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Interspecific Competition and the Evolution of Communal Breeding in Burying Beetles

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ABSTRACT.—Size of breeding groups and resource quality (carcass mass) were varied independently in experiments using the burying beetle, *Nicrophorus defodiens,* to examine reproductive output of beetles using carcasses exposed to carrion competitors. Male-female pairs experienced the same rate of brood failure as groups of four beetles (two males and two females). Groups of four produced more total larvae and a greater brood mass than pairs on large but not small carcasses, whereas reproductive output per female was lower for groups. Carcasses prepared by groups of two males and two females attracted similar numbers of free-flying congeners as carcasses prepared by pairs. The ability of more than two individuals to produce a larger brood than that of pairs may decrease the costs of communal breeding on larger carcasses, but by itself, is not sufficient to explain the evolution of breeding associations consisting of multiple females.

INTRODUCTION

One of the primary goals of socioecologists is to determine environmental factors t select for group vs. solitary breeding (reviews in Rubenstein and Wrangham, 1986; Slobodchikoff, 1988). As a first step toward addressing this issue, reproductive success of groups of different size and under different environmental conditions is frequently measured. Unfortunately, because larger groups often occupy superior territories or hold superior resources, an independent effect of group size on reproductive success may be difficult to ascertain (Brown *et al.,* 1982). Burying beetles (*Nicrophorus* spp.), which prepare vertebrate carcasses as a food source for their brood, are excellent subjects for examining the consequences of breeding in groups of different size. Burying beetles have a highly variable breeding system (monogamous, polygynous, polyandrous and polygynandrous associations), and important environmental variables (group size, resource quality, presence/absence of competitors) can be controlled and manipulated.

Studies of burying beetles in which potential competitors have been excluded from large carcasses have shown that groups of more than two beetles produce more total offspring but fewer offspring per female than pairs (Eggert and Müller, 1992; Scott and Williams, 1993; Trumbo and Wilson, 1993). However, when carcasses are exposed to carrion competitors before colonization by burying beetles, it is clear that competitors sometimes win a significant proportion of the resources (Springett, 1968; Wilson, 1983; Kneidel, 1984; Scott *et al.,* 1987; Trumbo, 1990, 1992). The effect of this competition on the formation of communal breeding groups is not known. In this study we determined the reproductive output of groups of four *Nicrophorus defodiens* (two males and two females) on carcasses previously exposed to carrion competitors, and compared these results with previously reported information (Trumbo, 1993) on the reproductive output of male-female pairs breeding under the same experimental conditions.

METHODS

Study animal and field site.—Burying beetles prepare a carcass for their young by burial, removal of hair, rounding into a ball and depositing anal secretions which affect the decomposition (Pukowski, 1933; Halffter *et al.*, 1983). Beetles use a wide size range of carcasses and sometimes form communal breeding associations (which include cooperative brood care) on larger carrion (Trumbo, 1992; Eggert and Müller, 1992; Scott and Williams, 1993; Trumbo and Wilson, 1993). *Nicrophorus defodiens* Mannerheim, the smallest burying beetle at The University of Michigan Biological Station (UMBS, near Pellston, Michigan (described in Wilson *et al.*, 1984), often breeds communally on carcasses over 40 g (Trumbo and Wilson, 1993).

Competition experiments.—A carcass used by burying beetles is not always discovered on the 1st night it is available (Trumbo, 1990; Scott and Traniello, 1990), and competition, especially with flies, can be intense in this situation (Wilson, 1983; Kneidel, 1984; Trumbo, 1992). To simulate a situation in which beetles discover a carcass after carrion flies have oviposited a large number of eggs, small (18–24 g) or large (50–90 g) rodent carcasses were left uncovered in a woodland at UMBS from 0900 to 1800 h the day before each trial. Carcasses were then taken inside overnight, re-exposed the following day from 0900 to 1400 h, and then visually inspected to confirm that flies had oviposited.

