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 (50–80 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 congers.
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 pastusatus, in contrast, appears to be unique among Nicrophorus in that it can raise nearly 200 young on larger carcasses.
7. Nicrophorus orbicollis and Nicrophorus nesi 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. pastusatus 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 quasi-social.

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 (Olson, 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 (Satz & Hölldobler, 1962; Woolfenden & Kirkpatrick, 1984; Brown, 1987). Unfortunately, it is often impossible to directly manipulate the purported environmental determinant of a social system (but see Sakagami & Merta (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, 1966; Kezel 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,
and the prevalence of communal breeding. Follow-up experiments in the laboratory examined potential reproductive output of single females and the necessity of paternal regurgitations for normal larval development.

The study animal. Burying beetles' utilization of small carcasses has long been known (Faber, 1909; Pukowski, 1933). A single female or male--female pair--can transport a small vertebrate carcass to a suitable burial spot and excavate a nest. As the carcass is buried, the fat removes any hair or feathers, shapes the resource into a broad ball, and deposits anal and oral secretions which affect the decomposition. Burying beetles carry phoretic mites (Pseudoleiurus carabi Vrémé) which pierce dipteran eggs that are oviposited on the carcass prior to and during nest preparation (Springett, 1968). Pseudoleiurus 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, 1981). Defeated females can remain in the leaf litter surrounding a nest for a number of days and paralyze 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 (Eggett & 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 & Eggett, 1990). Larvae are fed trophallactically by parents but dependence on these regurgitations wanes as larvae develop (Pukowski, 1933). Parents are able to regulate trophallaxis but this information is not yet available because 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, 1995; 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 Petoskey, Michigan. The phytology and diurnal activity patterns of Nicterophorus spp. at this site are described in Wilcox et al. (1993).

A 350 x 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 CO2 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 Mass musculus, medium, 50--90 g Rattus rattus; 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 hind legs of the carcass and to a stake driven into the soil. Carcasses were placed across the stake so that the head pointed in one of four compass directions. All placements, subsequent checks and final examinations 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 consumed 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 (S = 100%, 4 = 90%--99%, 3 = 50%--90%, 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 8.4 for a mean density of 4 undiscovered carcasses/20.848 m2. This was well below carcass density in previous studies (Wilcox et al., 1984).

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 6 cm radius. The following measurements were made of the carcasses: 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. Dipteran 'won' the carcass if there were thirty or more larvae with diameter >1.5 mm, dipteran larva had penetrated the interior of the carcass and at least one larva was 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 dispensed. 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.

All carcasses placed on the grid, nine very large carcasses (210–300 g) were placed on a suplemental transect (30 m between transect points). Three carcasses were placed on each of 25, 25 and 27 July and were examined 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 (CZ/S) and day of exhumation (DAY)). Categorical variables were analysed using log-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 Wilkenson (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. nomenosus 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 (40–90 g Musculus and 90–100 g Ratus ratus carcasses for N. defodiens, 50–100 g Rattus for N. nomenosus and 90–110 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. patula (eight per treatment) were provided with 35–40 g Musculus, 90–100 g or 220–240 g Rattus ratus carcasses and similar measurements were taken. Since there is no information available on the biology of N. patula, two pairs were observed caging for broods under red light. Necessities 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. patula, N. orbicollis and N. mayi Laperre were provided with a 20–25 g carcass and allowed to oviposit. Three eggs each from 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 liver (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 greatest potential for competition on larger carcasses; there were a greater number of beetles (species and sexes combined) 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 carcasses (Fig. 3); and the pronatal 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 x date interaction, G = 2.24, P > 0.20, 3 df, 2 x 2 x 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 (6.1%, 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. nomenosus and twenty-three N. orbicollis young).

For carcasses containing a brood, the proportion of nests with two congeneric adults in residence and the proportion with two consemal adults feeding young are shown in Fig. 7. For N. orbicollis, there was a higher probability of
finding same-sex adults in residence on larger rather than smaller carcasses ($G = 10.60, P < 0.005$; 1 df, small and medium versus large and supplemental carcasses). Communal associations were quite variable and included polygnomons, polyandrous and polygynandrous groups.

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

Fig. 1. Number of Nicrophorus (A) on and (B) off the cocoon at exhumation. Number on log-linear analysis, number of beetles classified as 'few' (0–3) or 'many' (≥4); carcass size (CSZ), $G = 28.58, 2$ df, $P < 0.001$; age of exhumation (DAY), $G = 22.86, 3$ df, $P < 0.005$; CSZ × DAY, $G = 3.64, 6$ df, $P = 0.49$, $n = 155$. Number off: few (0–1) or many (≥2); CSZ, $G = 9.48, 2$ df, $P < 0.01$; DAY, $G = 17.96, 3$ df, $P = 0.005$; CSZ × DAY, $G = 5.80, 4$ df, $P = 0.05$. Sample sizes are shown at the base of the bar graphs.

