *N. orbicollis* and *N. defodiens*. The former, a larger species, was able to displace *N. defodiens* from corpses in the field, but the smaller species could find and use corpses at lower temperatures and was able to survive in a temperature refuge (Wilson *et al* 1984). Competition between three species in Scotland was discussed by Easton (1979). He suggested that *N. humator* bred on larger corpses than could be used by either *N. vespilloides* or *N. investigator* and did not therefore compete directly with them. but that for the two smaller species the potential for competition might exist. In laboratory experiments (Easton 1979) *N. investigator* was able to displace *N. vespilloides* from corpses and in the field the eclosion of *N. investigator* in July coincided during the years of his study with the end of breeding by *N. vespilloides*. However, in spite of its apparent competitive superiority, *N. investigator* is far less common than the smaller *N. vespilloides* (Easton 1979; Christie 1981) and I found too few *N. investigator* to use it in any study of competition.

3.2. Size and weight at eclosion.

Method.

A set of 20 female and 20 male *N. vespilloides* were allowed to bury 25g mice in the laboratory, each pair in one of the boxes described in chapter 2. Larvae from their broods dispersed from the corpses 10 days later, and a sample of 150 of these were taken from the broods and allowed to pupate. 137 adults eclosed and their pronotum widths (see chapter 2) and wet weights were measured at eclosion.

The experiment was later repeated with a further set of 20 males and females bred on 25g mice, 100 adults from these broods being measured for size and weight 20 days after eclosion, by which time *Nicrophorus* is sexually mature. These data for mature beetles were compared with size and weight data for beetles caught in traps in the field between May and July 1986 (see chapter 2). The field beetles used came from 15 traps set out 100m apart in the study site at Penicuik.

Results.

Adult size is plotted against the cube root of weight at eclosion (Figure 3.1) and against cube root of weight 20 days after eclosion (Figure 3.2). Both slopes are significantly different from 0 (F=294.2; df=1,137; P<0.001 and F=195.5; df=1,99; P<0.001).

The distribution of pronotum width is plotted for the set of 100 laboratory adults 20 days after eclosion (Figure 3.3). There is no significant difference in the mean pronotum width of the mature laboratory population and that of *N. vespilloides* trapped in the field in 1986 (t test P>0.05) (see chapter 2).

Figure 3.1

Pronotum width and wet weight at eclosion for 137 laboratory *N.vespilloides* raised on 25g mice.

Regression equation: $y=7.92x+0.42$; $r^2=0.67$

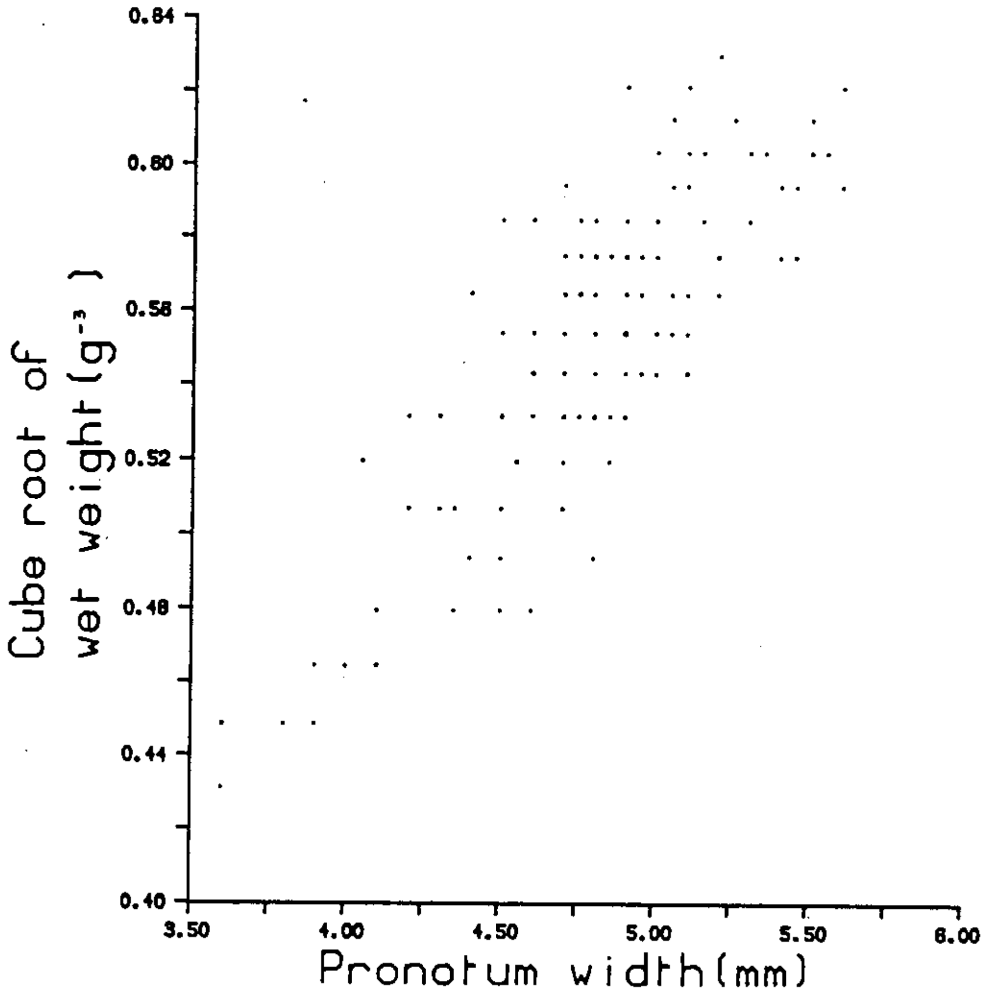


Figure 3.2

Pronotum width and wet weight 20 days after eclosion for 100 lab *N.vespilloides* raised on 25g mice. This is a different sample of beetles from that used for figure 3.1.

Regression equation: y=6.59x+0.97; r ^{2}=0.67

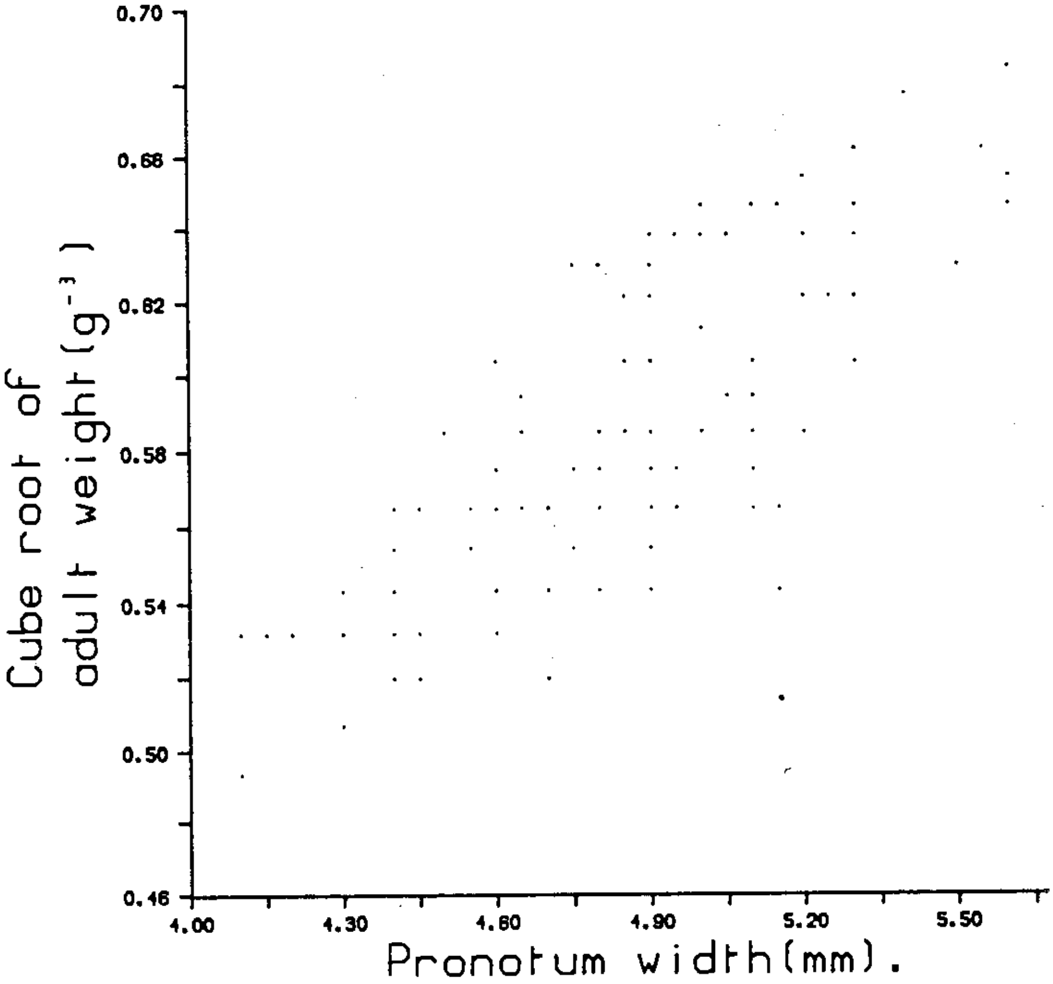
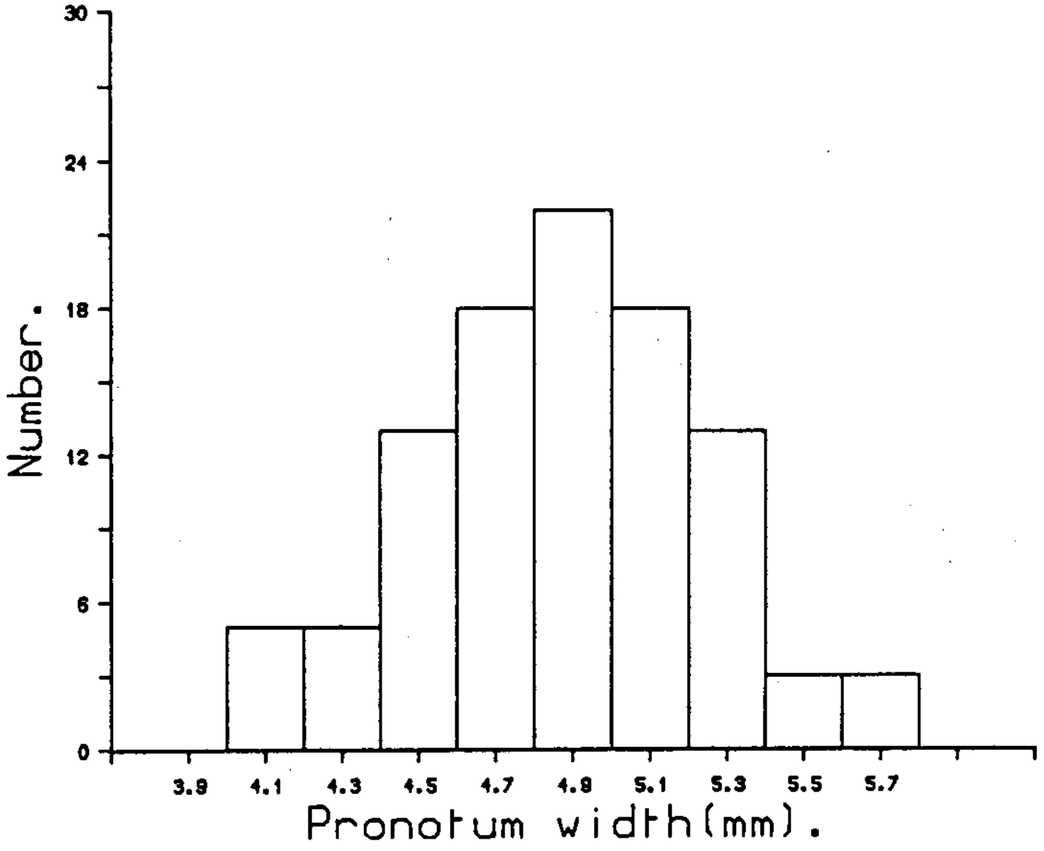


Figure 3.3

The distribution of pronotum width 20 days after eclosion for the laboratory sample of *N.vespilloides* shown in figure 3.2.

n=100, mean=4.83 ± 0.08



3.3. Sex ratio at eclosion in the laboratory.

Method.

20 pairs of male and female *N. vespilloides* 20 days after eclosion bred on 25g mice, a further 20 pairs on 10g mice. Adults from these broods eclosed a month later. 637 from the 25g mouse broods were sexed, 182 from the 10g mouse broods.

Results.

There was no significant deviation from a 1:1 sex ratio in either the population raised on 25g mice (χ^2=0.69, P>0.05) or that from 10g mice (χ^2=0.20, P>0.05) (Table 3.1).

3.4. Ovaries.

3.4.1. Development in the laboratory.

Method.

In order to test whether females in the laboratory show ovary maturation only after burial of a corpse, or have mature ovaries before a corpse has been found, females were taken at eclosion and kept in groups of ten in the boxes described in chapter 2. The females were kept away from males and fed on mealworms. They were stored in a room away from that in which experiments were normally carried out in case the smell of nearby carrion in the experimental room affected ovary development. Each group was dissected at a certain age, the ovaries removed at the common oviduct, blotted and weighed. At 20 days of age the members of one group were put into a box with a male and allowed to bury a 25g mouse. Another 20 day group was dissected

Table 3.1.

Corpse size	Females at eclosion	Males at eclosion	χ^2 test.
25g	308	329	$P>0.05$
10g	88	94	$P>0.05$

The sex ratio at eclosion of *N. vespilloides* raised on 25g corpses and 10g corpses. Both samples come from 20 broods raised on each size of corpse.

without being given a mouse. The females which had buried the mouse were removed after 24 hours, by which time a few had already laid some eggs but most had not. Those which had laid no eggs were dissected and their ovaries weighed. Females which had not buried a mouse were therefore dissected a day earlier than females which had. The two groups were still compared directly. It is most unlikely that the single day coincides with sudden ovary development occurring whether a mouse is buried or not. A further group was given mice at 20 days after eclosion and allowed to bury them and raise larvae. Some of these females were dissected 3 days after the dispersal of their larvae from the corpse and the rest 12 days after dispersal.

Results.

For each female the combined weight of the two ovaries was expressed as a proportion of total wet weight and plotted against time from eclosion (Figure 3.4). The proportion increased up to 10 days of age but did not increase significantly between 10 and 20 days of age. Females dissected on the first and fifth day had no sign of eggs, females at 10 and 20 days almost all had a well-developed egg in each ovariole and would have been classified as 'mature' by Easton (1979) and Christie (1981). After burial of the corpse ovary weight increased and was significantly higher than the mean ovary weight of the 20 day females which had not buried mice (Table 3.2). These females had two or more eggs in several of the ovarioles. The increase in weight supports the suggestion of a burst of egg production following corpse burial (Wilson & Knollenberg 1984). Following dispersal of the larvae the ovary weight of the female parents reverts to about the same level as that found just before breeding.

Figure 3.4

Ovary weight as a proportion of total weight for laboratory *N.vespilloides* at different times after eclosion. At 20 days three sets of females were given 25g mice: one set were dissected a day later, one 13 days later (3 days after dispersal of larvae) the third 25 days later (12 days after brood dispersal). Points represent the mean of ovary weight/body weight; bars 95% CL.

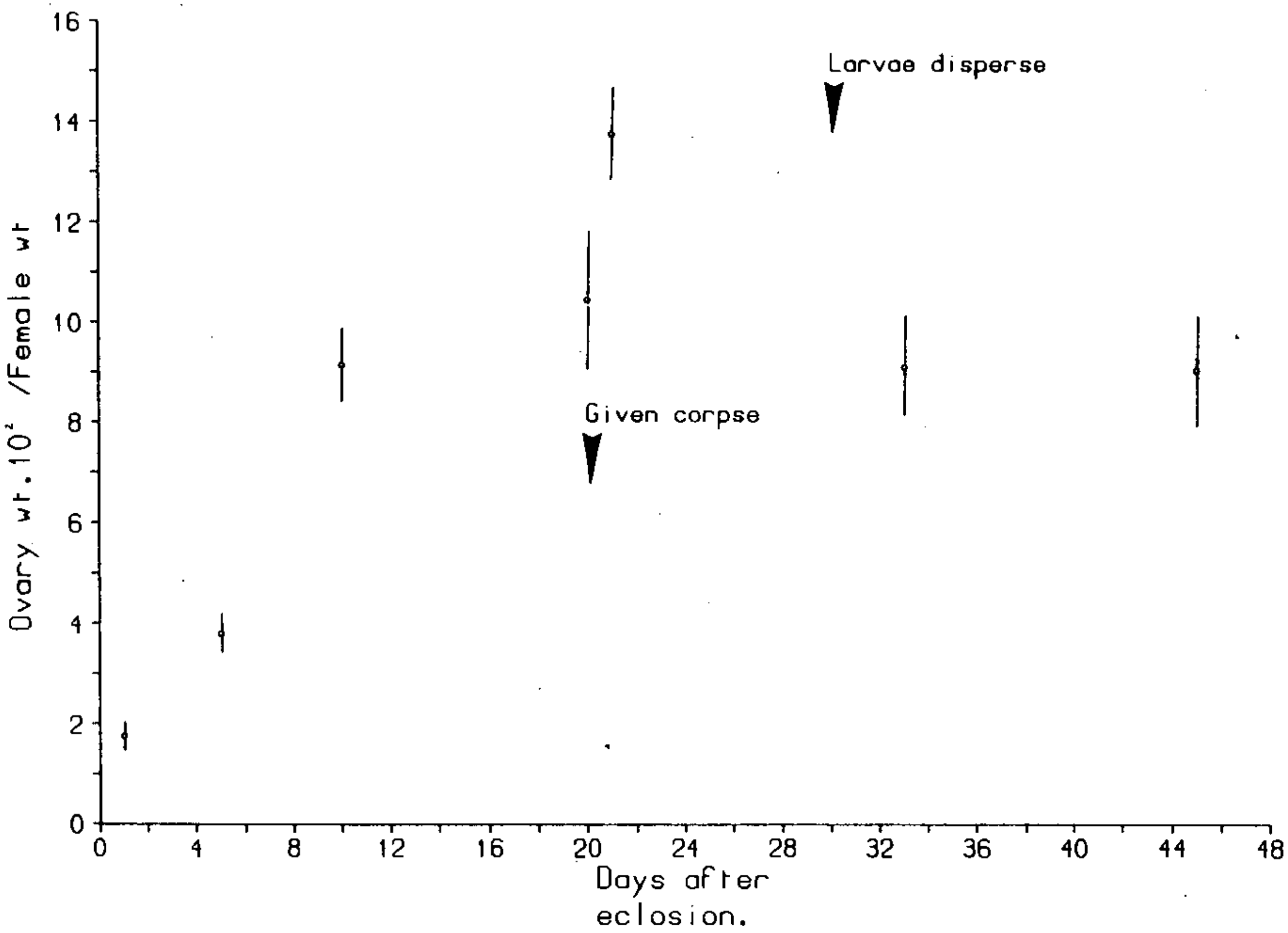

Larvae disperse
Given corpse
Ovary wt.10² /Female wt
0
2
4
6
8
10
12
14
16
0
4
8
12
16
20
24
28
32
36
40
44
48
Days after eclosion.

Table 3.2.

The ovary weights of *N. vespilloides* in the laboratory at different times after eclosion.

Days after eclosion	n	Ovary wt(mg)		Ovary wt.10^2 /body weight	
		mean	95% CL	mean	95% CL
1	16	2.98	0.81	1.74	0.23
5	7	9.66	1.32	3.79	0.89
10	20	25.15	1.14	9.50	0.45
20	27	26.30	4.64	10.37	1.44
21 (day after corpse burial)	21	34.78	3.39	13.93	1.89
33 (13 days after)	12	24.81	6.30	9.08	1.52

ANOVA table

Source	DF	SS	MS	F	
Between groups	5	1664.47	332.89	41.01	$P<0.001$
Within groups	94	763.00	8.12		
Total	99	2427.47			

Multiple range test (Scheffe; * = sig't at 5%)

Age	1	5	10	20	21	33
1		ns	*	*	*	*
5	ns		*	*	*	*
10	*	*		ns	*	ns
20	*	*	ns		*	ns
21	*	*	*	*		*
33	*	*	ns	ns	*	

3.4.2. The effect of traps on ovary development.

A second experiment was carried out to test whether burial of a corpse was needed to induce final ovary development, or whether contact with a corpse used to bait a trap could cause the same effect.

Method.

Laboratory females were taken at eclosion and kept away from the smell of carrion as described in the previous experiment. 20 days after eclosion each was placed inside a trap of the kind described in chapter 2. Each trap had already been baited with a freshly-killed mouse. The females were left in the traps for 24 hours and then dissected and the ovaries weighed. A control group of females was taken at eclosion and kept for 20 days without having any contact with carrion. They were then dissected.

Results.

For each female the combined weight of the ovaries was expressed as a proportion of total wet weight. The mean value for the females put into traps (8.86± 1.94, n=14) did not differ significantly from that for the control females (8.94± 1.80, n=14, t test $P>0.05$). The last stage of ovary maturation described by Wilson & Knollenberg (1984) and confirmed for *N. vespilloides* in the previous experiment is not induced simply by contact with a corpse in a trap of the type used by Easton (1979) and Christie (1981).

3.5. Carrion.

3.5.1. Success on rook corpses.

Method.

The rookeries were searched in the spring of 1985. The ground beneath the trees was searched regularly from the beginning of May until no more corpses were likely to be found. The position of any dead birds was marked with a bamboo cane and the corpse inspected on each subsequent visit.

Results.

Fourteen corpses were found. Of these, four were discovered by *N. humator* but none was buried. Three of the fourteen were removed by a farmer and hung from a nearby fence, one was eaten by maggots, one disappeared and the rest were eaten and the wings left smelling strongly of fox.

Although this attempt met with little success, others like it based on areas of high nest concentrations could be a valuable means of estimating the success of *Nicrophorus* in a natural, if specialised, site.

3.5.2. Competition with invertebrate carrion users.

Methods.

In an experiment designed to test the abundance of flies, twenty mice were laid out in the morning at the study site at Penicuik in July 1985 and collected twelve hours later and kept in the laboratory at 20° C.

A second experiment was done to study competition between *N. vespilloides* and flies. Twenty mice were laid out and collected as before. Half were left in the laboratory for 24 hours and then a pair of beetles was allowed to bury each corpse, the other half were left for 48 hours before beetles were allowed to bury them.

Results.

In the first experiment dipteran eggs were laid on all twenty corpses and all corpses were eaten by maggots hatching two or three days later. Under normal late-summer conditions burying beetles are probably never free from competition with flies. As suggested above, the speed with which maggots can eat a corpse makes them important competitors.

In the second experiment, beetles bred successfully on 14 of 15 corpses in the first group and 2 of 10 corpses in the second (Table 3.3).

In further field experiments the results of competition between burying beetles and their invertebrate and vertebrate competitors was studied by examining the fates of laboratory mice placed in the field.

3.5.3. Fates of corpses in the field.

Method.

Mice were tethered to canes on the field site and recorded as being used by *N. vespilloides*, eaten by maggots, or removed by scavengers. Canes were set 100m apart in Lower South Bank Wood and Hurley Cote and visited every day. The mice were recorded as being used by beetles if they were buried and a crypt built, as scavenged if the tethering thread had been broken and the mouse had disappeared. The ground on the study site is mostly soft; in many places a thick layer of leaf mould forms the surface. Under these conditions burying beetles need not move carrion far to find a place where it can easily

Table 3.3

Laboratory competition between *N. vespilloides* and maggots.

Time in lab before mice buried	n	Eaten by maggots	*Nicrophorus* successful	Uneaten
24 hours	15	0	14	1
48 hours	10	6	2	2

The table compares laboratory breeding success of *N. vespilloides* on mice which had been exposed in the field for 12 hours and then left in the laboratory for 24 hours with mice exposed for 12 hours but left in the lab for 48 hours. Fisher's exact test: measures probability of finding, by chance, the observed frequencies of beetle and maggot success at the two time intervals between removal from field and burial by *Nicrophorus*.

$P = 6.69.10^{-6}$

be buried and I never saw a corpse moved by beetles further than the range allowed for by the length of thread which they were given. In cases where the corpse was recorded as being taken by scavengers the thread had been pulled away and snapped, or it disappeared into a mole run. In cases where corpses were recorded as buried by *N. vespilloides* the thread remained at least partly coiled and could be traced into the crypt.

Results.

The success of *N. vespilloides* in burying corpses placed in the field is variable even within one site (Table 3.4). Factors such as time of year and temperature which affected the activity and abundance of flies altered the balance of competition; beetles themselves were also affected by weather. On evenings of heavy rain none were seen and if rain persisted for several days corpses could lie unused by either beetle or fly. (This was the case for the corpses set out on 24.8.86 (Table 3.4).

3.6. Discussion.

Size and weight at eclosion.

Size has often been found to have a significant effect on reproductive success. Among insects there are cases in which increasing size over the observed range has an increasingly beneficial effect (Thornhill 1980; Ward 1983a), others in which an intermediate size is favoured (Fincke 1982; Ward 1983b) and yet others in which the smallest class of individuals has some advantage (McLachlan 1986). Large size may be of advantage in winning fights with other animals for resources or territories, or in overcoming the resistance of females to mating (Partridge et al 1987). Intermediate or small size can be beneficial because of reduced wing loading (Takagi 1985) and/or increased

Table 3.4.

Date	n	Proportion used by			
		Nicrophorus	Maggots	Scavengers	Uneaten
1.7.85	10	0.6	0.3	0.1	0
24.7.85	15	0.7	0.1	0.2	0
3.8.85	15	0.17	0.27	0.56	0
22.5.86	15	0(0.45)*	0	0.45	0.10
13.6.86	15	0.45	0.20	0.35	0
13.7.86	10	0.20	0.10	0.70	0
24.8.86	15	0	0	0.50	0.50

* discovered by *Nicrophorus* but abandoned.

The fates of corpses tethered to poles 100m apart on the study site are shown as either buried by *N. vespilloides*, eaten by maggots, or taken by vertebrate scavengers.

manoeuvrability in flight. Such effects were considered in this study (chapters 4 & 5) but although the laboratory sizes agree well with those found in the field, lack of field results on breeding success precludes any direct application of the effects of size in the laboratory to reproductive success in the field.

Sex ratio at eclosion.

A male-biased sex ratio was reported by Easton (1979) during the early part of one field season. In 1985 and 1986 I also found a significant male bias in the sample of *N. vespilloides* caught in traps in the early months of the field seasons (chapter 2). At eclosion in the laboratory the ratio was not significantly different from 1:1. If adults can control the sex of their offspring, a female-biased sex ratio can be selected for (Hamilton 1967). This is often found amongst insect parasitoids (Werren 1980). Some Hymenoptera have been found to vary the female bias of the sex ratio of the eggs they lay according to variation in the extent of local mate competition (Charnov et al 1981, Waage & Lane 1984). Burying beetles can sometimes be usefully compared with such animals, in that both lay eggs on a discrete and valuable resource, but in the lab they do not show the same sex bias at eclosion. As diploid organisms, they may not be able to control the sex of the eggs they lay. There may also be ecological explanations. Two processes are involved in female bias (Taylor 1981; Grafen 1984; Harvey 1985, Harvey et al 1985), the diminishing returns (in numbers of grandchildren) to a mother which produces more sons, and the extra mating opportunities for the sons of a mother which produces more daughters. These processes can occur when siblings mate (Hamilton 1967) or when sib mating does not occur but populations are isolated and inbred (Bulmer & Taylor 1980; Charnov 1982). Burying beetles are probably inseminated at feeding aggregations and at the site of corpse burial: mate competition at the eclosion site is not significant. The alternative explanation for a biased sex ratio is also inapplicable: burying beetles are strong fliers and populations are unlikely to be isolated and inbred.

A 1:1 sex ratio at eclosion is therefore not unexpected. Any male-biased ratio found in the field probably represents an ecological effect: for example some corpses are buried by females without males (Wilson & Fudge 1984) leaving a higher proportion of males to be trapped during the breeding season.

Ovary development.

The European classification of *Nicrophorus* ovaries was based on morphology and termed 'mature' females with one well-formed egg in the base of most of the ovarioles. During the breeding season, the majority of female *N. vespilloides* trapped by Easton (1979) and Christie (1981) were of this type. Field work on the North American species *N. orbicollis* suggested that ovaries were never mature until a corpse had been buried. The ovaries of females trapped in the field always weighed less than the ovaries of females which had been allowed to bury a mouse in the laboratory. These experiments on *N. orbicollis* did not describe the ovaries of the beetles used, allowing no comparison with those of *N. vespilloides*.

My first experiment shows that *N. vespilloides* in the laboratory can have mature ovaries as defined by Easton (1979) and Christie (1981) (i.e. an egg in each ovariole) before being in contact with carrion. If all these eggs were laid, a clutch of 24-28 would result, less than the clutch size which *N. vespilloides* can lay in the laboratory (see chapter 5). Further ovary development occurs in the 24 hours after burial of a corpse, as described for *N. orbicollis* (Wilson & Knollenberg 1984). The two sets of work can be combined; the old definition of 'mature' now referring to a pre-burial state, and a new condition being recognised as that which is found after the corpse has been buried.

The second experiment shows that contact with a corpse in a trap is not sufficient to induce the final phase of ovary development. It has been pointed out that final ovarian development before a corpse has been buried might be wasteful, since the first burying beetle to arrive at a corpse is often displaced by a later, larger arrival (Wilson & Knollenberg 1984).

Competition with invertebrates.

The success of *N. vespilloides* in this laboratory competition varied with the time which the fly eggs had had to develop before the corpses were found by beetles. In a similar experiment on *N. orbicollis* laboratory mice were left in woodland for either 24 or 48 hours and then brought back to the laboratory and *N. orbicollis* allowed to breed on them. On the one day group success was 80%, and on the other 55% (Wilson et al 1984). As with vertebrate competition, it is the timing of beetle activity that is important, both in finding the corpse and in burying it.

The extent of the interspecific competition which *Nicrophorus* faces for corpses and the factors which affect its success are important pieces of its ecology and laboratory experiments on the significance of burying beetle characteristics cannot be completely realistic without their inclusion. Results are needed on the abundance of carrion and where it lies so that field and laboratory experiments can be more meaningfully designed.

Chapter 4.

Pair formation.

'All those who climb up from underground are maimed, with limbs amputated at the joints, some higher up, some lower down.'

J.H. Fabre: 'The Glow-Worm and other Beetles' 1919.

4.1 Introduction.

A corpse buried by *Nicrophorus* is almost always eaten by the brood of a single pair of adults. The only exception seems to be when the corpse used is so large or long (as with a snake) that two pairs can raise broods at either end (Milne & Milne 1976). However, several individuals may be involved in burial before the single pair is left in possession (Fabre 1919). This reduction to a pair was the original subject of Pukowski's (1933) study on *N. vespillo.* She confirmed the finding that a single female or else a heterosexual pair monopolises the corpse. By field experiments with marked beetles she showed also that individuals fight for possession, female with female and male with male. This chapter describes experiments investigating pair formation in *N. vespilloides.*

I first describe the attraction of females by males. *Nicrophorus* does not arrive in pairs at corpses in the field (Fabre 1919; pers.obs.). For some time either a male or a female is alone and, as was observed with *N. vespillo* (Pukowski 1933), behaviour differs according to sex. Females begin at once to bury the corpse. They are almost always already inseminated (Christie 1981) and can bury the corpse and raise a brood without the help of a male (see chapter 6).

In contrast, males adopt the 'sterzeln' position described by Pukowski (1933) in which the head of the beetle points down and the back legs are fully extended, pushing the tip of the abdomen into the air. On the basis of her observations on *N. vespillo* Pukowski (1933) suggested that a male in this position is releasing a signal, probably a pheromone, to which females are attracted. It has since been assumed that a pheromone is involved, but this has never been proved. I studied sterzeln behaviour in the laboratory and the field in order to investigate whether it is involved in the attraction of females and to discover something of the nature of the signal used (Bartlett 1987).

The next sequence of experiments investigates fighting in *N. vespilloides*. It is common to all studies of *Nicrophorus* that more beetles are attracted to a corpse than the pair which eventually breed upon it (Fabre 1919; Wilson & Fudge 1984). From this it has been argued that the reproduction of *Nicrophorus* is limited by the availability of suitable corpses (e.g. Springett 1967). The situation is one in which individuals might be expected to fight to gain the resource: it is valuable and rare; it is compact and, having been won, can be expected to yield a reward in fitness (Hamilton 1979). Fighting in *N. vespillo* was described as 'ferocious...the more startling for the calm of the summer evenings on which it takes place.' (Pukowski 1933). Fighting has since been seen or inferred in other species (Milne & Milne 1944; Wilson & Fudge 1984). Under certain conditions, co-operation can also be found. Wilson & Fudge studied *N. orbicollis* and *N. defodiens*. For *N. orbicollis*, the larger species, they found that in 90% of cases where two beetles of the same sex could be collected from a single mouse the animal positioned on the mouse was larger than that found in the leaf litter nearby. For *N. defodiens* a similar result was found, but in 42% of corpses with a pair of the same sex there was no single central animal: both were in a central position. This happened for *N. orbicollis* in only 8% of cases. They suggested that the smaller species, which could easily be displaced by the larger from the corpse, might more often co-operate in removing the corpse from the surface before competing for possession. A greater tendency for co-operation was also found in another small beetle, *N. tomentosus*, than in *N. orbicollis* (Milne & Milne 1944).

In Scotland work on *N. investigator* and *N. vespilloides* suggested that the former might displace *N. vespilloides* from corpses and so alter *N. vespilloides* competitive behaviour (Easton 1979). I found too few *N. investigator* to test this idea but was able to study fighting in *N. vespilloides* in the laboratory and in the field. The aim of these experiments was to describe the nature of fighting in this species, to discover the factors which affected the outcome of fights, and to find whether fights always took place or whether there were circumstances in which co-operation occurred.

