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Burying beetles: intraspecific interactions and reproductive success in the field

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ABSTRACT. 1. The discovery and utilization of small carcasses by burying beetles (Silphidae, *Nicrophorus*) was studied by placing dead mice at random points on large grids at two locations in Michigan, U.S.A.

2. The majority of mice are found within 24 h by more beetles than ultimately will utilize the carcass. If a carcass is likely to be usurped by a larger species of beetle or by a vertebrate, then intraspecific competition may be postponed until the carcass is concealed and buried.

3. Both males and females practice parental care. Maturing broods are tended by no adults, a single female, a single male, or a male–female pair. No differences in brood success were observed among these categories.

4. The female lays a larger clutch than ultimately will survive. Brood size is regulated after the egg stage, such that offspring number varies, but individual offspring size does not.

5. A large amount of unexplained variation exists in brood size, in both the laboratory and the field. This variation is probably caused by the environment, and not the reproductive physiology of the beetles. Competition with microbes is a likely candidate.

6. Differences exist not only between *Nicrophorus* species, but also between localities for a single species, suggesting adaptation to local environments.

Key words. Silphidae, *Nicrophorus*, burying beetles, cooperation, parental care, reproductive success.

Introduction

Burying beetles (Silphidae, *Nicrophorus*) are carrion feeders that specialize on small carcasses, such as dead rodents, that they bury in the ground to raise their brood upon. A single carcass is often found by several beetles, who sometimes bury it together, but eventually a single pair drives the others off and appropriates the carcass for itself. The pair then cooperates in building a burial chamber and modifying the carcass to receive the female's clutch of young. The male is reported to leave soon after oviposition, but the female remains with her brood until they pupate. She not only guards her offspring, but also tends and feeds them. This is the highest level of sociality attained by the Coleoptera (Wilson, 1971).

The first naturalists to observe burying beetles interring a carcass were so impressed that they thought the beetles must be capable of reasoned thought. Fabre (1919) conducted numerous experiments to show that their behaviours are purely instinctive. Most aspects

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of *Nicrophorus* ecology and behaviour were described in a remarkable monograph by Pukowski (1933) that remains the best work on the subject. Since then they have received only sporadic treatment (most notably Anderson, 1982a; Easton, 1979; Springett, 1967), with very little attention paid to their social behaviour (Milne & Milne, 1976).

From the standpoint of modern ecology and evolution, burying beetles pose a number of interesting questions, including cooperation and competition among unrelated individuals during the burial process, costs and benefits of parental care, male versus female investment, the regulation of brood size, competition between different species of burying beetles, and coevolution between burying beetles and their phoretic mites (Wilson, 1983). None of these specific questions can be answered, however, without a solid knowledge of the behaviours that exist and the selection pressures that operate in the field. To obtain this background information we have followed the discovery and utilization of over 1000 carcasses placed at random points of large grids at two locations in Michigan, U.S.A. The results, along with supplementary field and laboratory experiments, are reported in two papers. Interactions among congeners are analysed in Wilson *et al.* (1984); intraspecific interactions are presented here.

Methods

The studies were conducted at the University of Michigan Biological Station (UMBS) in Pellston (lat. 45°34′), and the Kellogg Biological Station (KBS) in Hickory Corners (lat. 42°34′), 315 km south of UMBS. The carcasses were laboratory *Mus musculus* L., killed with CO_2, sorted into weight categories and frozen until 12 h before use. A 0.5 m length of dental floss was tied to the hind legs, to help locate the mice after burial.

The KBS study was conducted from 28 June to 9 October 1980. Flags (100) were placed at 20 m intervals in a 5 × 20 grid in a mature oak–hickory forest characteristic of the area. On the first day of the study mice were placed at five randomly chosen flags in the early morning. Every morning thereafter the mice were checked and recorded into one of three categories: (1) undiscovered, (2) discovered by burying beetles, or (3) discovered (and removed) by a vertebrate. New mice were then placed at randomly chosen unoccupied flags, in equal numbers to the mice discovered. In this way exactly five mice were available for discovery every day, although their placement dates differed. Two weight categories of mice (30 g and 40 g) were used on alternate days.