Fig. 2. Proportion of individuals that were found with a same-sex conspecific on the carcass at the time of exhumation. Log-linear analysis, $N$. orthocerus, $CSZ, G = 7.45, P = 0.005$, 2 df, SEX, $G = 0.48, P = 0.50$, 1 df; $CSZ × SEX, G = 1.14$, $P = 0.29$, 2 df; $N$. nubilalis, $CSZ, G = 9.54, P < 0.005$, 1 df, SEX, $G = 2.24, 0.10 < P < 0.20$, 1 df; $CSZ × SEX, G = 3.06$, $P = 0.08$, 1 df. For statistical analyses, data from medium and large carcasses were combined for Cl. definitus 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 were by depressor not included in the analysis).
Fig. 3. Of carcasses held by *N. nevadensis* (n = 150), percentage held by *N. aridicola*. Log-linear analysis, CSIZ: G = 12.38, P = 0.0005, 2df. DAY, G = 49.33, P < 0.001, 3df; CSIZ × DAY, G = 6.67, P = 0.20, 6df. Sample sizes shown at the base of the bar graphs.

Fig. 4. Proportional width of the largest (A) *N. aridicola* female on the carcass at exhumation (one-way ANOVA, CSIZ, F,7,12 = 4.95, P = 0.0003) and *N. aridicola* male (CSIZ, F,7,12 = 1.99, P = 0.11). (B) *N. defodiens* female (CSIZ, F,7,12 = 3.78, P = 0.03) and *N. defodiens* male (CSIZ, F,7,12 = 0.48, P = 0.79). S3L = supplemetal teneral. Numbers of carcasses with at least one individual of the indicated sex and size shown at the base of the bar graphs.

Fig. 5. Percentage of carcasses exhumed on days 8, 12 or 18 with *N. nevadensis* using Log-linear analysis (all carcasses: CSIZ, G = 11.60, P < 0.005, 2df; DAY, G = 5.16, P = 0.025, 1df; CSIZ × DAY, G = 1.39, P = 0.26, 2df). Sample sizes shown at the base of the bar graphs.

Competition for carcasses (non-congeners)

Of the 238 carcasses placed in the field, 65–66% (22.7%) were scavenged by *N. nevadensis*. The scavenging rate was not affected by carcass size but was affected by the duration of the trial (log-linear analysis, carcass size, G = 1.57, P = 0.20, 2df; DAY, G = 14.61, P = 0.0003, 3df; CSIZ × DAY, G = 3.30, P = 0.20, 6df). Of the eight-four carcasses not scavenged in trials lasting 8 or more days, 32.1% met the criteria for significant presence of dipteron larvae and 10.7% were overrun by dipterans. Of carcasses even by dipterans, 66.7% were initially buried by beetles. Both measures of dipteran exploitation suggest that dipterans were more successful on larger carcasses (Table 1).

Handling the carcasses

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 the moment, 23.2% toward the tail) and 36.6% to either side; G = 13.51, P < 0.001, 3df, 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). Of 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. 7. Of carcasses with N. oricollis young (n = 50), the proportion without two consensual adults (open bars), proportion with two or more consensual adults (more than one not observed to feed young, hatched bars), and proportion with two or more consensual 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. oricollis, N. nontentus, N. defodiens and N. pantalatus are shown in Fig. 8. Pairs of N. oricollis, N. nontentus 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 Necrophorus to handle carcasses of different size.

<table>
<thead>
<tr>
<th>Carcase size</th>
<th>% significant diptera presence</th>
<th>% diptera won</th>
<th>Day of discovery (mean ± SE)</th>
<th>Burial score (mean ± SE)</th>
<th>% dragged in direction of head</th>
<th>% head further from stake than tail</th>
<th>Distance dragged from stake (cm) (mean ± SE)</th>
<th>% rounded</th>
</tr>
</thead>
<tbody>
<tr>
<td>Small</td>
<td>9.1</td>
<td>0.0</td>
<td>1.35 (0.09)</td>
<td>4.92 (0.09)</td>
<td>61.4</td>
<td>78.6</td>
<td>24.0 (1.9)</td>
<td>92.3</td>
</tr>
<tr>
<td>Median</td>
<td>36.2</td>
<td>8.8</td>
<td>1.45 (0.09)</td>
<td>4.69 (0.09)</td>
<td>55.8</td>
<td>64.3</td>
<td>25.3 (2.5)</td>
<td>94.4</td>
</tr>
<tr>
<td>Large</td>
<td>42.9</td>
<td>21.4</td>
<td>1.53 (0.10)</td>
<td>3.35 (0.17)</td>
<td>60.5</td>
<td>69.2</td>
<td>24.0 (1.6)</td>
<td>54.5</td>
</tr>
</tbody>
</table>