Having described something of the nature and likely outcome of fights I investigated the possibilities of reproductive success amongst those individuals which might only rarely win direct contests. Results from fights (see section 4.3) and the apparent shortage of corpses suggest that small beetles have little chance of reproduction. The size of a beetle is established during the period of juvenile feeding and moulting and is then fixed throughout life so that there is no increase in competitive ability as an individual grows older and body size increases such as occurs with vertebrates, e.g. elephant seals, where younger males infiltrate the harem of an older male by pretending to be females and only when older and larger try to defend harems of their own (Le Boeuf 1974). In many insects, alternative behaviours of this type, forced on an individual by small size, may persist throughout life. In the water bug *Gerris elongatus*, large males defend territories in which females can lay eggs and signal to females by creating waves on the water surface, whilst small males do not signal but roam the pond in search of chance matings or solitary females laying outside a male-held territory (Hayashi 1985). Small male spiders *Meta segmentata* mate monogamously with solitary females on poor-quality web sites and avoid fights with large males which mate at aggregations of females on high-quality sites (Rubenstein 1987).

I studied the arrival of burying beetles at corpses in the field to find any effect of size on order of arrival. The results of the experiments on fighting behaviour suggested that there might be a particular advantage to small beetles in arriving first at a corpse and having the opportunity to bury it without being challenged by a larger animal.

Small *Nicrophorus* males are in a different situation from females in that finding a corpse first does not confer the same immediate advantage if there is not a female already present. They may signal and only attract a male larger than themselves. If this does happen, or if a small male comes to a corpse and finds a larger male already there, field observations and the data of section 4.3. suggest that the small male will not be driven away but work in co-operation at least until a female comes. By this time he may have spent considerable effort in burying the corpse and perhaps also have taken some risk in signalling and if he is then expelled he may have worked for nothing. The same phenomenon of male co-operation was noticed by Fabre (1919): '...anxious to serve a lady they creep under the body, work at it with back and claw, bury it and then go their ways, leaving the master and mistress of the house to their happiness.' but the behaviour of the small male needs some explanation other than chivalry. It is possible that though he may not become the resident in the crypt he may father some offspring through 'sneak' matings with the female. I often saw such matings in laboratory experiments. Once driven off, the loser stayed on the surface and made several returns to the corpse. If the other male was still there the weaker ran away or was driven off again but often he copulated with the female before he was discovered. Even after the corpse is buried the female may come to the surface to work at the roof of the crypt and the defeated male can be seen to mate with her. This was not a product of laboratory conditions: the small male was free to fly away but usually only did so after several hours.

'Sneak' mating is a behaviour taken up by the weaker males of a variety of species, for example small frogs *Rana catesbeiana* crouch silently near the territories of larger, calling males and try to mate with the females they attract (Howard 1978). For *N. vespilloides* males it is a conditional behaviour dependent on the presence or absence of larger competitors. The gerrids described earlier change their strategy from patrolling to signalling according to such factors as the number of females and defensible oviposition sites, the time of year and the size of competing males (Hayashi 1985; Spense & Wilcox 1986) and a small *Nicrophorus* may similarly be able to alter its behaviour according to the degree of competition for corpses and so the likelihood of burying a corpse without challenge. I studied the success of small males when they bury a corpse in company with a large male.

Finally, I describe experiments investigating mate recognition in *N. vespilloides*. The corpse is buried and a single pair of beetles is in possession. At some point they become more than simply two individuals and each seems to have some recognition of the other as belonging in the crypt. This was suggested by W.D. Hamilton (pers. comm.) on the basis of observations by M.Otronen and examined in this study by a different technique.

4.2. Signalling for a mate.

General methods and description of behaviour.

In the laboratory a circular plastic container (a paddling pool) 1.5m in diameter was used as an enclosure. It was filled to a depth of 10cm with compost and a mouse corpse placed in the centre. Males were then released into the pool and left to find the corpse. They took up the sterzeln position as Pukowski (1933) described, with the last pair of legs extended and the tip of the abdomen pointing up. Usually they stood on a high point such as the mouse itself, or a stick or stone if these were put in the soil (Figure 4.1). They might signal for several hours, interrupting each bout of sterzeln behaviour with visits to the corpse and the area around it. If a female was placed in the pool and found the corpse, sterzeln behaviour stopped as soon as the male discovered her on one of his visits to the corpse and was never resumed unless the female was taken away for several hours. I only saw sterzeln behaviour if males were in contact with, or had recently been removed from, a corpse.

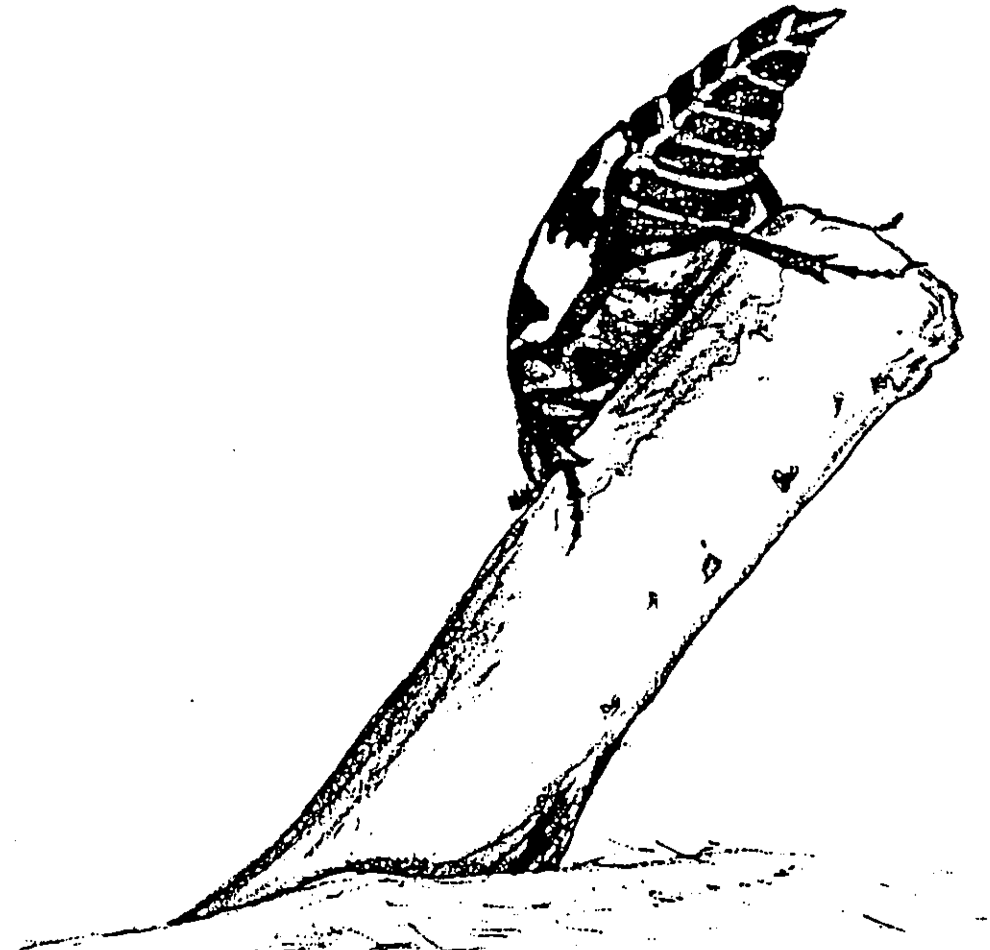
4.2.1. Timing of signal: methods.

I found that males which discovered a corpse in the pool sometimes took up the sterzeln position almost at once, or might instead spend up to five or six hours first burying the corpse. This seemed to vary with the time of day at which males were put into the pool. To study this, I released males into the pool at different times, noting the length of time before darkness in the room, the 16h:8h light:dark cycle being kept constant. I checked the pool every 30 minutes and noted the time when a male first took up the sterzeln position. Once the behaviour began it was maintained as the main activity.

Some males were used to measure the time of first signal on the day following that on which the corpse was found. I released these males at different times on the first day and checked the pool every half-hour throughout the following day.

Figure 4.1

The sterzeln position. A male *N.vespilloides* signalling from the top of a twig.



Results.

If a male was placed with a corpse in the morning he buried it during the day and did not show the sterzeln behaviour until an hour or so before the dark section of the laboratory light cycle (Figure 4.2). If a male was placed with a corpse just before darkness he began to signal soon afterwards, not burying the corpse at all. He returned often to the corpse and made some inspection and the beginnings of burial, but the sterzeln behaviour dominated throughout the time of observation, which went on for several hours after dark. The extent to which the corpse was buried therefore depended on the time between discovery and that when signalling began. A corpse discovered early in the day was covered with earth by the evening whilst one found only an hour or two before dark was hardly buried at all and no further progress was made for the rest of the observation time.

Males observed on the second day behaved in a similar manner. Those released in the morning buried the corpse during the day and signalled just before dark, whilst those released late in the afternoon signalled almost at once and only buried the corpse between midnight on the room light cycle, when I left the experiment, and the next morning. The sterzeln position was taken up again just before darkness on the second day (Figure 4.2).

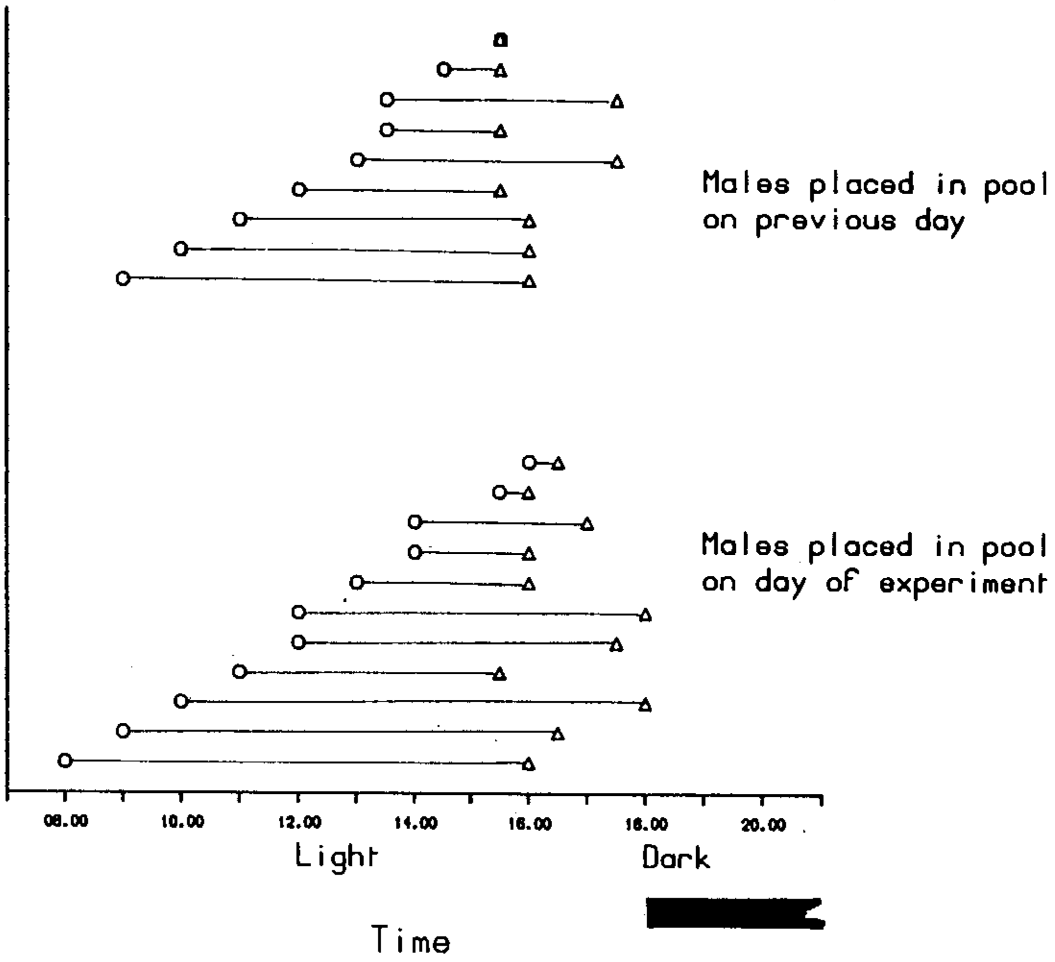
4.2.2. Evidence for a sex attractant.

Methods.

The paddling pool described above was used as a laboratory enclosure. It was filled to a depth of 10cm with earth and two boxes (see chapter 2) placed opposite each other so that their tops were level with the surface of the soil in the pool. Each box had a shallow layer of earth inside with its surface 5cm below the surface of the surrounding earth; in one container a dead mouse was

Figure 4.2

Each of 20 male *N. vespilloides* is represented by a circle and a triangle. The circles show when each male was released into the enclosure. For the lower set of males the triangles show when each male first signalled on the same day on which he was put into the enclosure. For the upper set the triangles show the time of first signalling on the following day. The light:dark cycle is shown. For both sets of males, therefore, signalling begins just before dark, regardless of the time at which males were allowed to find the corpse.


Males placed in pool on previous day
Males placed in pool on day of experiment
08.00
10.00
12.00
14.00
16.00
18.00
20.00
Light
Dark
Time

placed, in the other a mouse and a male beetle. The contents of the boxes were not visible from the centre of the pool.

At the beginning of the experiment I enclosed a female in a box in the centre of the pool. The experiments began at midday, six hours before darkness in the room, and the male buried the mouse during the afternoon. Over the same period I covered the other mouse with earth. In the evening the male took up the sterzeln position. Once the male had been 'signalling' for at least an hour the female was released.

In the field a similar choice was given. Pairs of open boxes, 10m apart, were laid in a row with 50m from one pair to the next. In one of each pair was a male beetle with a mouse which he had buried in the laboratory the previous day; in the other a mouse which I had buried over the same period. The boxes were taken in mid-afternoon to the study site at Penicuik. The males began signalling and were left overnight.

A further laboratory experiment was designed to study the nature of any signal involved. The original suggestion of a pheromone signal (Pukowski 1933) was challenged by Halffter et al (1983) who argued for an acoustic signal after being unable to find any glands in the male by which a pheromone could be produced. I tested for a vibration signal through the twigs or stones which males often climb and signal from. With the help of Dr. A.W. Ewing of the Zoology Department, Edinburgh, a stylus tip was attached against a signalling post (a stick placed upright in the soil) and connected either to earphones or to an oscilloscope. In either case the equipment was sensitive enough to record the footsteps of a beetle climbing the post.

Results.

In the indoor enclosure females were significantly more likely to go to the container with a male than to the one without (Table 4.1a). In the field experiments no beetles were attracted to the hand-buried mice, but each of the signalling males attracted a beetle, 7 of these being males and 9 females (Table 4.1b).

As soon as a beetle stopped moving on the stick and began to signal, no vibration was recorded through the stylus.

4.3. Pair formation.

General methods.

In the field the frequency of fights was studied for comparison with the laboratory data. During the 1985 field season 25 corpses tethered to poles at Penicuik (see chapter 2) were visited every day from the time of being taken to the field until they had been buried by *N. vespilloides* and a crypt formed. Poor weather during this experiment meant that there was a gap of several days between the start of the experiment and corpse burial. Any beetles present were sexed, measured for pronotum width and marked with a warm needle (see chapter 2). The beetles ran away from the corpse after this procedure, but I checked the corpses again after making a round of the poles and by this time (about an hour later) any beetles I had disturbed had returned. Corpses were recorded as being buried by the first beetles to find them or as being buried by later arrivals with displacement of the earlier individuals. Displacement is only a minimum measure of fights since it records only those fights which a challenger wins, but without staying at corpses continuously over several days it is the most accurate estimate that can be made.

Table 4.1

	Male & mouse	Mouse	(χ^2 test)
a. Laboratory.			
Females going to each container.	17	4	$P<0.01$
b. Field.			
Beetles of either sex going to each container.	16	0	$P<0.01$

Results of a choice experiment using female *N. vespilloides*, between a male signalling beside a buried corpse and a hand-buried corpse with no male present.

In the laboratory, fights were watched in the circular pool described above. A corpse was placed in the centre of the pool. The two beetles to be used were measured for size and weight on the day before the experiment and left in the pool overnight, confined in inverted boxes around the perimeter of the pool. Three size classes of beetles were used. Small animals had a prothorax width of between 4.20 and 4.40mm, medium animals measured between 4.80 and 5.00mm and the large class were 5.40-5.60mm. The middle class was chosen because it contains the mean size of beetles in my population (see Figure 3.3) which is itself similar to the mean size of beetles trapped in the field (see Figure 2.5). The other two classes are symmetrical about it and a reasonable number of beetles could be found in each.

In the morning the boxes were taken away and the beetles allowed to find the corpse. Fights were watched until one beetle either ran away or had clearly given up any attempt to bite its opponent and was only prevented from fleeing because the other was in the process of biting through its leg. Defeated beetles often returned to the corpse, but eventually tunnelled out of sight and remained hidden for an hour or more. They never flew away, although they were free to do so. There was an obvious difference between temporary retreats, after which the loser circled the arena for a few minutes and then came back to the corpse, and what was recorded as the final defeat, after which the loser made directly for the edge of the enclosure and went underground. Beetles from all size classes and of both sexes were used in these experiments.

Sex differences in fighting.

Results from the experiments above suggested that males and females differed in their tendency to fight and I therefore studied this directly. Pairs of males or pairs of females from the middle size class were put into the enclosure in the morning. Corpses were inspected at half-hourly intervals and the presence of beetles on the corpse recorded. Once a beetle has found a corpse it will not leave it for long, and if both beetles are known to have found the corpse but only one is found on it by the end of the day and on the following morning, it can be assumed that a fight has taken place. A fight was recorded in these experiments if it was seen, or if both beetles were recorded as having been on the corpse (i.e. had begun the inspection behaviour that precedes burial) and only one was found on the corpse at later inspections and on the morning following the day of the experiment. The pair was recorded as co-operating if both were still found on the corpse in the inspections made after each had found the corpse and if both were still on the corpse on the following morning.

Two sets of experiments were done with male pairs. In the first, males were put together with no female present. In the second, to test whether the presence of a female had any effect on the tendency of males to fight, a female was released into the enclosure and allowed to find the corpse before the males were released. Males arriving at the corpse in these experiments therefore found a female already present.

The outcome of fights.

A field study on the North American species *N. orbicollis* found that the beetle occupying the central position on a corpse was likely to be larger than any beetles in the leaf litter nearby (Wilson & Fudge 1984). I tested whether size difference alone could account for the results of fights between *N.*

vespilloides. Pairs of females (which were found to fight more readily than males) from different size classes were matched against one another. Pairs of females from within the medium size class were also matched. These differed in pronotum width by 0.1–0.2mm. In some cases the corpse was watched until a fight took place, in others the corpse was visited at intervals as described above and the outcome of a fight recorded.

In these experiments the first beetle to arrive at the corpse was noted to test whether first arrival had any effect on the result of a fight. In further experiments to study this point, a female of the medium class was put into the enclosure with a mouse and allowed to find and begin to bury it, and a second female of the medium class, at least 0.1mm larger or smaller in pronotum width than the first, was then added to determine whether it would displace the earlier arrival. Following the first fight, the loser was removed, a third female added and the result of the next fight recorded. The size sequence of the females put into the enclosure was varied and the sequence of results noted.

The duration of fights: symmetric and asymmetric for size.

Fight length was compared between females matched and unmatched for size. Females of equal pronotum width and weight (to the nearest 0.05mm and 0.01g) within the medium size class were matched against each other. Females from different size classes were also allowed to fight. The corpse was watched continuously and the length of the fight was recorded from the first time one opponent bit the other until one beetle fled from the corpse. Fight length was also measured for pairs of females over a range of pronotum widths, with pronotum width and body weight equal within each pair.

Results.

Frequency of displacements in the field.

A high proportion of burials in the field involved displacement of the first beetle to arrive at a corpse (Table 4.2). On the 25 corpses watched, 8 beetles of either sex buried their mouse without being known to be involved in a fight but 23 of either sex definitely displaced another beetle to take possession of their corpse. This represents a minimum estimate of the frequency of fights and shows that fighting is likely to be common, as has often been suggested (Fabre 1919, Springett 1967). Laboratory experiments on fighting are therefore of relevance to the field.

The nature of fights.

When they occur fights are similar for both sexes of *N. vespilloides*. Beetles meeting on a corpse inspect one another, head to abdomen. If a fight is to take place one bites at the other's abdomen and the struggle typically escalates at once with each seizing an opponent's leg between its mandibles and the pair rolling over one another, first one and then the other on top. They may stridulate loudly during the fight and the sound of their mandibles closing on elytra and legs can be clearly heard. Even after the weaker has run away it may return several times to the mouse, always running at once if challenged. After each such encounter the winner chases its opponent a few centimetres from the corpse and then goes back to it. For several minutes the holder of the corpse shows a characteristic behaviour, not seen at any other time, of short, jerky movements across all parts of the corpse.

The fight may end almost at once but can sometimes go on for an hour or more, periods of biting and tumbling alternating with periods when both are still, each lying with an opponent's leg between its mandibles but neither

Table 4.2.

	Number of corpses	Number involving displacement	Number buried by first arrival
Females	21	15	6
Males	10	8	2

Intraspecific displacement by *N. vespilloides* at Penicuik. 25 corpses in the field were scored either as being buried by the first female or male to find them, or as involving displacement of one or both sexes by later arrivals.

attempting to move. It is in the longest fights that the worst damage is suffered. Fights lasting up to five or ten minutes seem to cause no harm, but in encounters of half an hour or more elytra were seen to be torn away and wings damaged, or a leg could be bitten through. If a beetle became so damaged that it could not leave the area around the corpse it would repeatedly be attacked and in some cases all the legs would be bitten through and the abdomen punctured several times. In the field I sometimes trapped beetles which had damage to the elytra similar to that found in beetles which had fought in the laboratory. Such damage could possibly have been caused within the trap, but observation of beetles in a similar situation in the laboratory suggests that this is unlikely: interactions in such a situation are always brief and not of the kind which cause damage. Field beetles and beetles which have been in laboratory fights also occasionally show loss of one or both antennae, which, since the antennae contain the carrion receptors, must affect their ability to find corpses.

Sex differences in fighting.

Males and females in the laboratory were found to differ in their tendency to fight. Of 21 female x female pairs, 20 fought as soon as they met on the corpse. Only the winning female buried the corpse in these cases.

27 male x male fights were set up without a female present (Table 4.3a). Four of these resulted in a fight as immediate as those between females but in the rest the males tolerated one another on the corpse, signalled together in the evening and buried the corpse together overnight. If a female was then introduced, only the larger male and the female would later be found on the corpse.

In sixteen further male x male pairs a female was allowed to find the corpse before the males were released. When a male came to the corpse he

Table 4.3

a. Fights between females with no male present and between males with no female present.

	Immediate fight	Pair together on corpse overnight
Females	20	1
Males	4	23

Females are significantly more likely than males to fight as soon as they meet on the corpse. ($\chi^2 = 27.18$, $P<0.001$)

b. Fights between males meeting on a corpse at which a female is already present and between males on a corpse without a female.

	Immediate fight	Both males together on corpse overnight
Female present	12	4
No female	4	23

Males are significantly more likely to fight as soon as they meet if there is a female already at the corpse when they arrive. ($\chi^2 = 13.11$ $P<0.001$)

found a female already there. In twelve of these cases the two males fought at once and only one buried the corpse with the female; in four the three beetles buried the corpse together. Males are more likely to fight at once if a female is present at the corpse when they arrive (Table 4.3b).

Fabre (1919) noted cases where several males buried a corpse with one female but reported none where females worked together. Females fight one another for a corpse and so fight at once, whilst males seem to fight for corpse and female and delay their fights until a female arrives. Fighting can result in serious injury and it might be advantageous for males to delay risking a fight until the winner at least is assured of some reward.

The outcome of fights.

Size seems to be the main asymmetry deciding which beetle wins a fight (Table 4.4). In all cases a beetle from a larger size class could displace a beetle from a smaller size class. For pairs within the medium size class, the larger individual always won the fight (Table 4.4). Priority of arrival had no effect on the outcome of a fight. Residency may have an initial effect in that a larger beetle just arriving at a corpse is sometimes chased away by a smaller beetle that has been in possession of the corpse for a while, but the large individual seems always to come back, and once it has been on the corpse for a few moments the attacks of the resident are at first ignored and then returned, and the fight proceeds as usual with the small beetle being chased away. 10 experiments of the second type described in the methods, where a sequence of different sized challengers were released to fight with a resident, were done. In all cases it was found that a larger beetle could displace a smaller from the corpse at which the smaller was the resident, even if the smaller had already beaten an individual smaller than itself. If a smaller beetle than the resident was added to the enclosure, the owner always won (Table 4.4).

Table 4.4.

The effect of size and residency on the outcome of fights between female *N. vespilloides*.

a. Members of large(L), medium(M) and small(S) size classes matched against one another.

Classes	n	Winner		Fisher's exact	First arrival		Fisher's exact
		Larger	Smaller	probability	Larger	Smaller	probability
LxM	9	9	0	$2.06.10^{-5}$	3	6	0.31
MxS	11	10	1	$1.73.10^{-4}$	7	4	0.27
LxS	8	8	0	$7.70.10^{-5}$	3	5	0.31
MxM	6	6	0	$1.08.10^{-4}$	2	4	0.24

	Larger wins	Smaller wins	Fisher's exact probability
Larger first	13	0	
Smaller first	14	1	0.54

b. Sequence of larger(L) or smaller(S) females than resident(R) allowed to challenge(C) for mouse.

Experiment	n	Sequence added	Sequence winners	Probability
1	2	L L S	C C R	$1.6.10^{-2}$
2	3	L S L	C R C	$1.95.10^{-2}$
3	2	S L S	R C R	$1.6.10^{-2}$
4	2	S S L	R R C	$1.6.10^{-2}$

Duration of fights.

Fights between females matched for size and weight lasted significantly longer than fights between females of different size classes (Table 4.5).

The duration of fights symmetric for size and weight increased sharply with the pronotum width of the combatants (Figure 4.3). This result could in part be caused by the method of measurement. Error in measuring width would have been proportionately greater for the smaller pairs, making them less evenly matched than the larger pairs and so reducing the likely length of a fight. The effect of increasing size shown in Figure 4.3. however, seems so marked that measurement error alone could not account for it entirely.

4.4. Reproductive success of small individuals through alternative strategies.

Method.

Each night for two weeks five corpses were placed 100m apart on the study site. The experiment began at 16.00, and the corpses were inspected throughout the late afternoon and evening. The first beetle to arrive at the corpse was captured and measured across the pronotum. Over the same period a line of ten traps 100m apart was set out in another part of the field site and the sizes of beetles caught in these was measured. A further comparison was made with beetles which successfully buried corpses and raised larvae during this field season. These corpses were laid as described in chapter 2.

Table 4.5.

		Duration(mins)	
Pairs	n	mean	95% CL
Asymmetric	18	0.36	0.46
Symmetric	19	4.76	1.44

Mann–Whitney U test: W = 185.0

$P<0.001$

The duration of lab fights between female *N. vespilloides* matched for size and weight and between females of different size classes.

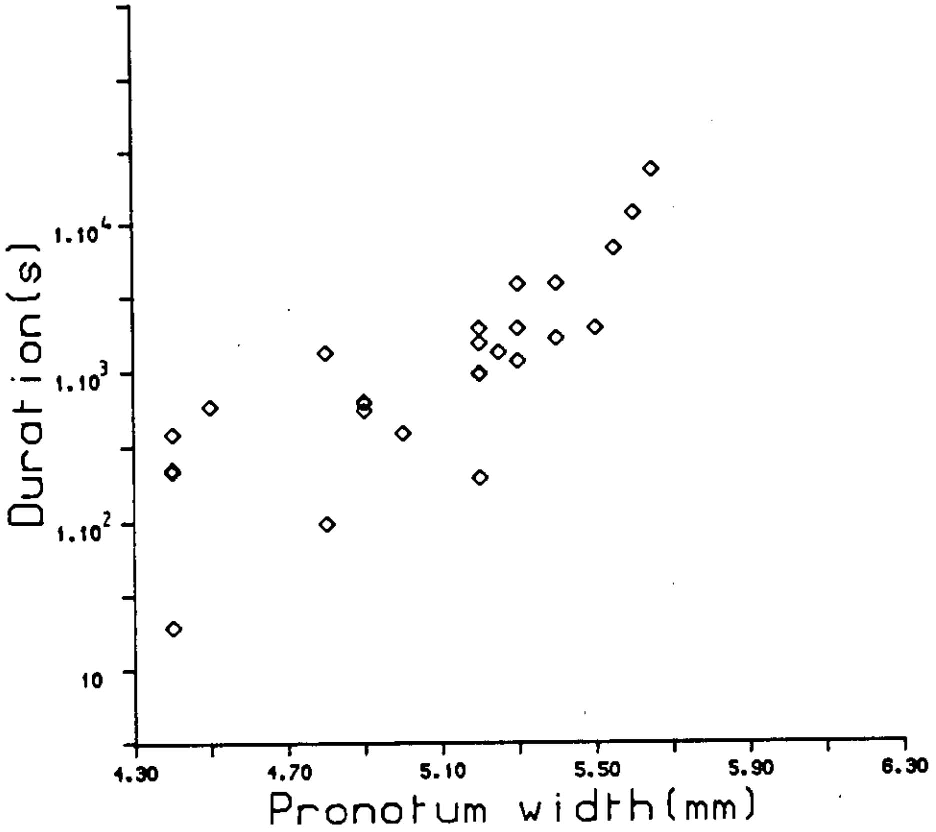


Figure 4.3

The length of a fight plotted against pronotum width for pairs of female *N.vespilloides* matched for pronotum width to the nearest 0.05mm. Fight duration is plotted on a log scale.

Results.

The mean size of the first beetle to arrive at a corpse was significantly less than the mean size of beetles caught in traps (Table 4.6). The mean size of the first arrival was also significantly less than that of the mean size of successfully breeding animals (Table 4.6).

4.4.1. Reproductive success of small males.

Methods.

Following the technique used by Parker (1970) to sterilise dungflies, males were irradiated with gamma rays. A Cs137 source was used and the males exposed to 10k rads. The technique is intended to allow sperm to compete normally for fertilisation of an egg but to cause such abnormalities in the zygote that development stops at an early stage and the egg fails to hatch. Treated males showed no obvious behavioural effects of the irradiation and lived for more than two weeks afterwards. They were used a day after treatment.

Firstly the technique was tested. Each irradiated male was placed with a virgin female and a 25g corpse. The number of eggs laid could not be counted because this would have affected hatching success, but if a clutch was laid at least some of the eggs could be seen against the sides and base of the box. Pairs were used in the experiment if eggs were known to have been laid. The number of larvae on the corpse was counted for these pairs. A control group consisted of untreated males, of the same age as the treated set, mated with females as above.

For sperm competition experiments, pairs of males were used. One of each pair came from the large size class, the other from the medium size class. In a fight the larger male could easily displace the smaller; this is clear from

Table 4.6.

	First arrival	Trapped beetles	Successfully breeding
n	18	24	20
mean(mm)	4.48	4.85	5.13
95% CL	0.11	0.11	0.10
t test		$P<0.01$	$P<0.01$

The size (pronotum width) of the first beetle to arrive at a corpse in the field compared with the sizes of beetles caught in traps and of beetles successfully breeding in the field.

the experiments described above. In half of the pairs the smaller male was irradiated, in the other half the larger. Each pair was placed with a female and a mouse and scored as before.

Results.

The control experiment showed that females mated with treated males laid eggs as usual but that the eggs failed to hatch (Table 4.7). The control group females all produced broods of larvae when eggs were laid.

In the experimental broods, mean brood size was much larger when the smaller male was sterilised than when the larger male had been treated. In several cases where the large male was sterile no eggs hatched, showing that the small male had fertilised none of the eggs laid. In other cases a few of the eggs did hatch and the larvae from these must have been fathered by the smaller male. In some cases therefore, a small male can benefit by burying a corpse with a large male and not leaving in spite of being beaten in a fight.

4.5. Mate recognition.

Method.

Pairs of *N. vespilloides* were each allowed to bury a 10g mouse. From each pair the male was removed and attached with sealing wax to a cotton thread. Another male from the laboratory stock that had not buried a corpse was also attached to a thread. Each female was then presented three times in succession with her own male and three times with a strange male, 'presented' meaning that the male was lowered into the crypt and kept stationary on the corpse until discovered by the female. In half of the broods the strange male was presented first, in the other half the resident male first. A female was recorded as showing aggression if she made the jerking movements typically

Table 4.7.

a. Control.

	Irradiated males			Untreated males	
n	No.boxes with eggs	No.boxes with larvae	n	No.boxes with eggs	No.boxes with larvae
10	10	0	12	11	11

b. Paternity experiment.

	Larger male irradiated			Smaller male irradiated	
n	No.boxes with eggs	mean ± 95%CL no.larvae	n	No.boxes with eggs	mean ± 95%CL no.larvae
12	12	1.75± 1.51	12	12	23.67± 5.71

t test

for mean no.larvae P<0.001

Reproductive success of small *N. vespilloides* males.

The control experiment shows the effect of Cs137 irradiation on the fertility of males mated with virgin females. The paternity experiment pairs untreated and irradiated males and compares egg hatching success between cases where the smaller male is irradiated and cases where the larger male is irradiated.

seen in *Nicrophorus* when the crypt is invaded or disturbed, stridulated and made a biting attack on the male.

Results.

The strange male was attacked on 89% of presentations, the resident never. This did not vary with the order of presentation (Table 4.8).

4.6. Discussion.

Timing of signal.

Signalling at the corpse only begins an hour or two before darkness in the laboratory. There may be a 'window' for signalling analogous to the dawn signalling of the cricket *Gryllus integer* (Cade 1979) or the timing of song bouts in many birds and some primates (Tenaza 1976). A number of theories considering the function of the dawn chorus in birds have been proposed (Mace 1986) and some may be relevant to the behaviour of *Nicrophorus*. A signal might travel further under the thermal conditions found at dawn and dusk (Henwood & Fabrick 1979) or the period might be the most cost-effective in which to signal (c.f. Kacelnik & Krebs 1983): if climbing to an exposed place and signalling there increases the risk of predation then signalling might be confined to a period in which females are most active and so the risk most worth taking. *Nicrophorus* is thought to be most active in the early evening (Pukowski 1933). An alternative interpretation is that signalling does not occur in a specific 'window' defined by thermal conditions but simply after a time when light has begun to fade and predation risks are reduced.