Of those mice discovered by burying beetles, half were collected immediately and the following data recorded: (1) location on the grid, (2) mouse weight, (3) placement date, (4) discovery date, (5) degree of burial (subjectively estimated as the fraction of the mouse above ground), (6) number, species, size (width of pronotum) and sex of beetles in vicinity of the mouse, and (7) position of beetle(s) relative to the mouse. Item 7 distinguishes between beetles that were actually with the mouse (central) from beetles that were a short distance away in the leaf litter (peripheral).

The other half of the mice discovered by burying beetles were left undisturbed for 10 days, by which time the beetle broods were usually nearing the prepupal stage. Then adults and larvae were collected and the following data recorded: (1) items 1–4 above, (2) number, species, size and sex of adult beetle(s) within the chamber, (3) number of larvae within the chamber, and (4) wet weight of entire larval brood (after preservation in 70% ETOH). When no adults were present, larvae were identified to species using Anderson (1982b).

The UMBS study was conducted from 15 May to 30 August 1981 in a northern hardwood forest characteristic of the area. The grid was doubled in size to 200 flags placed 20 m apart in a 10 × 20 grid, and ten mice were made available for discovery every day. The procedure was identical to KBS with two additional items recorded: (1) for mice collected the day after discovery, the degree to which the mouse was concealed by leaf litter was subjectively estimated, in addition to the degree of burial, and (2) for mice collected 10 days after discovery, the depth of the burial chamber was measured, from floor of chamber to soil surface.

The laboratory experiments were conducted in July 1982 on *Nicrophorus orbicollis* from UMBS, captured in baited pitfall traps. Fifty pairs of beetles were bred in plastic shoeboxes filled with gently compressed unsterilized top soil to a depth of 6 cm. The boxes were stored at 19–21°C and the natural photoperiod. The boxes were divided into two treatments, with mouse sizes of 15–20 g and 30–35 g respectively. Half of each treatment was dismantled after oviposition, the adults removed, the eggs counted and replaced. The other halves were allowed to develop to the prepupal stage, then dismantled to record offspring number and live weight of the brood. These experiments provided a more controlled setting to explore the following subjects: effect of parent on offspring survival, clutch size, the regulation of brood size, effect of adult size and mouse weight on brood number and size, and variance in reproductive success.

Results

Carcasses were utilized by four *Nicrophorus* species at UMBS (*N.sayi* LaPorte, *N.defodiens* Mannerheim, *N. orbicollis* Say, *N.tomentosus* Weber), and two species at KBS (*N.orbicollis, N.tomentosus*). *N.sayi* and *N.tomentosus* breed in the spring and autumn respectively, and were reproductively inactive during most of the study. This paper therefore concentrates on *N.orbicollis* and *N.defodiens*, for which large sample sizes exist. *N.orbicollis* is twice as large as *N.defodiens*, whom it often displaces at carcasses (see Wilson *et al.*, 1984, for a full account).

Discovery of mice. The proportion of mice found by burying beetles is influenced by many factors, including density of competing vertebrates, density of beetles, individual searching ability, reproductive condition (Wilson & Knollenberg, 1984) and temperature (Wilson *et al.*, 1984). Table 1 shows that at KBS, 255/330 = 0.77 of the mice were found within 24 h of their placement, and 117/330 = 0.35 of all mice were discovered and removed by vertebrates prior to burial by *Nicrophorus* (some mice removed by vertebrates may have previously been found by *Nicrophorus*). By contrast, at UMBS 735/778 = 0.94 of the mice were found within 24 h, and only 46/778 = 0.06 of all mice were discovered and removed by vertebrates prior to burial by *Nicrophorus*. KBS therefore appears to have a lower density of beetles and a higher density of vertebrates.