Nicrophorus defodiens were caught in pitfall traps baited with a large quantity (>100 g) of carrion and fed chicken liver before experimental trials. In Experiment 1, two small and two large carcasses were taken, along with beetles, to the experimental site (a birch-beech-aspen woodland) on 18 days between 3 July and 6 August 1991 (only large carcasses were taken for five additional days). At four randomly chosen points (on one of six transects, spaced 50 m apart), a rectangular section of soil was dug from the forest floor and trimmed to fit snugly into an 8 × 15 × 30 cm container. Male-female pairs or four beetles (two males and two females) were placed into a container holding either a small (n = 18/treatment) or large (n = 23/treatment) carcass. Wire screening (0.3-cm mesh) was placed over the container to prevent free-flying beetles from gaining access to the resource. The container was buried flush with the soil and after 6 days was brought back to the laboratory. Wire screening was then removed and adult beetles were allowed to disperse. Within 24 h of beetle larvae crawling away from the carcass, the number and mass of the brood were determined.

Experiment 2 was designed so that information on the attraction of congeners, as well as reproductive success, could be obtained. Small (24–30 g) and large (90–100 g) carcasses were exposed to fly oviposition as in Experiment 1. On each of 13 days in July or August 1991, and 5 days in July 1992, two pairs and two groups of four beetles were transported, along with two small and two large carcasses, to the field site. Circular plugs of forest soil were dug up and fitted into the base of a plastic drum (36 cm height, 29 cm diam). Beetles and a small (n = 18/treatment) or large (n = 18/treatment) carcass were placed into the drum and the drum was buried so that its rim was flush with the soil surface. The top of the drum was covered with a fine wire mesh (0.2 cm) into which a circular hole had been cut. Free-flying beetles that were attracted to the carcass would fall into the hole, drop through a funnel, and land in a cup. Free-flying beetles were collected each day for 6 days, after which time the drum was taken to the laboratory, the wire screening was removed, and resident beetles were allowed to disperse. Brood number and mass were determined as in Experiment 1. All statistical analyses were performed using SYSTAT (Wilkinson, 1989).

RESULTS

In both Experiments 1 and 2, brood failures (no beetle young produced) were more common on larger rather than smaller carcasses (24% vs. 0%, and 55% vs. 17% in Experiments 1 and 2, respectively). The majority of carcasses on which beetles failed was consumed by fly larvae (88%). The number of residents (NR) on the carcass, however, did not affect

TABLE 1.—Mean (±SE) number of larvae and brood mass produced by pairs and groups of four beetles on carcasses previously exposed to oviposition by carrion flies (sample sizes shown in parentheses)

	Small carcass		Large carcass	
Group composition	Number of larvae	Total brood mass (g)	Number of larvae	Total brood mass (g)
Exp. 1				
1 male, 1 female	24.1 ± 1.7 (18)	3.4 ± 0.2 (18)	28.4 ± 2.3 (16)	4.3 ± 0.4 (16)
2 males, 2 females	27.9 ± 1.3 (18)	3.7 ± 0.2 (18)	40.2 ± 3.4 (19)	5.9 ± 0.5 (19)
P[a]	=0.07	>0.20	<0.01	<0.05
Exp. 2				
1 male, 1 female	19.9 ± 2.1 (14)	3.3 ± 0.4 (14)	29.7 ± 5.7 (9)	4.8 ± 0.8 (9)
2 males, 2 females	21.2 ± 2.3 (16)	3.3 ± 0.4 (16)	53.0 ± 5.0 (7)	8.7 ± 0.9 (7)
P[a]	>0.20	>0.20	<0.01	<0.01

[a] P values determined by one-way ANOVAs (brood failures excluded from the analysis)