Table 4.8.

a. Own male presented first.

Brood	1	2	3	4	5	6
Aggressive response to own male	0	0	0	0	0	0
Aggressive response to strange male	2	3	3	3	3	2

b. Strange male presented first.

Brood	1	2	3	4	5	6
Aggressive response to strange male	2	3	3	3	3	3
Aggressive response to own male	0	0	0	0	0	0

The response of female *N. vespilloides* in a crypt to the introduction into the crypt of the male with which she buried the corpse and of a strange male. The aggressive response is recorded as the number out of three presentations of each male.

Fisher's exact probability for independence of order of presentation = 1.0
Probability of response to strange/own males being due to chance: $1.16.10^{-9}$

Evidence for a sex attractant.

It is clear that males attract other beetles to a corpse. The sterzeln position is almost certainly associated with the release of an attractive signal. Males sometimes signal close by an unburied corpse and their attraction must then act in addition to the attraction provided by the carrion itself. It is not surprising that males as well as females should respond to a male signal if it announces the presence of a corpse: a larger male which responds has a chance of displacing the signalling male.

Attraction of other males by a signalling male is not uncommon (Thornhill & Alcock 1983). Aggregations of males, typified by the bark beetles (Scolytidae) (Birch 1978) occur when males gather in large numbers and add their signals to those of previous arrivals. This can happen with burying beetles: if several *N. vespilloides* males collect on a corpse where no female is present, all may signal together (pers.obs.). However, it is unlikely that attracting other males is an advantage of signalling. Several males together might be more successful in attracting a female (individual males interrupt their signalling bouts to visit the corpse and the presence of several males may mean a more continuous signal) but this increased success would almost certainly be outweighed by the increased competition for the female attracted. Groups are more likely to collect because of the advantage to males of responding to a male signal than because of any advantage to the signalling male of calling in another male with whom he may then have to fight. The advantage to the respondent will vary with size. Large males can displace smaller males from a corpse (section 4.3) and it might be predicted that the smallest of males should not respond to a male signal because the signaller is likely to be able to defeat them in fighting for any females later attracted to the corpse.

These experiments show that male beetles have some way of attracting other individuals but do not prove that a pheromone is involved. An acoustic signal, however, seems unlikely. Burying beetles stridulate, using a 'file' structure on the underside of the elytra (Niemitz 1972), but the obvious movements performed when stridulating never occur during sterzeln signalling at which time the tip of the abdomen quivers slightly and is stroked by the hind legs but no sound can be heard. Furthermore, no vibration is passed through the twigs or stones which males often climb and signal from: I recorded no vibration through a stylus tip attached to the signalling post once the male stopped moving and began sterzeln signalling. It seems likely that the means of the attraction demonstrated here will prove to be pheromonal rather than acoustic.

It has been suggested that long distance pheromones are rare amongst male insects compared with females (Jacobsen 1972). In general females signal and males, which usually compete more vigorously than females for mates, undergo the costs and risks of travelling to the signal. Different examples where a male pheromone occurs can have different explanations (Thornhill 1979). One likely to apply to *Nicrophorus* is that males have possession of a resource such as a breeding site or a 'gift' of food to be exchanged for mating whose reproductive benefits to a female outweigh the costs of travelling. *Nicrophorus* males clearly illustrate this point. A female responding to a male signal will find a corpse on which she can breed. Females are, of course capable of finding corpses by the smell of carrion alone and can bury and raise a brood without the help of males (Pukowski 1933; Wilson & Fudge 1984; chapter 6). There may be reasons why a female should respond preferentially to a male signal rather than to just the smell of a corpse. The male signal might travel more effectively than the odour of a corpse, particularly if the corpse has only just begun to decay. Even if there is no difference in detectability between the perfume of carrion and that of the male pheromone there might be an advantage in increased speed of burying the corpse when a male is already there to help, so reducing the chance that the corpse will be lost to other beetles or to a vertebrate scavenger before it can be buried out of reach. Later on, if the male contributes to parental care (chapter 6), the presence of the male may help in feeding the brood and in brood defence.

Release of a pheromone may be costly. A cost of signalling can be increased risk of predation (Walker 1964) or attack by parasites (Mitchell & Mai 1971). There is no evidence for *Nicrophorus* to suggest that predators respond to any pheromone a signalling male might release, but a male in the sterzeln position, often signalling from an exposed position, must be more visible to predators. A possible explanation of delaying the signal until just before dark is that predation risk might be reduced as light fades.

The male signal in *N. vespilloides* involves risks to the signalling male, possibly in increased risk of predation and, as shown in field experiments, in attracting male competitors. The benefit, however, if a female is attracted, is the difference between fathering a brood on the corpse he has found and being unable to reproduce. Females respond to the male signal although they can breed without the help of a male. The main advantage to them may be in increased chances of finding a corpse through the efficiency of a male signal and in greater speed of burial of a corpse when a male is there to help.

Pair formation.

Fights are an extreme manifestation of competition; they will occur when competition is direct and extreme: that is, when a resource is discrete, accessible and in short supply. As an example, the wingless male morphs of some fig wasp species engage in mortal struggles for females inside a fig fruit

(Hamilton 1979). In this case the fights are particularly damaging (which may be more common among insects than vertebrates (Matthews & Matthews 1978) although vertebrate examples do occur (e.g. Silverman & Dunbar 1980)) but it is more usual that contests do not escalate to the point where there is a risk of severe damage or death but are rather settled by display or by the first contacts between opponents (Maynard Smith & Parker 1976). This limitation of individual risk is one of the predictions of the game theory analysis of fighting (Maynard Smith 1982) whereby it is proposed that the behaviour of an individual in a contest should not depend solely on its own requirements and capabilities but also on those of its opponents in the population. Capabilities and requirements are the ability of an individual to fight for a resource - its resource holding potential or RHP - and the value of that resource to the individual in terms of fitness - a corpse to lay eggs on or a female with which to mate - a value which is not simply the absolute fitness value of the resource but what can be gained from it by that individual relative to the gains possible from available alternatives. The outcome of a contest, which reflects the decisions of its protagonists to escalate or to run away, depends on the information they receive as to the inherent RHP of their opponent - for example its size - and the value of the resource in question: the adjustment of inherent RHP according to need.

Information may be transferred in various ways. An arbitrary convention may settle the contest, as when zebra spiders seem to use their mode of behaviour at the time of meeting so that stationary spiders repel wandering ones (Jacques & Dill 1980). This can be interpreted as the 'owner' of a piece of wall or ground repelling the intruder, a situation seen also in the dragonfly *Pyrrhosoma nymphula* where contests amongst the larvae for feeding sites are determined not by size but by status as resident (Harvey & Corbet 1986). Residency is important too in the spider *Meta segmentata* (Rubenstein 1987).

The outcome of a fight in this species usually depends on size, but a resident at a web can defeat opponents up to 10% heavier than itself. A burying beetle resident at a corpse can chase any individual it meets away from the corpse regardless of size and can drive off larger beetles if it meets these as soon as they arrive. A contest for possession is not finally settled by such a convention, however; the intruding beetle will always return and after only a few moments on the corpse will engage in a full-scale contest, responding fiercely to the 'resident's' attack. If successively larger beetles are introduced to a corpse so that the first challenger becomes the resident and then faces a challenger larger than itself, the challengers continue to win until one smaller than the resident is tried.

A signal indicating relative strength may be used as a predictor of the likely outcome of a fight and allow the weaker to back down without suffering damage and the stronger to avoid even the slight risk of a fight. The roaring of red deer stags in the mating season (Clutton-Brock et al 1979) may be an example of such a signal since the challenger of a harem holder usually retreats if the owner can roar at a quicker rate than he. The physical strength and condition required to roar loudly and often is used to signify the potential to fight well. The depth of croak in the common toad *Bufo bufo* seems to be used in the same way (Davies & Halliday 1978). An alternative signal may simply be that of size, which may be assessed by appearance. The next stage in stag contests involves a parallel walk during which the opponents can measure one another's size; in a thrips (Insecta: Thysanoptera) parallel positioning of males seems to allow the same function (Crespi 1986). Males of the common toad also have the ability visually to assess their rivals (Davies & Halliday 1978) and size 'demonstrations' occur in several insects. The digger bee *Centris pallida* rears up and spreads its forelegs during agonistic displays (Alcock 1979) and rival diptera *Achias australis* spread their eyestalks parallel to one another and can judge head width and so body size (McAlpine 1979).

In some cases assessment may require contact, such as the grappling that occurs between horned Hercules beetles (*Dynastes*) before the weaker breaks free and runs away (Beebe 1944), or fighting between dungfly males (Parker & Thompson 1980). No preliminary assessment has been seen in *N. vespilloides*; some kind of direct struggle has to take place before a contest is decided. The length of a contest, or its intensity - how far each escalates the risks involved - depends on when the weaker animal gives up. This may be a function of how closely matched the opponents are in RHP; the less the asymmetry between them the more likely it is that escalation will occur and the contest be prolonged (Parker 1974; Sigurjonsdottir & Parker 1981; Maynard Smith 1982). Intensity of cichlid fighting was found to be inversely related to the size difference between the individuals (Turner & Huntingford 1986) and male weevils *Claeoderes bivittata* were more likely to engage in a contest of lashing one another's legs with their antennae if they were similar in size (Johnson 1983).

I found that fights in the laboratory between female *N. vespilloides* lasted longer if the beetles were matched for size and weight than if they were asymmetric for size. The asymmetric fights normally lasted only a few seconds before the loser ran from the corpse; the matched pairs fought for up to two hours.

The length of fights might be expected to correlate with damage suffered, but this may not always be true. With stag beetles (Lucanidae) it was found that damage rarely occurred with matched pairs even in long contests but was the fate only of small beetles in unbalanced pairs. Horned beetles in general use leverage rather than piercing or biting tactics to win their contests (Palmer 1978; Eberhard 1979); use of spines or mandibles may be more likely to cause length of contest to be related to risk; nonetheless, for the shrimp *Alpheus* *armatus* which uses a modified claw to snap at its opponents, greatest damage and more frequent damage occurred in the shortest fights, those between large females (Knowlton & Keller 1982). Only the longest fights caused obvious damage to *N. vespilloides*, except in occasional cases where an antenna was lost in fights lasting one or two minutes. Legs were lost, elytra torn away, wings frayed and beetles killed only in the fights of half an hour or more.

Fight intensity can also depend on the value of the resource fought for compared with that of available alternatives. Male brentid weevils fought more fiercely for large females than for small (Johnson 1982) and male bugs *Acanthocephala femorata* were more likely to attack intruders when their territory contained females than when it was empty (Mitchell 1980). Fights between female spiders *Meta segmentata* lasted longer in higher quality web sites (measured as the amount of prey available) than in lower quality sites (Rubenstein 1987). *Nicrophorus* might be predicted to fight more fiercely for a larger corpse, or when corpses were particularly rare. It is usually assumed, however, that corpses are always limiting for *Nicrophorus* (Springett 1967) and the value of any corpse might be so high that the beetles always fight at a maximum intensity.

The point at which a weaker animal gives up may also be a function of an asymmetry in the value of a resource. If RHP is equal the animal with most to gain from victory relative to available alternatives should be more prepared to escalate (Parker 1984). Even an animal weaker in RHP but with more to gain than its opponent might be expected to risk more under certain circumstances, defined by Parker (1984) as whether a stronger animal reaches, before its opponent does, a point where the expense of further contest exceeds resource value should the contest then be won. This may explain the observation that starved pygmy sunfish (Rubenstein 1981) are more likely than well-fed fish to attack and to defeat opponents larger than themselves. The effect of starvation was not tested for *N. vespilloides*. If corpses are sufficiently limiting, their value may never be asymmetrical to the extent of allowing a weaker competitor to win.

Absolute size in matched pairs may affect the nature of a contest. Fights between small thrips (Crespi 1986) were more likely to escalate than fights between a large pair. This could be because small thrips have less risk of damage from their small stabbing appendages or because the chances of victory for a small animal are so rare that competing with another small animal offers a disproportionate reward. However, fights between large females of the shrimp *Alpheus armatus* escalated more quickly and involved greater risk of damage (Knowlton & Keller 1982). I found that fights between *N. vespilloides* of the large size class were those which lasted long enough for serious damage and death to occur: fight length increased markedly with the size of the beetles involved (Figure 4.3) although the result might be exaggerated by errors in measurement of the smaller pairs. Fights between large *N. vespilloides* are thus most likely to be costly in terms of damage suffered. The relationship could be explained if individuals fought for a time dependent only on their own size and not that of an opponent, but then any fight between pairs of different size classes is likely to be shorter than a fight between a matched pair from the smaller class of the two. Mean duration of fights between matched pairs of the medium size class was about 4 minutes (Table 4.5), whilst a fight between a medium and a large female never lasted more than a minute and was usually over in a few seconds. The result seems surprising: as for the thrips it can be argued that the smallest beetles are those which have least chance of winning any fight and that they should therefore risk a great deal in any contest in which they find themselves at least evenly matched since such contests are likely to be rare. For *Alpheus armatus* it was argued that the largest females were evenly matched so rarely that their assessment ability was poor and fights between two large females escalated most rapidly because of this (Knowlton & Keller 1982); the same might be suggested for *N. vespilloides*: a large beetle might have a poor ability to 'know' when to give up.

Alternative behaviours.

Smaller beetles may adjust their behaviour in order to have more chance of finding a corpse before larger animals do, perhaps spending more time in flight, with the benefit of first arrival balanced against the energetic and possible predatory costs of flying. A similar case is that of the sugar-cane beetle *Podischus agenor* where small males emerge earlier in the season than large males and disperse more from the site of emergence, both behaviours that are argued to reduce competition with larger males (Eberhard 1982). First arrival is not a guarantee of breeding success, as is shown by the result that beetles breeding successfully at Penicuik that summer were much larger on average than the first-arriving beetles; for females at least, however, it must give some chance of reproduction.

Reproductive success of small males.

Small males lose fights with larger competitors but through sneak matings may enter a new competition at the level of sperm. Insect sperm generally remain potent throughout the life of the female in which they are placed, so that sperm of earlier or later matings by the same or different males may compete to fertilise eggs (Walker 1980). There may be free mixing of sperm from different matings; or the sperm of the first mating may take precedence, as in the parasitic wasp *Nasonia vitripennis* (Holmes 1974); or the sperm of the last male may take precedence: this latter seems to be the usual case (Walker 1980). Observed patterns of sperm displacement may result from the behaviour of the male. A dramatic example is found in the damselfly

Calopteryx maculata (Waage 1979) where a male removes previously deposited sperm from a female before inserting his own. Observed patterns may also result from selection on female behaviour and reproductive structure: female behaviour may prevent or encourage matings by more than one male and the structure of the spermatheca may determine the extent of displacement; spherical or ovoid shapes are usually associated with low levels and an elongated shape with high (Walker 1980).

A male in the crypt mates frequently with the female; if either has gone outside he will copulate again as soon as they meet. The male which wins a fight therefore has the best chance of being last to mate and can put more sperm in total into the spermatheca, so that the odds in this second competition are still against the loser of the fight. The results of the paternity experiment, however, suggest that some success is still possible and this must occur as a result of the female's willingness to accept matings from a male other than the resident of the crypt. The acceptance of multiple matings may be advantageous in a number of ways (Walker 1980): a female may receive a nuptial gift of food from each male she mates with or use nutrients in fluids transferred with sperm (Boggs & Gilbert 1979); these food items may then increase her reproductive ability; harassment by males may be less if they are allowed to mate; there may be genetic benefits in allowing fertilisation by a diversity of sperm (Walker 1980). Another adaptive argument is that multiple mating provides 'insurance' against any one male being sterile (Gibson & Jewell 1982). A consideration more relevant for *Nicrophorus* might be that if the losing male has some chance of paternity, there may be no risk of his attacking the brood. Once larvae hatch a female will attack any strange male in the crypt and burying beetles will readily eat larvae that cannot be their own. A similar explanation is proposed for the willingness of the female dunnock (*Prunella modularis*) to mate with the weaker of two males which may share a territory with her (Davies 1985): a subdominant male which has no matings may destroy the female's brood. Alternatively, multiple mating by females may not be adaptive for females but may have evolved because of genetic correlation between the sexes which has drawn female reproductive behaviour along a path of multiple mating selected for only amongst males (Halliday & Arnold 1987).

Mate recognition.

Females seem to be able to recognise the male with which they are raising a brood. A strange male may be treated as a threat to the brood in the same way as are carabid and staphylinid beetles if these are placed in the crypt (see chapter 6): *Nicrophorus* will readily eat maggots on a corpse (Steele 1927) and would probably treat the larvae of other burying beetles in the same way. In the laboratory non-breeding *Nicrophorus* placed with larvae whose parents had been removed have been seen to kill and eat the brood.

Chapter 5.

Corpse burial and egg laying.

'Transcendent alchemists, they were transforming that horrible putrescence into a living and inoffensive product.'

J.H. Fabre 'The Glow-Worm and other Beetles' 1919.

5.1. Introduction.

Burial of the corpse is the most conspicuous and best-known feature of the behaviour of *Nicrophorus*. Burial takes the corpse beyond the reach of competitors such as blowflies and some of the vertebrate scavengers. The beetles create a more secure situation and for a while impose a new kind of order on their environment. In this they are unique amongst the carrion community. Another silphid, *Necrodes surinamensis*, uses carrion for feeding and reproduction but does not bury the corpse; its eggs are laid on the surface around the corpse and the larvae are left without care (Ratcliffe 1972). The same is true of the Japanese carrion beetle *Promascopus morio* (Peck 1982). The investment represented by burial and subsequent aspects of parental care increases the importance of each individual brood to *Nicrophorus* and emphasises the questions to be examined in this and the following chapter, of how to trade costs and gains in the raising of offspring. The stability created in the crypt (Easton 1979) lends further emphasis: when the influence of the environment is reduced the importance of individual action is relatively greater (Horn & Rubenstein 1981). The purpose of this chapter is to compare burial and egg laying in *N. vespilloides* with the work on *N. vespillo* (Pukowski 1933) which has until now been used to describe the whole genus, and to discuss the number of eggs laid by *N. vespilloides* and some of the factors which affect this clutch size. I first describe corpse burial and the distribution of eggs. The eggs of *N. vespillo* are laid in a chamber built off the side of the crypt (Pukowski 1933; Ling 1957). I was not able to study egg laying in the field, but the distribution of eggs in laboratory broods of *N. vespilloides* was examined. The second part of the chapter discusses the clutch sizes found in *N. vespilloides*. Clutch size, the number of eggs in a discrete batch, is a key life history trait (Stearns 1976; Sibley & Calow 1985). A large body of work dealing with clutch size in vertebrates, particularly birds, has been accumulated, and more recently interest in invertebrate clutch size has grown, mainly dealing with parasitoids (Klomp & Teerink 1962; Waage & Ng 1984; Takagi 1985) and gall-forming insects (Weiss et al 1983, Godfray 1986). *Nicrophorus* is an animal of particular interest for clutch size studies in that it illustrates the situation used for many insect oviposition models, a clutch laid on a limited resource (Parker & Courtney 1984), but also shows parental care of the hatching brood, making it relevant to some of the results and predictions of work on birds. A few other insects show parental care of comparable complexity, e.g. the earwig *Forficula auricularia* (Lamb 1976) and the salt marsh beetle *Bledius spectabilis* (Wyatt 1986) but I am aware of no studies of clutch size in such animals.

Much work on clutch size, in vertebrates and invertebrates, has been based on optimality models designed to predict the clutch sizes that should be laid under particular circumstances if a parent is to maximise its lifetime fitness. Some of the general statements that result from such work were used as the basis of the work on *N. vespilloides* which is described in this chapter. A predicted optimum may vary with the condition and circumstances of an individual; its age, for example, or the availability of food. It may lie outside the possible range for the parent: clutch size, like any life history trait, is governed by what is desirable in terms of fitness and what is possible according to the capacity of the individual involved. A predicted optimum to maximise the productivity of a single clutch may differ from an optimum designed to maximise the sum of several clutches over an individual's lifetime. If an animal only breeds once or if chances to breed are the chief limiting factors in reproduction, then the predicted optimum for each clutch is to maximise the productivity of that clutch. If the animal can breed several times with opportunities to breed not being the main limiting factor then each clutch may be lower than the maximum-production clutch in order to reduce the costs of reproduction at each clutch and produce a greater lifetime sum. Too little is known of the biology of *Nicrophorus* in the field to predict what its clutch-laying behaviour should be and the laboratory experiments described below were intended to begin to define the boundaries of what may occur. First I studied the variation of clutch size with the circumstances of individual females. A series of experiments was done to examine variation in clutch size for females of different sizes, ages and nutritional state. Age, nutritional state and the number of clutches already laid might affect residual reproductive value: the reproductive capacity of an organism at its next breeding opportunity multiplied by the probability of its survival to that next opportunity (Williams 1966). Previous experience may also affect clutch size considerations although this was not studied in these experiments. For example, considering clutch size on a patchy, limited resource as an optimal foraging problem it was predicted that an increase in search time between suitable oviposition sites should lead to an increase in optimal clutch size (Skinner 1985). Food intake of the female before breeding may also affect the breeding effort that can be made (Hirshfield 1980; Murphy et al 1983). These are all factors which may vary during the lifetime of an individual. The size of *Nicrophorus*, in contrast, is established at eclosion and does not change thereafter. Size has often been found to affect the egg-laying capacities of invertebrates (Peters & Barbosa 1977; Blueweiss et al 1978; Derr et al 1981; Kasule 1985) and was studied here for its effect on a single clutch on a large corpse and on several clutches laid on 25g corpses throughout individuals' lifetimes.

The second part of the investigation of clutch size then examines variation with resource size. The careful manipulations and movements of a corpse reported by all observers of burying beetles may have as one function assessment of the value of a corpse as a food source for larvae, leading to an adjustment of the clutch laid (Springett 1967; Easton 1979). An analogy can be drawn with certain insect parasites. The chalcid wasp *Trichogramma embryophagum* adjusts its clutch according to the size of the host egg. The egg is assessed by walking over it with antennae 'drumming' across the surface. If a larger egg is provided for drumming and then substituted with a smaller, a clutch is laid suitable for the first egg (Klomp & Teerink 1967). An effect of resource value on clutch size seems to be common in parasitoids (Luck et al 1982; Sato & Tanaka 1984; Godfray 1986) and certain other cases: the weevil *Apoderus balteatus* for example, forms an egg-cradle from a leaf and adjusts the number of eggs it lays according to the size of cradle it can make (Sakurai 1986).

Previous studies on *Nicrophorus*, however, have not been as clear. Resource value is assumed to be weight of a particular type of corpse, usually a laboratory mouse. No correlation between the two variables and no difference in mean clutch size laid on mice and on rats was found by Easton (1979). His combined mean for the two types of corpse was 12.79 eggs. For *N. orbicollis* bred in the laboratory on two size classes of mice (15-20g and 30-35g) no difference between mean clutch size was found (Wilson & Fudge 1984) although the size of brood was subsequently different.

For some insects there may be no shortage of sites to lay eggs, for example where eggs are laid on the leaves of common plants. Burying beetles experience fierce competition for each site and each corpse imposes a limit on clutch size. I therefore compare the clutch sizes found for *N. vespilloides* with the capacity of corpses of different weights. For *N. vespilloides* in the laboratory Easton (1979) made broods larger than those normally found by adding larvae to existing broods and calculating a threshold brood which a corpse could support without a sudden increase in larval mortality. The threshold for 25g mice was about 27 larvae, for 15g mice 23 larvae, for 10g mice 26 and for 5g mice 19. I did not repeat Easton's experiments but measured laboratory brood sizes on different sizes of mice and studied the effects of brood size on the members of the brood. I hoped to interpret the significance of clutch size in terms of subsequent effects on the brood. Since the lifetime fitness of adults is measured not simply by their own productivity but that of their offspring, that is, by the number of grandchildren they produce, consideration of optimum clutch meant studying the fitness as well as number of offspring produced by a given clutch. *Nicrophorus* lays its eggs on a corpse, a discrete resource, and as for other insects which do this, the size of offspring might be expected, at least for smaller corpses, to be inversely related to the number of eggs laid (Klomp & Teerink 1967; Mitchell 1975). The size of offspring has profound effects on their fitness (Chapter 4, section 5.4.). The size of larvae on different corpses was therefore also studied. In all cases effects were measured in terms of larval weights. Larval weight at dispersal is the quickest and most easily measured index of offspring fitness, but the assumption is being made that larval weight is an accurate index of adult size, which is the true basis of competition for corpses. This assumption is tested in the next part of this chapter. Finally I describe experiments looking at egg size. The size of each unit of a clutch, as well as the size of the whole, may be a component of the role of clutch size in an individual's life-history strategy (Smith & Fretwell 1974). Models of predicted egg size under different circumstances have been produced (Parker & Begon 1986; Begon & Parker

1986). They emphasise the importance of egg size by proposing an inverse relationship with clutch size: a female is likely to be able to lay many small eggs or fewer large ones. Such a relationship has been recorded for the speckled wood butterfly *Pararge aegeria* (Wiklund & Persson 1983). Using *N. vespilloides* in the laboratory, I examined the effect of female size, corpse weight and repeat laying on egg weight. Work on butterflies showed that egg size decreased with female age (Wiklund & Persson 1983; Karlsson & Wiklund 1984). This was explained in mechanistic terms: as a female aged the reserves available for eggs were depleted and smaller eggs were laid (Wiklund & Karlsson 1984), and as an adaptive female strategy (Begon & Parker 1986). Both explanations refer to organisms which obtain the food reserves for egg production before reaching maturity. Burying beetles feed throughout their adult lives and may not, in the field, suffer from gradually depleting reserves.

Begon & Parker (1986) predicted that larger females should lay larger eggs than smaller females in the first clutches. The argument assumes that there is an advantage in fitness to larvae hatching from larger eggs. Such an effect seems to occur in birds (Parsons 1970; Schifferli 1973), but was not found in the speckled wood butterfly *Pararge aegeria* (Wiklund & Persson 1983) or the wall brown butterfly *Lasiommata megera* (Karlsson & Wiklund 1984). The measures of fitness for the butterflies were made in the laboratory, and it was pointed out that effects not apparent under those conditions may be important in the field (Begon & Parker 1986).

5.2. The process of burial.

Corpse burial, which is the first stage of parental care in *Nicrophorus*, is foreshadowed in silphids which show no care of their young. For example, *Necrodes surinamensis* strips the hair from a corpse, apparently in search of maggots beneath the skin (Ratcliffe 1972), and the same behaviour is part of the burial process in *Nicrophorus*. This account of burial is based on my observations on *N. vespilloides* in the laboratory, where mouse corpses were buried in the boxes described in chapter 2, and in the field, where mouse corpses were placed on the ground and left until discovered by beetles.

A corpse is inspected carefully and may be moved a considerable distance before burial. A single beetle can gradually move a rat or a rook, and a mouse is easily shifted. The beetle crawls underneath so that it lies on its back, and the corpse is moved by the insect's legs as though resting on a conveyor belt. A corpse can be moved from a spot where burial is impossible, on a concrete slab, for example, to softer ground (Ling 1957). Close inspection of the corpse probably allows the discovery of fly eggs (the hair is combed apart by mandibles and front tarsi and the orifices and crevices of the body explored) and detects any obstruction to burial. A corpse can be released from the branches of a bush or bitten free from raffia tying it to a stake (Fabre 1919). When the site is settled a slanting tunnel is dug into the earth and the corpse pulled into it. A chamber is hollowed out at the end of the tunnel; this is the crypt. The corpse is packed into the crypt; during burial it is rolled into a ball and the hair stripped away with the mandibles (Figure 5.1). The wall of the crypt becomes tightly packed as a result of the beetles pressing against it as they work around the corpse. The hair of the corpse mingles with the soil in the wall and the soil fragments and hair fibres form a reinforced structure which will stand securely if the surrounding soil is removed. Within the crypt, variation in temperature and humidity is dampened (Easton 1979). The corpse is covered with mud and faeces; according to Halffter et al (1983) the excrement repels flies and inhibits fungal growth. It is deposited throughout the nesting period by both parents and larvae. Antibiotic secretions from the saliva may also play a part in inhibiting microbial growth on the corpse (Springett 1967). It is obvious that the burial process in some way slows

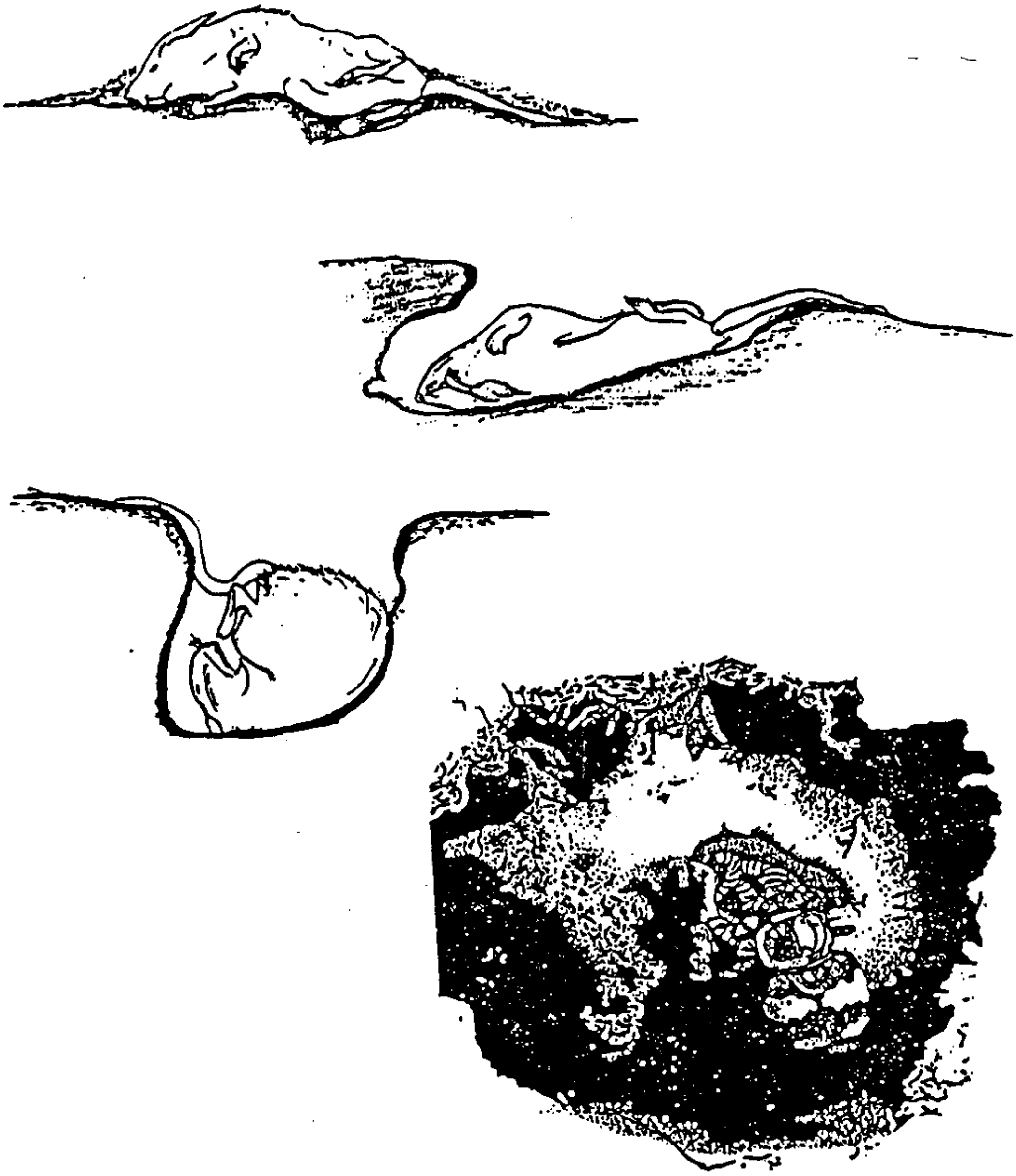


Figure 5.1

Corpse burial by *N.vespilloides*

corpse decay: a corpse buried by beetles remains unchanged long after a corpse left on the surface has putrefied.

5.3. The distribution of eggs.

Method.

Eggs are laid after the corpse has been buried and the crypt built. Once the eggs have been laid the adults continue to remove the hair from the corpse and to pack the walls of the crypt. In my experiments, eggs in boxes were scattered through the soil instead of being laid in a chamber, but this might have been caused by conditions in the box being too crowded. Ten pairs of *N. vespilloides* were each allowed to bury a 25g mouse in a flower pot 0.5m in diameter and containing soil to a depth of 0.75m. Three days later, when egg laying was complete, the crypt was dug out.

Results.

No chamber was found. Eggs were scattered in the soil exactly as they had been in the normal broods in food boxes. They were found all around the corpse, between one and ten centimetres away.

5.4. Clutch size.

5.4.1. Food intake and clutch size.

Method.

20 days after eclosion in the laboratory, 40 females of average size were treated in two groups. 20 'fed' females were given an excess of mealworms, 20 'starved' females one mealworm every fourth day. After twelve days the fed group had gained on average 4% in weight, the starved group had lost 4%. Both groups were then given 25g mice and paired with males and allowed to breed. The number of eggs laid was counted.

Results.

Females from the starved group laid significantly more eggs than females from the fed group (Table 5.1).

5.4.2. Female size and clutch size.

Methods

The variation of clutch size with female size, measured as pronotum width, was studied by two experiments, the first to measure the size of a single, maximum clutch, the second to measure the total number of eggs produced in a lifetime.

Two sets of females, 20 days after eclosion in the laboratory, were used to test the effect of size on a single clutch. The first had a mean pronotum width of 4.41 ± 0.06mm, the second of 5.21 ± 0.04mm. They were paired at random with a sample of males representing the range of pronotum widths normally found in the laboratory population (see chapter 3). The pairs bred on 75g corpses. These corpses consisted of two large mice sewn together and were rolled up and buried as if one corpse. They were used so that females were given enough carrion to induce them to lay a maximum clutch (see section 5.4.2).