Number and sex ratio of beetles colonizing single mice. Table 2 shows the number of beetles found either on or near mice that were collected the morning after discovery. At UMBS, more than one *Nicrophorus* species was often collected on a single mouse. The column marked 'all species' shows the number of beetles found on mice, irrespective of beetle species. The other columns show data

TABLE 2. The number of beetles found on single mice on the morning after discovery. N.o. and N.d. refer to *Nicrophorus orbicollis* and *Nicrophorus defodiens* respectively. For example, at KBS a single beetle was collected from thirty-one mice, two beetles from thirty-seven mice, and so on.

No. beetles	KBS	UMBS		
	N.o.	All species	N.o.	N.d.
1	31	75	15	52
2	37	135	36	72
3	21	70	22	24
4	2	44	18	10
5	2	27	10	6
>5	1	11	1	2
	94	362	102	166

TABLE 1. Number of mice discovered by *Nicrophorus* and vertebrates within 24 h, 48 h and ⩾ 72 h.

Time to discovery (h)	KBS			UMBS		
	Beetles	Vertebrates	Total	Beetles	Vertebrates	Total
24 h	163	92	255	694	41	735
48 h	38	13	51	34	4	38
⩾ 72 h	12	12	24	4	1	5
Total	213	117	330	732	46	778

for mice that were found by one species only.

Table 2 would accurately estimate the number of beetles arriving at mice, if every beetle remained to be collected the following morning. If this were so, then 0.42 of the mice at UMBS are found by three or more individual beetles (all species). There are strong indications, however, that other beetles have arrived and left during the night, which makes Table 2 a minimum estimate. For example, two individual beetles of the same species were collected at 163 mice (KBS and UMBS data combined). Of these, 0.87 of the pairs were a male and a female, which would never be expected by chance ($\chi^2 = 90.03$, $P< 0.001$). The beetles are either remarkably proficient at 'calling in' the opposite sex (which seems unlikely), or else a larger number of beetles arrived at the mice, of which only one of each sex remained. It therefore appears that the majority of mice are found by more beetles than the final successful pair.

Concealment and burial after the first night. In the field experiments, mice were always placed on top of the leaf litter. When collecting mice that had been discovered the night before, we noted (a) the proportion of the mouse that was concealed from view (e.g. dragged under the leaf litter; UMBS only), and (b) the proportion of the mouse that was actually covered by soil. These can be related to mouse weight, species, position and body size of the beetles.

Virtually all the mice were completely concealed from view, for both *N.orbicollis* and *N.defodiens* (0.97 of 277 mice). Burial, however, was usually incomplete. For *N.orbicollis* only 0.40 of the mice were completely covered by soil, while 0.21 were unburied. Mice found by single males only were significantly less buried than mice found by single females or a male and female (t-test, $t = 2.96$, d.f. = 18, $P< 0.01$). This was the only significant trend; degree of burial did not correlate with mouse size, beetle size, total number of beetles, or number of beetles occupying the central position.

For *N.defodiens*, only 0.08 of the mice were completely covered by soil (of these a third were rolled down rodent holes, which did not require digging), while 0.62 were unburied. No differences existed between mice found by single males and single females, nor were there any other significant trends.

Competition and cooperation. The presence of several beetles at a carcass creates a very interesting ecological situation. On the one hand, the carcass presumably can be buried faster if several beetles work together (Pukowski, 1933). On the other hand, only two of the participants will benefit from such cooperation. Are interactions among beetles during burial purely competitive, or do they have an element of cooperation?

Before addressing this question, it is important to realize that the benefits of cooperation can vary between species and between localities. Because *N.defodiens* is a small species, the physical task of moving and burying the carcass is greater. Furthermore, at UMBS *N.defodiens* is in constant danger of losing its mice to *N.orbicollis* (Wilson *et al.*, 1984). *N.orbicollis* is the 'top scavenger' at UMBS, but at KBS it is placed in the position of *N.defodiens*, by being in constant danger of losing its mice to vertebrates.

