Monogamy to communal breeding: exploitation of a broad resource base by burying beetles (*Nicrophorus*)

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Abstract. 1. To investigate the range of resource size that burying beetles (*Nicrophorus*) exploit, small (21–33 g), medium (50–90 g) and large (120–210 g) carcasses, were placed in the field and then exhumed after 1, 4, 8, 12 or 18 days.

2. *Nicrophorus* attempts to utilize carcasses over this entire size range but has greater success on smaller carcasses.

3. Larger carcasses were more difficult to exploit because: (a) they took longer to conceal beneath the leaf litter; (b) they were less likely to be rounded into brood balls; (c) they were more likely to be utilized by dipterans; and (d) they were occupied by greater numbers of congeners.

4. Larger carcasses, however, did support greater numbers of larvae and contained broods of greater total mass than smaller carcasses.

5. Beetles sometimes bred communally on larger carcasses in the field and same-sex adults were observed to feed young.

6. Two follow-up experiments were conducted in the laboratory. On a large carcass *N.defodiens*, *N.tomentosus* or *N.orbicollis* can raise a maximum of 35–50 young. *Nicrophorus pustulatus*, in contrast, appears to be unique among *Nicrophorus* in that it can raise nearly 200 young on larger carcasses.

7. *Nicrophorus orbicollis* and *Nicrophorus sayi* are extremely dependent on parental regurgitations and young fail to survive to the second instar if parents are removed. Young of *Nicrophorus defodiens*, *N.tomentosus* and *N.pustulatus* can develop normally without parental regurgitations.

8. I discuss these results in the context of reproduction on carcasses of different size and hypothesize that this breeding system is facultatively quasisocial.

Key words. *Nicrophorus*, burying beetles, carrion, competition, reproductive success, parental care, communal breeding, cooperation.

Introduction

The resource base that a population utilizes for reproduction is thought to be a chief environmental determinant of its social structure and mating system. A necessary approach to identifying important variables has been to correlate geographical, seasonal or interspecific differences in social structure with differences in environmental conditions (Orians, 1961; Crook, 1965; Jarman, 1974; Noonan, 1981; Evans & Hook, 1982). A frequent conclusion is that difficult conditions such as a lack of territories of high quality or nest sites have led to the evolution of cooperative breeding (Bartz & Hölldobler, 1982; Woolfenden & Kirkpatrick, 1984; Brown, 1987). Unfortunately, it is often impossible to directly manipulate the purported environmental determinant of a social system [but see Sakagami & Maeta (1982) and Koenig & Mumme (1987)].

Carrion is a resource which can be manipulated relatively easily because it is discrete, compact and varies considerably in size. Animals which reproduce on a broad size range of carrion are excellent organisms for investigating variable breeding systems. Except for smaller scaled studies (Arnett, 1946; Peck, 1986; Kozol *et al.*, 1992), previous field work on *Nicrophorus* has employed only smaller carcasses (<80 g). In the present study, carcasses of different size were placed in the field to examine the ability of *Nicrophorus* to handle a carcass, competition,

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and the prevalence of communal breeding. Follow-up experiments in the laboratory examined potential reproductive output of single females and the necessity of parental regurgitations for normal larval development.

The study animal. Burying beetles' utilization of small carcasses has long been known (Fabre, 1899; Pukowski, 1933). A single female or male–female pair will transport a small vertebrate carcass to a suitable burial spot and excavate a nest. As the carcass is buried, the pair removes any hair or feathers, shapes the resource into a brood ball, and deposits anal and oral secretions which affect the decomposition. Burying beetles carry phoretic mites (*Poecilochirus carabi* Vitzthum) which pierce dipteran eggs that are oviposited on the carcass prior to and during nest preparation (Springett, 1968). *Poecilochirus carabi* has a mildly mutualistic effect on the reproductive success of its beetle host (Wilson & Knollenberg, 1987).

There is evidence that, in special circumstances, beetles tolerate rivals for a brief period on small carcasses (Wilson & Fudge, 1984; Bartlett, 1988). Intrasexual contests begin prior to oviposition if not immediately upon the discovery of the carcass and observers consistently report that only the dominant male and female remain to finish the burial and raise a brood on a small carcass (Pukowski, 1933; Wilson & Knollenberg, 1984). Defeated females can remain in the leaf litter surrounding a nest for a number of days and parasitize the brood (Müller *et al.*, 1990a) and defeated males can achieve some reproductive success by adopting a satellite strategy and copulating with the dominant female (Bartlett, 1988). If a male fails to discover the carcass, a female will utilize stored sperm to fertilize eggs and will attempt to raise a brood on her own (Eggert & Müller, 1989, 1992). Eggs are oviposited in the surrounding soil and females accept young that arrive on the carcass during a specific window of time (Müller & Eggert, 1990). Larvae are fed trophallactically by parents but dependence on these regurgitations wanes as larvae develop (Pukowski, 1933). Parents are able to regulate brood size (selective infanticide on smaller carcasses) so that larvae have adequate resources (Bartlett, 1987). The result is that larvae produced on a range of carcass sizes disperse from the carcass at an equivalent weight (Wilson & Knollenberg, 1984; Trumbo, 1990a, b). The presence of the male parent reduces the probability of a takeover by a congener (Scott, 1990; Trumbo, 1990c). Possible benefits of having additional adults on a carcass have not yet been investigated.

Methods

Field experiment. The study was conducted at the University of Michigan Biological Station (UMBS) located near Pellston, Michigan. The phenology and diurnal activity patterns of *Nicrophorus* spp. at this site are described in Wilson *et al.* (1984).