Table 5.1

	Fed females	Starved females
n	19	16
Initial weight	0.23(0.01)	0.23(0.01)
Breeding weight	0.24(0.02)	0.22(0.05)
Mouse weight	26.59(1.20)	24.85(1.50)
Clutch size	20.26(1.73)	28.19(1.92)
t test between clutch sizes	P<0.01	

Clutch size and food intake before breeding.
All weights in grammes, 95% CL in brackets.
Starved females were given one mealworm every fourth day for twelve days, fed females an excess of mealworms.

In the second experiment, to measure total egg production, a further set of females representing the range of pronotum widths were paired at random with a set of males and allowed to bury 25g corpses. Once first stage larvae appeared on the corpse the soil was removed from around the crypt, so removing any unhatched eggs, and replaced with fresh soil. The number of eggs in the old soil was counted. The larvae on the corpse were picked off with forceps, counted and put back on the corpse. The number of eggs and the number of larvae were added to give the size of the initial clutch. Egg total could not be counted before hatching because of the poor hatching success of eggs that had been removed from the soil. This process was repeated every ten or eleven days as each brood was raised and dispersed from the corpse. For each new set of corpses the sexes were paired again at random so that any effect of size difference between male and female was cancelled out over the experiment. Throughout the experiment the beetles were given access to food (mealworms) but these were never eaten.

Results

On 75g corpses, the mean clutch size for the large females was greater than that for the small females (Table 5.2).

In the second experiment, using a sequence of 25g corpses, there was a strong relationship between female pronotum width and the total number of eggs laid (Figure 5.2).

5.4.3. Clutch size and clutch number.

Table 5.2

	Small females	Large females
n	20	12
Pronotum width(95%CL)mm.	4.41(0.06)	5.21(0.04)
Mouse weight(95%CL)g.	75.00(2.05)	77.00(2.20)
Mean clutch(95% CL)	26.85(7.41)	46.42(8.08)
t test between clutches	P<0.01	

Clutch size on 75g corpses: small and large females.

Small females 20 days from eclosion allowed to breed on 75g corpses and clutch size counted and compared with that of large females of same age burying corpses of the same weight.

75g corpses were made by sewing two mice together.

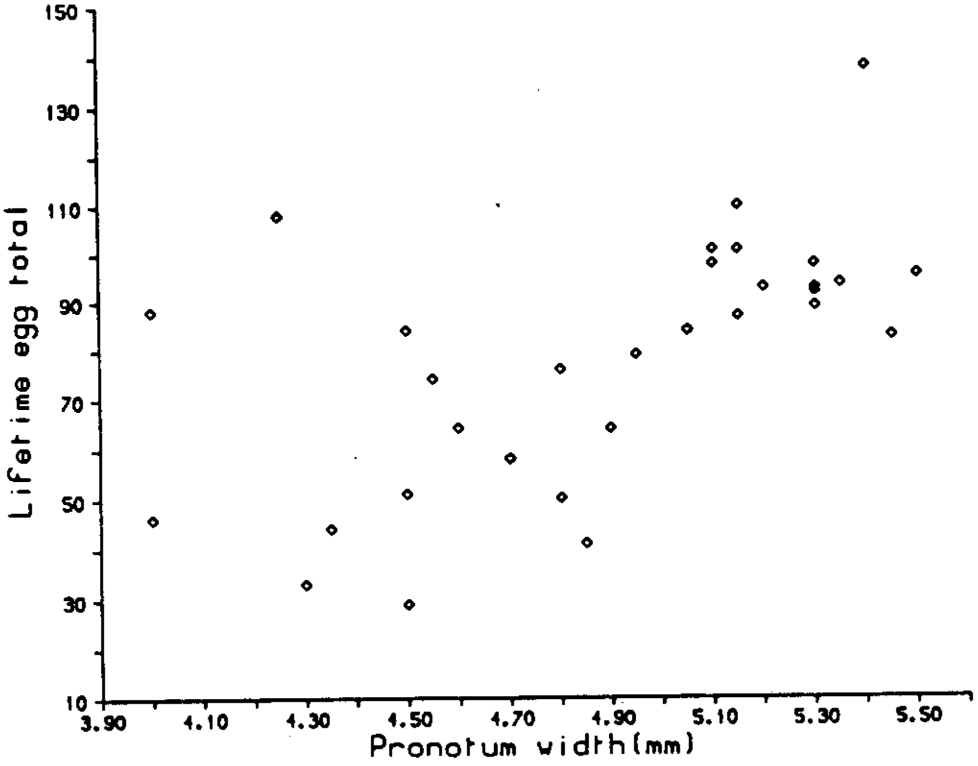


Figure 5.2

The lifetime egg totals laid by females of different pronotum widths bred repeatedly on 25g corpses until death.

n = 32, Spearman's rank correlation coefficient = 0.61, P<0.001.

Method.

The effect of a succession of breeding attempts on clutch size was studied by giving females a sequence of 25g mice. Female age and past breeding effort might therefore both affect the results. Each of 20 females (all 20 days from eclosion) was paired with a male and allowed to bury a 25g mouse. Once first stage larvae had collected on the mouse the soil around the crypt was replaced and any unhatched eggs in the old soil counted to give a total for clutch size. The broods were allowed to develop as normal until the larvae had dispersed. The adults were then collected, sexes paired again at random and each pair allowed to bury another 25g mouse. Clutch size was counted for each mouse buried until all females had bred four times. 16 were still alive when given the fourth mouse, but only four survived this attempt. Throughout the experiment, adults were given access to mealworms which, however, they never ate.

Results.

The numbers of females still alive at each attempt, and the mean clutch size laid are shown in Table 5.3. Mean clutch size did not differ significantly between the first two breeding attempts, but the mean for the third attempt was significantly less than that for the second and for the fourth less than for the third.

5.4.4. Clutch size and resource value.

Table 5.3.

Breeding attempt	1	2	3	4
No.of females burying mice	19	19	18	16
Mean clutch size	24.89(2.96)	28.26(5.24)	17.05(4.10)	4.32(3.36)

ANOVA Table

Source	D.F.	S.S.	M.S.	F ratio
Between groups	3	64.69	21.50	23.45
Within groups	72	66.01	0.90	
Total	75	130.50		

Multiple range test (Scheffe method; * = sig't at 5%)

Attempt	1	2	3	4
1		ns	ns	*
2	ns		*	*
3	ns	*		*
4	*	*	*	

Clutch size with repeated breeding attempts on 25g mice.
Females of mean pronotum width 5.16± 0.12mm 20 days after eclosion bred on a sequence of 25g mice until dead and clutch size on each mouse counted. Successive breeding attempts were started as the last ended, giving an interval of 10–11 days between starts.
95% CL for clutch sizes given in brackets.

Method.

In the laboratory, pairs of beetles 20 days from eclosion bred on corpses of different weights and the number of eggs laid was counted. Eggs were laid usually within 24 hours of the experiment beginning. They were counted just before they could be expected to hatch. No female was ever found to lay eggs after this time and so it can be assumed that all the eggs were found. As before, 75g corpses consisted of two mice sewn together and these were rolled up and buried as if one corpse.

Results

There was no significant difference in clutch size between 15g and 30g mice, (1 way ANOVA with multiple range test $P>0.05$) but significantly fewer eggs were laid on 5g mice than on 15g ($P<0.05$) and significantly more laid on 75g mice than on 30g ($P<0.05$). There was no significant difference between the mean clutch size on 75g corpses and on the corpses of rats weighing 160g ($P>0.05$) (Table 5.4).

In the laboratory *N. vespilloides* is therefore capable of some adjustment of clutch size to corpse size. There was no significant difference, however, between the clutches laid on 15g and 30g mice. This was also found for *N. orbicollis* and for this species it was claimed that survival of the brood was different after larvae had reached the mouse (Wilson & Fudge 1984). I therefore studied the survival of *N. vespilloides* broods on 15g and 30g mice in the laboratory (Bartlett 1987b).

Table 5.4.

Corpse wt(g)	n	Mean clutch size
5.21(0.84)	20	15.60(2.05)
10.51(1.01)	19	27.53(3.32)
15.31(1.10)	26	29.96(4.23)
30.89(1.90)	21	33.71(2.81)
75.00(2.38)	18	46.83(5.86)
162.61(8.91)	10	44.60(8.66)

ANOVA table

Source	D.F.	S.S.	M.S.	F ratio
Between groups	5	114.65	22.93	26.64
Within groups	108	92.96	0.86	
Total	113	207.61		

Multiple range test (Scheffe's method; * = sig't at 5%).

Corpse	5g	10g	15g	30g	75g	rat
5g		*	*	*	*	*
10g	*		ns	ns	*	*
15g	*	ns		ns	*	*
30g	*	ns	ns		*	ns
75g	*	*	*	*		ns
rat	*	*	*	ns	ns	

Variation of clutch size with corpse weight.
Pairs of adults allowed to breed on different size classes of corpse and the clutch size counted. 5–30g corpses were of single mice, 75g corpses of two mice sewn together, 162g corpses of rats. All adults 20 days from eclosion. 95% CL in brackets.

Brood survival on 15g and 30g mice.

Method.

36 pairs of adults were given a 15g mouse and allowed to bury it and lay eggs. For twelve of the pairs the number of eggs laid was counted, for a further twelve the eggs were allowed to hatch and the number of first stage larvae reaching the corpse was counted by inspecting the corpse every two or three hours and removing them as they arrived and for the final twelve the brood was left undisturbed until the third stage larvae dispersed from the corpse and the number of larvae dispersing was counted. A further 36 pairs of adults were bred on 30g mice and divided into twelves as before. The two corpse sizes could therefore be compared at three different stages of brood development.

Results.

Clutch size on 30g mice was not significantly different from clutch size on 15g mice and hatching success was high on both sizes of corpse, but subsequent survival of the brood was very different (Table 5.5). On 30g mice there were no significant differences in the numbers at the egg stage, first instar and larvae at dispersal. As many larvae as reach the corpse are likely to disperse from it. On 15g mice there was no significant difference between the mean number of eggs laid and the mean number of first stage larvae reaching the corpse. Hatching success was therefore again high, but the difference between the mean number of first stage larvae and the mean number of larvae at dispersal shows that only half of the larvae which reach a 15g corpse are likely to complete development. These results closely resemble those of Wilson & Fudge (1984) and suggest that the clutch size laid around 15g mice is such that normal hatching success produces more larvae than can complete

Table 5.5.

a. 15g mice: means ± 95% CL

Clutch size	First stage larvae	Dispersing larvae
29.69 ± 3.31	30.21 ± 1.88	16.16 ± 1.68
(n=12)	(n=12)	(n=12)

b. 30g mice: means ± 95% CL

30.92 ± 2.80	33.92 ± 2.06	30.08 ± 2.34
(n=12)	(n=12)	(n=12)

The table shows natural clutch sizes, number of first stage larvae and number of dispersing larvae in three independent sub-groups of twelve on each of two mouse sizes.

development on the corpse. Further experiments were done on small corpses to find the stage of development at which larvae were lost.

Timing of mortality on small corpses.

Method.

15 broods with a mean of thirty first stage larvae (to match the brood size found in the previous experiment) were created on 15g mice by pooling the hatchlings of several families and dividing them between the mice. Each brood was attended by the male and female which had buried the corpse on which the brood was placed. Previous experience suggested that adult *N. vespilloides* cannot recognise their own larvae and will raise a foster brood (also found by Easton (1979)) but as a control for abandonment of foster broods clutches laid around a set of 10g mice were taken from the soil just before hatching and the larvae that had hatched returned to their own corpse. The adults on the 10g mice therefore had broods of their own larvae and the survival of these broods could be compared with the artificial broods on the 15g mice. Availability of corpses meant that 10g rather than 15g mice had to be used for the control experiment. All broods were counted as the number surviving to second instar, to third instar and to dispersal from the corpse.

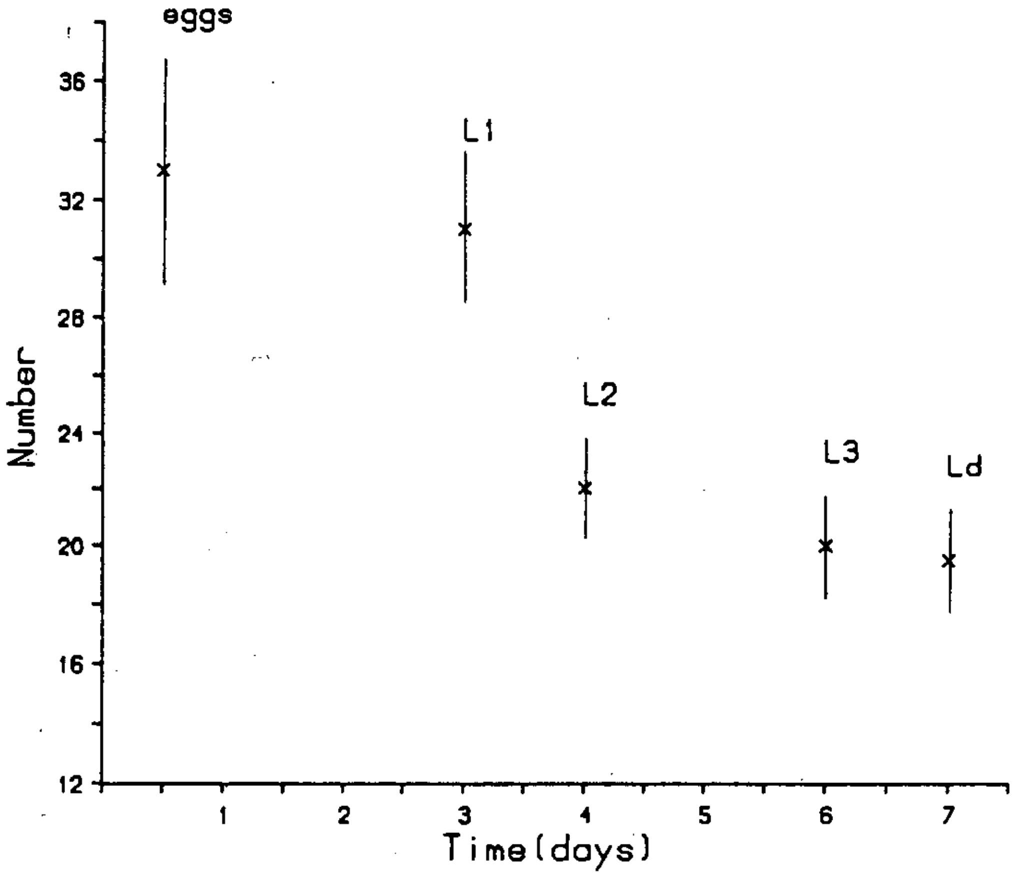
Results.

No experimental broods on 15g mice or control broods on 10g mice were abandoned, showing that the parents on the 15g mice did not recognise the larvae they were given as strange. The artificial broods created on a set of 15g mice showed a significant fall in mean larval numbers between first and second instars but no significant mortality between second and third instars and up to dispersal (Figure 5.3). The control broods on 10g mice were of

Figure 5.3

Survival of artificial broods on 15g mice.

Using the broods of 25 females, 15 broods of first stage larvae (L1) were made, with a mean brood size of 30. These were then introduced to 15g mice previously buried and tended by a pair of adults. The figure shows the numbers of larvae surviving 24 hours, 72 hours and 96 hours later, as second stage larvae (L2), third stage larvae (L3) and dispersing third stage larvae (Ld).



variable size because of differences in the number of eggs laid. There was no mortality between first and second instars if the brood size was below about 15, but for broods larger than this numbers fell sharply in the first 24 hours on the mouse, which is the period of the first instar (Figure 5.4). On both 15g and 10g mice, therefore, using artificial or natural broods, reduction of excessive numbers of larvae was found to happen on the first day of larval development.

In three cases during these experiments adults were seen to kill and eat first stage larvae. It is unlikely that food was limited during the first 24 hours on the mouse and so it seemed that killing by parents might be the main cause of larval mortality. An experiment was done to examine this point.

Cause of mortality on small corpses.

Method.

The cause of the observed larval mortality was studied by watching broods on 15g mice. Pairs of adults were allowed to bury corpses and the crypt roof was replaced with a leaf as described in chapter 2. The brood was not disturbed for counting and so the initial brood sizes were not known. The broods were watched until the movements of the parents in the crypt turned the larvae out of sight, giving a different period of observation for each brood (Table 5.6). The number of larvae surviving to second instar was counted and this number compared with that for broods on 15g corpses which had not been watched.

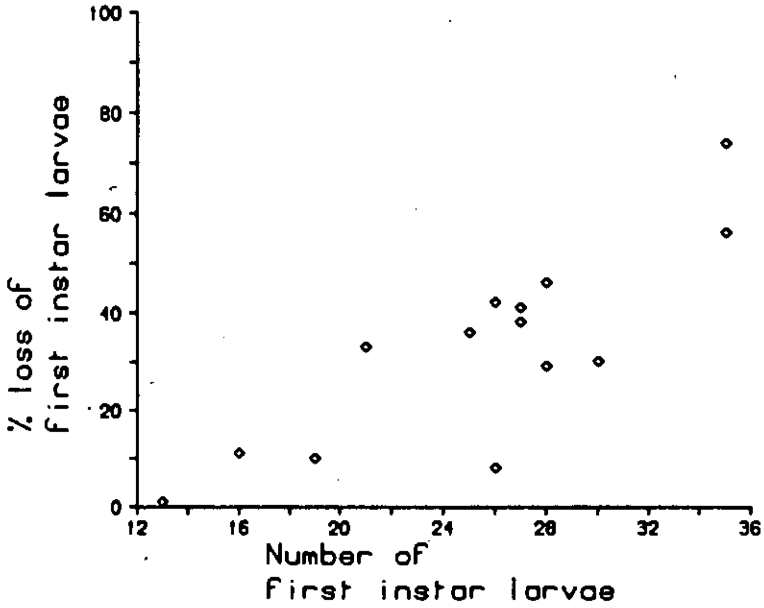


Figure 5.4

Mortality among natural broods on 10g mice.

The percentage survival to the second instar is shown for broods on 10g mice. The broods were made by removing clutches of eggs from the soil and putting the first stage larvae back on their corpse as they hatched.

Table 5.6.

Brood	Hours in view	Larvae seen killed	Parent responsible	Mean L2 (exp't) (n=5)	Mean L2 (control) (n=11)
1	1	1	Female		
2	2	3	Female		
3	15	14	Male	18.00	17.65
4	10	16	Male+Female	± 2.10	± 2.05
5	4	7	Male		

Infanticide on 15g mice.

Broods were watched until the hole in the corpse where the brood fed was turned out of sight by the movements of the adults in the crypt. The number of second stage larvae in these broods is similar in each case to the mean number of second stage larvae in the controls, broods set up at the same time on the same size of mice (15g) but not watched during the first larval instar.

Results.

In all the broods set up for observation the parents were seen to kill and eat first stage larvae (Table 5.6). This could explain the observed brood reduction. The main period of larval mortality on 10g and 15g corpses is at the first instar, during the first 24 hours after the larvae have reached the corpse. It is most unlikely that food is limiting at this time since only a small hole has been eaten in the skin of the mouse and the larvae have not begun to penetrate the body. Table 5.6 shows that if broods can be watched for long enough, sufficient larvae will be eaten to account for the 50% or 60% brood reductions that the earlier experiments recorded.

There was no significant difference between the number of second stage larvae on the mice used for observation and on the mice buried at the same time but not watched.

5.4.5. Corpse size and brood size.

Method.

Twenty days from eclosion three sets of females were paired at random with males and bred on three sizes of mouse, 10g, 20g and 30g. For each pair of beetles the mouse given was weighed before and after breeding. The size of brood was measured as number of larvae dispersing from the mouse. The mean weight of dispersing larvae was measured.

Results.

As in earlier experiments, the average size of the brood dispersing from the set of 10g mice was about 15 (Table 5.7). In all cases the mouse was completely eaten. Larger broods dispersed from 20g and 30g corpses; for the 30g corpses the brood size is what would be expected after complete survival

Table 5.7.

Corpse weight	10.52(0.31)	20.59(0.41)	29.42(0.40)
n	14	20	17
Brood size at dispersal	15.78(2.47)	24.71(2.40)	31.14(4.30)
Proportion mouse used.	1.00	0.80(0.12)	0.73(0.11)
g mouse used/larva	0.67(0.03)	0.67(0.03)	0.69(0.04)

ANOVA table: brood size at dispersal

Source	D.F.	S.S.	M.S.	F ratio
Between groups	2	16.99	8.49	12.38
Within groups	48	32.94	6.90	
Total	50	49.93		

Multiple range test (Scheffe's method; * = sig't at 5%)

Mouse	10g	20g	30g
10g		*	*
20g	*		ns
30g	*	ns	

Laboratory broods on 10, 20 and 30g mice.
Weights in grammes, 95% CL in brackets.
Brood sizes are shown for three sets of *N. vespilloides* bred on three weight classes of mouse. The proportion of corpse eaten during the breeding attempt and the production of larvae per gramme of mouse are also shown.

of the normal clutch laid on this weight of mouse. These corpses were not completely eaten; usually in such cases the skin is almost complete and the hindquarters are left untouched. Mean larval weight at dispersal (MLWD) was significantly lower for larvae dispersing from 10g corpses than for larvae from either of the other two sizes of corpse. Larvae from 20g and 30g corpses did not differ significantly in mean weight (Table 5.8). The same pattern was found for total brood weight (Table 5.8).

Table 5.8.

Corpse weight	10.52(0.31)	20.59(0.41)	29.42(0.40)
n	14	20	17
Mean larval weight at dispersal	0.142(0.01)	0.193(0.01)	0.192(0.01)
Total brood weight	2.24(0.25)	4.77(0.70)	5.98(1.20)

ANOVA table: mean larval weight at dispersal.

Source	D.F.	S.S.	M.S.	F ratio
Between groups	2	0.024	0.012	17.63
Within groups	48	0.033	0.001	
Total	50	0.057		

Multiple range test (Scheffe's method; * = sig't at 5%).

Mouse	10g	20g	30g
10g		*	*
20g	*		ns
30g	*		

Laboratory broods on 10,20 and 30g mice.

Weights in grammes, 95% CL in brackets.

The mean larval weights at dispersal are shown for three sets of *N. vespilloides* bred on three weight classes of mouse. The total brood weights are also shown.

5.4.6. Brood size and larval weight at dispersal.

Method

Using 30g and 10g mice, artificial broods of different sizes were created to test the effect of brood size on the weight of the dispersing larvae.

10g mice.

Pairs of adults were allowed to bury 10g mice. The crypts were looked at regularly on the third day after burial until first stage larvae began to appear on the corpses. The required number were put on each corpse and the corpse, brood and parents were all transferred to a crypt hollowed out by hand in another box of compost. The adults soon adjusted to the new situation and cared for the brood as before. In this way broods of up to 15 larvae were made. The transfer ensured that no more larvae came to the corpse, so that the brood size was accurately known. In all cases in this experiment parents were caring for larvae from a mixture of broods. By this stage of the study it was clear that adult *N. vespilloides* would raise a foster-brood as well as they would their own larvae.

To make broods larger than fifteen, which normally would be culled by the parents, a different technique was used. Pairs of adults buried 30g mice on the day before another set of adults buried 10g mice. Once a brood of the required number of first stage larvae (20, 25 or 30) had arrived on the 30g corpse these larvae and their parents were transferred with one of the buried 10g mice to a new crypt in another box of compost. In this way it was hoped that adults would behave throughout as though they were raising a brood on a 30g mouse and had no need to cull their young. The method assumes that females assess the value of the corpse during the process of burial and take no notice of a change after that. The brood size was measured between 30 and

36 hours after transfer to see if any culling had been done. The experiments of section 5.4. suggest that if this had been so, half or more of the brood would be missing.

The total weight of the brood and the number of larvae surviving were measured at dispersal.

30g mice.

The method for 30g mice was the same as for the broods of less than 15 larvae on the 10g mice. Pairs of adults were allowed to bury their mice and the mouse and brood transferred once the required number of larvae had been put on the corpse. As before, total brood weight and number dispersing were measured.

Results.

10g mice.

In one case the adults were not deceived by the transfer of mouse and their brood was reduced from 25 to 12. In the others, survival from first to second stage larvae was 90% or above (Figure 5.5). There was a strong relationship between the size of the hatching brood and the mean weight of the larvae dispersing from the corpse (Figure 5.6).

30g mice.

In all cases survival of larvae from first instar to dispersal was high (Figure 5.7). Mean larval weight at dispersal (MLWD) was plotted against brood size and the regression line calculated. The slope was significantly different from 0 (Figure 5.8) but significantly shallower than the slope of the regression line for 10g mice ($F=15.59$; $df=1,62$; $P<0.001$). Brood size therefore has an

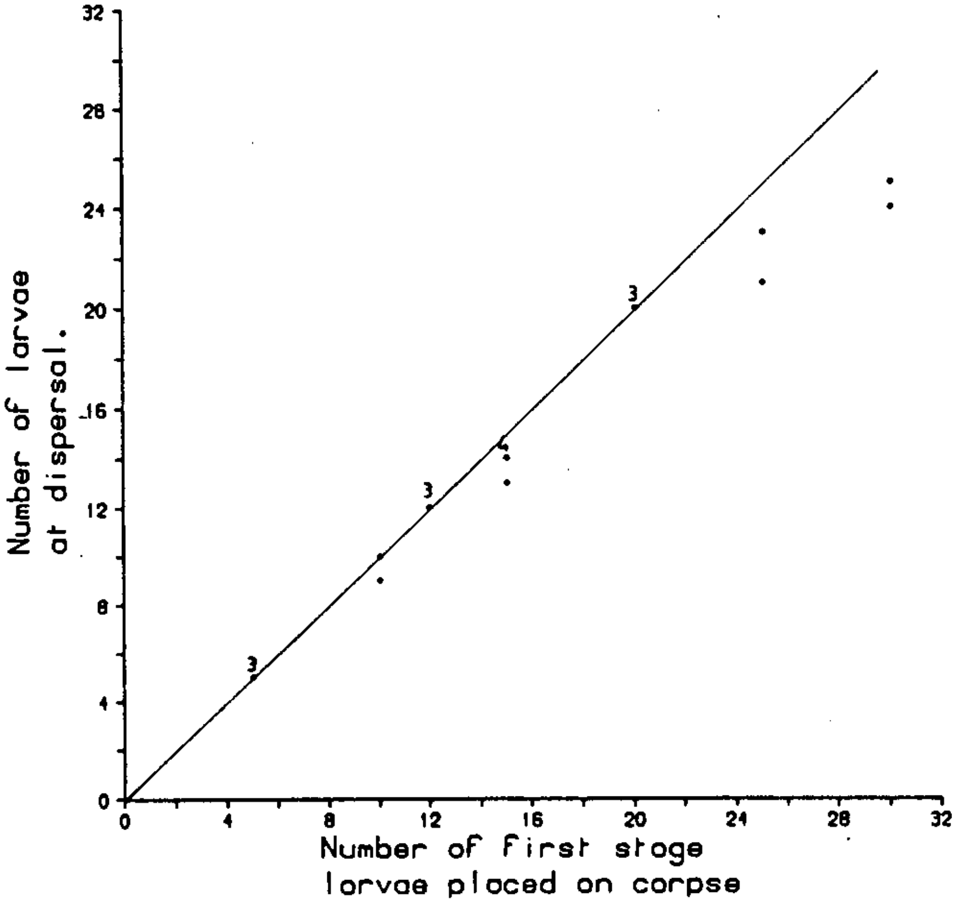


Figure 5.5

Survival of artificial broods created on 10g mice. Broods of 20 or more larvae were put on 10g mice but given to adults which had buried a 30g mouse in order to prevent culling of the brood. The line through the origin shows 100% survival. Figures next to symbols show the number of data points superimposed there.

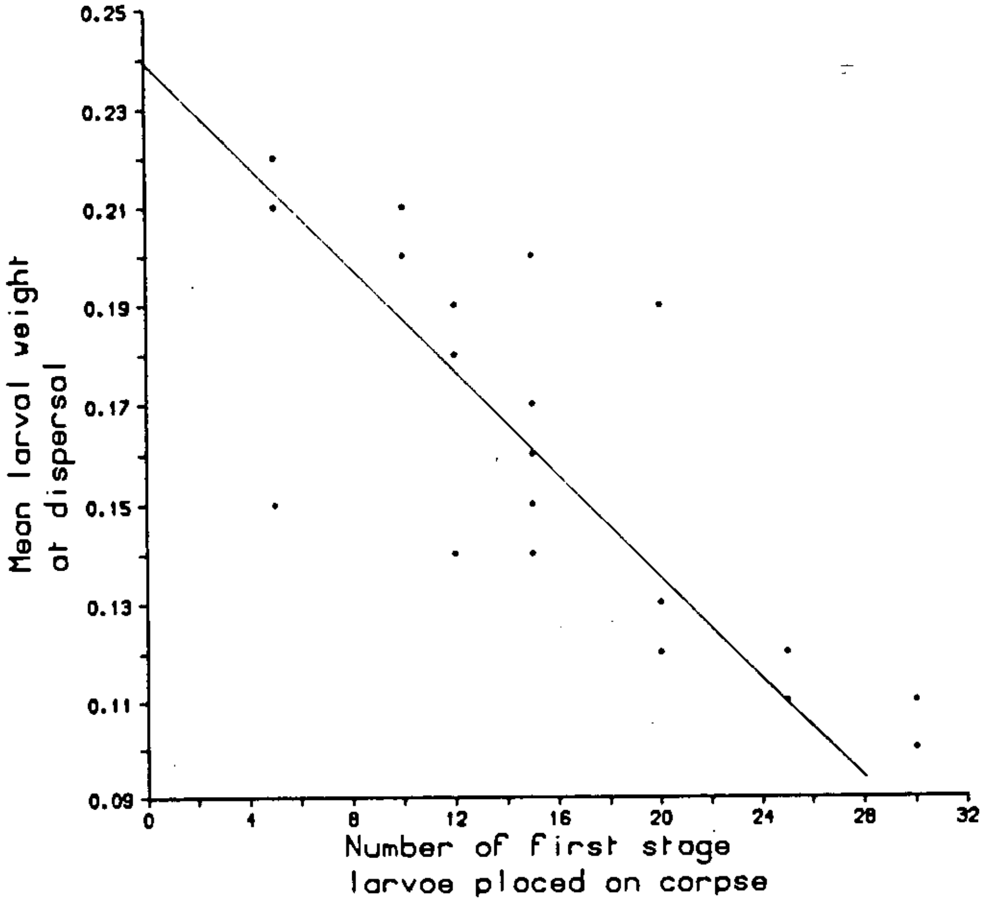


Figure 5.6

Mean larval weight at dispersal (MLWD) plotted against brood size for the artificial broods on 10g mice shown in figure 5.5

Regression equation: $y=-0.0053x + 0.24$, F ratio=54.8(1,17);$P<0.001$.

Figure 5.7

Survival of artificial broods on 30g mice. Details of graph as for Figure 5.5.