Information on cooperation and competition is provided by the spatial arrangement of beetles around the carcass. Table 3(a) shows that for *N.orbicollis* at UMBS, single males were collected at sixty mice (one or more females might have been collected at the same mice); $57/60 = 0.95$ of these males were found in the immediate vicinity of the mouse (central). The other three were found a short distance away in the leaf litter (peripheral). If males make no attempt to exclude each other, then one might expect that for $0.95^2 = 0.90$ of the mice from which two males were collected, both would occupy the central position. This is not the case; two males were collected from twenty-four mice, and in twenty-one cases only one male occupied the central position ($\chi^2 = 34$, $P< 0.001$). Much the same pattern exists for females (Table 3, section b, not significantly different than section a). These data suggest that most peripherals are losers in intrasexual competition for the mice, and this hypothesis can independently be tested by comparing the sizes of centrals and peripherals of the same sex on the same mouse. The centrals are larger in sixty-one out of sixty-eight comparisons, which strongly supports the hypothesis ($\chi^2 = 42.8$, $P< 0.001$). To summarize, for *N.orbi-*

TABLE 3. Spatial arrangement of beetles collected the morning after discovery. Beetles were found either with the mouse (central) or a short distance away in the leaf litter (peripheral). The tables show how many individuals occupy the central position, out of the total number of that sex collected. For example, in section c, two male *N.defodiens* were collected on each of nineteen mice. Of these, both occupied the peripheral position on two mice, one was central and the other peripheral on eleven mice, and both were central on six mice.

		No. central males						No. central females				
UMBS *N.orbicollis*	No. males collected (a)	0	1	2	3	Σ	No. females collected (b)	0	1	2	3	Σ
	1	3	57			60	1	5	51			56
	2	2	21	1		24	2	0	20	4		24
	3	0	1			3	3	1	5	3	1	10
		No. central males						No. central females				
UMBS *N.defodiens*	No. males collected (c)	0	1	2	3	Σ	No. females collected (d)	0	1	2	3	Σ
	1	18	77			95	1	25	71			96
	2	2	11	6		19	2	4	12	15		31
	3	2	3	1	0	6	3	1	3	2	1	7
		No. central males						No. central females				
KBS *N.orbicollis*	No. males collected (e)	0	1	2	3	Σ	No. females collected (f)	0	1	2	3	Σ
	1	0	47			47	1	0	69			69
	2	0	10	9		19	2	0	3	7		10
	3	0	0	0		0	3	0	1	0	4	5

collis at UMBS, intrasexual interactions appear to be purely competitive.

N.defodiens differs from *N.orbicollis* at UMBS in at least two important ways (Table 3, c and d). First, a higher proportion occupy the peripheral position, even when no other individual of the same sex is present (43/191 = 0.23 for both sexes combined, compared to 0.07 of *N.orbicollis*; $\chi^2 = 12.71$, $P < 0.001$). To see if this was caused by intersexual competition, we compared the sizes of fifteen heterosexual pairs in which one individual occupied the central and the other the peripheral position. Males were as likely as females to be peripheral, and there was no tendency for the central individual to be larger. *N.defodiens* apparently occupy the peripheral position by choice, for unknown reasons.

Second, when two individuals of the same sex are found on a mouse, they often both occupy the central position (21/50 = 0.42 for both sexes combined, compared to 0.08 for *N.orbicollis* at UMBS; $\chi^2 = 16.87$, $P < 0.001$). In fact in the absence of intrasexual competition one might expect both to occupy the central position for $0.77^2 = 0.59$ of the cases, which is quite close to the observed value ($\chi^2 = 3.46$, d.f. = 2, n.s.). However, when intrasexual competition is independently tested by comparing the sizes of central and peripherals of the same sex from the same mouse, the centrals are larger in thirty-three of forty-one comparisons ($\chi^2 = 8.40$, $P < 0.005$). It is possible that two *N.defodiens* of the same sex occupy the central position only when they are competitively equal and cannot oust each other; if so, then these individuals should be closer in size than pairs in which only one occupies the central position. This is not the case (t-test, $t = 0.63$, d.f. = 23, n.s. for males, $t = 1.39$, d.f. = 33, n.s. for females).