α 84 84 216 212 130 41 157 42

P < 0.005 < 0.05 > 0.05 > 0.05 > 0.20 > 0.20 > 0.20 < 0.025

* α = 0.05, 2 df, 2 x 2 contingency test; * α = 0.05, 2 df, 2 x 2 contingency test; * α = 0.05, 2 df, 2 x 2 contingency test. Carcases scavenged before discovery were included. * α = 0.05, 2 df, 2 x 2 contingency test. Carcases scavenged before discovery were included. * α = 0.05, 2 df, 2 x 2 contingency test. Carcases scavenged before discovery were included. * α = 0.05, 2 df, 2 x 2 contingency test. Carcases scavenged before discovery were included. * α = 0.05, 2 df, 2 x 2 contingency test. Carcases scavenged before discovery were included. * α = 0.05, 2 df, 2 x 2 contingency test. Carcases scavenged before discovery were included. * α = 0.05, 2 df, 2 x 2 contingency test. Carcases scavenged before discovery were included. * α = 0.05, 2 df, 2 x 2 contingency test. Carcases scavenged before discovery were included. * α = 0.05, 2 df, 2 x 2 contingency test. Carcases scavenged before discovery were included.
Fig. 8. Mean number of larvae (A) and mean total mass of brood (B) as a function of carcass mass for *N. orbicollis*, *N. donaci*, *N. defodiens* and *N. punctatus*. Each point is based on a minimum sample of six. The horizontal line represents the range of values for each species. The results are presented in this study. Open symbols represent data taken from Wilson & Fudge (1984), Scott (1986), Scott & Trudjio (1990) and Trombo (1990a, b, 1991). Curves were drawn by logarithmic approximation.

was 50% greater on the larger carcasses than on smaller carcasses (0.18 < 0.48, Mann-Whitney U test, *P < 0.05*). In contrast, nearly all the available resource was consumed by the largest *N. punctatus* broods, even on 220–260 g carcasses. Large carcasses prepared by *N. punctatus* 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 stimuliations. Parents stayed with their young until the young were about to disperse.

Necessity of feeding

When *N. defodiens* and *N. punctatus* larvae were provided with a superbundant supply of chicken livers (parents removed), survival was quite high (88% of *N. defodiens* and 84% of *N. punctatus*). Larvae attained a weight similar to that attained when parents are present (mean ±SE: 0.12 ± 0.04 g, *N. defodiens*; 0.47 ± 0.06 g, *N. punctatus*). *N. punctatus* and *N. orbicollis* young failed to reach the second instar when provided chicken liver or a combination of chicken liver and chopped cheddar and thistle instars (comparisons with *N. defodiens* and *N. punctatus*, Fisher's Exact Probability test, *P < 0.05*). Only one *N. orbicollis* achieved the second instar on a diet of chopped thistle 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. punctatus* (2.14 ± 0.15 mg) but considerably larger in *N. orbicollis* (2.09 ± 0.19 mg; FEP, *P < 0.05*).

Discussion

To understand how a variable resource base influences the success of beetles, it is necessary to describe the system, its role in the environment, and its impact on the species involved. More potential competitors around large carcasses might lead to a higher probability of interspecific brood competition. 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, we suggest 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 Trombo (1990b)].

There is also indirect evidence for greater tolerance of concomitant on larger carcasses (also see Scott & Trudjio, 1990). There was an absence of communal brooding on smaller carcasses in the field and in the laboratory. I have been able to induce communal brooding on large but not small carcasses (unpublished results). This study confirmed that communal brooding is a regular feature of reproduction on large carcasses and that group composition is quasi-fixed. 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 carasses. I hypothesize that the breeding system is facultatively polygynous.

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 carasses, the exact number of communal breeders might have been underestimated, and brood parasitism is probably more common on larger carasses. 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 carasses.

Beetles with larvae on the carasses were most likely to be injured than beetles without larvae. One possible explanation is that the tendency to fight increases on the carass is prepared, the nest near completion and the probability of successful reproduction increases.