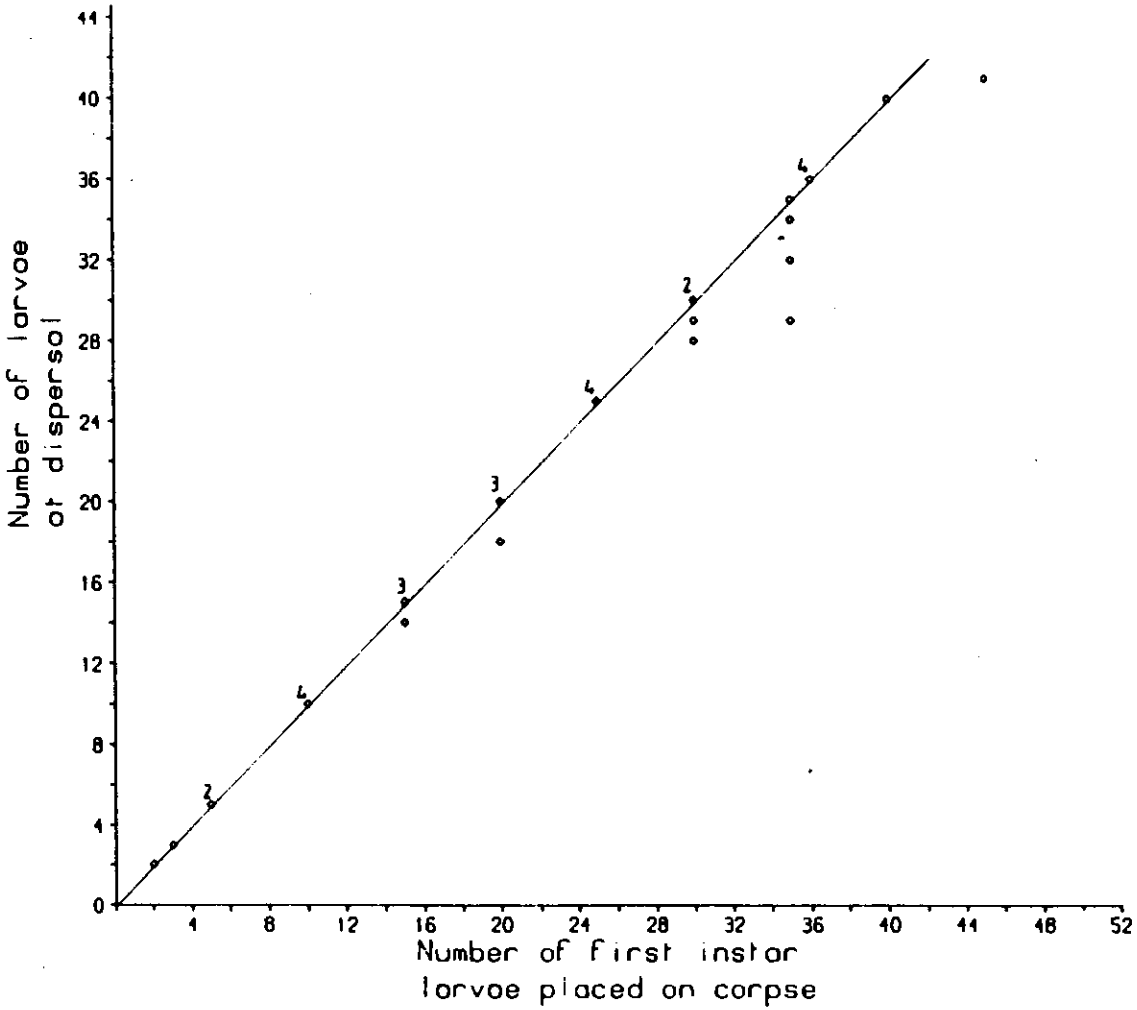
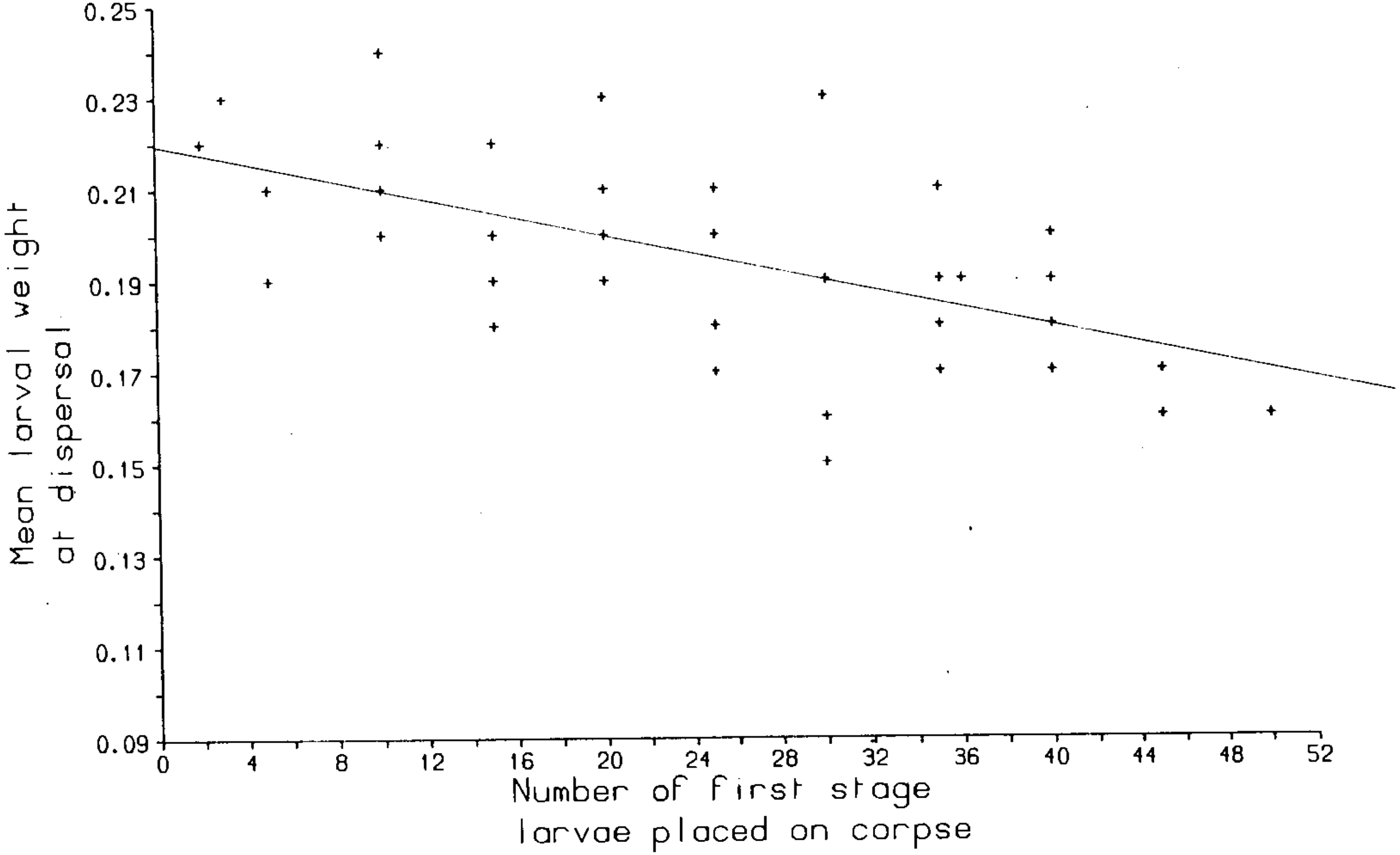


Figure 5.8

MLWD plotted against brood size for the artificial broods on 30g mice shown in figure 5.7

Regression equation: $y=-0.0011x+0.22$, F ratio=22.37(1,36);$P<0.001$


Mean larval weight
at dispersal
0.25
0.23
0.21
0.19
0.17
0.15
0.13
0.11
0.09
0
4
8
12
16
20
24
28
32
36
40
44
48
52
Number of first stage
larvae placed on corpse

effect on MLWD even on the larger mice, but the effect is much less marked than on smaller corpses. Larval weight is not as direct a measure as adult size of adult fitness. Larval weight obviously limits the resources available to the eclosing adult, but these resources might be used in different ways by larvae of different weights. The next experiment examines the ratio of adult size and weight in relation to larval weight at dispersal.

5.4.7. Larval weight and adult size.

Method.

Larvae were taken from a number of broods at dispersal so that a range of larval weights was represented. Each larva was allowed to pupate in a plastic container 60mm x 60mm x 180mm three-quarters filled with compost. At eclosion the adults were weighed and their pronotum widths measured. The ratio of pronotum width to cube root of weight at eclosion was plotted against larval weight at dispersal. The adults were also measured and weighed 20 days after eclosion and the same graph plotted.

Results.

If adult size at eclosion was directly proportional to larval weight at dispersal, the slope of the regression line in Figure 5.9 would not be significantly different from 0. The slope is significantly negative, showing that the smallest adults at eclosion have a relatively high size:weight ratio. The slope is significantly different from that of Figure 5.10, the graph plotted for the same adults at maturity.

Figure 5.9

The ratio of pronotum width to the cube root of weight at eclosion plotted against weight as dispersing larvae for a set of beetles weighed at dispersal and weighed and measured at eclosion.

Regression equation: $y=-8.07x + 10.4$, F ratio=15.67(1,21) $P<0.01$. 95% CL for slope = 4.28.

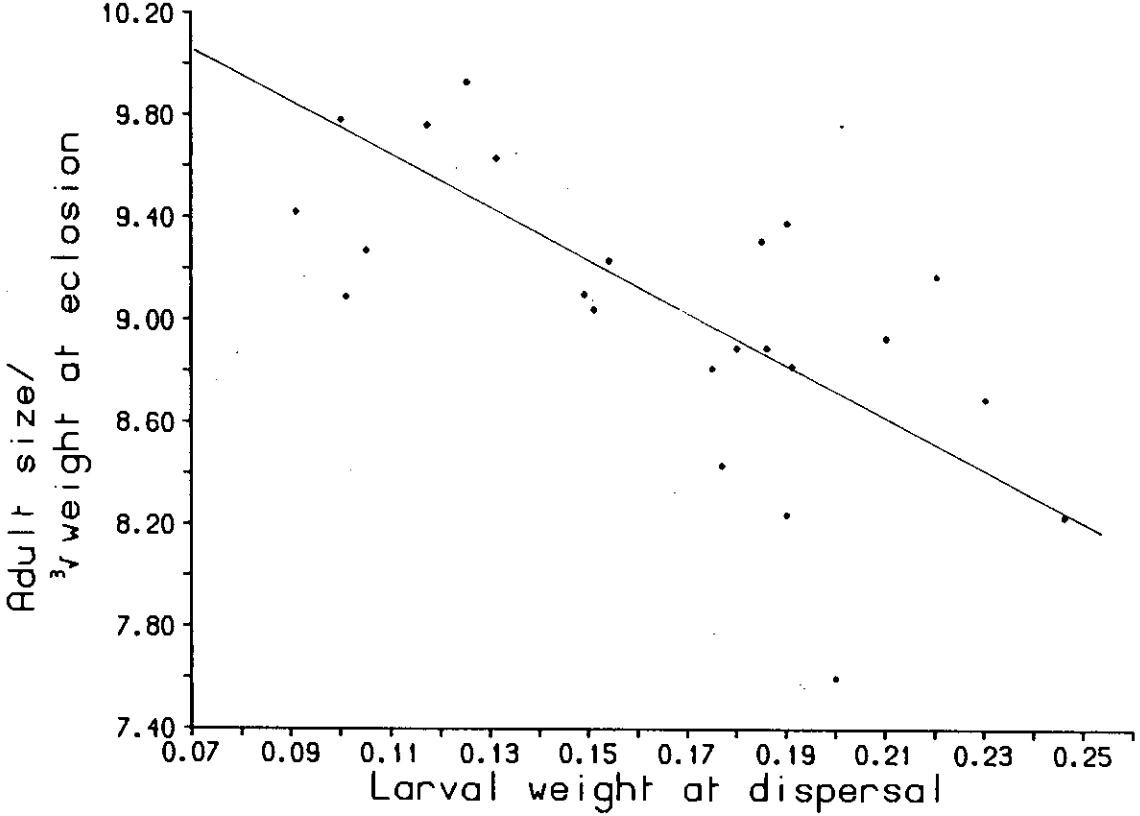
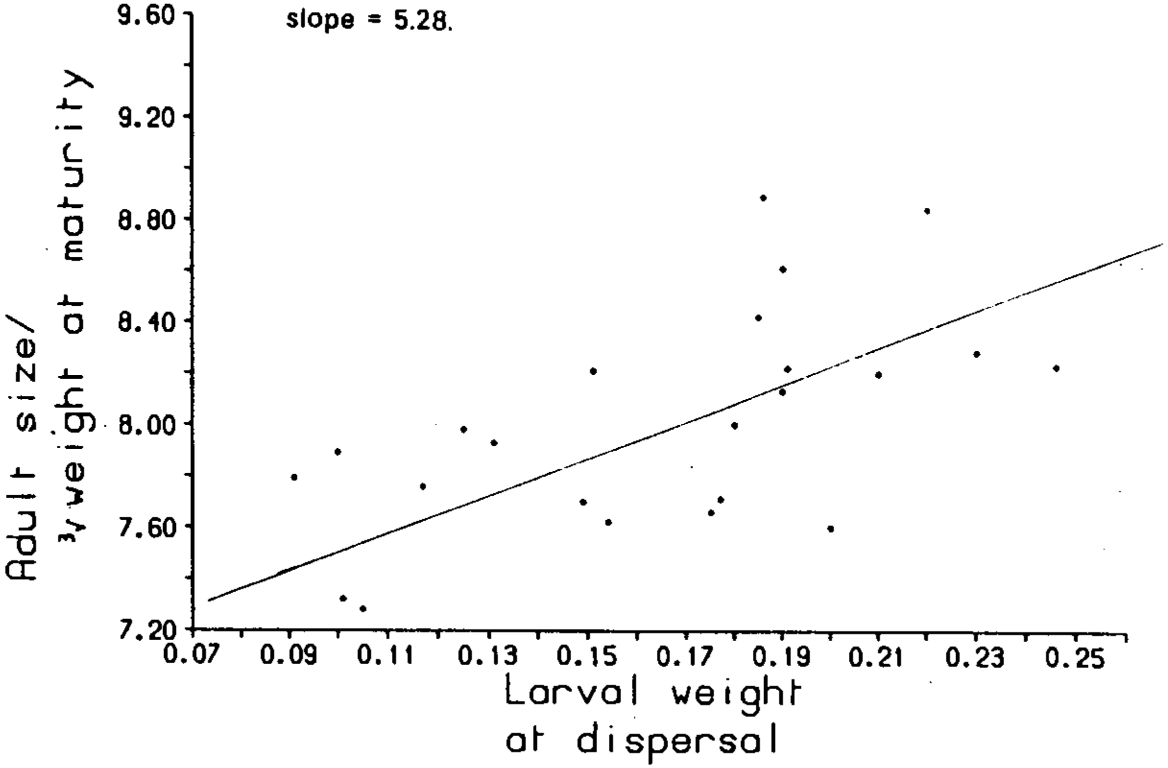

Adult size/
$^3\sqrt{}$weight at eclosion
10.20
9.80
9.40
9.00
8.60
8.20
7.80
7.40
0.07
0.09
0.11
0.13
0.15
0.17
0.19
0.21
0.23
0.25
Larval weight at dispersal

Figure 5.10

The ratio of pronotum width to the cube root of weight 20 days after eclosion for the set of beetles shown in Figure 5.9.

Regression equation: $y=5.83x + 7.05$, F ratio=12.25(1,21) $P<0.01$. 95% CL for slope = 5.28.



5.4.8. MLWD and adult size for natural broods on 10g and 30g mice.

Method.

One set of adults was allowed to breed on 10g mice, another on 30g mice. Both sets were left undisturbed until their larvae dispersed from the corpses. The larvae of all broods were then individually weighed and allowed to pupate. The pronotum width of each adult was measured at eclosion.

Results.

Mean larval weight at dispersal and adult pronotum width were both significantly less for beetles raised on 10g mice than for beetles raised on 30g mice (Table 5.9)

5.5. Egg size.

5.5.1. Corpse weight and egg weight.

Method.

The mean weight of the eggs laid on 15g, 30g and 75g corpses was measured. Pairs of adults 20 days from eclosion were allowed to bury the corpses. All females had a pronotum width of between 4.8 and 5.0mm. 75g corpses, as in other experiments, were made by sewing two mice together. Eggs were removed from the soil two days after corpse burial and any particles of earth brushed away. The total clutch was counted and weighed on a balance reading to 0.0001g.

Table 5.9

The weights of larvae from 10g and 30g mice and the pronotum width at eclosion of adults from these broods.

	10g mice			30g mice		
	n	mean	95% CL	n	mean	95% CL
Larval weight(g)	282	0.145	0.014	427	0.194	0.015
Adult pronotum width(mm)	179	4.58	0.20	330	5.00	0.21

ANOVA for larval weight at dispersal.

Source	DF	SS	MS	F ratio	Sig'f F
Between mice	1	0.386	0.386	28.19	P<0.001
Broods within mice	26	0.356	0.014	9.65	P<0.001
Within broods	681	0.967	0.0014		

ANOVA for adult pronotum widths.

Source	DF	SS	MS	F ratio	Sig'f F
Between mice	1	18.63	18.63	19.89	P<0.001
Broods within mice	26	24.35	0.937	7.66	P<0.001
Within broods	481	58.82	0.122		

Results.

There was no significant difference between the mean weight of eggs laid on 15g and 30g mice but mean egg weight on 75g corpses was significantly less than on either of the lighter corpses (Table 5.10). For each of the three corpse weights there was no significant correlation between the clutch size and the mean egg weight (Spearman's rank correlation $P>0.05$).

5.5.2. Female size and egg weight.

Method.

The mean weight of eggs in clutches laid on 25g mice by females 20 days from eclosion was measured. Thirty five females with pronotum widths over the range normally found in the laboratory population were paired with males and allowed to bury corpses. Eggs were removed, counted and weighed two days later.

Results.

There was no significant correlation between female pronotum width and egg weight (Spearman's rank correlation = 0.13, $n=33$ $P>0.05$ Figure 5.11).

5.5.3. Repeated breeding and egg weights.

Method.

Fifteen females 20 days from eclosion and with pronotum widths between 4.80 and 5.00mm were paired with males and allowed to bury 25g mice. When a first group of larvae had appeared on the corpse, the earth around the crypt was replaced and the adults left to raise this group of larvae. Unhatched eggs were removed from the original earth and weighed. It might be argued that

Table 5.10

Corpse wt(g)	n	Egg weight(mg)	
		mean	95%CL
15	22	2.42	0.08
30	17	2.48	0.13
75	23	2.09	0.13

ANOVA table

Source	D.F.	S.S.	M.S.	F ratio
Between groups	2	1.910	0.955	14.54
Within groups	59	3.873	0.066	
Total	61	5.783		

Multiple range test (Scheffe's method; * = sig't at 5%).

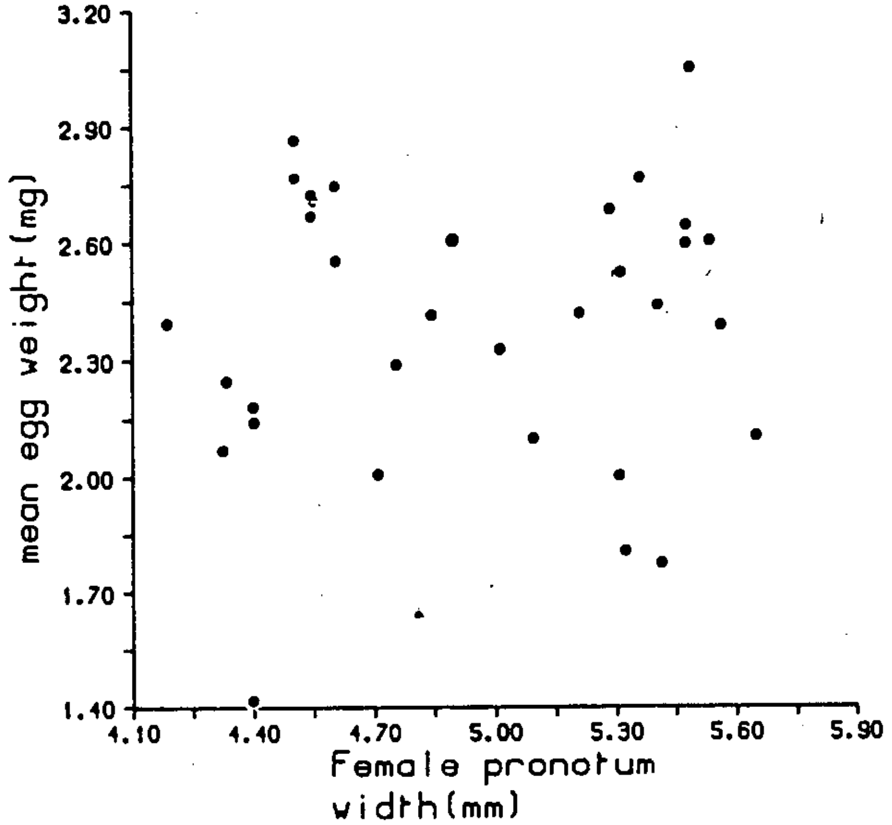
Mouse	15g	30g	75g
15g		ns	*
30g	ns		*
	*	*	

The mean weight of the eggs laid in single clutches on 3 weights of mouse. Within all three weights of mouse there was no significant correlation between clutch size and mean egg weight.

Figure 5.11

Mean egg weight in a single clutch on a 25g mouse for 33 females of varying pronotum width.

Spearman's rank correlation coefficient = 0.13, P>0.05



these eggs were infertile and possibly lighter than fertile eggs. However, there are normally very few infertile eggs (see Table 5.5). Eggs in these experiments were taken as soon as larvae appeared on the corpse and would probably have hatched if left only a few hours longer in the soil. The number of eggs was added to that of the larvae on the corpse to give the total clutch size. When the brood had dispersed, ten days later, the females were paired with different males and given another 25g mouse. The process was repeated over four breeding attempts.

Results.

There were no significant differences between mean egg weights for any of the four breeding attempts (Figure 5.12).

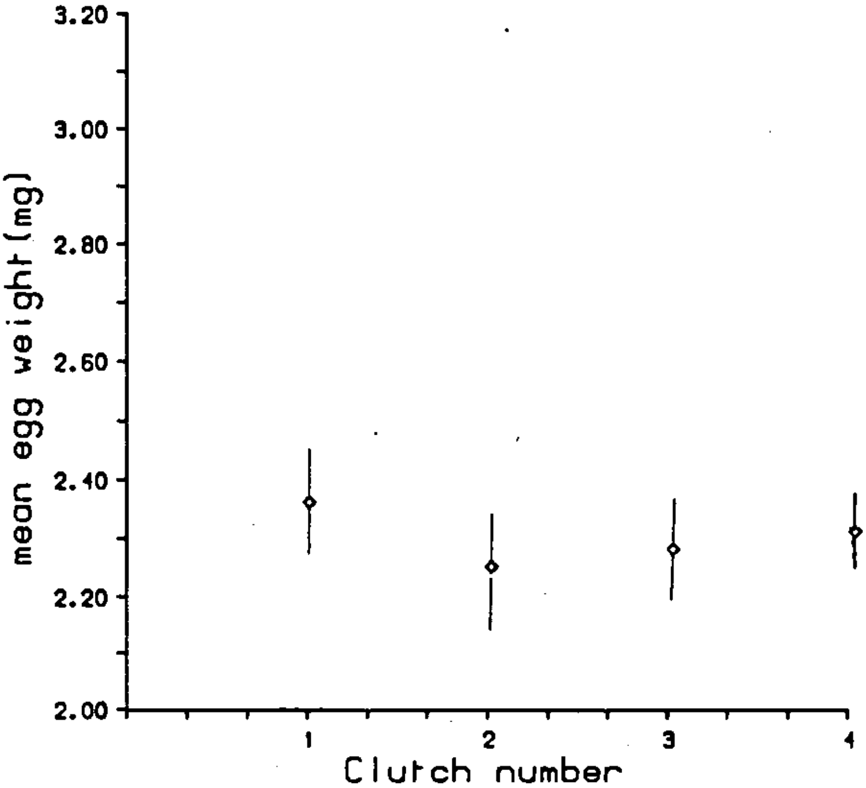
5.6. Discussion.

Egg distribution.

I found that the eggs of *N. vespilloides* were not laid in a chamber, as was reported for *N. vespillo* (Pukowski 1933; Ling 1957) but scattered in the soil around the crypt. Clustering and spacing of eggs has often been discussed with regard to predation for Lepidoptera (e.g. Stamp 1980) but the distances involved do not apply for *Nicrophorus*. It is possible that the egg distribution patterns reflect differences in the danger of fungal infection, this danger in turn reflecting habitat differences. Eggs laid in a chamber might be wiped out by an infection growing from one to the next whilst more isolated eggs would be less at risk. A chamber might have the alternative advantage of allowing the adults to protect their clutch more effectively against invertebrate predators. *N. vespillo* and *N. vespilloides* were found respectively in meadow and woodland habitats (Pukowski 1933) and the separation, with possible differences

Figure 5.12

Each point shows the mean and 95% CL of egg weight for 15 females. 95% CL based on pooled standard deviation after analysis of variance. The females were bred on a sequence of four 25g mice.



in the balance of fungal and invertebrate predator risk, may help to explain the difference in egg distribution. Scattering by *N. vespilloides* is unlikely to be a product of my particular laboratory conditions, since it was also seen in another study (C. Easton pers.comm.) and occurs in *N. mexicanus* (Halffter et al 1983). The experiment in flowerpots, where space was not restricted, is further confirmation that egg distribution probably differs between *N. vespillo* and *N. vespilloides*.

Food intake and clutch size.

Extra food intake is usually associated with an increased clutch (Hughes & Walker 1970; Murphy et al 1983). I found that for *N. vespilloides* the clutches of fed females were significantly lower than those of females starved before breeding. Females may respond to loss of condition as though to decreased future breeding opportunities (reduced residual reproductive value) and increase reproductive effort in the present breeding attempt.

Female pronotum width and clutch size.

On a single 75g corpse I found that large females laid a significantly larger clutch than small females. Total lifetime egg production was positively correlated with pronotum width. Female size may thus impose one of the boundaries on possible clutch size, affecting whether a predicted optimum on a large corpse can be attained. This is seen in other insects, (Ratcliffe 1972; Peters & Barbosa 1977; Derr at al 1981; Kasule 1985). Lifetime totals are also affected by size. However, the significance of these results to the field cannot be fully judged until the number of breeding opportunities an individual may have is known. For a small female, given the difficulty of winning a corpse in competition with larger members of the population, the handicap of small size in fighting may far outweigh that in lifetime egg production capability.

Clutch size and clutch number.

The number of eggs laid on a sequence of 25g corpses decreased after the first two breeding attempts. These results may suggest something of the effects of previous breeding effort and of age on clutch size. They probably represent an extreme case, since in the field it is unlikely that *N. vespilloides* could breed so frequently, but they may be useful in helping to define what can occur. Clutch size variation with age was modelled by Begon & Parker (1986). They considered a female which gathered resources in a pre-reproductive phase and expended them over several clutches. They assumed that random mortality would be more significant than reproduction-dependent mortality. The model predicted an optimal female strategy of decreasing reproductive effort over the sequence of clutches. If egg size was constrained, clutch size should decrease; if clutch size was constrained, egg size should fall. The prediction contrasts with that usually produced by a consideration of residual reproductive value (Williams 1966). Increasing reproductive effort with age in several lizard species, for example, was analysed by Pianka & Parker (1975) as a case of ageing causing reduced residual reproductive value with a consequent increase in effort. They pointed out, however, that falling clutch size may not mean a decrease in reproductive effort. The depletion of resources may mean that a greater proportional effort is put into later clutches for lower numbers or weights actually produced. Begon & Parker's (1986) model, inspired by experimental data from butterflies, was based on females gathering resources before reproduction and then expending them with little or no replenishment between clutches and the depletion effect might be applied to remove the apparent discrepancy between predictions. Further, the two theoretical studies were based on different animal groups. Begon & Parker state that the assumption of greater importance for random rather than reproduction-dependent mortality makes their model suitable for most invertebrates. *Nicrophorus* is an unusual member of this grouping, and the extent of its parental care might make it an exception to the assumption. Nonetheless, as predicted by the Begon & Parker (1986) model, clutch size declines over a sequence of breeding attempts. Whether this represents a decrease in reproductive effort in terms of the proportion of available resources expended was not studied. Females lose little weight over a sequence of breeding efforts (chapter 6) and the carrion eaten during breeding may allow reserves to be replenished between each attempt. If this is so, then effort may fall over the sequence.

Clutch size and corpse capacity.

On 10g corpses I found that the mice were completely eaten by broods of about 15 larvae. 30g mice were only partly eaten by broods of about 30. There was some adjustment of clutch size with size of corpse, but similar numbers were laid on 10g and 30g corpses. The mean clutch found on 10g mice was greater than the apparent capacity of such corpses, that on 30g mice was less. On the 30g mice the females had enough carrion to raise more larvae and could, since this is done on 75g mice (Table 5.4.), have laid more eggs. On the 10g mice the corpse is completely eaten by a mean brood comparable in size to that found after the brood reduction described in the experiments above and the clutch laid around such mice in the lab will produce more larvae than the corpse, even uneaten by micro-organisms, can support. As well as number of larvae, however, their individual weights must be taken into account in estimating corpse capacity. A corpse could theoretically be eaten by a large number of larvae which are low in weight when they disperse or a small number of heavier larvae. On 10g mice mean larval weight at dispersal and total brood weight were both significantly lower than on 20g or 30g mice. Larval weight affects adult size at eclosion (section 5.4.7.) and so has an effect on the fitness of the next generation.

The effect of brood size on the weights of brood members was then studied. A start can be made to predicting an optimum single-clutch size by measuring fitness of brood members as their weights. The size of eclosing adults has been shown to affect success in winning corpses (chapter 4) and subsequent reproductive ability (section 5.4.2). It is not, however, possible, to relate size to field success and so to come to any conclusion about optimum clutch or brood size. These laboratory experiments are only the beginning of what must be known before such conclusions can be reached. One assumption made above is that larval weight is a good estimate of adult size. Larval weight is easily and quickly measured, but may not be directly related to the quantity, adult size, which actually affects fitness. This was tested and I found that small larvae metamorphose into adults relatively large for their weight. The small larvae have compensated at least partly for the disadvantage of low weight at dispersal, and must have done so by diverting resources into external structures, whose size is fixed at eclosion, at the expense of internal structures and reserves of fat and protein which can be increased after eclosion. They are 'hollow' compared with a similar-sized adult eclosing from a heavier larva. Such adults are obviously at risk compared with their heavier neighbours if food at eclosion happens to be scarce but large size provides such an increase in fitness (chapter 4, chapter 6) that the risk could be outweighed. The result suggests that there is a threshold adult size below which adults have very little chance of breeding because of the importance of size in settling the possession of corpses. The balance between adult size and adult food reserves might be based upon the need to exceed this threshold and on the risk of starvation soon after eclosion. Larvae which are heavy enough to exceed the threshold without sacrificing food reserves might increase their total chance of breeding success (the sum of the chances of surviving the immature period after eclosion and of winning a corpse) by eclosing as smaller, but fatter adults than they could have become. Larvae too light to reach the size threshold without a disproportionate investment in structure, however, might only have a chance of success if they risk starvation by increasing their size. The results can be considered as an example of risk-sensitive behaviour (Caraco 1980; Real 1980), the heavier larvae adopting a risk-averting strategy, the lighter a risk-prone strategy. Conservative behaviour is common amongst animals, such as these heavier larvae, with high reserves (Caraco et al 1980; Rubenstein 1987).

The control and the effects of brood size.

The results discussed so far have shown that the weight of larvae at dispersal is affected by brood size, to an extent which varies with corpse weight. There are species, for example certain parasitic hymenoptera (Godfray 1987) in which larvae determine brood size by killing their siblings or unrelated larvae which share their host. For *Nicrophorus* no siblicide of this kind has been seen; larvae do not attack one another with their mandibles or even seem to eat the bodies of larvae which have died during development. Their only effect is to occasionally trample one of their number into the flesh of the corpse and suffocate it. Burying beetle larvae therefore develop in a brood whose size has been set by their parents and it is on the parental decisions of how many eggs to lay and how many larvae to allow to survive that any discussion of optimum clutches and broods must be based.

Females adjusted their clutch size according to corpse weight, as was suggested by Easton (1979). However, on mice weighing less than 25-30g complete hatching success, which is the usual case in the laboratory, produced more larvae than could survive on that weight of corpse. On mice heavier than this brood survival was high but the mouse was not completely eaten, suggesting that a larger clutch could have been laid and the brood successfully raised. These are the main findings to be discussed. The alternatives available and the results found will be interpreted in terms of parental and offspring fitness, but for *Nicrophorus* such interpretations will be limited. The measure of fitness taken is a narrow one, being based on only one factor, that of larval weight or adult pronotum width, and its significance in the field has hardly been studied.

On small corpses I have shown that adult *N. vespilloides* in the laboratory produce an excess of larvae and reduce their broods by culling larvae at the first instar. Filial infanticide of this kind is extremely unusual. In several teleost fish species the male may eat some of the eggs he is guarding (Dominey & Blumer 1984). The coral reef fish *Acanthochromis polyacanthus* has been seen to kill some of its young in the process of driving an early-season brood from its own territory, apparently to be fostered by neighbouring adults (Thresher 1985). In colonies of social insects, queens have been reported as using eggs or young larvae as food (Wilson 1971), a behaviour found at a time of food emergency in the colony, and even under normal conditions the haemolymph of larval *Amblyopone silvestrii* (Hymenoptera) is used as food, though without killing the larvae (Masuko 1986). Coot chicks were seen to be killed by the male parent during behaviour used to regulate food allocation to the brood (Horsfall 1984). *N. vespilloides* is different from any of these. Hatched, viable larvae rather than infertile eggs are eaten; the killing is not a consequence of takeover by a strange male, which is the usual proximate cause of vertebrate infanticide, nor an accidental product of another behaviour, but apparently a normal adaptation to a particular size-class of corpse. The uneaten members of the brood are fed and defended as normal. The culling practised by *N. vespilloides* and possibly *N. orbicollis* (Wilson & Fudge 1984) seems to occur regularly on corpses weighing less than about

15g. It may occur in order to balance the eventual ratio of larvae with available carrion food.

The explanation of this unusual behaviour must answer two questions. First, why are larvae killed, in other words what would be the effect of not culling the brood ? Second, if there is a valid reason for this, why are so many eggs laid that the problem arises at all ? The first was approached by creating artificial broods on 10g mice and deceiving the parents into not culling the brood (section 5.4.6.). The results showed a sharp decrease in larval weight at dispersal with brood size. If broods were not culled on this size of mouse, offspring size might be reduced below whatever level makes the chance of breeding success in the field unacceptably low. It was suggested by Wilson & Fudge (1984) that brood reduction in *N. orbicollis* might occur because of uncertainty as to the amount of corpse that might be eaten by micro-organisms between burial of the corpse and arrival of the larvae. This implies that if 15g corpses were not eaten by micro-organisms they would be able to support the larvae hatching from clutches of the size that are laid around them. My results suggest that this is not so. In the laboratory, the time between burial and arrival of larvae is so short and the action of micro-organisms probably so much reduced compared with that in the field that very little of a corpse can have been eaten when the larvae reach it and yet brood reduction on small corpses still occurs. It seems likely that complete hatching success of the size of clutch laid around 10g or 15g corpses produces more larvae than even a complete corpse of that size could support to dispersal. The argument of Wilson & Fudge can be compared with one proposed to account for the brood reduction practised in many bird species (O'Connor 1978; Mock & Parker 1986). Here reduction might be carried out in response to uncertain food availability: when food is scarce the last of an asynchronous brood to hatch is allowed to starve, whereas all offspring are fed when food is plentiful. In these laboratory experiments the food supply for *N. vespilloides*, once buried, is assured and an uncertainty argument at this level does not apply. There may, however, be uncertainty in the field about the number of larvae which will arrive at a corpse and the explanation of why so many eggs are laid may be that the excess acts as an insurance against predation of eggs or of larvae making their way to the corpse. The eggs of *N. vespilloides* seem to be scattered in the soil away from the corpse (section 5.3) rather that being laid together in a chamber as is the case for *N. vespillo* (Pukowski 1933; Ling 1957). I argued earlier that scattering may reduce the risk of mould spreading through a clutch, but increase vulnerability to predation. Increased predation risk might make an excess of eggs valuable insurance in the field. An insurance hypothesis has been proposed as an alternative explanation for asynchronous hatching in birds (Dorward 1962; Stinson 1979; Clark & Wilson 1981). Only one young is raised and the one or two additional eggs serve as an insurance against the failure of the first. Variable mortality of eggs or hatchlings making their way to the crypt may explain why a *Nicrophorus* female with a small corpse lays many more eggs around it than are raised. A corpse attracts a wide range of insect predators (see e.g. Nabaglo 1973); the staphylinid *Philonthus decorus* is one which has been seen to kill newly-hatched larvae (chapter 6).