A 350×700 m grid was established in a birch–beech–aspen secondary woodland so that grid points along E–W transects were separated by 50 m and points along N–S transects by 25 m. Mice and rats were killed with CO_2, frozen until needed and thawed overnight in a refrigerator prior to being placed on the grid. Three sizes of carcasses were placed at randomly selected grid points from 25 June to 4 August 1990 (small, 21–33 g *Mus musculus*; medium, 50–90 g *Rattus rattus*; and large, 120–210 g *Rattus rattus*). To help locate the carcass after burial, opposite ends of a 1 m length of dental floss were tied to the hindleg of the carcass and to a stake driven into the soil. Carcasses were laid across the stake so that the head pointed in one of four compass directions. All placements, subsequent checks and final exhumations occurred between 9 a.m. and 12 noon.

Newly placed carcasses were checked daily until discovered by scavengers (removed from the site), discovered by burying beetles (taken fully or partially beneath the leaf litter), or it was evident that the carcass was won by other invertebrates. On the first day after discovery every carcass received a day 1 burial score indicating the percentage of the carcass taken beneath the leaf litter ($5 = 100\%$, $4 = 90–99\%$, $3 = 50–89\%$, $2 = 10–49\%$ and $1 = 1–9\%$). Carcasses discovered by burying beetles were exhumed on the first day after discovery, day 4, day 8, day 12 or day 18. Only medium and large carcasses were exhumed on day 18 because small carcasses are generally exploited and abandoned by beetles or dipteran larvae by that time. Thus, there were a total of fourteen carcass size-day of exhumation treatments. On each day that carcasses were placed, seven carcasses were put on the grid. In this way, over a 2-day period, one carcass in each treatment was placed in the field. Each treatment was allocated seventeen carcasses such that a total of 238 placements were made. During brief cold or rainy periods in which beetle activity was reduced, placement of carcasses ceased so that undiscovered carcasses did not accumulate on the grid. The number of undiscovered carcasses on the grid per night averaged 8.6 for a mean density of 1 undiscovered carcass/28,488 m². This was well below carcass density in previous studies (Wilson *et al.*, 1984; Trumbo, 1990c).

Carcasses were exhumed by removing leaf litter in the vicinity of the nest, carefully digging down to crypts and searching the surrounding soil surface within a 60 cm radius. The following measurements were made of the carcass: distance from the head and tail to the stake, burial depth, whether the carcass was dragged into the N, S, E or W quadrant, and whether the carcass was rounded (head brought to rest on the abdomen). Dipteran larvae were recorded as 'present' if there were five or more larvae of diameter >1.5 mm on the carcass. Dipterans 'won' the carcass if there were thirty or more larvae with diameter >1.5 mm, dipteran larvae had penetrated the interior of the carcass and no beetle larvae were present. In addition, the species, sex, pronotal width, injury status of legs and antennae and position of each adult beetle in relation to the carcass was recorded at exhumation.

Measurements of reproductive performance were taken on carcasses exhumed on day 8, 12 or 18. If burying beetle larvae were present at exhumation, the carcass, larvae and resident adults were brought back to the laboratory

and placed into plastic rearing containers filled with soil. Broods were reared until larvae dispersed. If more than one adult of the same sex was present on the carcass with a brood, 1–2 h observations were made under red light to determine whether adults fed young. At dispersal, the number of larvae and total mass of the brood were recorded. To make species determinations of broods, larvae were transferred into cups filled with soil until they emerged as adults.

In addition to carcasses placed on the grid, nine very large carcasses (210–300 g) were placed on a supplemental transect (50 m between transect points). Three carcasses were placed on each of 23, 25 and 27 July and were exhumed 12 days later. If burying beetle larvae were present, measurements were taken as before. Data from the supplemental transect were not included in the analysis unless specified.

For most statistical analyses, each trial was placed into a two-way classification table [e.g. carcass size (CSIZ) and day of exhumation (DAY)]. Categorical variables were analysed using long-linear techniques (Sokal & Rohlf, 1981) and continuous variables by two-way ANOVA. In some analyses, treatment levels were collapsed to increase sample size (day 12 and day 18 treatments were regularly collapsed) and in other analyses, day of exhumation treatment levels were combined because carcass size was the only variable of interest. Contrasts between selected levels of treatment are labelled as such. Data were analysed using Wilkinson (1989).

Limitations of female reproductive output. Information on reproductive output (number of larvae and total brood mass as a function of carcass mass) was gathered from the literature for *N.defodiens*, *N.tomentosus* and *N.orbicollis*. To fill in gaps in the available information, pairs (six to eight per treatment) were provided a carcass within a specified size range in containers filled with potting soil (40–50 g *Mus musculus* and 90–100 g *Rattus rattus* carcasses for *N.defodiens*, 70–100 g *Rattus* for *N.tomentosus* and 90–100 g and 250–300 g *Rattus* for *N.orbicollis*). The male parent was removed 2–4 days after larvae arrived on the carcass. At the time of larval dispersal, larvae were counted and weighed. In addition, pairs of *N.pustulatus* (eight per treatment) were provided with 35–40 g *Mus musculus*, 90–100 g or 220–260 g *Rattus rattus* carcasses and similar measurements were taken. Since there is no information available on the biology of *N.pustulatus*, two pairs were observed caring for broods under red light.

Necessity of feeding. Since parents might have less time to feed individual larvae in large broods on larger carcasses, I examined the ability of young of different species to survive without parental feedings. Females of *N.defodiens*, *N.pustulatus*, *N.orbicollis* and *N.sayi* Laporte were provided a 20–25 g carcass and allowed to oviposit. Three eggs from each of six females were weighed and then discarded. Additional eggs were removed in groups of five and placed into cups with soil and a superabundant supply of chicken livers ($n = 6$ per species). After hatching, liver was added each day and old liver (more than 2 days) was removed. In addition, an attempt was made to rear groups

of five *N.orbicollis* larvae on freshly chopped *N.orbicollis* third instars or on a combination of liver and chopped third instars ($n = 6$ per treatment).