In the laboratory, N.defendant and N. orbicularis tend to utilize most of the available resource of a small carass for larval growth and development. Pair utilize only a fraction of larger carasses, however, because clutch size seems to be limited to 30–50 eggs, a maximum that appears typical for Nicrophorus (Pukowski, 1933; Halfker et al., 1987; Bartlett & Ashworth, 1988; Mulfinger et al., 1998b; Kozel et al., 1992). On a small carass which is almost fully exploited, pairs regulate brood size (Bartlett, 1987) so that mean mass of individual larvae is equivalent over a range of carass sizes (e.g. 5–15 in N.defendant, 10–30g in N.ornamentus; Trumbo, 1990a, b). If a carass exceeds the resource requirements of the maximum brood that can be produced by a single female, then individual larval dispersive at greater mass (there also was evidence for this in the field). Even with enhanced larval growth, larger carasses cannot be fully exploited by the offspring of a single female. This should lower the costs of tolerating a second nesting female, especially when the available resource is greater than what that required by the brood of a single female. Since a single N.defendant female can produce her maximum brood size of 23–34g carasses while N. orbicularis female requires a 89–10g carass to do the same, N.defendant is expected to adopt communal breeding strategies on much smaller carasses than N. orbicularis.

Reproduction in N.pustulata is clearly different from anything reported to date for burying beetles. Pairs reared up > 80% of their larvae on larger carasses but sometimes rejected small carasses (<20g, unpublished result) suggesting that N.pustulata is specialized to reproduce on large carasses. Andersen (1926b) associated N.pustulata with reproduction on small carasses but no evidence was provided. Nicrophorus pustulatus has neven been found on thousands of small carasses placed in the field in northern Michigan (Trumbo, 1990b, 1992; Wilson & Fudge, 1984; Wilson et al., 1984). The life history of Nicrophorus privatulus remains enigmatic, however, because it was not found on large carasses 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 arise on the carass at the 'expected' time (unpublished results). Despite considerable seasonal overlap between Nicrophorus and N.defendant, there was no evidence of interspecific brood parasitism by N.defendant in the field. The possibility of N.ornamentus acting as an interspecific brood parasitic should be examined since Nicrophorus did bear one mixed broom containing N. ornamentus larve and N.ornamentus was just becoming active as the field experiment came to an end.

It is clear that large carasses present considerable difficulties for burying beetles in the field. Beetles took longer to bury large carasses beneath the leaf litter and larger carasses were not rounded into a brood ball as often as smaller carasses. Using N.vespilloides, Bartlett (1988) noted that the quality of preparation of carasses declined with size of the range of 15–30g. In addition, hair is not always removed from an entire large carass as it is on smaller carasses. The longer exposure and greater surface area of a larger carass is likely to lead to greater oviposition by dipterans. Once underground, the inability to round the carasses 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 carasses. Scott et al. (1987) noted greater dipteran success on 30–60g rather than 20g carasses in New Hampshire.

Another difficulty that burying beetles might encounter on larger carasses 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 and five species, N.ornamentus, has been similarly studied (Trumbo, 1990a). Young of the three smallest species, N.defendant, N.ornamentus and N.pustulata, survived to the adult stage on chicken liver in the absence of parents. Nicrophorus defendant and N.pustulata reared in this manner were able to reproduce successfully (unpublished results). Young of the two larger species, N. orbicularis and N. saizi, failed to survive to the second instar without post-hatching parthenial care. Wilson & Fudge (1984) found that a few small-sized N. orbicularis survived to the third instar when they were left on the original brood ball without parents. I suspect this occurred because parents fed and then regurgitated directly into a small depression at the top of the carrion ball before larvae hatched (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. N. crassus and N. haemator are good-sized species which failed to survive to the second instar without parents (Springett, 1967). Halfter et al. (1983) reported that N. menestrans larvae suffered slightly higher mortality without parents that when the female provided care, but development was otherwise normal. No information is available on the sex of this species.

Larger species may achieve greater size more from rapid larval growth than from continued growth at a larger size as at the egg stage. The dispersal mass of N. orbicollis larva is 200–500% greater than that of N. defodiens while egg mass is only about 40% greater. Nymphopus punctulatus seems to produce small eggs relative to its dispersal mass, perhaps as an adaptation for producing extremely large clutches. It seems probable that N. orbicollis evolved from a group that did not require post-hatching parental care [see Peak (1982) for the life history of the closely related Promopsus from which Nymphopus is thought to be derived]. I hypothesize that although preparation of the case 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 "nocebo" for larger size in some extant Nymphopus species, however, and may have important implications for reproduction on larger clutches. All else being equal, a species with young less dependent on parental care would have an advantage on larger clutches with larger broods if parents have less time to feed individual larvae.

This study confirms that Nymphopus utilizes a wide resource base for reproduction and demonstrates considerable variation in the breeding system. On smaller clutches a male and female can pair and cooperate through nest preparation with the male deserting shortly after larvae active on the licorice. On intermediately-sized clutches, nuptial care is provided throughout most of larval development (Trumbo, 1991). On larger clutches, associations among conspecifics are more likely to rise 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 (brachial saturation, Brave, 1975).

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 costs and 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, Nymphopus are quite amenable 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 provide insights into the physiological and social determinants of mating systems.

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