Predators such as *Philonthus* or fungal infection could cause the unpredictable mortality proposed here. An alternative explanation is that the beetles fail to assess accurately the capacity of the corpse; but since clutch size is different between 5g and 15g corpses, or between 30g and 75g, some assessment is clearly possible. It might also be argued that *N. vespilloides* is incapable of laying a clutch smaller than that found on 10-15g corpses, if there is a physiological requirement that at least one egg from each ovariole must be laid when a clutch is produced, for example. However, a smaller clutch is laid on 5g corpses.

The raptors discussed by Stinson (1979) do not raise the hatchlings of their 'extra' eggs; these are killed by their older sibling or starve in competition with it. The adults can only bring enough food to raise one young. Similar constraints make the clutch laid by *Nicrophorus* on small mice excessive: a small mouse represents too small a reserve of food to support the brood that is produced on it.

Brood reduction in *Nicrophorus* is therefore a phenomenon which probably occurs in response to a shortfall of food relative to the requirements of the larvae arriving at a corpse. The laying of an excessive number of eggs is more likely to reflect uncertainty about the number of larvae successfully reaching the corpse than about how much food will be available and so conforms to a type of the 'insurance' hypothesis discussed by Clark & Wilson (1981). The situation differs from that in birds in that larvae can feed themselves as well as receiving regurgitated carrion from their parents. The adults cannot afford to let the members of an excessively large brood compete amongst themselves for the corpse and they therefore reduce the number by culling rather than by allowing some to starve. It is a direct action, and a consequence of the unique biology of burying beetles.

The experiments described here did not look at the question of how *Nicrophorus* adjusts the numbers of larvae that are culled. The simplest hypothesis was that adults allowed a certain number of hatchlings to reach the corpse and killed all later arrivals, but culling was found to occur whether larvae were allowed to reach the corpse naturally or added in a single batch.

There seems to be no sex bias in culling. Table 3.1 shows that a population which had been raised on 10g mice with the broods not adjusted in any experiments had a sex ratio not significantly different from 1:1. It is possible to argue that a male bias might be adaptive: if the adults eclosing from small mice are likely to be small, then small males might have a better chance of reproductive success, through sneak matings, for example (chapter 4), than small females. Sex bias has been suggested in brood reduction in coots (Horsfall 1984), and some hymenopteran parasites lay male eggs on smaller hosts: the cost of small size in the resulting adult is less for a male than for a female, as argued here for *N. vespilloides* (Charnov et al 1981; Simbolotti et al 1987).

On corpses of 25-30g and larger almost all the larvae that hatch and reach the corpse survive. Only 73% on average of a 30g corpse is eaten by these larvae, suggesting that a clutch below the corpse capacity is usually laid. Larger clutches are laid on larger mice and larger broods are successfully reared, showing that females are capable of laying more eggs and parents capable of feeding the resulting brood. As with the small corpses, it is difficult to make any prediction about the optimal clutch that should be laid since the relationship between laboratory weight or size and field success is unknown. It is surprising, however, that even after such striking behaviours as culling and disproportionate allocation to adult size, adults eclosing from broods raised on 10g mice are still smaller than those from broods on 30g mice. Either adults lay too few eggs around 30g mice in that the extra weight of their larvae provides no significant increase in breeding success compared with larvae from smaller mice, or adults allow too many larvae to survive culling on 10g mice and the subsequent low weight of the larvae is a disadvantage for eventual breeding success.

Why might culling not be severe enough ? Conditions in the lab might account for this. Culling is necessary when a high proportion of eggs survive and produce larvae which reach the corpse. If, in the field, this proportion is normally lower than in the lab, then *N. vespilloides* might be adapted to culling from totals lower than those it is faced with in the lab and not be able to adjust to higher numbers. However, the data of Figure 5.4 show that culling is progressively more severe the more larvae arrive at a corpse, and this is true for up to 100% survival of the size of clutch normally laid around 10g mice. An alternative explanation might be that adults cull not to a final total, but to a total which allows for some later mortality in the brood that is not usually found in the lab.

Why should adults lay too few eggs around a 30g corpse ? Burial of 30g corpses in the laboratory is not as accomplished as that of smaller corpses: the corpse is not rolled up as neatly, nor do the beetles build such a well-defined crypt. If this is also true in the field, it might hinder the adults from preventing the growth of mould as effectively as on a small corpse. The effects of mould are likely to be more severe in the field than in the lab and might reduce the field capacity of a 30g corpse.

Another factor in reducing the clutch laid on a 30g corpse might be the costs of increasing clutch size. Clutch size below the theoretical capacity of a resource has been found in a wide range of animals, whether capacity is set by the ability of parents to feed their young, as with birds, or the value of an oviposition site (Charnov & Skinner 1983; Waage & Godfray 1985). Lack (1954) suggested that nesting birds should be selected to lay a clutch maximising the survival of young to maturity. This clutch would be equivalent to the capacity of the corpse in terms of the larvae it could support, leaving out any variation in the amount eaten by the adults. For birds it was pointed out (e.g. Williams 1966) that such a clutch (the maximum number parents could feed) was an incomplete measure of fitness because it failed to take into account the effect of brood size on survival of the parents to the next breeding season. Charnov & Krebs (1974) proposed the idea of an optimal clutch size that maximised an individual's fitness over its lifetime. In the laboratory *Nicrophorus* can breed many times and may therefore compromise or trade off clutch size against future breeding in the way that Charnov & Krebs suggested might explain the common finding that observed clutch is lower than Lack's predicted most-productive clutch. For *Nicrophorus* as for birds, clutch size must be discussed in terms of adult as well as juvenile survival. The Charnov & Krebs argument suggests that clutches below the 'Lack clutch' may have evolved in response to increased lifetime fitness of individuals laying several clutches, each below the resource capacity, and maintaining their residual reproductive value after each at a higher level than would have been the case if they had laid a maximum clutch each time. As discussed above, it is difficult to apply such arguments to *Nicrophorus* given the lack of knowledge about the number of breeding opportunities available in the field. Results presented in chapter 6, however, show that there are costs to reproduction in terms of parental care and this factor may affect the sizes of clutches laid. It is possible, therefore, that clutch size on 25-30g corpses is partly established by a strategy of maximising the productivity not of a single clutch but of the sum of several.

A discussion of this point should also consider the effect of variance in clutch size. Increased variance in the numbers of offspring produced by an organism has been predicted to reduce its fitness (Gillespie 1977). The strength of selection on variance of offspring number may equal that on the mean under conditions where environmental fluctuations are important (Gillespie 1977). The argument leads to a prediction of small, repeat clutches in order for variance to be reduced. This may partly explain the reduction in clutch size on 30g mice below their apparent capacity.

On larger corpses than this, the lack of a difference between clutch size on 75g mouse corpses and 160g rats argues that a physiological limit has been reached. The value of such a resource may induce a female *N. vespilloides* to lay a maximum clutch in spite of any costs this may incur if this value is such as to exceed the summed value of more smaller corpses than the female can expect to find. The discussion of clutch size in burying beetles is still at early stage. One obvious line of progress, however, would be to examine the cost of raising broods of different sizes to the lifespan and future fecundity of a set of females. It would be more difficult to measure the cost of clutch size because of the confounding effect of the different costs of burying and maintaining the very different corpse sizes that would be needed to induce differences in clutch size, but brood size can easily be manipulated and the costs found. Such a cost was recorded for blue tits by Nur (1984), who manipulated the brood sizes of adults and recorded survival to the following season. The major problem remains the lack of field data, but such an experiment would at least be another step to completing an outline of the reproductive strategies of burying beetles.

Egg size.

It has been predicted that egg size should increase when eggs are laid on a poor resource or when competition between siblings is likely to be significant (Sibley & Calow 1983; Parker & Begon 1986). The observed reduction here on 75g corpses compared with lighter mice is compatible with these predictions. The lack of any difference between the two smaller weight-classes might be due to a physiological limit: females might lay eggs of maximum weight on 30g as well as 15g corpses. Culling on 15g corpses means that competition between larvae on such corpses is not as severe compared with that on 30g corpses as might be expected. Eggs of similar weight might therefore be laid on both.

The other results show no effect of female size or of clutch number on egg weight. An increase in egg weight with female size has been recorded in another beetle (Johnson 1983) and decrease in egg size with female age predicted (Begon & Parker 1986). On 25g mice, the size used in these experiments, females of all sizes may be capable of laying a clutch consisting of the maximum egg size the species can achieve, or the size above which the hatching larva receives no extra benefit. The Begon & Parker prediction was based on constant clutch size. In burying beetles clutch size tends to decrease with repeated breeding and this decrease may allow eggs of constant size to be laid. On 25g and 30g mice the results are consistent with the proposal that there is an egg size which females of all sizes can lay over the size of clutch found on this weight of mouse and that this egg size confers maximum benefit on the hatching larvae, so that clutch size rather than egg size will be decreased in repeat broods.

Chapter 6.

Parental care in *N. vespilloides*.

'These grave diggers in truth are remarkable fathers. They have nothing of the happy-go-lucky paternal carelessness that is the general rule among insects, which pester the mother for a moment with their attentions and then leave her to care for the offspring!'

J.H. Fabre: 'The Glow-Worm and other Beetles' 1919.

6.1. Introduction.

The peculiarity of an insect caring for its young was among the features first noted in 18th century work on *Nicrophorus* (Pukowski 1933). Insect parental care is more common than was then realised; subsocial species, where larvae or nymphs are cared for by adults for some time after hatching (Wilson 1971), are found in many orders of insects (Eickwort 1981), but the parental care of *Nicrophorus* can still be regarded as amongst the most complex seen outside the eusocial Isoptera and Hymenoptera (Tallamy 1984).

Insect parental care may arise in response to harsh environmental conditions (Wilson 1971). Under these circumstances, the attention of the parents may be necessary to allow the young to survive the physical requirements of their environment. The female of the salt marsh staphylinid *Bledius spectabilis* protects her eggs and young brood from flooding and anoxia (Wyatt 1986). Female earwigs *Forficula auricularia* show care to rival that of *Nicrophorus*, defending their nymphs, bringing them food and constantly attending the eggs by manipulating them with their palps, without which eggs are attacked by mould and fail to hatch (Lamb 1976). Parental care may also be valuable when a rich, discrete resource is used for breeding and intense intraspecific or interspecific competition may make it advantageous in terms of surviving offspring for parents to defend their young or to speed their development. Burying beetles have been suggested as an example of this situation (Tallamy 1984) where parents need to defend their larvae and their corpse, a resource valued by other individuals and other species, if breeding is to succeed.

Burial of the corpse is the beginning of care for the brood. During burial the crypt which will buffer the larvae from changes in temperature and humidity (Easton 1979) is made, and the corpse seems to be treated so that the growth of mould is inhibited (Halffter et al 1983).

After hatching, the larvae are on the mouse for about seven days in the laboratory as first, second and third instars and throughout this time are cared for by at least one parent. Care consists of feeding and defence; these will be discussed and work on the benefits and costs of care will be described. Finally, I shall discuss the role of the male in parental care.

Defence of the brood.

A corpse attracts a number of insect predators, most notably staphylinid and carabid beetles. Use of a compact, rich resource requires behaviour to deal with these predators and Pukowski (1933) noted that adult *Nicrophorus* would defend their crypt against other insects. I tested brood defence in the laboratory using a species of *Philonthus* (Coleoptera:Staphylinidae) probably *Philonthus decorus* which was known to attack *Nicrophorus* pupae (Easton 1979) and was found in preliminary studies to eat *Nicrophorus* larvae if the parents were not present.

N. vespilloides will also defend its brood against other members of its own species and this was tested in the laboratory. *N. vespilloides* was seen during this study to eat larvae of other broods and so could be a threat in the field.

Feeding the brood.

The larvae of *N. vespilloides* cluster at a hole in the body of the corpse, eaten out by the adults just before the eggs hatch. They eat the rim of the hole, sometimes in a row like grazing sheep; they eat inwards too, into the body where occasionally one or two may drown in blood and soft flesh. The parents may stay in the crypt below the corpse or may themselves eat at the hole. When they are close to the brood one larva will touch the adult's legs and at once rear up so that the front of its body is lifted in the air and its head touches the adult's mandibles (Figure 6.1). Droplets of brown fluid pass from adult to larva until the adult pulls itself away or another larva knocks the first away and takes its place to be fed. At times five or six larvae may reach up together like young birds when an adult returns to the nest.

There has been some disagreement as to when parents feed their brood. One suggestion was that feeding occurred only during the first 60-72 hours of larval development (Pukowski 1933), another that the larvae were fed for 24 hours after each moult (Milne & Milne 1976) which was explained by suggesting that the mouthparts were still soft after the moult and the larvae could not feed themselves (Easton 1979). I watched broods throughout development to establish when the larvae of *N. vespilloides* are fed.

Costs and benefits of parental care.

The experiments described above show something of the efforts made by adult *N. vespilloides* in feeding and defending their young. Further experiments were done to establish any cost to adults of caring for broods in terms of future reproductive success, and to determine the nature of the benefit received by the larvae compared with the situation in which parents were removed. It is sometimes suggested (e.g. Godfray 1987) that the costs of repeated reproduction in insects might be less significant than for birds

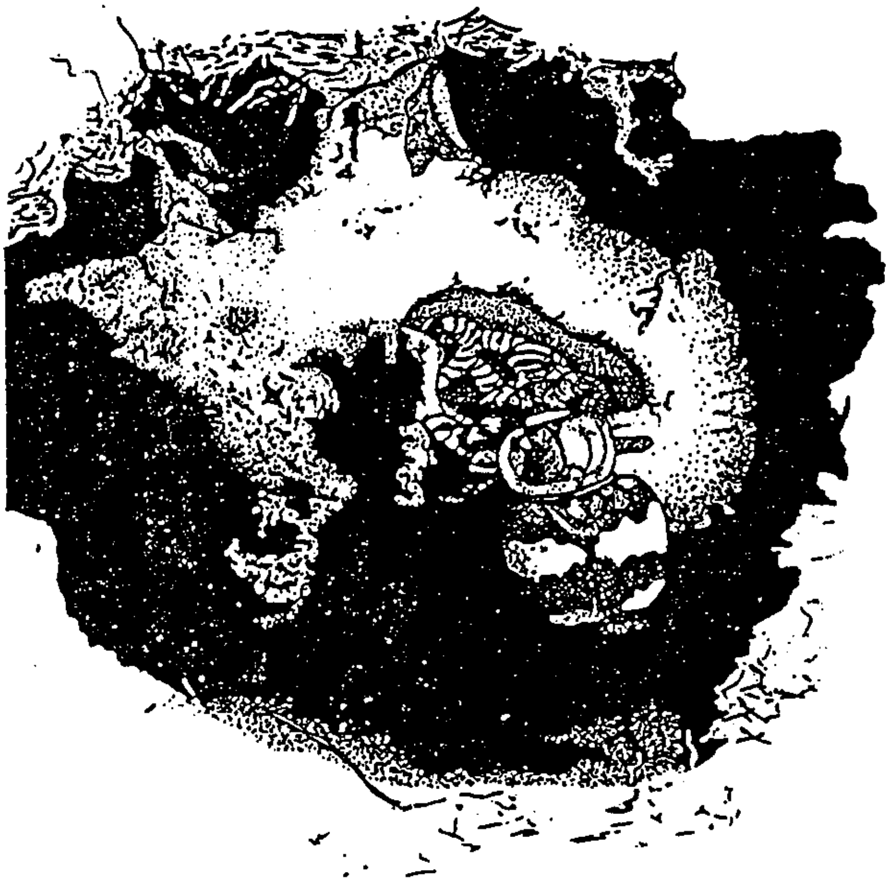


Figure 6.1

A female *N.vespilloides* is shown in the crypt, standing on the partially eaten corpse of a mouse. The larvae are gathered in a hole in the body. One is reaching to the parent to be fed, another is chewing at the edge of the hole.

because of the usual lack of costly parental care. The extensive care found in *N. vespilloides* might make it an exception to this suggestion.

The value of parental care was studied by comparing orphaned and normal broods on 25g and 10g mice. Two corpse sizes were used in case larval competition had any effect on the need for parental feeding. The experiments described in chapter 5 show that in spite of brood reduction on 10g mice, larvae raised on such mice weigh less at dispersal than larvae raised on 25g mice and therefore faced stronger competition for food during development.

The value of parental care for the survival of a brood needs to be balanced against any cost to the parent in terms of future reproductive success. The parent may be exposed to risk of predation, lose breeding opportunities during the time spent caring, or be weakened by the energetic demands of parental care such that longevity or future fecundity is reduced. Risk of predation and the extent of lost breeding opportunities cannot be measured in the laboratory, but the effect of effort spent in caring for offspring can be measured by a comparison with parents allowed to breed but not to care for their brood. The cost is likely to be important only if a significant proportion of resources is diverted into reproduction from another potential and necessary function (Calow 1979). An example of a case where energetic costs were small compared with those of lost breeding opportunities is that of the male of the tropical frog *Eleutherodactylus coqui* (Townsend 1986). There was a measurable cost to care in that egg-brooders lost weight during breeding and were more likely to have an empty stomach than non-brooders, but this cost was described as small. The more significant cost was in lost opportunities to mate again and this cost could be quantified, which is not yet possible for *N. vespilloides*. I first measured the cost of care in terms of weight loss for breeding *N. vespilloides*.

Further experiments were done to examine the costs of parental care in terms of reduced future fecundity and lifespan. This was achieved by a direct comparison of adults caring for their brood throughout development and adults removed after egg laying. In this way the cost of producing offspring, which is undergone by all insects, and the cost of caring for them during their development, which happens in a small proportion and rarely so extensively as in *Nicrophorus,* are separated. In the lacebug *Gargaphia solani* females removed from their eggs after laying laid twice as many eggs in their lifetimes as females allowed to care for the nymphs after hatching (Tallamy & Denno 1982). Green lynx spiders showed the same cost of care: females allowed to care for the first egg sac laid a second batch less often than females removed after the first sac had been produced (Fink 1986). In both cases, however, the costs of predation on unguarded eggs and young meant that caring adults produced more surviving offspring in spite of the reduction in lifetime fecundity (Tallamy & Denno 1981; Fink 1986).

Sex roles in *Nicrophorus* care.

Work with *N. vespillo* (Pukowski 1933) showed that in 80% of cases the female raised the young alone after apparently expelling the male from the crypt soon after the eggs were laid. *N. vespilloides* may be different from the majority of its genus in the greater frequency of male parental care (Hinton 1981). One study has suggested that biparental care may occur in 50% of *N. vespilloides* broods, the females caring alone in the other half (Pukowski 1933).

I examined the frequency and efficiency of male care in laboratory broods. In general in laboratory broods males seemed to stay with the larvae until a day or at most two days before they dispersed; the females stayed until dispersal. I tested for any effect of male size on the length of time for which males stayed. The presence of the male may mean a gain in the survival or the quality of the offspring but a cost in the amount of corpse he eats which is then not available for female or young. This cost may become particularly significant on small corpses. and so male care was compared between broods on 5g and 25g corpses.

I tested the ability of the male to care for the brood by experiment and observation. It has been claimed that although males rarely cared for the larvae they were capable of feeding them as well as could a female (Pukowski 1933).

As explained above, the cost of parental care can be expressed as the physiological cost of tending to a brood or as the cost in terms of the number of breeding opportunities lost; it must be balanced by considering the advantage of parental care in increasing reproductive success. I investigated the costs to males of parental care.

6.2. Defence of the brood.

6.2.1. Defence against *Philonthus*.

Methods.

30 pairs of *N. vespilloides* were allowed to breed on 25g mice. Once twenty or more first stage larvae had arrived at the corpse, I reduced the brood to twenty and replaced the soil around the crypt so that no more larvae would arrive and the brood size was known. In twenty of the broods the parents were then removed and in ten they were left. Half of the twenty broods without parents present were kept as controls and the others used in the experiment. Two *Philonthus* which had been trapped in pitfalls on the study site and kept without food for three days were placed with each experimental brood and the number of larvae alive was counted every other day. The

control broods had neither parents nor *Philonthus* in the boxes and were also counted every other day.

The experiment was also tried with a carabid, *Feronia nigrita*, which was another beetle regularly trapped in pitfalls around corpses on the study site, but the carabid was quickly killed by *Nicrophorus* adults in the crypt before any larvae could be eaten.

Results.

The presence of the parents greatly reduced *Philonthus* predation. Mean brood size at dispersal for the controls was 19.02 ± 1.3 and for the broods with parents and *Philonthus* 18.80 ± 1.1 (t test $P>0.05$). Mean brood size when the predator was present and parents had been removed was 11.20 ± 4.20. This differed significantly from the mean brood size when parents were present (t test $P<0.01$). *Philonthus* was chased by the parents but was too quick to be caught.

6.2.2. Defence against *N. vespilloides*.

Methods.

A dead or etherised beetle placed in the crypt causes no response but a beetle attached with sealing wax to a thread and lowered on to the corpse may be vigorously attacked. Females in three sets of breeding pairs were offered a strange female on a thread. One set was challenged within 15 minutes of finding the corpse, the second after the corpse had been buried and eggs laid and the third after the eggs had hatched and the larvae had moulted to the second instar. The tethered female was presented five times and the reaction to each presentation recorded (Table 6.1). An aggressive response was taken as biting and chasing of the intruder followed by the jerky movements described in chapter 4 as being typical of a burying beetle which has just chased another insect from its corpse.

Results.

Females just arrived at a corpse are less likely to attack the tethered beetle than females which have laid eggs. The latter group attacks almost 100% of the time and is not significantly different in this from females with larvae on the mouse (Table 6.1).

6.3. Feeding the brood.

Method.

Pairs of beetles were allowed to bury 25g mice. As described above, broods of twenty first stage larvae were allowed to form and the soil around the crypt was then replaced. The brood size was therefore known and constant between all observed corpses. On each day of the larval period the crypt was watched twice in the morning and twice in the afternoon, for ten minutes each time. In each 30s interval of the ten minute watches the male and female were scored as feeding any larvae or feeding none. For each morning and each afternoon there was therefore a maximum score of 20 per sex per 10 minute watch x two 10 minute watches = 40 for each sex. The results for each sex are discussed below; in this analysis the sexes were lumped together.

Table 6.1

Stage of breeding attempt	n	Aggressive response	
		mean	95%CL
15 minutes after finding mouse	10	0.48	0.09
Eggs laid	17	0.98	0.01
Second stage larvae	10	1.00	-

The laboratory response of three sets of female *N. vespilloides* to a strange female appearing on the mouse. The first set of females had found the mouse 15 minutes earlier, the second set had buried the mouse and laid eggs, the third had a brood of second stage larvae on the corpse.

Results.

The second instar larvae were those most often fed (Figure 6.2). Soon after moulting to the third instar the larvae were hardly fed at all. All three instars, however, received some food from their parents.

6.4. The costs and benefits of parental care.

6.4.1. The value of parental care.

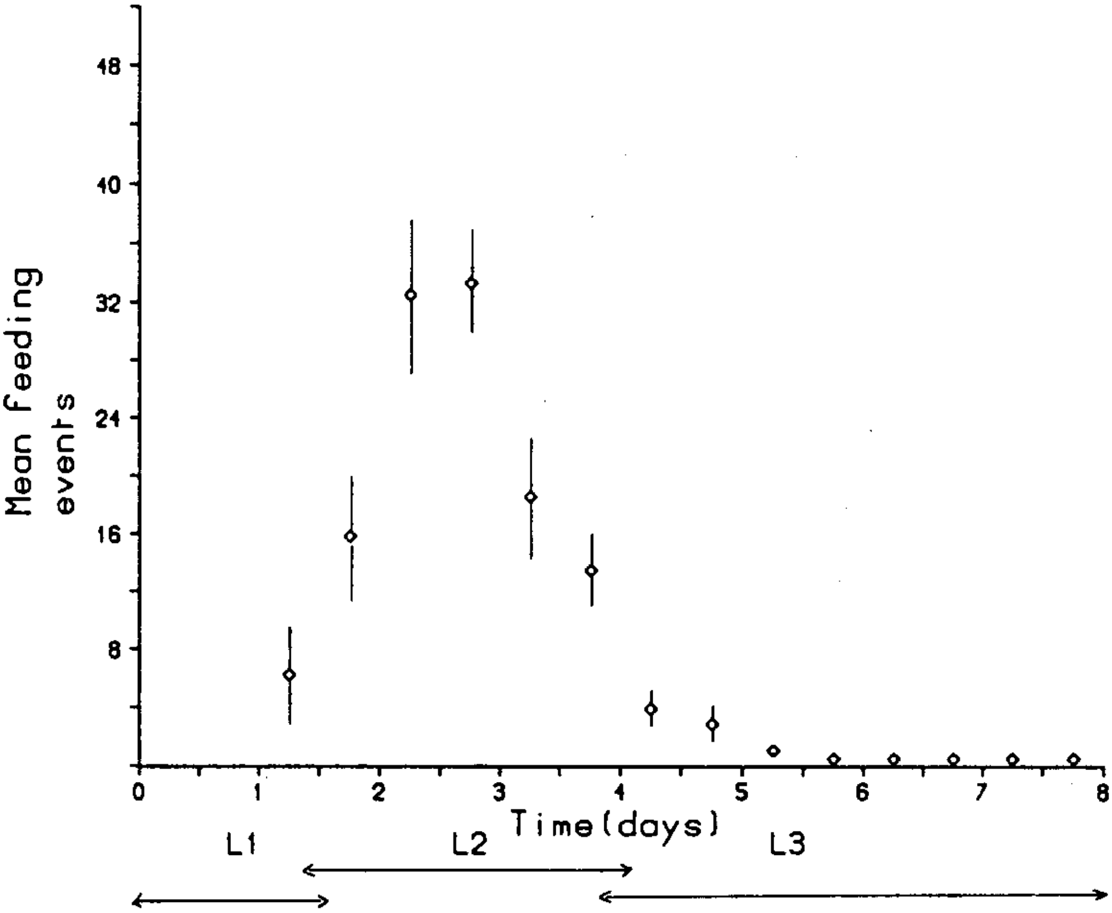
Methods.

a.25g mice.

Pairs of adults were allowed to breed on 25g mice. Half of the broods were left undisturbed until the larvae dispersed: the larvae were then counted and weighed. For the rest of the broods the parents were removed just before the eggs were expected to hatch i.e. after a hole had been eaten into the body of the mouse ready for the larvae to arrive. Larvae found their way to the corpse and began to feed. They were left undisturbed until dispersal and then counted and weighed. Although parental stridulation has been shown to attract the newly hatched larvae of *N. vespillo* to the crypt (Niemitz & Krampe 1972) I found that first-instar *N. vespilloides* under the conditions in which they were bred for this study made their way to the crypt without parents being present. Any differences in brood size at dispersal in this experiment would not therefore be caused by larvae without parents failing to reach the mouse.

Figure 6.2

Each point represents the mean (bars 95% CL) of 10 broods and shows the summed feeding efforts by a male and female pair at different stages in larval development (L1–L3). Totals were measured by recording whether a feeding event occurred in each 30s period of 2 10 minute observations in the morning and two in the afternoon of each day. The two morning observations and the two afternoon observations were each combined to give 2 points for each day. The maximum for a brood at each point is therefore 80 (20 in each 10 minute period x 2 10 minute periods x 2 adults).



b.10g mice.

The method was the same as above, except that to avoid any culling of the brood where parents were present, broods were in all cases reduced to twelve after the first-stage larvae had gathered at the mouse and the earth around the crypt was replaced to prevent any more larvae arriving.

Results.

a. 25g mice.

There was no significant difference between the mean brood size when parents were removed and when parents were left, nor between the mean larval weight at dispersal for the two situations (Table 6.2).

b. 10g mice.

In every case at least 11 of the 12 larvae placed on these corpses survived to dispersal, giving further confirmation that larvae in the laboratory are capable of feeding themselves. However, the mean larval weight at dispersal (MLWD) for broods without parental care was significantly less than that for broods where parents were left in the crypt (Table 6.3).

6.4.2. The costs of care.

Methods.

19 pairs of beetles were allowed to breed on 25g mice. The females were weighed throughout the breeding period and their weights compared with those of 17 non-breeding control females given over the same period an excess of mealworms as food.

Table 6.2

	n	Brood size at dispersal		Larval weight at dispersal	
		mean	95%CL	mean(g)	95%CL
With parents	18	25.59	5.02	0.181	0.02
Without parents	13	22.00	3.88	0.177	0.02
t test		P>0.05		P>0.05	

Pairs of adults allowed to bury 24-26g mice and lay eggs. Brood size at dispersal and MLWD are shown as the mean of 18 cases where both parents cared for the brood and 13 cases where parents were removed before eggs hatched.

Table 6.3

Value of parental care on 10g mice.

	n	Larval weight(g)	
		mean	95%CL
With parents	171	0.187	0.01
Without parents	170	0.167	0.01

Nested ANOVA table.

Source	D.F.	SS	MS	F ratio	Significance of F
Between care types	1	0.038	0.038	16.93	$P<0.001$
Broods within types	28	0.063	0.0023	6.99	$P<0.001$
Within broods	311	0.100	0.0003		

In an experiment designed for a different purpose females were bred repeatedly on 25g mice and allowed to care for their young and compared with females also bred repeatedly but removed from their mice after egg laying and kept for the period normally taken up by parental care with an excess of mealworms as food before being bred again. The weights of these two sets of females were measured before each breeding attempt and are presented here to examine any cost in terms of weight loss of repeated parental care compared with egg-laying only. Both sets of females are compared with a second non-laying control group of the same age which were kept individually and fed on an excess of mealworms during the period of the experiment.

The males paired with the two sets of females since the beginning of the experiment were also weighed before each breeding attempt. They were treated in the same way as the females: one set cared for broods and one was removed after egg-laying and kept with excess food for the normal period of parental care.

Results.

In the single breeding attempt on 25g mice, the graph suggests that the mean weight of the breeding group tends to decrease during breeding (Figure 6.3). However, there was no significant difference between the mean weights of breeding and non-breeding females at any point during the experiment.

In the experiment with repeated breeding attempts, there was no significant difference between the mean weights of the two sets of females before the first burial. Before the next three breeding attempts the mean weight of non-caring females was significantly greater than that of caring females (Figure 6.4 t test, $P<0.001$ for each case) but the mean weight of the caring females was never significantly different from that of the control group (t test, $P>0.05$).

Figure 6.3

A comparison of mean weight of 19 females during breeding on 25g mice with mean weight of 17 females not bred but kept over the same period with an excess of food. Points show mean and 95%CL. The labels show that the mice were given on day 1, eggs laid on day 2-3 and larvae dispersed on day 9.

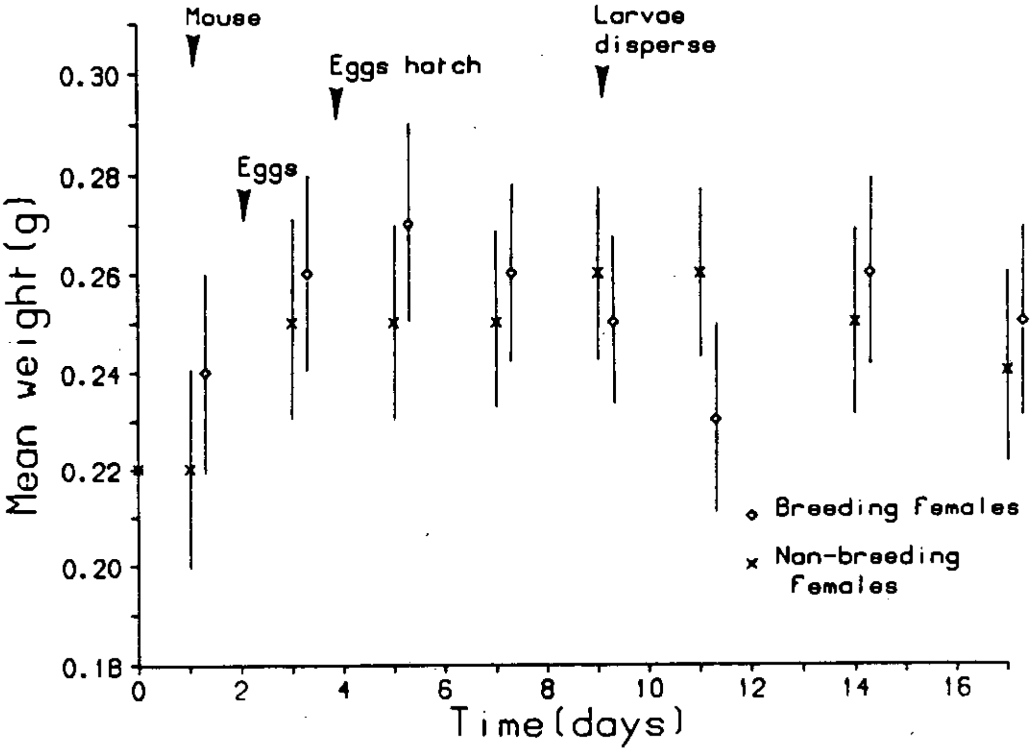
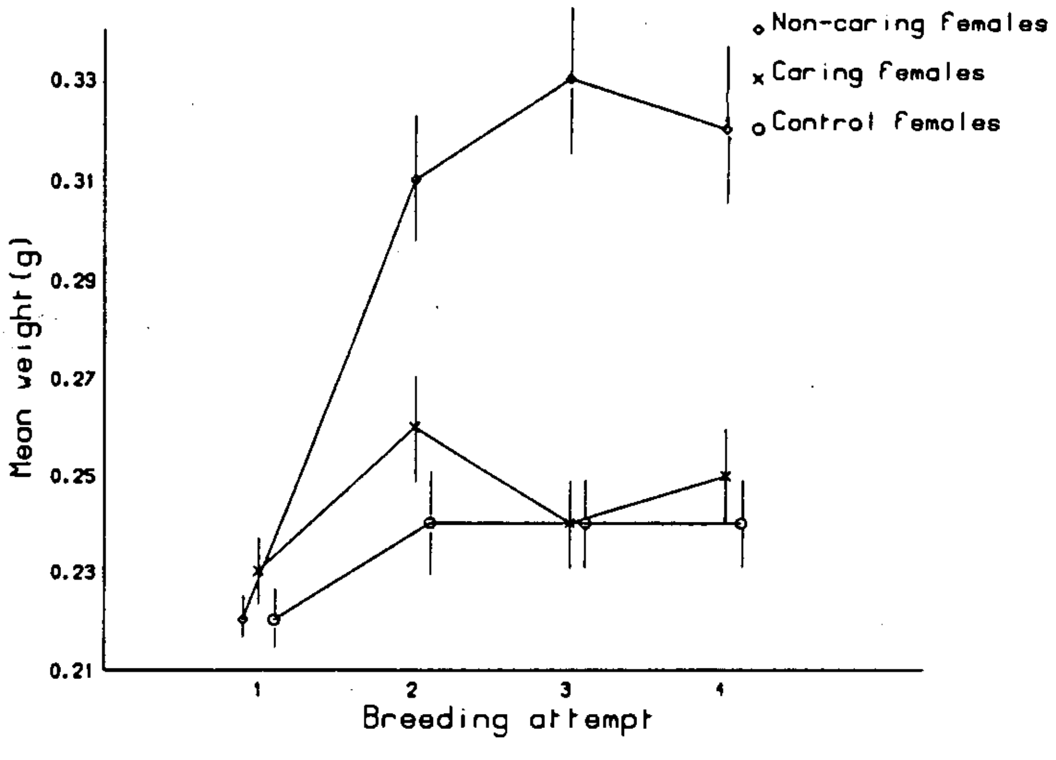


Figure 6.4

The mean weight and 95% CL for females bred on a sequence of 4 25g mice and allowed to care for the offspring of each brood, females allowed to bury a sequence of four 25g mice but removed after egg laying and kept between broods with an excess of food and females not bred but kept over the same period with an excess of food.