Results

Field experiment: competition for carcasses (congeners)

A number of findings pointed to the greater potential for competition on larger carcasses; there were a greater number of beetles (species and sexes combined) both on and off the carcass at exhumation on larger carcasses (Fig. 1); both *N.orbicollis* and *N.defodiens* were more likely to face a direct competitor on larger carcasses (Fig. 2); the competitive dominant, *N.orbicollis*, was more likely to be in residence on larger rather than smaller carcass (Fig. 3); and the pronotal size of the largest individual tended to be greater on larger carcasses for females (but not males) in both *N.orbicollis* and *N.defodiens* (Fig. 4). In trials lasting a longer duration, total number of beetles declined and *N.orbicollis* was favoured over its competitor *N.defodiens* (Figs 1 and 3).

22% of *N.orbicollis* caught at exhumation had sustained an injury to the legs or antennae. Individuals caught later in the season (the season was divided into four equal time periods for analysis) were more likely to be injured ($G = 14.30$, $P < 0.005$, 3 df, $n = 222$) and individuals present with larvae were more likely to be injured than when larvae were not present at exhumation ($G = 4.58$, $P < 0.05$, 1 df; larvae × date interaction, $G = 2.24$, $P > 0.20$, 3 df, $2 \times 2 \times 4$ contingency table, log-linear analysis). The presence of larvae did not affect the injury rate in *N.defodiens* ($G = 0.45$, $P > 0.20$, 1 df) and the overall injury rate (8.1%, $n = 148$) was about one-third that of *N.orbicollis*.

Reproductive success

Burying beetles' difficulty in utilizing large carcasses was reflected by a lower probability of producing a brood as carcass size is increased (Fig. 5). Larger carcasses did produce more *N.orbicollis* larvae although productivity appeared to be lower on carcasses exploited by dipterans. The same relationships held for total mass of *N.orbicollis* broods (Fig. 6A, B). A test contrasting mean individual larval mass on small and medium-sized carcasses with mass on larger carcasses was significant (Fig. 6C), suggesting that resources available to individual larvae are greater on larger carcasses, at least at the upper end of the carcass size range. Of the seven broods cared for by *N.defodiens* adults and forty-three broods cared for by *N.orbicollis* adults (supplemental transect included), only one *N.orbicollis* brood contained larvae of a congener (mixed brood of seventeen *N.tomentosus* and twenty-three *N.orbicollis* young).

For carcasses containing a brood, the proportion of nests with two consexual adults in residence and the proportion with two consexuals feeding young are shown in Fig. 7. For *N.orbicollis*, there was a higher probability of
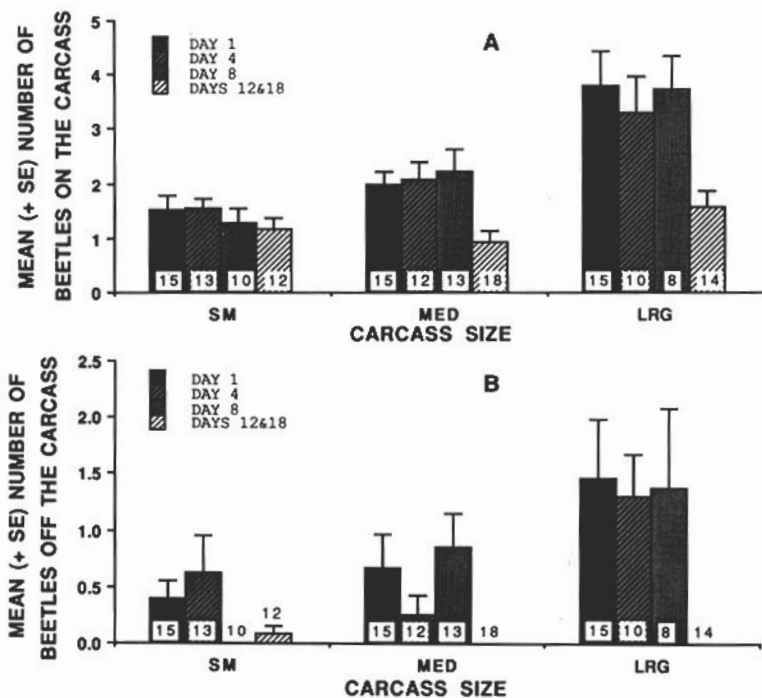
Fig. 1. Number of *Nicrophorus* (A) on and (B) off the carcass at exhumation. Number on [log-linear analysis, number of beetles categorized as 'few' (0–2) or 'many' (3+); carcass size (CSIZ), $G = 28.58$, 2 df, $P < 0.001$; day of exhumation (DAY), $G = 12.96$, 3 df, $P < 0.005$; CSIZ × DAY, $G = 3.64$, 6 df, $P > 0.20$, $n = 155$]. Number off ['few' (0–1) or 'many' (2+); CSIZ, $G = 9.40$, 2 df, $P < 0.01$; DAY, $G = 17.96$, 3 df, $P < 0.001$; CSIZ × DAY, $G = 4.50$, 6 df, $P > 0.20$]. Sample sizes are shown at the base of the bar graphs.

finding same-sex adults in residence on larger rather than smaller carcasses ($G = 10.80$, $P < 0.005$; 1 df, small and medium versus large and supplemental carcasses). Communal associations were quite variable and included polygynous, polyandrous and polygynandrous groups.