To summarize, the size comparisons show that some intrasexual competition does exist in *N.defodiens*. Nevertheless, two or more individuals of the same sex often share the central position the morning after discovery. This of course is only a prerequisite for cooperation, and not a proof of it.

The data for *N.orbicollis* at KBS are shown in Table 3, e and f. Remarkably, over half of the homosexual pairs shared the central position (16/29 = 0.55 for both sexes combined, compared to 0.08 for the same species at UMBS; $\chi^2 = 17.32$, $P < 0.001$). For those pairs in which one occupied the central position, the central was larger in fourteen out of seventeen comparisons. These patterns more closely resemble *N.defodiens* than *N.orbicollis* at UMBS.

Reproductive success. For those mice left for 10 days after discovery by burying beetles, 0.13 at UMBS and 0.38 at KBS were found by vertebrates. Table 4 presents data for burial chambers that contained either adults and/or larvae when the mice were retrieved. *N.defodiens* buries its mice less deeply and has more offspring than *N.orbicollis*, as might be expected from a smaller beetle. In fact, many *N.defodiens* chambers were merely shallow depressions, covered only by leaf litter.

Table 4, section 5 shows an unexpected variation in the number and sex of adults found in the burial chamber with the maturing brood. Larvae could be untended, tended by either sex, or by the pair. Some of this variation might be an artefact caused by adults escaping; e.g. a brood tended by a male and female might be recorded as male only if the female escapes. In our opinion this could not account for the large numbers in each category, although the pattern should be confirmed in the laboratory.

Brood success can be related to mouse size, burial depth, date, number of days before discovery, and the number, sex and sizes of adults tending the brood. In general, the data are remarkable for the lack of significant trends. Brood size increases with mouse weight for both *N.defodiens* and *N.orbicollis* at UMBS, but only the latter is significant (Anova, $P < 0.004$). For *N.orbicollis* at KBS, mean brood size does not increase with mouse weight, but the variance in brood size does (Levene's test, $P < 0.005$), which suggests that although a larger brood can be raised on a larger mouse, the probability of failure also increases. At UMBS, *N.orbicollis* have fewer offspring in the early summer (1–19 June), while *N.defodiens* have fewer offspring in the late summer (1–20 August).

The lack of significance for the other variables does not necessarily imply that no differences exist. The unexplained variation is so large that average brood sizes could differ by as much as 20% among treatments and still not reach significance. The unexplained variation could come from two sources: (a) some aspect of the environment that was not measured, and (b) the physiological state of the beetle, such as the number of eggs laid by the female. The laboratory experiments were conducted to reduce the former and monitor the latter.

Laboratory experiments. When *N.orbicollis* is bred in the laboratory, the number of eggs

TABLE 4. Data for mice retrieved 10 days after discovery by *Nicrophorus*. N.o. and N.d. refer to *N.orbicollis* and *N.defodiens* respectively. Standard deviations are in parentheses.

	UMBS		KBS
	N.o.	N.d.	N.o.
(1) Number of chambers examined	171	80	54
(2) Average burial depth (cm)	6.02 (2.28)	3.93 (2.47)	–
(3) Proportion of broods that failed	0.105	0.01	0.11
(4) Average brood size	14.9 (4.97)	23.95 (9.75)	14.9 (7.42)
(5) Proportion of chambers with 0 adults	0.33	0.23	0.39
Proportion of chambers with 1♀	0.35	0.56	0.48
Proportion of chambers with 1♂	0.13	0.04	0.07
Proportion of chambers with 1♀, 1♂	0.16	0.18	0.06
Proportion of chambers with 2♀	0.02	0	0
Proportion of chambers with 2♂	0.01	0	0

TABLE 5. Results of laboratory experiments in which pairs of *N.orbicollis* were provided with two size-classes of mice in the laboratory. Standard deviations are in parentheses.