For males, the mean weight of the non-caring group was again significantly greater than that of the caring group over the second, third and fourth breeding attempts (Figure 6.5).

6.4.3. Lifetime costs of parental care.

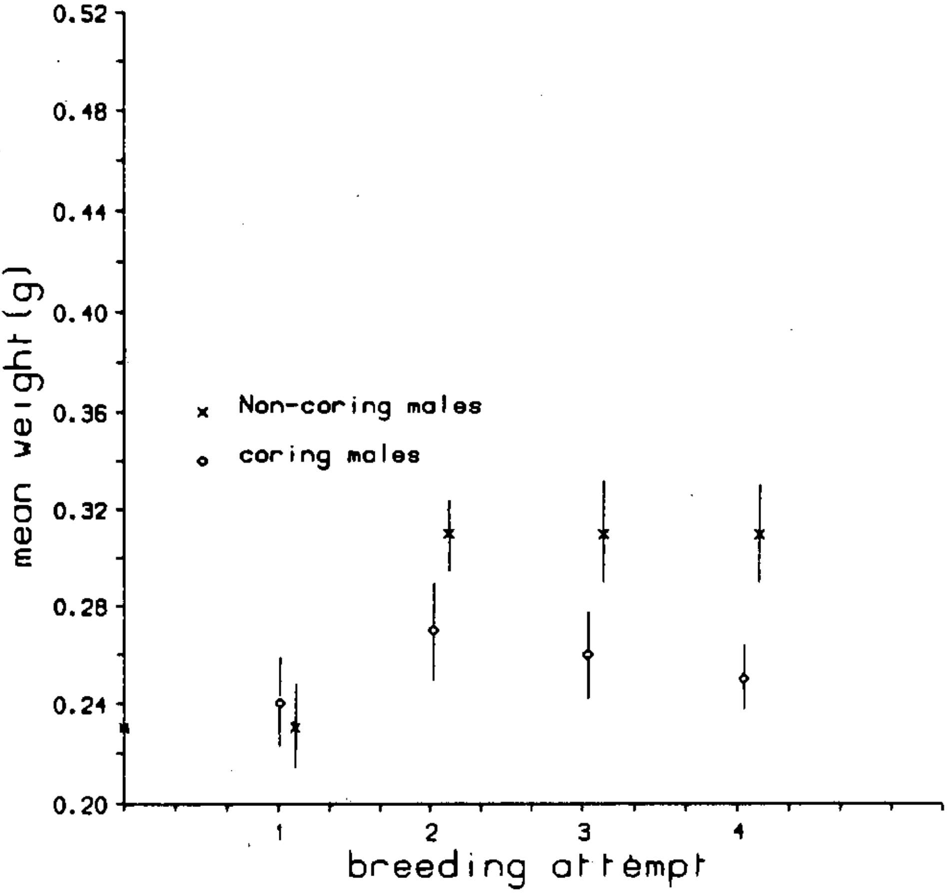
Methods.

Two sets of twenty females aged twenty days from eclosion were paired with two sets of males and allowed to breed on a succession of 25g mice until all the beetles were dead. A third set of females of the same age were used as controls and were never bred. There was no significant difference between the mean pronotum widths of the three sets of females nor between the mean wet weights at the start of the experiment (t test, $P>0.05$). For each new breeding attempt the surviving males and females were paired again at random. One set of females and males were allowed to raise their broods as normal and given a new mouse as soon as the last brood had dispersed. The other set were taken from their mice before their eggs had hatched and kept in boxes for a week with an excess of mealworms as food, until their broods, had they been allowed to survive, would have dispersed. They were then given new mice. The control females were kept individually throughout the experiment and fed on an excess of mealworms.

For the first set of beetles clutch size was counted by allowing first stage larvae to reach the corpse and then replacing the earth around the crypt and searching the old earth for any unhatched eggs. The total of eggs and larvae then gave the clutch size. Eggs could not be counted before hatching because of the poor hatching success of eggs taken from the soil and counted. For the second set of beetles, where larvae were not needed, eggs were counted directly to give clutch size. All beetles, including controls, were checked every

Figure 6.5

Mean weight and 95% CL of males paired with the two sets of breeding females shown in Figure 6.4. All caring males stayed with their broods for at least 7 days.



day, if possible, to see whether they were still alive. Data was therefore collected on the longevity of non-breeding controls, the longevity of adults caring for their brood and adults not giving parental care, and on the lifetime total of eggs produced by females caring or not caring for their brood. Within each set of adults longevity and number of eggs produced could also be compared.

Results.

The survival of the three sets of females is shown in Figure 6.6. When the last of the egg-laying and caring females died, 20% of the non-caring females and 75% of the control females were still alive. 70% of these controls were alive when the last of the non-caring females died. Lifespan of the controls was not measured after this point, but it would seem likely that non-breeding females tend to live longer than either type of breeding female. There was no difference in median lifespan between caring and non-caring females or males (Table 6.4) (Mann-Whitney U test, $P>0.05$ all cases). However, females not caring for their broods laid significantly more eggs over their lifetimes than females which cared for their young (Table 6.4: Mann- Whitney U test, $P<0.01$).

Within each of the two sets of breeding females the total number of eggs laid was strongly correlated with lifespan and so with the number of breeding attempts (Spearman's rank correlation: caring females $n=19$, $r=0.74$ $P<0.01$; non-caring $n=18$, $r=0.66$ $P<0.01$).

6.5. Male parental care.

Figure 6.6

The lifespan in days from eclosion of three sets of females: controls fed on an excess of mealworms and never bred; caring females bred on a sequence of 25g mice at ten-day intervals and allowed to care for the young of each brood; non-caring females also bred sequentially on 25g mice at ten-day intervals but removed after egg-laying and kept for the rest of the time with an excess of food.

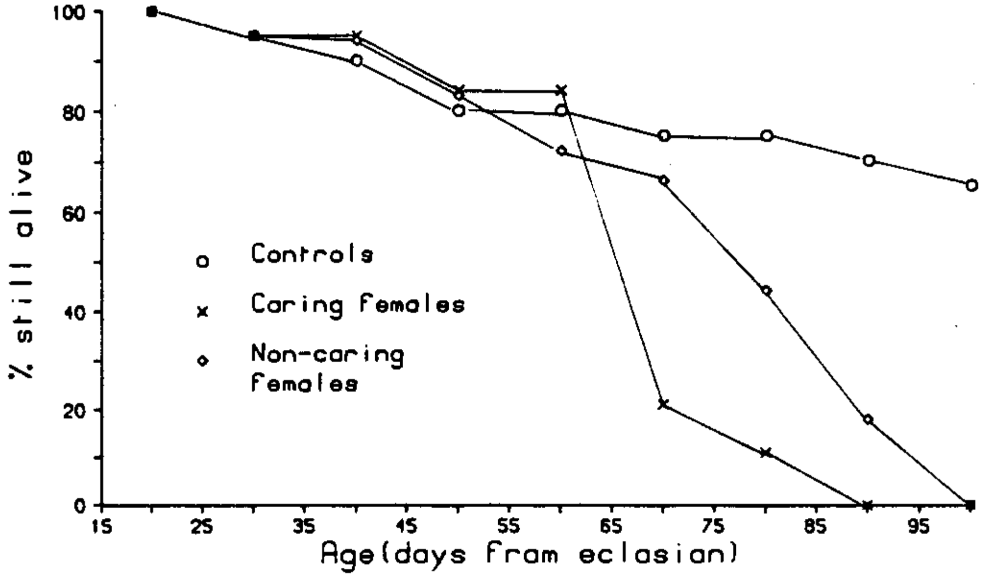


Table 6.4

Costs of parental care.

	Caring		Non-caring		Mann-Whitney
	median	95%CL	median	95%CL	U test
Total eggs	83.00	5	163.0	5	P<0.01
Female lifespan	65.00	5	77.50	5	P>0.05
Male lifespan	58.00	5	61.00	5	P>0.05

Two sets of 20 adult *N. vespilloides* in the laboratory allowed to make successive breeding attempts until dead. One set raised larvae as normal, the members of the other were taken from each mouse after egg laying. The lifespan of males and females as days from eclosion and the mean of the total number of eggs laid by each female in her lifetime are shown for the two sets.

General methods.

The presence of a male was easily checked by lifting away the leaf covering the crypt (Chapter 2) and looking inside. When a male did leave he stayed on the soil surface, occasionally opening his elytra as if to fly away. Leaving did not seem to be a 'decision', therefore, that was at all inhibited by being confined to the breeding box. A further sign was that males which were considered to have left were covered by a swarm of the mites which had bred on the corpse and were now dispersing with the male. Males still in the crypt carry far fewer mites; most are still feeding on the corpse.

6.5.1. Male care on 5g and 25g mice.

Method.

I first studied the length of times males of different sizes stayed with broods on 25g mice. Small males, with little chance of winning another corpse, might stay more readily than larger males. Males with a range of pronotum widths representing that usually found in the lab population were paired with females and bred on 25g corpses. The corpse was checked three times a day to see whether the male was still present. The next experiment examined the effect of corpse size on the tendency of males to care for the brood. 16 pairs of beetles were each allowed to breed on 25g mice and 16 pairs on 5g mice. Two of the pairs on the larger mice produced no offspring and were removed from the experiment. The rest all produced broods, although these were not counted so as not to disturb the parents. The crypt was examined three times a day and scored for the presence of each parent.

Results.

First stage larvae appeared on the corpse on the third or fourth day after burial. They were on the corpse until the ninth or tenth day. The day on which the male left the brood was not correlated with male pronotum width (Spearman's rank correlation = 0.06, n=21). Most males stayed until the eighth or ninth day (Figure 6.7). By this time, both parents have virtually ceased to feed the larvae. In the experiment using different sizes of corpse, nearly 80% of the males on the 5g corpses had abandoned their broods by the time first-stage larvae arrived at the corpse, and the rest were gone on the following day (Figure 6.8). The males from three of the 5g broods were found dead. They had lost their antennae and one or more legs and had punctures along the abdomen. They had clearly been killed by the female with which they had been paired. Males only gradually left the 25g broods, following the pattern usually seen for male care in broods used in other experiments. None of these males was found dead.

6.5.2. Efficiency of male care.

Method: experimental.

Three sets of beetles bred on 10g mice. In one set both parents were left with the brood. The male stayed for the usual length of time and the larvae had biparental care throughout the feeding period. In the second set the female was removed as soon as the eggs had hatched and the larvae reached the corpse; in the third set males were removed once the larvae had arrived. Brood size and mean larval weight at dispersal (MLWD) were measured.

Figure 6.7

The day (from mouse burial) on which each of 18 males left his crypt is plotted against male pronotum width.

Spearman's rank correlation: $r_s = -0.06$

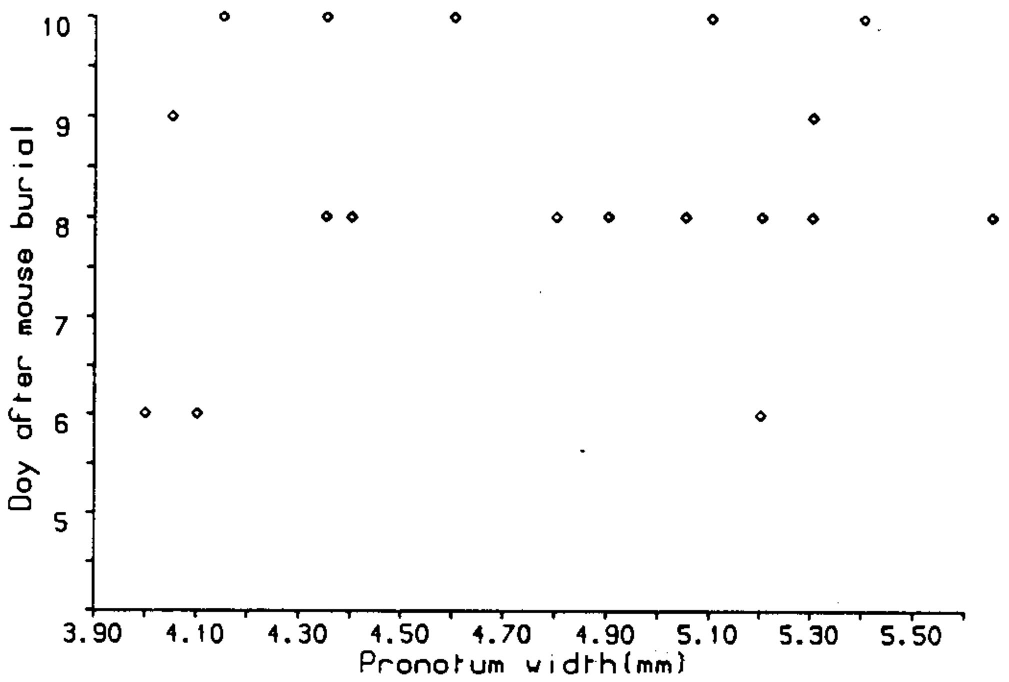
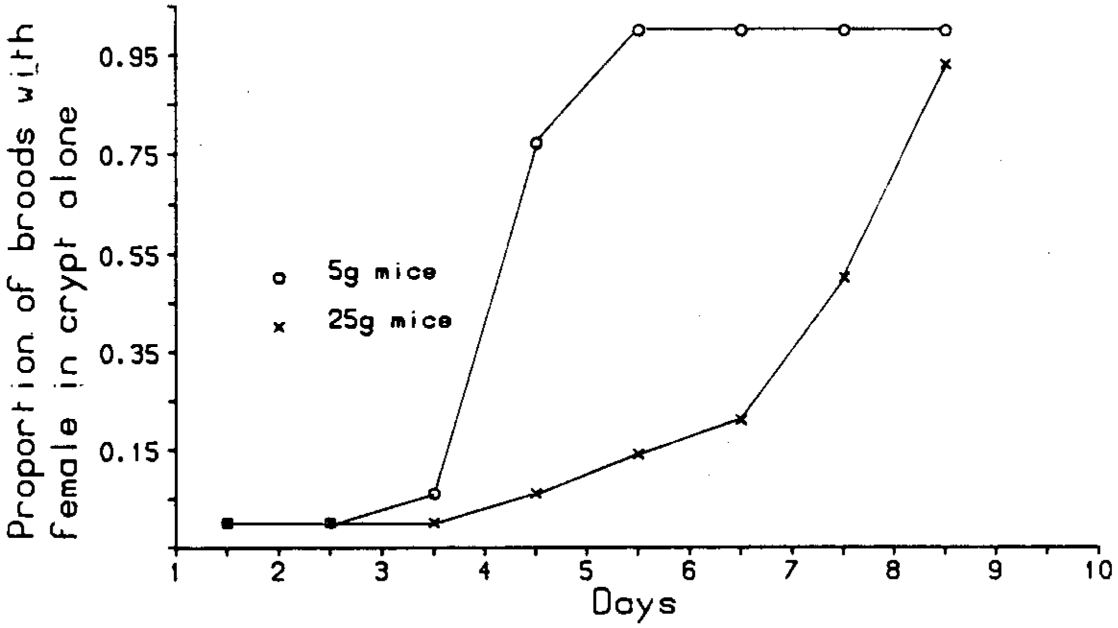


Figure 6.8

The proportion of broods on 5g mice and 25g mice with only a female in the crypt. Crypts were looked at three times a day and a female recorded as alone that day if she was alone on all three inspections. Larvae appeared on the corpses on day 4.



Results.

There were no significant differences between sizes or weights of broods between the three groups, (Table 6.5) suggesting that either parent can raise a brood in the laboratory as well as the other or as both parents together.

Methods: observations.

A further set of pairs of adults were allowed to breed on 25g mice and these broods were watched to compare directly the amount of feeding done by males and females. The method used was that described in section 6.3, with broods of 20 larvae watched for ten minutes twice in the morning and twice in the afternoon on each day of brood development and adults scored for feeding larvae within each 30 second interval of the 10 minute period, giving a maximum score of 20 for each adult for each 10 minute observation. The scores for the two observations in each half-day were combined, giving a maximum of 40 for each sex.

Results.

There are no significant differences between male and female mean feeding effort at any time during larval development (Figure 6.9). Males tended to leave the brood a day or two before females, as was usually the case in the laboratory, but this was after the larvae had ceased to be fed by the parents (compare Figure 6.2).

Table 6.5.

	Male only	Female only	Two parents
n	110	109	113
Mean larval wt(g)	0.168	0.171	0.175
95% CL	0.01	0.01	0.01

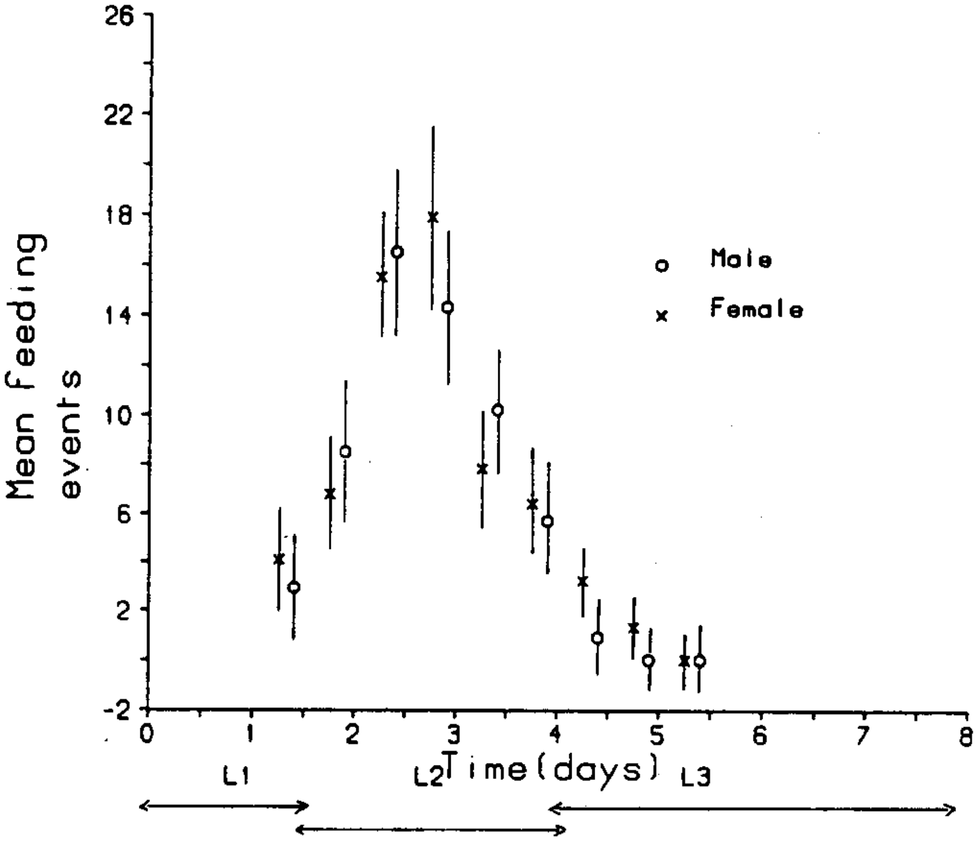
Nested ANOVA table

Source	D.F.	S.S.	M.S.	F ratio	
Between parental types	2	0.006	0.003	0.489	$P>0.05$
Broods within types	27	0.116	0.004	7.348	$P<0.001$
Within broods	302	0.177	0.0006		

A comparison of larval weights at dispersal for 10 broods of 12 larvae raised by male only, 10 broods by female only and 10 by both parents.

Figure 6.9

Comparison of male and female feeding efforts on 25g mice, each point mean of ten broods, bars 95% CL. Details of data collection as for Figure 6.2.



6.6. Discussion.

Defence of the brood.

The results of the experiment with *Philonthus* shows the potential value of *N. vespilloides* adults in defending their young. Two parents might be better than one at defending a brood, but this was not directly tested. If a brood is watched for some time it can be seen that adults are not constantly attending to the larvae but may spend time in the crypt below or around the corpse. At such times a predator as quick as *Philonthus* might take its chance to carry off a larva (larvae were not eaten in the corpse but seized and carried away and eaten outside the crypt). If two parents are present it is more likely that an adult will always be in position to drive off such an attack. This may be one advantage of the two-parent care that seems to be the usual situation for *N. vespilloides* (see section 6.3).

N. vespilloides females in the crypt show maximum aggression to other females at an early stage of a breeding attempt. In contrast lacebug (*Gargaphia solani*) females are progressively more aggressive as their brood ages (Tallamy 1982). The difference may reflect differences in what is fought over. For lacebugs oviposition sites (the surface of leaves) are likely to be less limiting than corpses are for burying beetles: the site is relatively less valuable than the ageing brood (whose value increases with age and so time invested). For *Nicrophorus*, sites may be so rare that a mouse once secured is already worth defending as fiercely as possible and no extra value of the brood with age can cause an increase in effort.

Feeding the brood.

The period of feeding seems roughly to correspond with Pukowski's (1933) observation that larvae were fed in the first 72 hours on the corpse. The larvae do not seem to be fed because they are incapable of feeding themselves: they eat the corpse without difficulty between bouts of begging from the parents.

The value of parental care.

The result for 25g mice confirms that there is no period for lab broods when larvae are incapable of feeding themselves for so long that they would starve without their parents to feed them. On 10g mice, however, it seems that parents are of some value in feeding the larvae and that this benefit exceeds the cost of the carrion that the parents themselves eat. Perhaps carrion is used more efficiently if already chewed or part-digested by an adult or perhaps the mould which grows more noticeably on mice without adult burying beetles in attendance has a greater proportional effect on the small corpses than on the large.

Neither single nor repeated breeding showed an energetic cost as weight loss when females breeding normally were compared with non-breeding controls. Breeding females seem to feed on the corpse, in contrast to Springett's (1967) claim that females do not feed at all during breeding. The experiment used 25g mice and it might be argued that on smaller mice breeding adults could not eat so freely as to maintain their weight, but in laboratory experiments on 15g or even 10g mice neither females nor males lost much weight, perhaps 10mg in an average weight of 250mg. Females allowed to bury a corpse and lay eggs but not to care for the hatching brood show an increase in weight over both normally-breeding females and non-breeding controls (Figure 6.4). The increase may be caused by non-caring females eating a large amount of corpse in preparation for raising the brood: the hole in which the larvae collect is eaten at this time. If this was the explanation, however, then it would be expected that the females weighed throughout a single breeding attempt should show a sharp increase at the start, followed by a decline. This pattern is shown in Figure 6.3, but the initial increase is not as great as might be expected, nor did it, in this experiment, make the mean weight of breeding females significantly greater than that of the controls. It can be concluded from the experiment only that breeding causes no significant effect on body weight compared with not breeding at all, and that under the conditions of the experiment burying mice but not caring for the brood leads to a substantial increase in weight.

Although no loss in weight was found, caring females laid significantly fewer eggs over their lifetimes than did non-caring females. There is a cost to parental care therefore, as specified by Calow (1979), in that care seems to use resources that could otherwise have gone into producing more eggs.

Insect parental care has several functions e.g. to maintain an environment in which the young can develop and to protect the young from predation or competition. The costs and benefits in the laboratory of parental care in *N. vespilloides* have been examined in the experiments above. Over a series of breeding attempts, females can produce more eggs if they do not care for their larvae than if they stay with their brood, although median lifespan is not significantly different for each case.

In the lacebug *Gargaphia solani* the effect of parental care on egg production was the same: females not allowed to care for their clutches laid many more eggs than females which defended their young (Tallamy & Denno 1982). (For these insects, longevity was reduced in the non-caring group, but these females were bred without gaps between bouts of egg-laying. It was suggested that reduced lifespan was caused by this repeated egg laying.)

Lacebug lifetime reproductive success in the field, however, was increased by parental care because of the advantage to the brood in reduced predation if a female was present (Tallamy & Denno 1982). This was also true for the green lynx spider (Fink 1986) and the frog *Eleutherodactylus coqui* (Townsend 1986).

These findings for other species show that the perceived cost in egg production to *N. vespilloides* females of staying with their brood must be balanced by a discussion of the benefits in survival of each brood. Burial behaviour removes the brood and its food source from some predators and competitors; furthermore, the crypt regulates the environment (Easton 1979). Other carrion beetles, for example *Necrodes surinamensis* (Ratcliffe 1972) and *Promascopus morio* (Peck 1982) lay their eggs in the soil around a corpse and leave the larvae to compete with blowfly maggots and to face the risk of predation. However, the experiments described above show that it is the care which occurs after burial and egg laying which results in the observed cost. The value of *Nicrophorus* in protecting its young from predators is clear from the laboratory experiments with *Philonthus*. There may be a further advantage in the continued suppression of mould. In *N. orbicollis* broods without parents hatched successfully but the broods often failed and the corpses became covered with a thick layer of mould (Wilson & Fudge 1984). The importance of adults in reducing fungal and microbial competition was emphasised by Halffter et al (1983). In the laboratory in this study the parents had an obvious effect in slowing the decay of the corpse but in their absence the brood still usually survived. In the field, where the burial process is slower and the corpse may already be partly decayed when discovered, the presence of parents may be much more significant.

Feeding by the parents was not found to be necessary for larval survival; the larvae could successfully eat the corpse throughout development. I measured the effect of parental care on the weight of dispersing larvae for broods on 25g and 10g mice. Orphaned broods on 25g mice survived as well as broods with two parents. There was no significant difference in brood size or mean larval weight at dispersal between the two sets of broods. In the same experiment on 10g mice, but using broods reduced to twelve to prevent culling by the parents, orphaned broods survived as well as broods with parents, but individual larvae were on average lighter. In the laboratory parental care can reduce the costs of predation and under some circumstances increase larval weight at dispersal. In the field, defence against predators and against mould is likely to be even more important and might well be expected to counterbalance the observed cost in reduced egg production. In discussing *N. vespilloides*, however, an extra point must be considered: that males as well as females care for the brood. The females of *N. vespillo*, in contrast, were reported to drive their mates from the crypt after egg laying (Pukowski 1933); the same behaviour was noted for *Forficula auricularia* (Lamb 1976). The extent of male care and its value in *N. vespilloides* were therefore studied.

Frequency of male care.

In the laboratory, parental care in *N. vespilloides* seems to almost always involve the male, the exception being on very small corpses where the female may behave like the females of *N. vespillo* and drive the male away (Pukowski 1933). It was not possible to see whether males abandoned these 5g broods voluntarily or were driven away. Only a small brood can be raised on a 5g mouse and so few larvae might be cared for as well by a female alone as by a female and male pair, allowing the male to abandon the brood without risking its future. The deaths of three of the males from the 5g broods suggests that they were driven away rather than abandoned the brood although they may have left voluntarily and then, being unable to leave the box, have come back to the crypt and been treated by the female as predators.

Males make competent parents; they feed the larvae as often as females do and the numbers and mean weights of larvae dispersing from broods on 10g mice tended exclusively by them are not significantly different from results from broods tended either by a solitary female or both parents together.

Generally, paternal care in insects is unexpected (Thornhill 1979; Tallamy 1984). It is occasionally found in subsocial wasps (Eickwort 1981) and is best known, as exclusive paternal care, in a few families of Hemiptera (Ralston 1977; Smith 1980). Several arguments have been produced to explain the occasional occurrence of male brood care.

The presence of the male may help the current brood: the bugs (Hemiptera: Reduviidae; Belostomatidae) described by Smith (1980) offer a safe environment for eggs by carrying them on their backs until hatching. In several species of dung beetle (Scarabaeidae) the processing and securing of a rich but transient resource may require the male and female to work together as far as burial is probably explained for *Nicrophorus* males in the same way. Advantages after hatching are more difficult to find. Once the eggs are hatched a male cannot be cuckolded; a single female seems to be able to feed a brood as efficiently as an adult pair. The male may be needed for defence of the brood (see section 6.3.1); habitat differences in the extent of predation may then explain differences in male care between *Nicrophorus* species. The answer may lie, however, not only in the positive aspects of male care but in the balance of these and the advantage of leaving. It has been pointed out that a decision to desert or to stay should be based on the likely chances and cost of raising another brood and on the effect of desertion or staying on the survival of the current group of offspring (Dawkins & Carlisle 1976). The alternatives for a male were summarised by Maynard Smith (1977) as those of deserting with a variable chance to breed again and of staying with whatever difference that might make to the survival of the current brood. These are the factors that can be examined for *Nicrophorus* in an attempt to understand the variation that seems to exist in paternal care within the genus. Any advantage to *Nicrophorus* males in helping to raise a brood must be balanced against the energetic costs of the care and the loss of mating opportunities. In the frog *Eleutherodactylus coqui*, for example, the costs of paternal care were divided into the energetic costs of not feeding during the period of care and the reproductive cost of not mating with other females. The latter was judged to be more important and showed that there was an advantage to be gained by desertion in terms of future breeding success. However, this potential advantage was outweighed by the benefits to the male of caring for the present brood (Townsend 1986).

In *N. vespilloides*, the benefits to brood success of males helping to care are not obvious from the experiments described here: single females can raise as many young as two parents and the young are not significantly lighter at dispersal. The experiments do not, however, take account of the benefit of two parents in defending the brood from predation.

As for costs, males which cared for several broods in succession showed no significant loss in weight (Figure 6.5) over the experiment and were comparable in this to females caring for several broods and non-breeding females (Figure 6.4). Males must eat the corpse during breeding. Males which were removed from a succession of broods after egg-laying had occurred on each were much heavier on average than males which were left with their broods (Figure 6.5), a result again comparable to that for females. Under the conditions of the experiment, then, abandonment of the brood after corpse burial and egg-laying can result in increased weight. It is not known whether such an increase could be of any advantage in the field; it can be considered as a disadvantage in reduction of dispersal ability (Takagi 1985) and may simply be an effect of the experimental procedure: males removed after corpse burial may have only put on the excess weight in preparation for feeding the brood.

Males which are left to care for their brood do not show any reduction in lifespan compared with males which are removed after egg laying (Table 6.4). Physiological costs of parental care may therefore be small.

Mating and breeding opportunities may be rare. The male biased sex ratio reported among beetles trapped at corpses by Easton (1979) during the peak of the breeding season and found also in this study (chapter 3) may reduce the chances of finding another mate and affect the tendency of males to leave. This should be particularly true for small males and a size difference in the tendency to care might be expected although this has not been found in the laboratory where males of any size seem always to stay until almost the end of larval development.

In *N. vespillo* it is the female which is said to determine the situation of the male by driving him from the crypt (Pukowski 1933). In the experiment with 5g mice (section 6.6.2) three of the males were found to have been killed by their mates and the solitude of the female may therefore reflect her own rather than the male's course of action. The occurrence of male care needs to be examined also from the viewpoint of the female. Since males show no significant weight loss over several breeding attempts, they must feed on the corpse they bury. If the female is determining whether the male should stay or not then this loss of corpse for herself and her brood may be a factor. It may explain the apparent driving away of males from 5g corpses, where the effect of the male eating any of the corpse is likely to be relatively severe. The benefit to the female of a male helping to raise the brood has not been tested. I have speculated that males may be of significant use in defending the brood; a further advantage might lie in reducing any physiological costs of care, even though the experiments described in this chapter show that these are low in the laboratory. Under field conditions the effect might be more apparent. In the eastern bluebird, for example, although no immediate advantage of two-parent care was found, it was suggested that in the long term male help might benefit a female (Gowaty 1983). An effect on reducing the effort of defence was offered to help explain monogamy in the lesser snow goose (Martin et al 1985): single females spent more time in the alert posture during incubation than females with mates. Finally, it was argued in a discussion of the willow ptarmigan that the smallest advantage to male help might be significant if there was sufficient lack of alternatives (Martin & Ccoke 1987) and this could well apply to *N. vespilloides*. Any final explanation needs to confirm and account for differences within the genus, differences also recorded for the earwig genus *Forficula* (Lamb 1976). Confirmation would require direct comparison of several species, a comparison attempted in this study but not achieved (chapter 2). An explanation might come from comparing the relative risks of different habitats; the need for defence seems more likely to vary than the chances of mating and breeding again.

Chapter 7.

General discussion.

'When the cares of the family are finished, the joys of life are finished likewise. The insect then sometimes becomes depraved; and its disordered mechanism ends in aberration.'

J.H. Fabre 'The Glow-Worm and other Beetles' 1919.