Since side by side consexual adults were observed to feed one larva after another within a single large group of young, facultative quasisociality [cooperative brood care (Michener, 1969)] appears likely. No agonistic interactions were observed between consexuals that were feeding young.
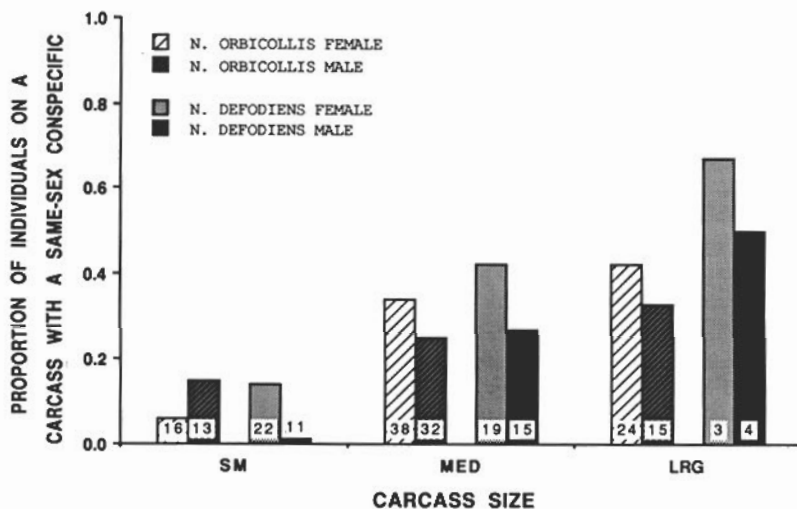

Fig. 2. Proportion of individuals that were found with a same-sex conspecific on the carcass at the time of exhumation. Log-linear analysis, *N.orbicollis*, CSIZ, $G = 7.45$, $P < 0.025$, 2 df; SEX, $G = 0.45$, $P > 0.20$, 1 df; CSIZ × SEX, $G = 1.14$, $P > 0.20$, 2 df; *N.defodiens*, CSIZ, $G = 9.54$, $P < 0.005$, 1 df; SEX, G = 2.24, $0.10 < P < 0.20$, 1 df; CSIZ × SEX, $G = 1.26$, $P > 0.20$, 1 df. For statistical analysis, data from medium and large carcasses were combined for *N.defodiens* because of the small sample size. Number of carcasses with at least one individual of the indicated species and sex shown at the base of the bar graphs (carcasses won by dipterans not included in the analysis).
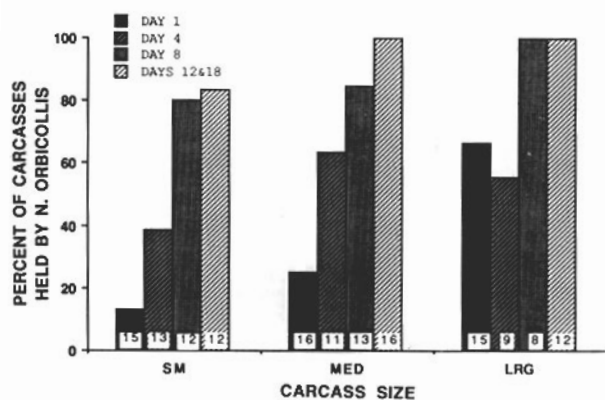
Fig. 3. Of carcasses held by *Nicrophorus* ($n = 150$), percentage held by *N.orbicollis*. Log-linear analysis, CSIZ, $G = 12.38$, $P < 0.005$, 2 df; DAY, $G = 49.33$, $P < 0.001$, 3 df; CSIZ × DAY, $G = 6.67$, $P > 0.20$, 6 df. Sample sizes shown at the base of the bar graphs.
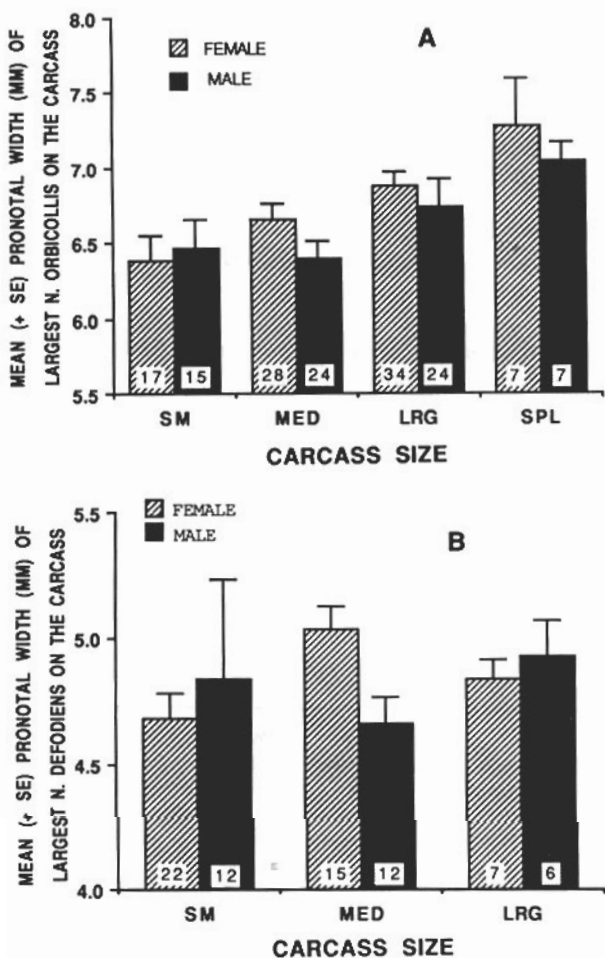