(1) Mouse size	30–35	15–20
(2) Average number of eggs	32.14 (11.26)	29.75 (3.76)
Sample size	12	11
(3) With adult:		
Per cent success	100	92
Average number of larvae	15.85 (7.03)	7.58 (2.97)
Average weight of brood (g)	6.60 (3.20)	4.12 (1.58)
Average larva weight (g)	0.49	0.55
Sample size	13	12
(4) Without adult:		
Per cent success	42	9
Average number larvae	3.02 (1.12)	2.0 (–).
Average weight of brood (g)	0.93 (0.73)	0.73 (–)
Average larva weight (g)	0.29	0.37
Sample size	5	1

deposited varies directly with female size (r^2 = 0.336, $P < 0.002$), but not with the size of the mouse (Table 5, line 2). The smallest number of eggs laid was twenty-two, and hatching success was excellent. The largest number of larvae that survived to pupation was twenty-six; thus, virtually all females lay more eggs than ultimately will survive.

When the adult beetle(s) are present, some offspring are almost always produced (Table 5, line 3). Total brood weight and number of larvae are unrelated to female size (r^2 = 0.001, n.s.), but strongly related to mouse size (Analysis of Covariance, $P < 0.001$). Furthermore, the differences are reflected in the number of larvae. Individual larvae from 15–20 g carcasses are actually slightly larger than those from 30–35 g carcasses (t = 1.97, d.f. = 23, $P < 0.05$). This is not expected from scramble competition, and strongly suggests an organized regulation of brood size.

Nevertheless, there is a large amount of unexplained variation in brood size. Even when the adults were present, brood sizes ranged from seven to twenty-six larvae on 30–35 g mice, and from three to twelve larvae on 15–20 g mice. Fig. 1 shows the relationship between brood weight and larvae number for both treatments. The data points for large and small mice fall along the same line (analysis of covariance, n.s.). In other words, a relatively unsuccessful brood raised from a

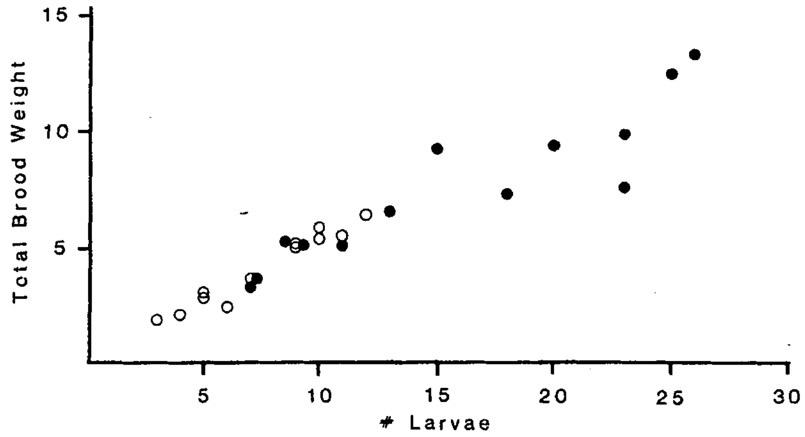

FIG. 1. Relationship between number of larvae and total weight of brood for laboratory experiments. Points represent broods from 30–35 g mice, and open circles represent from 15–20 g mice.

large mouse is indistinguishable from a successful brood raised from a small mouse.

When the adults are removed prior to hatching, many broods fail completely, those that succeed produce few larvae, and these larvae are much smaller than when the adult is present. Observations showed that hatching success was excellent, but that a thick mould grew over the carcasses in most cases.

Discussion

One of the most intriguing results of this study concerns the spatial arrangement of beetles around the mouse, which suggests that the timing of intraspecific competition is influenced by the intensity of interspecific competition. In other words, if a carcass is likely to be usurped by a larger species of beetle or by a vertebrate, then intraspecific competition is postponed until the mouse is securely concealed and buried. Furthermore, differences exist not only between species, but also for the same species between localities. Has *N.orbicollis* adapted to regional differences in vertebrate density? This hypothesis can easily be tested by rearing F1 generations and observing the burial process in the laboratory. Different numbers of beetles can also be placed on mice in the field, to observe their effect on the speed and extent of burial.