Burying beetles remain little-known creatures. A relatively small number of studies scattered across more than two hundred years make up the sum of published work. A single literary reference praises not their beauty or their strength but their quality of unobtrusiveness (Ford 1924). It is not possible yet to describe their life history with any pretence to comprehensiveness, but this, together with suggestions for future work, is the purpose of this chapter. All the experiments described above focused on a specific question posed at one point in the animals' lives. Usually, for example, age of beetles used was held constant at 20 days from eclosion. The significance of the results is therefore not primary; it lies in their effect on the whole of the subject's life history (Cole 1954; Stearns 1976; Bradshaw 1986). The difficulty of doing suitable experiments usually prevents life history as a whole from being studied directly; this was the case in this work on *N. vespilloides*. Experiments and results were taken at single points, or else lifetimes were simulated under laboratory conditions whose relevance is not fully known, and a discussion of life history strategy, the 'schedule of fecundity and survival' (Horn & Rubenstein 1984), can be no more than informed speculation.

It is, however, possible to consider some of the more significant problems of burying beetle life-history, for example, the question of repeat breeding.

In the laboratory *N. vespilloides* can raise broods on as many as six 25g corpses, although most beetles die after four (chapter 6). On very large corpses they seem to lay as many eggs as they can produce for a single clutch, but at the upper end of the range of the most common field corpse weights (Bobek 1969; Easton 1979) they lay fewer eggs than this and probably fewer than such corpses could support (chapter 5). In the field, adults which eclose as part of the first generation often survive to be trapped amongst the second generation (Easton 1979; Christie 1981). Early in the year I have trapped *N. vespilloides* which, judging from experience with lab beetles seemed old enough and scarred enough to be survivors from the first generation of the summer before. All of these observations point to at least the capacity for repeated breeding in the field, usually as uniseasonal but possibly even multiseasonal iteroparity, using the definition of Kirkendall & Stenseth (1985). Whether this does occur will vary between site and season as part of the unknown variable of corpse availability.

Comparison of the success of semelparity and iteroparity has predicted that selection will be balanced on the relative probability of parents surviving to breed again (P) and young surviving to breed for the first time (Y). Specifically, to match a perennial breeder producing x young per breeding attempt, a one-off breeder would need to produce 2P/Y + x young (Cole 1954; Charnov & Schaffer 1973; Waller & Green 1981; Horn & Rubenstein 1984). Discussion of P and Y for *Nicrophorus* should help to clarify the validity or otherwise of the proposed iteroparity.

The period of greatest mortality in laboratory burying beetles or during breeding in the field is that of the prepupa and pupa (Easton 1979). This suggests that Y may be low compared with P and favours iteroparity by increasing the 2P/Y + x needed by the semelparous alternative to match the brood x. The prepupal stage is greatly lengthened in *N. investigator* by being the overwintering stage. P/Y may therefore be even greater for this species and I have found in both field seasons that apparent second-season adults were more common amongst *N. investigator* (admittedly with a small total sample) than *N. vespilloides*.

Even though *N. vespilloides* overwinters as the second-generation adult, overwintering, simply by its length, must reduce the chances of an offspring surviving to breed next year compared with the chances of its parent surviving perhaps only days or weeks until the next opportunity to breed. P/Y is again increased, favouring iteroparity (Murphy 1968; Hirshfield & Tinkle 1975). This argument is an interesting addition to the extension of Cole's (1954) definition of semelparity and iteroparity to include within-season and between-season differences (Fritz et al 1982; Kirkendell & Stenseth 1985). Adults have the potential to breed within a season but juveniles must wait to the next for their first reproduction (Easton 1979; Christie 1981).

Iteroparity is further favoured by selection for small litters and large offspring (Horn & Rubenstein 1984). In most cases the constraint of corpse weight will cause burying beetles to raise broods smaller than those of which they are capable. This constraint will in most cases preclude successful semelparity. There are also strong advantages for large offspring (chapter 4 & 5).

Both the potential for an iteroparous strategy and advantages of it seem to exist for *N. vespilloides*. More detailed analysis of such a strategy has been attempted for other species, considering whether total effort should be distributed equally over the several breeding episodes or decrease from the first (Mouer & Istock 1980; Bradshaw 1986). In a laboratory experiment with *N. vespilloides* (chapter 5) I found that clutch size increased in the second attempt and then decreased in the third and again in the fourth. The likely shortage of corpses in the field might favour bias to earlier broods, depending on the weight of each corpse and the ability of the adults to win whatever corpses there are. The decrease might also be the result of senescence or the cumulative costs of reproduction. The initial increase in laboratory clutches might be explained by an increase in breeding efficiency between the two breeding efforts.

Any strategy is likely to vary within a species, according to age and size of individuals and the particular circumstances of the habitat (Horn & Rubenstein 1984). For *Nicrophorus*, size can have a profound effect on success and may affect many aspects of breeding behaviour (chapter 4). The habitat too, by affecting the number of corpses and perhaps the extent of competition with vertebrate scavengers, will exert an effect. However, *N. vespilloides* shows in the laboratory the potential for iteroparity, and the limit imposed by each corpse on brood size and the greater unpredictability of juvenile compared with adult survival in the field suggest an advantage to at least uniseasonal repeat breeding. It seems likely that if reproductive behaviour of individuals could be followed in the field, this would be the strategy found.

Future work.

A comparison of this study on *N. vespilloides* with earlier work on *N. vespillo* (Pukowski 1933) and the North American species *N. orbicollis* and *N. defodiens* (Wilson & Fudge 1984) points to differences within the genus which could be looked at by breeding the different species under the same conditions. Clutch size in *N. vespilloides* and *N. orbicollis* is larger than in *N. vespillo*. *N. vespilloides* (see chapter 5) and *N. mexicanus* (Halffter et al 1983) scatter their eggs rather than laying them in a chamber. Two-parent care seems to be more common in *N. vespilloides* than was thought, and provides another contrast with *N. vespillo*. There are several European species for which these behaviours are unknown. If direct comparison found these differences to hold, they could be investigated further by comparing the habitat types in which the different species are found, work begun by Pukowski (1933) and (Wilson et al 1984), seeking differences in, for example, predation pressure.

I was unable to confirm many of my results in the field, partly due to concentration on lab work, partly to poor weather in both field seasons of 1985 and 1986 and partly because some time was spent in an unsuccessful search for *N. vespillo*, a beetle once common in the areas where traps were laid. A number of experiments in the field could be done without great difficulty; there are also many which are desirable but less practicable. Amongst the former are a study of the value of parental care (and of two-parent care in particular) by removing parent(s) from field broods and of culling to see whether it occurs in the field and under what circumstances. More difficult experiments are those investigating the background to *Nicrophorus* breeding success: the availability of corpses and the extent of competition for them. A discussion of life-history strategy requires discussion of breeding opportunities in a lifetime, and for burying beetles this in part depends on how many corpses there are to be buried and how intense is the competition to use them. For example, a number of my experiments have considered larval weight and adult size as a measure of fitness, but as yet the relationship in the field between size and reproductive success is unknown. The importance of size in settling corpse ownership means that measurement of the benefit of size only for increased fecundity and the cost in increased development time, as was done for *Drosophila melanogaster* (Roff 1981), is insufficient for burying beetles. Nor is it enough to record the mean size of adults breeding successfully on corpses placed in the field until the density of corpses used in the experiment can be made to match that which might naturally occur.

Although little studied, there is a sense in which burying beetles are well known: their remarkable habits of burial and of parental care have often been described and find their way, sometimes inaccurately, into many popular books on insects. This study, however, on one of the better-known members of the genus, has still produced new aspects of their behaviour and suggests that much more remains to be known. Burying beetles are striking members of their community, not only in their size and their handsome appearance, but in a unique strategy of life. Where the typical carrion user is a frail opportunist, relying on chance, speed and large numbers to overcome an unpredictable environment, *Nicrophorus* attempts to create order and for a while suspend the usual course of things by establishing an environment of its own. Compare a frantic, heaving mass of dipteran maggots with the stately progress, enclosed in its own chamber, of the burying beetle's brood and though the claims of Lacordaire and the praise of Fabre may seem absurd or quaint, the attraction of *Nicrophorus* remains and the fascination that has been recorded for two hundred years can still be felt.

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'In this important matter of the Necrophori, my assistants were a small boy and an illiterate.'

J.H. Fabre 'The Glow-Worm and other Beetles' 1919.

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Evidence for a sex attractant in burying beetles.

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Introduction

In common with other members of its genus, the burying beetle *Nicrophorus vespilloides* Herbst (Coleoptera: Silphidae) buries carrion and uses it as a food source on which larvae are raised. Large numbers of burying beetles may arrive at a corpse; individuals of the same sex then fight one another until one male and one female are left in possession (Pukowski 1933). Pukowski noted that if a male arrived at a corpse and found no female there, he adopted a characteristic 'sterzeln' position, with hind legs extended and abdomen pointing up. Subsequent authors have assumed, as Pukowski herself suggested, that the position indicated the release of an attractant by which females were drawn to the site. The original suggestion of a pheromone signal (Pukowski 1933) was challenged by Halffter et al (1983) who argued for an acoustic signal after being unable to find any glands in the male by which a pheromone could be produced. The behaviour is limited to males: females arriving at a corpse are almost always already inseminated (Christie 1981) and can bury the corpse and raise young without assistance from a male. However, Pukowski did not try to show directly that females were attracted by males.

This was the purpose of the experiments described here.

Methods.

A circular plastic container (a paddling pool) 1.5m in diameter was used as a lab enclosure. It was filled with earth and two containers placed opposite each other near the sides so that their tops were level with the surface of the soil in the pool. Each container had a shallow layer of earth inside with its surface 5cm below the surface of the surrounding earth; in one container a mouse was placed, in the other a mouse and a male beetle. The contents of the containers were not visible from the centre of the pool.

The experiments began at midday (artificial lighting was used with a cycle of 16h light:8h dark) and the male buried the mouse during the afternoon. Over the same period I covered the other mouse with earth. In the evening the male adopted the sterzeln position. The behaviour seems to begin only an hour or so before dark. Once the male had been 'signalling' for at least an hour, a female was allowed to leave a container in the centre of the pool where she had been enclosed at the beginning of the experiment.

In the field, a similar choice was given. Pairs of containers, 10m apart, were laid in a row with 50m from one pair to the next. In one of each pair was a male beetle with a mouse which he had buried in the lab the previous day, in the other a mouse which had been buried by hand over the same period. The containers were taken in mid-afternoon to an area of deciduous woodland known to contain *N. vespilloides*. The males began signalling and the containers were left overnight.

A test for a vibration signal through the twigs or stones from which males often signal was done with the help of Dr. A.W. Ewing of the Zoology Department, Edinburgh. A stylus tip was placed against the post and connected either to earphones or to an oscilloscope. In either case the equipment was sensitive enough to record the footsteps of a beetle climbing the post.

Results and Discussion.

In the laboratory enclosure, females were significantly more likely to go to the container with a male than to the one without. (Table 1a). In the field experiment, no beetles were attracted to the hand-buried mice but each of the signalling males attracted a beetle. Of the beetles attracted, 7 were male, 9 female. (Table 1b).

No acoustic signal was found. Burying beetles stridulate, using the 'file' structure on the underside of the elytra (Niemitz 1972), but the obvious movements performed when stridulating never occur during sterzeln signalling, at which time the tip of the abdomen quivers slightly and is stroked by the hind legs but no sound can be heard. No vibration is passed through the signalling post: once the beetle stopped moving and began to signal there was no vibration recorded through the stylus. It seems likely that the means of the attraction demonstrated here will prove to be pheromonal rather than acoustic.

It is clear that males attract other beetles to a corpse. The 'sterzeln' position is probably associated with the release of an attractive signal. Males sometimes signal close by an unburied corpse and their attraction must then act in addition to the attraction provided by the carrion itself. It is not surprising that males as well as females should respond to a male signal if it announces the presence of a corpse: the outcome of fights is determined by size (pers.obs.) and a large male which responds has a chance of displacing the signalling male in the subsequent struggle for female and corpse.

I would like to thank Philip Ashmole and Linda Partridge for their comments on the manuscript, and Sian Coe for translation.

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Table I: Proportion of beetles going to signalling male.

a.Lab.

	Male & mouse	Mouse	(χ^2test)
Females going to each container.	17	4	$P<0.01$

b.Field.

	Male & mouse	Mouse	(χ^2test)
Beetles going to each container.	16	0	$P<0.01$

Summary.

Infanticide is a common phenomenon in many animal groups, but filial cannibalism, The deliberate killing and consumption by parents of their own young, is extremely unusual. The burying beetle *Nicrophorus vespilloides* Herbst has a limited food supply, in the form of a buried corpse, on which to raise its young. On corpses weighing 10-15g, clutch size in the lab is such that complete hatching success will produce more larvae than the corpse can support without severe reduction in the individual weights of final instars. The parents reduce the brood by killing and eating almost half of the first stage larvae. It is suggested that, in the field, predation of eggs and newly hatched larvae may be heavy, and that the excess eggs are laid as an insurance. If survival is then unusually high, superfluous young are killed by the parents before competition for food can occur.

Filial cannibalism in burying beetles.

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Introduction.

Few cases of filial infanticide have been reported. Brood reduction through siblicide or starvation is common among birds (O'Connor 1978) and may occur in some marsupials (Wooler et al 1981) but the parents in these cases do not directly kill their young. Direct infanticide may be accidental, as when the coral reef fish *Acanthochromis polyacanthus* kills some of its young in the process of driving an early-season brood from its own territory, apparently to be fostered by neighbouring adults (Thresher 1985), or when coot chicks are killed during behaviour used to regulate food allocation to the brood (Horsfall 1984). It may be a response to unusual circumstances, as when queens in colonies of social insects use eggs or young larvae as food during a time of shortage in the colony (Wilson 1971; Masuko 1986). In the case of *N.vespilloides*, brood reduction is shown here to be caused by adults killing and eating their own young during the normal raising of a brood. It is suggested that the consequent brood reduction can be interpreted as a means of optimising the eventual ratio of larvae to available carrion food.

Beetles of the genus *Nicrophorus* (Coleoptera; Silphidae) bury the corpses of vertebrates and use them as a food source for their larvae. *N.vespilloides,* the species used here, creates a burial chamber or crypt around the buried corpse and scatters its eggs up to several centimetres away. The hatched larvae make their way to the crypt, and there develop through three instars before returning to the soil to pupate. The larvae eat the corpse, and are also fed regurgitated carrion by their parents. Both adults are normally present throughout larval development, feeding the young, repairing any damage to the chamber, and driving off insects which trespass on the crypt.

The number of *Nicrophorus* larvae a corpse can support increases with corpse size (Easton 1979; Wilson & Fudge 1984). However, the North American species *N.orbicollis* was found not to adjust its clutch size according to corpse size and to lay more eggs on a 15g corpse than the corpse could support (Wilson & Fudge 1984). The purpose of this study was to compare the behaviour of *N.vespilloides*, a smaller species than *N.orbicollis* and the most common in Britain, and to examine the mechanism of any brood reduction that might take place.

Methods.

Beetles were trapped near Edinburgh and a breeding population maintained in the lab for several months. They were kept at a room temperature of 21°C with a 16h : 8h light:dark cycle. The corpses used were of lab mice (*Mus musculus*). The mice were frozen within an hour of death and thawed before use in experiments. Each pair of beetles was bred in a plastic container 225mm x 120mm x 90mm three-quarters filled with potting compost. Once burial was complete the soil above the crypt was removed and replaced by a beech leaf. This could then be lifted away for observations into the crypt. Three sets of experiments were done.

a. Variation in brood survival with corpse size.

The success of broods was compared on 15g and 30g mice to see if there was any difference in the number of eggs laid and the number of larvae developing on the different sizes of corpse. 36 adults were given a 15g mouse and allowed to bury it and lay eggs. For twelve of the pairs the number of eggs laid was counted by removing all the soil from the breeding-box and picking out the eggs. For a further twelve pairs the eggs were not disturbed before hatching and the number of first stage larvae reaching the corpse was counted by inspecting the corpse every two or three hours and removing the larvae as they arrived. The final twelve pairs were left undisturbed until the third stage larvae dispersed from the corpse and the number of larvae dispersing was counted. A further 36 pairs of adults were bred on 30g mice and divided into three groups of twelve, treated as above.

b. Timing of mortality on small corpses.

Once mortality of the brood on 15g corpses had been established it was necessary to know at what stage the larvae disappeared. 15 broods with a mean of thirty first stage larvae (to match the brood size found in the previous experiment) were created on 15g mice by pooling the hatchlings of several families and dividing them between the mice. Each brood was attended by the male and female which had buried the corpse on which it was placed. Previous experience suggested that adult *N.vespilloides* cannot recognise their own larvae and will raise a foster-brood, but as a control for abandonment of foster-broods clutches laid around a set of 10g mice were taken from the soil just before hatching and the larvae that hatched returned to their own corpse. The adults on the 10g mice therefore had broods of their own larvae and the survival of these broods could be compared with the artificial broods on the 15g mice. Availability of different corpse sizes meant that 10g rather than 15g mice had to be used for the control experiment. The size difference has no effect on the principle being tested. All broods were counted as the number surviving to second instar, to third instar and to dispersal from the corpse.

c. Cause of larval mortality.

The cause of the observed larval mortality was studied by watching broods on 15g mice. Pairs of adults were allowed to bury corpses and the crypt roof was replaced with a leaf as described above. The brood was not disturbed for counting and so the initial brood sizes were not known. The broods were watched until the movements of the parents in the crypt turned the larvae out of sight, giving a different period of observation for each brood (Table 2). The number of larvae surviving to second instar was counted and this number compared with that for broods on 15g corpses which had not been watched.

d. Larval weight at dispersal in relation to brood size on 15g mice.

The effect of brood size on larval weight and so the significance of brood reduction in terms of weight of the dispersing larvae was tested in the laboratory on 15g mice. Pairs of adults were allowed to bury mice and lay eggs, eggs were removed from the soil just before hatching and different numbers of first-stage larvae placed on the corpse. The number surviving to second instar was counted and the number and mean weight of the larvae at dispersal recorded.

Results

a. Brood survival on 15g and 30g mice.

Clutch size on 30g mice is not significantly different from clutch size on 15g mice, but subsequent survival of the brood is very different (Table 1). On 30g mice there are no significant differences in the numbers at the egg stage, first instar and larvae at dispersal. On this size of corpse hatching success is high and as many larvae as reach the corpse are likely to disperse from it. On 15g mice there is no significant difference between the mean number of eggs laid and the mean number of first stage larvae reaching the mouse but the difference between the mean number of first stage larvae and the mean number of larvae at dispersal shows that only about half of the larvae which reach a 15g corpse are likely to complete development. These results are similar to those for *N.orbicollis* (Wilson & Fudge 1984) and suggest that the clutch size laid around 15g mice is such that normal hatching success produces more larvae than can complete development on the corpse.

b. Timing of mortality on small corpses.

No experimental broods on 15g mice or control broods on 10g mice were abandoned, suggesting that the parents on the 15g mice did not recognise the larvae they were given as strange. The artificial broods of thirty first stage larvae created on a set of 15g mice showed a significant fall in larval numbers between first and second instars but no significant mortality between second and third instars and up to dispersal (Figure 1). The control broods on 10g mice were of variable size because of differences in numbers of eggs laid. There was no mortality between first and second instars if the brood size was below about 15, but for broods larger than this numbers dropped sharply in the first 24 hours on the mouse, which is the period of the first instar (Figure 2). On both 15g and 10g mice, therefore, using artificial or natural broods, reduction of excessive numbers of larvae is found to happen on the first day of larval development.

c. Cause of mortality.

In all the broods set up for observation the parents were seen to kill and eat first stage larvae (Table 2). This had also been seen in three other broods in earlier experiments and could explain the brood reduction found in the experiments above. The main period of larval mortality on 10g and 15g corpses is at the first instar, during the first 24 hours after the larvae have reached the corpse. It is most unlikely that food is limiting at this time since only a small hole has been eaten in the skin of the mouse and the larvae have not begun to penetrate the body. Table 2 shows that if broods can be watched for long enough, sufficient larvae will be eaten to account for the 50% or 60% brood reductions that the earlier experiments recorded.

There was no significant difference between the number of second stage larvae on the mice used for observation and on the mice buried at the same time but not watched (Table 2).

Discussion.

The infanticide described in these experiments is of an unusual kind. These are not trophic eggs which are eaten but viable larvae. They are not killed by mistake nor in response to suddenly stressed or altered conditions but are deliberately lifted from the brood and eaten as part of a normal breeding attempt in which their surviving siblings continue to be fed and defended.

Brood reduction is best known in birds (O'Connor 1978). It has been argued that reduction is practised in response to uncertain food availability; when food is scarce the last of an asynchronous brood to hatch is allowed to starve, whereas all offspring are fed when food is plentiful. This explanation is unlikely to apply to *Nicrophorus*, for which the food supply, once secured for breeding, is assured. Clark and Wilson (1981) proposed alternative explanations for asynchronous hatching in birds: the nest failure hypothesis, where incubation begins as early as possible in order to offset the risk of predation, and the insurance hypothesis (Dorward 1962; Stinson 1979), where only one young is raised and the one or two additional eggs serve only as insurance against the failure of the first. Variable mortality of eggs or of hatchlings making their way to the corpse may explain why *Nicrophorus* lays many more eggs than are raised around a small corpse. A staphylinid *Philonthus decorus*, often found at corpses, has been seen to kill the young of *Nicrophorus* (Easton 1979) and will eat as many as half the larvae of an untended brood in the lab whilst failing to kill any of the larvae where parents are present (pers.obs.).

Fungal infection, or predators such as *Philonthus* which a corpse attracts in large numbers, could cause the unpredictable mortality proposed here. An alternative explanation for the high number of eggs laid is that the beetles fail to assess accurately the capacity of the corpse or are bound by a physiological constraint such that they must lay a minimum clutch which is greater than the capacity of a small corpse. In the laboratory *N.vespilloides* will lay 46.83 ± 5.86 eggs on a 75g corpse (n=18) and 18.44 ± 2.05 eggs on a 5g corpse (n=27), showing that some adjustment of egg number with clutch size is possible and that it is physiologically possible to lay a clutch smaller than the capacity of a 15g corpse.

The raptors discussed by Stinson (1979) do not raise the hatchlings of their 'extra' eggs; these are killed by their older sibling or starve in competition with it. The adults can only bring enough food to raise one young. Similar constraints make the clutch laid by *Nicrophorus* on small mice excessive. The strong relationship between brood size and mean larval weight at dispersal (Figure 3) is found even over a range of brood sizes less than that at which culling would be expected to occur. At higher densities, without culling, there might be insufficient food for all larvae to complete development and emerging adults would certainly be very much smaller than the products of less crowded crypts. Intraspecific competition over corpses, the result of which is largely determined by body size (Wilson & Fudge 1984), means that small beetles have a greatly reduced chance of breeding. Small size also restricts the number of eggs a female can lay, both in a single episode on a large corpse and over several breeding attempts on a sequence of corpses (pers.obs.).

Brood reduction in *Nicrophorus* is therefore a phenomenon which probably occurs in response to a shortfall of food relative to the requirements of the larvae arriving at the corpse. The laying of an excessive number of eggs is more likely to reflect uncertainty about the number of larvae successfully reaching the corpse than about how much food will be available and would, if this is true, conform to the 'insurance' hypothesis discussed by Clark and Wilson (1981). The situation differs from that in birds in that larvae can feed themselves as well as receiving regurgitated carrion from their parents. The adults cannot afford to let the members of an excessively large brood compete amongst themselves for the corpse and they therefore reduce the number by culling rather than by allowing some to starve. They cull the brood at the earliest stage: the larvae are feeding on a fixed resource and the sooner the brood is reduced the more food will remain for those which survive. Direct and early action, the most unusual features of *Nicrophorus* infanticide, are a consequence of their particular biology.

The experiments described here did not examine the question of how *Nicrophorus* adjusts the number of larvae that are culled. The simplest hypothesis was that adults allowed a certain number of hatchlings to reach the corpse and killed all subsequent arrivals, but culling was found to occur whether larvae were allowed the reach the corpse naturally or added in a single batch. It is hoped in future experiments to test whether larvae are killed at random or selected on the basis of size or sex (Horsfall 1984). If filial cannibalism is to benefit *Nicrophorus* parents, then their total number of grandchildren must be greater, through the increased reproductive success of their surviving offspring, than it would have been through a larger brood of individually smaller young. The high costs of small size in an animal which must fight for the chance to breed on a rare resource argue that the behaviour is likely to have this effect.

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a. 15g mice: means ± 95% CL

Clutch size	First stage larvae	Dispersing larvae
29.69 ± 3.31	30.21 ± 1.88	16.16 ± 1.68
(n=12)	(n=12)	(n=12)

b. 30g mice: means ± 95% CL

30.92 ± 2.80	33.92 ± 2.06	30.08 ± 2.34
(n=12)	(n=12)	(n=12)

Table 1. Success of broods on 15g and 30g mice.

The table shows natural clutch sizes, number of first stage larvae and number of dispersing larvae in three independent sub-groups of twelve on each of two mouse sizes.

Brood	Hours in view	Larvae seen killed	Parent responsible	Mean L2 (exp't) (n=5)	Mean L2 (control) (n=11)
1	1	1	Female		
2	2	3	Female		
3	15	14	Male	18.00	17.65
4	10	16	Male+Female	± 2.10	± 2.05
5	4	7	Male		

Table 2. Broods were watched until the hole in the corpse where the brood fed was turned out of sight by the movements of the adults in the crypt. The number of second stage larvae in these broods is similar in each case to the mean number of second stage larvae in the controls, broods set up at the same time on the same size of mice (15g) but not watched during the first larval instar.

Figure legends.

Figure 1.

Survival of artificial broods on 15g mice.

Using the broods of 25 females, 15 broods of first stage larvae (L1) were made, with a mean brood size of 30. These were then introduced to 15g mice previously buried and tended by a pair of adults. The figure shows the numbers of larvae surviving 24 hours, 72 hours and 96 hours later, as second stage larvae (L2), third stage larvae (L3) and dispersing third stage larvae (Ld).

Figure 2.

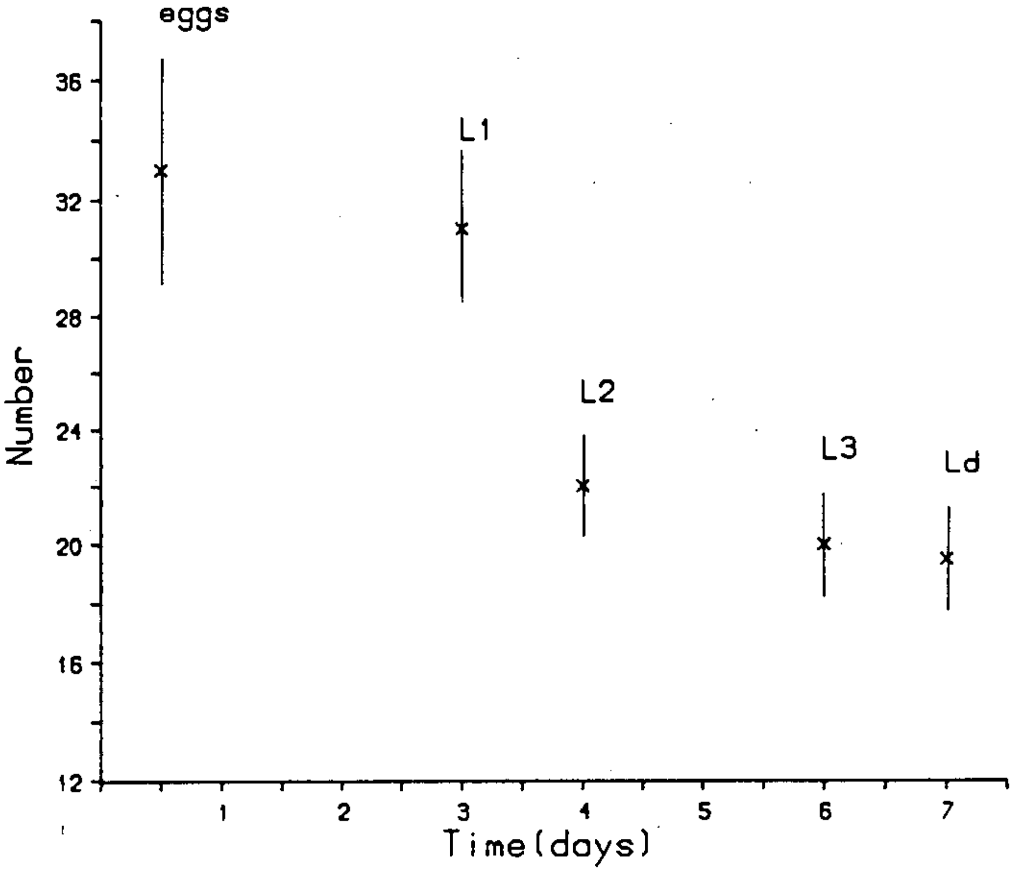
Mortality among natural broods on 10g mice.

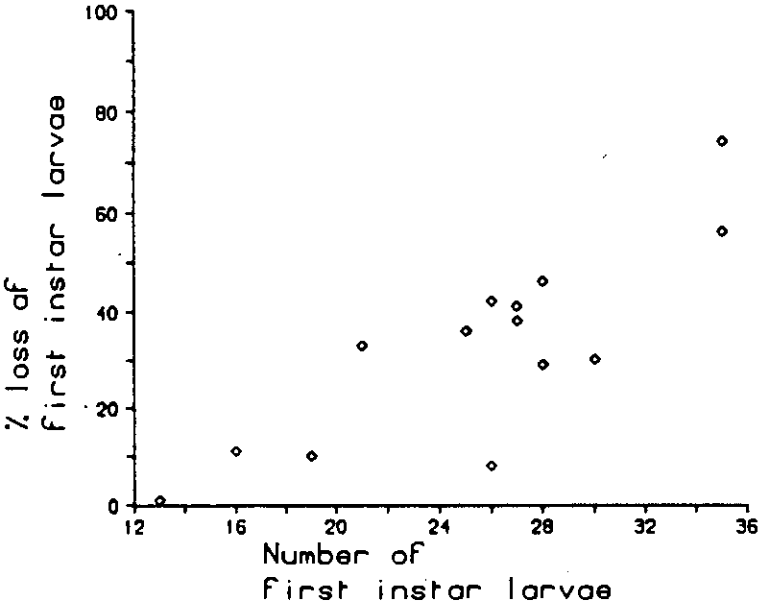
The percentage survival to the second instar is shown for broods on 10g mice. The broods were made by removing clutches of eggs from the soil and putting the first stage larvae back on their corpse as they hatched.

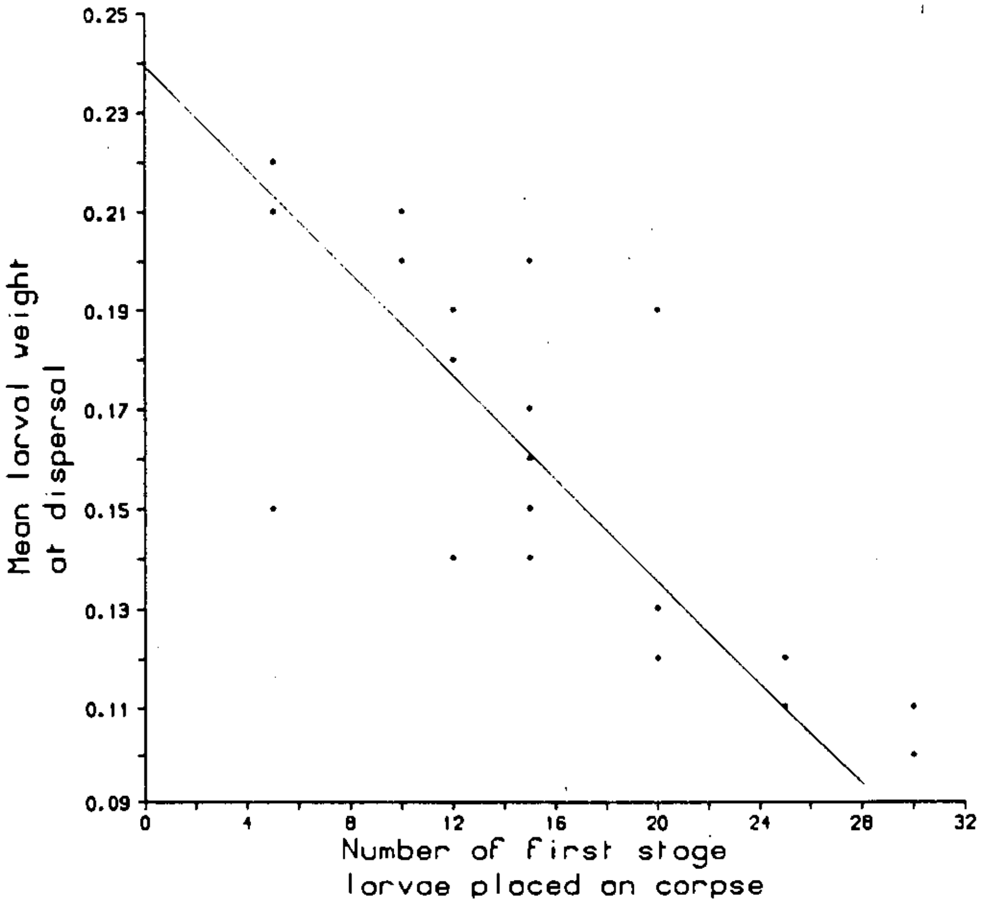
Figure 3.

Mean larval weight at dispersal : broods size at dispersal.

First stage larvae were placed on the 10g corpse around which they had been born such that 19 broods of between 5 and 20 larvae were created. In all cases survival of the brood was >90%. The regression line is plotted; slope is significantly different from 0 ($P<0.001$).


eggs
L1
L2
L3
Ld
Number
36
32
28
24
20
16
12
1
2
3
4
5
6
7
Time (days)


% loss of
first instar larvae
100
80
60
40
20
0
12
16
20
24
28
32
36
Number of
first instar larvae



Mean larval weight at dispersal
0.25
0.23
0.21
0.19
0.17
0.15
0.13
0.11
0.09
0
4
8
12
16
20
24
28
32
Number of first stage larvae placed on corpse