Fig. 4. Pronotal width of the largest (A) *N.orbicollis* female on the carcass at exhumation (one-way ANOVA, CSIZ, $F_{3,82} = 4.95$, $P = 0.003$) and *N.orbicollis* male (CSIZ, $F_{3,66} = 1.95$, $P = 0.13$). (B) *N.defodiens* female (CSIZ, $F_{2,41} = 3.78$, $P = 0.03$) and *N.defodiens* male (CSIZ, $F_{2,27} = 0.40$, $P > 0.20$). SPL = supplemental transect. Number of carcasses with at least one individual of the indicated species and sex shown at the base of the bar graphs.
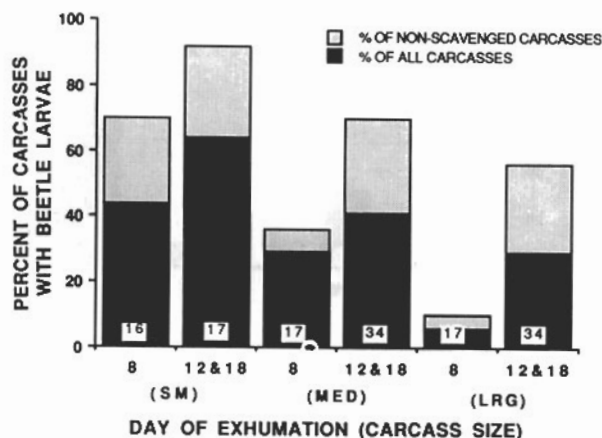

Fig. 5. Percentage of carcasses exhumed on days 8, 12 or 18 with *Nicrophorus* young. Log-linear analysis (all carcasses: CSIZ, $G = 11.63$, $P < 0.005$, 2 df; DAY, $G = 5.16$, $P < 0.025$, 1 df; CSIZ × DAY, $G = 1.39$, $P > 0.20$, 2 df). Sample sizes shown at the base of the bar graphs.

Competition for carcasses (non-congeners)

Of the 238 carcasses placed in the field, fifty-four (22.7%) were scavenged by vertebrates. The scavenging rate was not affected by carcass size but was affected by the duration of the trial (log-linear analysis, carcass size, $G = 1.35$, $P > 0.20$, 2 df; DAY, $G = 14.61$, $P < 0.005$, 3 df; CSIZ × DAY, $G = 3.30$, $P > 0.20$, 6 df). Of the eighty-four carcasses not scavenged in trials lasting 8 or more days, 32.1% met the criteria for 'significant presence of dipteran larvae' and 10.7% were won outright by dipterans. Of carcasses won by dipterans, 86.7% were initially buried by beetles. Both measures of dipteran exploitation suggest that dipterans were more successful on larger carcasses (Table 1).

Handling the carcass

The day (1, 2 or 3+) on which a carcass was discovered by beetles was not related to carcass size while a comparison of burial scores indicates that larger carcasses took longer to conceal under the leaf litter (Table 1). The distance that the carcass was dragged away from the stake was not affected by carcass size but larger carcasses were less likely to be rounded at exhumation (day 4 and 8 carcasses).

The direction in which the carcass was dragged by beetles was not random (34.1% in the direction that the head was pointing at placement, 27.3% toward the tail and 38.6% to either side; $G = 13.51$, $P < 0.005$, 3 df, $n = 130$). The head of the carcass was more likely to be further from the stake than the tail at the time of exhumation ($G = 7.27$, $P < 0.01$, 1 df; $n = 41$; day 1 and 4 carcasses that were not rounded included in the sample). This likely results because beetles focus their activity on the head and proceed to move the carcass in that direction (unpublished results). Since neither measurement was affected by size of the carcass (Table 1), carcass size apparently does not
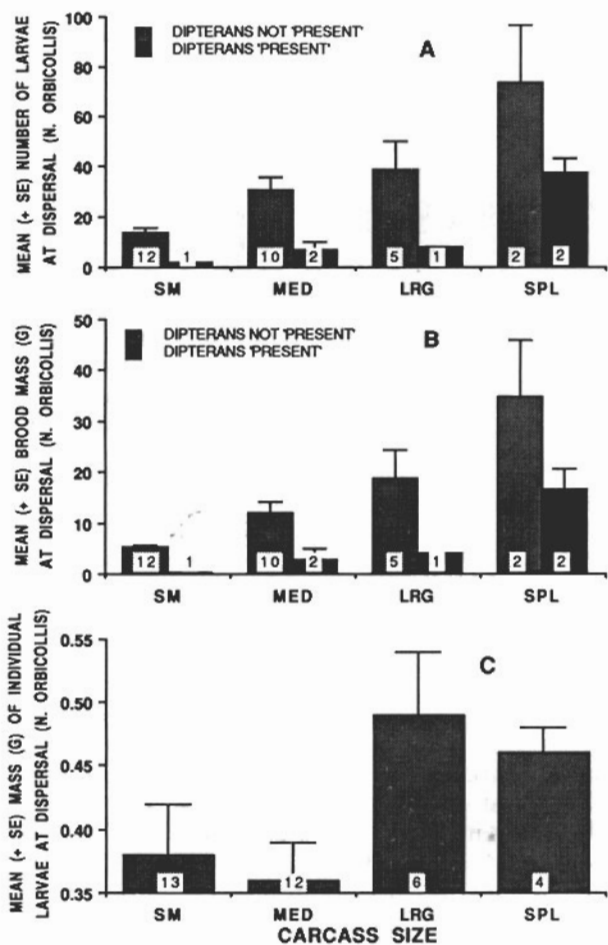
Fig. 6. (A) Number of *N.orbicollis* larvae produced (one-way ANOVA, CSIZ, $F_{2,26} = 8.68$, $P < 0.001$). (B) Total brood mass (CSIZ, $F_{2,23} = 10.34$, $P < 0.001$). Results for large and supplemental carcasses were combined for analysis. The effects of the presence of dipterans was not analysed because of the small sample size. (C) Mean mass of individual larvae [(CSIZ, $F_{1,28} = 5.40$, $P = 0.03$ (see text for statistical contrast)]. SPL = supplemental transect. Sample sizes shown at the base of the bar graphs.
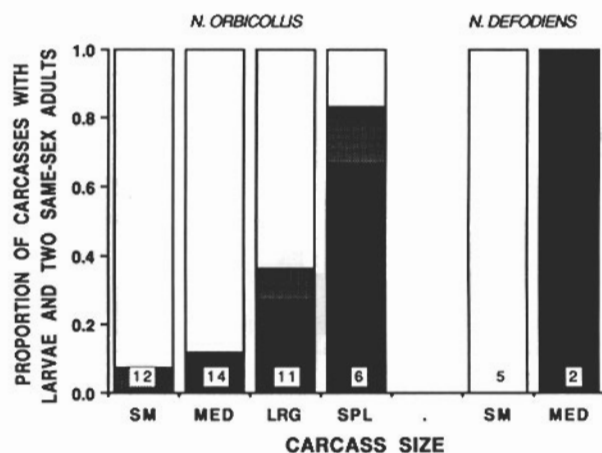