This study revealed few differences between males and females. Pukowski (1933) reported that if a male is the first to arrive at a carcass, it conceals but does not bury it. Rather, it climbs a nearby projection and releases a pheromone from its abdomen. We have also observed this behaviour; often the male has climbed to the top of the flag by which the mouse has been placed. By contrast, females set immediately to work. It therefore makes sense that mice found by single males only are less buried on the morning after discovery. Our study also shows that competition among females is as intense as that among males. The lack of size dimorphism is therefore not surprising (Wilson, unpublished data). We suspect, however, that numerous behavioural differences will be found between males and females upon closer examination, especially during the period spent below ground (Pukowski, 1933).

The laboratory experiment shows at least for *N.orbicollis* that some degree of parental care is vital for brood success (see also Pukowski, 1933; Easton, 1979). This does not mean, however, the parent(s) must remain until the larvae pupate. If the parents are removed after the first instar stage, the brood is often successful (Pukowski, 1933; Wilson, unpublished data). Pukowski (1933) demonstrated differences in parental care among European species. *N.vespillo* females usually drove away the males and remained with their brood until pupation. For *N.vespilloides* the pair remained in nearly half the cases. We have shown an even greater range of variation, representing all possible combinations (e.g. no parent, a single female, a single male, and the pair). This natural variation makes *Nicrophorus* an ideal organism to study male and female roles in parental care. Even though the presence of adults 10 days after discovery had no effect on brood success in this study, we suspect that important effects will be revealed in the future.

The laboratory experiments strongly suggest an organized regulation of brood size. It is interesting that this regulation occurs after the egg stage. We know that when the parents are removed, the carcass is often covered by a mould. Assume that toxic microbes are not entirely eliminated by the parent, but are in fact responsible for the unexplained variation in brood success. If so, then the amount of available resource depends on both the size of the carcass (that can be assessed before oviposition) and the amount made unsuitable by microbes (that cannot be assessed before oviposition). If the latter factor is important, then brood size cannot effectively be regulated at the egg stage.

Some of our results conflict with the studies of Springett (1967) and Easton (1979), both conducted on small islands off Britain. Unfortunately, both of these studies suffer from a serious design flaw. Carrion is a widely dispersed and ephemeral resource. Any field study of *Nicrophorus* must not raise the availability of carrion too far above ambient levels. In our study, we raised the density of small carcasses by 1 mouse/8000 m^2, and did not use baited pitfall traps within 1 km of the grid. Springett and Easton maintained grids of permanently baited pitfall traps over the entire islands, such that a burying beetle was never further than 50 m from a carrion source in Easton's study, and 20 m from a carrion source in Springett's study. Furthermore, beetles that entered pitfall traps could remain for as long as 1 week before being collected. Not only does this reduce the population of beetles searching for small carcasses, but it also has unfortunate implications when the beetles are used in laboratory experiments. Wilson & Knollenberg (1984) have shown that *Nicrophorus orbicollis* females have reduced ovaries until they actually find a small carcass suitable for burying, whereupon the eggs are produced in a 48 h burst (see also Anderson, 1982a). Our trapping procedure is designed to represent a large carcass that does not stimulate ovarian development. The beetles are collected within 14 h of entering the trap and used in experiments very shortly thereafter. Conditions within Springett's and Easton's pitfall traps were sufficient to trigger ovarian development for many females. The subsequent use of these females in experiments therefore represents a somewhat abnormal sequence of events, with unknown consequences for number of eggs ultimately laid, regulation of brood size, and so on. Easton (1979) recorded an average clutch size of only 7.89 for *N.investigator* and 12.79 for *N.vespilloides*. By adding larvae he demonstrated a threshold density above which mortality sharply increased, but average brood sizes were below this threshold. We suspect that the discrepancy between our results and Easton's is caused by the difference in our methods, although other interpretations are possible.

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