Fig. 7. Of carcasses with *Nicrophorus* young ($n = 50$), the proportion without two consexual adults (open bars), proportion with two or more consexual adults (more than one not observed to feed young, hatched bars), and proportion with two or more consexual adults observed feeding young (solid bars). SPL = supplemental transect. Sample sizes shown at the base of the bar graphs.

affect beetles' ability to turn the carcass and drag it in a preferred direction.

Laboratory experiments: limitations of female reproductive output

The relationship between carcass size and two measures of reproductive output (number and total mass of larvae) for *N.orbicollis*, *N.tomentosus*, *N.defodiens* and *N.pustulatus* are shown in Fig. 8. Pairs of *N.orbicollis*, *N.tomentosus* and *N.defodiens* are limited to a maximum of 35–50 young which leaves a significant proportion of a large carcass unused. The greatest mean individual larval mass for each of these species was obtained on the two largest carcass sizes. For *N.defodiens*, the mean mass

Table 1. Eight measures of the ability of *Nicrophorus* to handle carcasses of different size.

Carcass size	% significant dipteran presence	% dipterans won	Day of discovery (mean ± SE)	Burial score (mean ± SE)	% dragged in direction of head	% head further from stake than tail	Distance dragged from stake (cm) % (mean ± SE)	% rounded
Small	9.1	0.0	1.35 (0.09)	4.92 (0.05)	61.4	78.6	24.0 (1.9)	92.3
Medium	38.2	8.8	1.45 (0.09)	4.65 (0.09)	55.8	64.3	25.3 (2.0)	94.4
Large	42.9	21.4	1.53 (0.10)	3.55 (0.17)	69.5	69.2	24.0 (1.6)	54.5
n	84	84	216	212	130	41	157	42
P	<0.05[a]	<0.05[b]	>0.20[c]	<0.001[d]	>0.20[e]	>0.20[f]	>0.20[g]	<0.025[h]

* [a]$G = 6.85$, 2 df, 2 × 3 contingency test; [b]$G = 7.55$, 2 df, 2 × 3 contingency test; [c]$G = 2.38$, 4 df, 3 × 3 contingency test, carcasses scavenged before discovery excluded; [d]2 df, Kruskal-Wallis one-way ANOVA; [e]$G = 2.63$, 2 df, 2 × 3 contingency test; [f]$G = 0.63$, 2 df, 2 × 3 contingency test, rounded carcasses excluded; [g]$F_{1,155} = 0.70$, one-way ANOVA; [h]$G = 7.56$, 2 df, 2 × 3 contingency test, day 4 and 8 carcasses only.
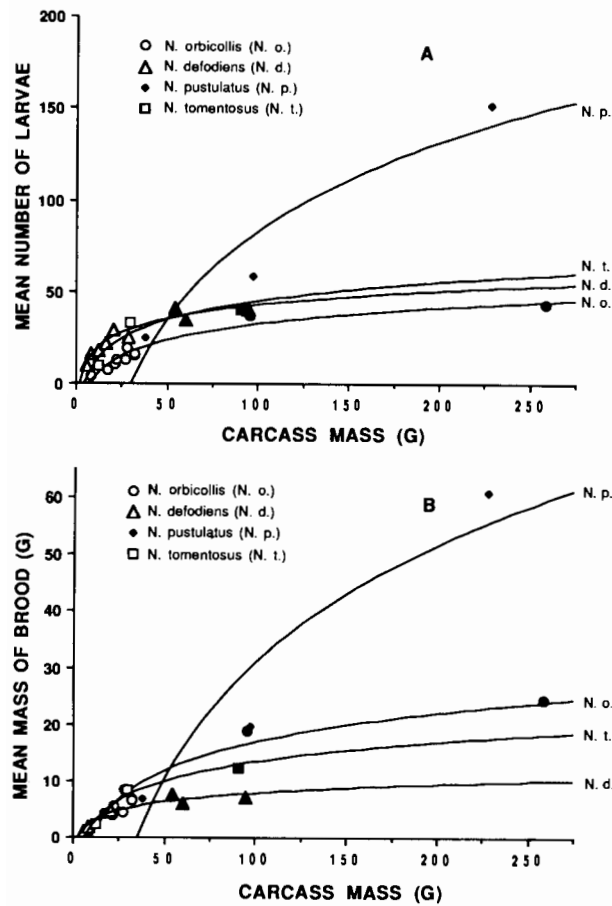
Fig. 8. Mean number of larvae (A) and mean total mass of broods (B) as a function of carcass mass for *N.orbicollis*, *N.tomentosus*, *N.defodiens* and *N.pustulatus*. Each point is based on a minimum sample of six. Darkened symbols represent data collected in this study. Open symbols represent data taken from Wilson & Fudge (1984), Scott (1989), Scott & Traniello (1990) and Trumbo (1990a, b, 1991). Curves were drawn by logarithmic approximation.

was 50% greater on the largest carcasses than on smaller carcasses (0.18 *v.* 0.12 g; Mann-Whitney U test, $P < 0.05$). In contrast, nearly all the available resource was consumed by the largest *N.pustulatus* broods, even on 220–260 g carcasses. Large carcasses prepared by *N.pustulatus* were sunk but not completely buried and were not rounded into well-formed brood balls. During the first few days of larval development in the largest broods, both males and females spent considerable time feeding larvae and emitting soft stridulations. Parents stayed with their young until the young were about to disperse.

Necessity of feeding

When *N.defodiens* and *N.pustulatus* larvae were provided with a superabundant supply of chicken livers (parents removed), survival was quite high (88% of *N.defodiens* and 84% of *N.pustulatus*). Larvae attained a weight similar

to that attained when parents are present (mean ±SE, 0.12 ± 0.01 g, *N.defodiens*; 0.47 ± 0.06, *N.pustulatus*). *N.sayi* and *N.orbicollis* young failed to reach the second instar when provided chicken liver or a combination of chicken liver and chopped third instars (comparisons with *N.defodiens* and *N.pustulatus*, Fisher's Exact Probability test, $P < 0.05$). Only one *N.orbicollis* achieved the second instar on a diet of chopped third instars (this individual subsequently died before reaching the third instar). Mean (±SE) egg mass was similar for *N.defodiens* (2.13 ± 0.15 mg) and *N.pustulatus* (2.14 ± 0.15 mg) but considerably larger in *N.orbicollis* (2.97 ± 0.19 mg; FEP, $P < 0.05$).

Discussion

To understand how a variable resource base influences behavioural plasticity and the flexibility of breeding systems, it must be determined how resource levels affect the ability to handle a resource, competition and reproductive success. *Nicrophorus* can utilize a remarkable size range of carcasses as a breeding resource (8–300+ g for *N.orbicollis* and 4–120+ g for *N.defodiens*; see Trumbo (1990b) and Müller *et al.* (1990b) for information about use of carrion of less than 10 g]. Little is known about reproduction at the upper end of this range [but see Milne & Milne (1944), Arnett (1946), Peck (1986) and Kozol *et al.* (1992)]. The present study demonstrates that *Nicrophorus* are extremely active on larger carcasses of up to 300 g in the field, that nearly all unscavenged large carcasses are buried by *Nicrophorus*, and that a significant proportion of large carcasses produce a *Nicrophorus* brood.

Beetles that attempt to exploit a large carcass in the field are more likely to confront conspecifics of greater size (at least for females) and greater numbers of congeners. More potential competitors around large carcasses might lead to a higher probability of intraspecific brood parasitism by subordinate females and satellite copulatory strategies by subordinate males. From this study it was not possible to determine whether more beetles were present on larger carcasses at exhumation because greater numbers discovered the carcass or because beetles were more tolerant of potential competitors. I suspect that both are true. The greater probability of finding *N.orbicollis* rather than *N.defodiens* on larger carcasses suggests that *N.orbicollis* found it easier to discover and then displace *N.defodiens* from large rather than small carcasses [also see Trumbo (1990b)].

There is also indirect evidence for greater tolerance of consexuals on larger carcasses (also see Scott & Traniello, 1990). There was an absence of communal breeding on smaller carcasses in the field and in the laboratory I have been able to induce communal breeding on large but not small carcasses (unpublished results). This study confirmed that communal breeding is a regular feature of reproduction on large carcasses and that group composition is quite flexible. Social interactions are complex and include competitive displacement, short-term associations (through nest preparation) and long-term communal care

of young. Future studies employing genetic markers can determine whether adults feed each others' young on larger carcasses. I hypothesize that the breeding system is facultatively quasisocial.

It seems doubtful that greater number of larvae and greater total brood mass on a larger resource translates into greater reproductive output per resident in the field. This is because communal breeding occurred on large but not small carcasses, the exact number of communal breeders might have been underestimated, and brood parasitism is probably more common on larger carcasses. These variables can be controlled in future experiments. Reproductive failures, the probability of being excluded by congeners and adverse effects of larval dipteran activity also appear to be more common on larger carcasses.

Beetles with larvae on the carcass were more likely to be injured than beetles without larvae. One possible explanation is that the tendency to fight increases as the carcass is prepared, the nest nears completion and the probability of successful reproduction increases.

In the laboratory, *N.defodiens* and *N.orbicollis* tend to utilize most of the available resource of a small carcass for larval growth and development. Pairs utilize only a fraction of larger carcasses, however, because clutch size seems to be limited to 30–50 eggs, a maximum that appears typical for *Nicrophorus* (Pukowski, 1933; Halffter et al., 1983; Bartlett & Ashworth, 1988; Müller et al., 1990b; Kozol et al., 1992). On a smaller carcass which is almost fully exploited, pairs regulate brood size (Bartlett, 1987) so that mean mass of individual larvae is equivalent over a range of carcass sizes (e.g. 5–15 g in *N.defodiens*, 10–30 g in *N.tomentosus*; Trumbo, 1990a, b). If a carcass exceeds the resource requirements of the maximum brood that can be produced by a single female, then individual larvae disperse at greater mass (there also was evidence for this in the field). Even with enhanced larval growth, larger carcasses cannot be fully exploited by the offspring of a single female. This should lower the costs of tolerating a second breeding female, especially when the available resource is greater than twice that required by the brood of a single female. Since a single *N.defodiens* female can produce her maximum brood on a 20–30 g carcass while a *N.orbicollis* female requires a 80–100 g carcass to do the same, *N.defodiens* is expected to adopt communal breeding strategies on much smaller carcasses than *N.orbicollis*.

Reproduction in *N.pustulatus* is clearly different from anything reported to date for burying beetles. Pairs reared up to 187 offspring on larger carcasses but sometimes rejected small carcasses (<20 g, unpublished results) suggesting that *N.pustulatus* is specialized to reproduce on large carcasses. Anderson (1982b) associated *N.pustulatus* with reproduction on small carcasses but no evidence was provided. *Nicrophorus pustulatus* has never been found on thousands of small carcasses placed in the field in northern Michigan (Trumbo, 1990b, 1991; Wilson & Fudge, 1984; Wilson et al., 1984). The life history of *Nicrophorus pustulatus* remains enigmatic, however, because it was not found on large carcasses in the field.

There was one case of a mixed-species brood in the field,

possibly resulting from interspecific brood parasitism. *Nicrophorus* appears vulnerable to interspecific brood parasitism; foster parents will raise heterospecific young that arrive on the carcass at the 'expected' time (unpublished results). Despite considerable seasonal overlap between *N.orbicollis* and *N.defodiens*, there was no evidence of interspecific brood parasitism by *N.defodiens* in the field. The possibility of *N.tomentosus* acting as an interspecific brood parasite should be examined since *N.orbicollis* did rear one mixed brood containing *N.tomentosus* larvae and *N.tomentosus* was just becoming active as the field experiment came to an end.

It is clear that large carcasses present considerable difficulties for burying beetles in the field. Beetles took longer to bury large carcasses beneath the leaf litter and larger carcasses were not rounded into a brood ball as often as smaller carcasses. Using *N.vespilloides*, Bartlett (1988) noted that the quality of preparation of carcasses declined even over the size range of 10–30 g. In addition, hair is not always removed from an entire large carcass as it is on smaller carcasses. The longer exposure and greater surface area of a larger carcass is likely to lead to greater oviposition by dipterans. Once underground, the inability to round the carcass into a ball and thereby to reduce the exposed surface area likely makes it more difficult to control microbial activity. The presence of microbes and especially dipteran larvae were primary reasons for the lower probability of reproduction on large carcasses. Scott et al. (1987) noted greater dipteran success on 30–60 g rather 8–29 g carcasses in New Hampshire.

Another difficulty that burying beetles might encounter on larger carcasses is the increased parental effort that might be required for larger broods. There has been confusion in the literature regarding the necessity of parental regurgitations for normal larval development. Pukowski (1933) reported that in the absence of parents, larvae fed normally and developed to the pupal stage but then failed to survive to the adult stage. Unfortunately, methodology has differed among subsequent investigators and Pukowski (1933) did not report the species with which she worked. The present study attempted to standardize procedures to investigate four species [a fifth species, *N.tomentosus*, has been similarly studied (Trumbo, 1990a)]. Young of the three smallest species, *N.defodiens*, *N.tomentosus* and *N.pustulatus*, survived to the adult stage on chicken liver in the absence of parents. *Nicrophorus defodiens* and *N.pustulatus* reared in this manner were able to reproduce successfully (unpublished results). Young of the two larger species, *N.orbicollis* and *N.sayi*, failed to survive to the second instar without post-hatching parental care. Wilson & Fudge (1984) found that a few small-sized *N.orbicollis* survived to the third instar when they were left on the original brood ball without parents. I suspect this occurred because parents feed and then regurgitate directly into a small depression at the top of the carrion ball before larvae hatch (Pukowski, 1933), and that some larvae were able to derive a limited benefit from this regurgitation in Wilson & Fudge's experiments. Young of larger *Nicrophorus* species may be more dependent on parental regurgitations

for normal larval development. *Nicrophorus investigator* and *N. humator* are good-sized species which failed to survive to the second instar without parents (Springett, 1967). Halffter *et al*. (1983) reported that *N. mexicanus* larvae suffered slightly higher mortality without parents than when the female provided care, but development was otherwise normal. No information is available on the size of this species.

Larger species may achieve greater size more from rapid larval growth than from starting out at a larger size at the egg stage. The dispersal mass of *N. orbicollis* larvae is 200–300% greater than that of *N. defodiens* while egg mass is only about 40% greater. *Nicrophorus pustulatus* seems to produce small eggs relative to its dispersal mass, perhaps as an adaptation for producing extremely large clutches.

It seems probable that *Nicrophorus* evolved from a group that did not require post-hatching parental care [see Peck (1982) for the life history of the closely related *Ptomascopus* from which *Nicrophorus* is thought to be derived]. I hypothesize that although preparation of the carcass by parents is necessary for normal larval development, parental aid in digesting carrion was not the primary selective force in the evolution of parental care in this group. A greater dependence on parental care might be a tradeoff for larger size in some extant *Nicrophorus* species, however, and may have important implications for reproduction on larger carcasses. All else being equal, a species with young less dependent on parental care would have an advantage on larger carcasses with larger broods if parents have less time to feed individual larvae.

This study confirms that *Nicrophorus* utilizes a wide resource base for reproduction and demonstrates considerable variation in the breeding system. On smaller carcasses a male and female can pair and cooperate through nest preparation with the male deserting shortly after larvae arrive on the carcass. On intermediate-sized carcasses, biparental care is provided throughout most of larval development (Trumbo, 1991). On larger carcasses, associations among consexuals are more likely to occur throughout nest preparation and can extend to the parental period. Numerous questions concerning the causes of communal breeding remain unanswered. A lack of available carcasses that can be exploited by male–female pairs (Wilson & Fudge, 1984) might be one factor promoting communal breeding [habitat saturation, Brown (1974)]. In addition, the greater number of young that can be supported on a larger carcass undoubtedly lowers the costs of tolerating rivals, especially for females which are limited to a clutch size of about 35–50. Future experiments can address possible benefits of communal breeding and the cost/benefits of fighting to monopolize a resource. To date, few experiments to manipulate both group size and the environmental determinants of a social system have been carried out. Fortunately, *Nicrophorus* is quite accessible to manipulation. Many species can be reared in the laboratory or under controlled settings in the field where group size and resource size can be varied independently. Given the broad understanding of the biology of this group and the availability of genetic markers, further investigation of this system promises to produce insight into the physical and social determinants of mating ststems.

Acknowledgments

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