the likelihood of brood failure (Exp. 1, $G_{\text{carcass size (CS)}} = 14.17$, $P < 0.001$, $G_{NR} = 1.09$, $P > 0.20$; Exp. 2, $G_{CS} = 12.29$, $P < 0.001$, $G_{NR} = 0.00$, $P > 0.20$; 2 × 2 × 2 Contingency tests, CS × NR interactions, ns). In both experiments, number of larvae and brood mass were significantly greater for groups of four than for pairs on large carcasses (brood failures excluded from the analysis). No differences in reproductive output were found on small carcasses (Table 1). Reproductive output per female for groups of four was lower than for pairs on both small and large carcasses in Experiment 1, and on small carcasses in Experiment 2 (Ps < 0.01, one-way ANOVAs). Number of larvae and brood mass per female did not vary significantly with group size on large carcasses in Experiment 2 ($P > 0.20$). There also were no differences in the number of free-flying beetles attracted to carcasses prepared by pairs and groups of four (mean ± SE on small carcasses, 1.3 ± 0.3 vs. 1.1 ± 0.3; large carcasses, 9.0 ± 2.0 vs. 9.4 ± 2.1; Mann-Whitney U tests, Ps > 0.20).

In 13 of 14 comparisons of group size that have been made to date, reproductive output was greater in multiple- than in single-female groups. Reproductive output per female, however, was always less in multiple-female groups (Table 2). In six different experiments, the decline in reproductive output per female (for multiple-female groups) was less on large as compared to small carcasses (Sign test, $P < 0.05$).

DISCUSSION

Information on reproductive output is fundamental for understanding the evolution and maintenance of breeding systems. In many cases, groups of multiple females can perform functions such as nest preparation (Rissing and Pollock, 1987) or nest defense (Gamboa, 1978) better than a single female or male-female pair. Previous manipulations of group size in burying beetles (using carcasses protected from carrion competitors) have demonstrated that total reproductive output on small carcasses is the same for groups containing one or two females. On large carcasses, groups with multiple females generally produce more young than single-female groups, but output per female is 23–40% less (Table 2). Thus, reproductive success of a second female comes partially, but not completely, at the expense of the first female (*see* Eggert and Müller, 1992; Scott and Williams, 1993, for analyses using genetic markers). The ability of multiple-female groups to produce more young than single-female groups reduces, but does not eliminate, the costs of communal breeding on large carcasses. This study demonstrates that this conclusion is valid even when

TABLE 2.—Comparisons of reproductive output from single- vs. multiple-female experiments (*Nicrophorus* spp.)

Comparison	Carcass size (g)	Location of experiment	% difference in number of larvae for multiple-female treatment[a]	% difference in number of larvae per female for multiple female treatment	Reference
N. defodiens					
1 male, 1 female vs. 1 male, 2 females	15–18	Field	+9	−45	Trumbo and Eggert (1993)
1 male, 1 female vs. 1 male, 2 females	40–60	Field	+50***	−25	Trumbo and Eggert (1993)
1 female vs. 2 females[b]	15–25	Laboratory	+10	−45	Trumbo and Wilson (1993)
1 female vs. 2 females[b]	50–90	Laboratory	+53***	−23	Trumbo and Wilson (1993)
1 male, 1 female vs. 2 males, 2 females	18–24	Field	+16*	−42	Experiment 1
1 male, 1 female vs. 2 males, 2 females	60–90	Field	+42***	−29	Experiment 1
1 male, 1 female vs. 2 males, 2 females	24–30	Field	+7	−47	Experiment 2
1 male, 1 female vs. 2 males, 2 females	90–100	Field	+78***	−11	Experiment 2
1 male, 1 female vs. 1 male, 4 females	60–100	Laboratory	+148***	−38	Trumbo and Eggert (1993)
N. vespilloides					
1 female vs. 2 females	5	Laboratory	+16[b]	−42	Eggert and Müller (1992)
1 female vs. 2 females	35	Laboratory	+24[b]	−38	Eggert and Müller (1992)
N. orbicollis					
1 female vs. 2 females[b]	25–30	Laboratory	−12	−56	Trumbo and Wilson (1993)
1 female vs. 2 females[b]	180–300	Laboratory	+20	−40	Trumbo and Wilson (1993)
N. tomentosus					
1 male, 1 female vs. 2 males, 2 females	35–40	Field	+20**	−40	Scott and Williams (1993)

[a] Statistical comparisons are one-way ANOVAs based on comparisons of single- vs. multiple-female treatments; *0.10 < P < 0.05; ** 0.05 < P < 0.01; *** P < 0.01

[b] Statistic not available

beetles attempt to breed on carcasses from which potential competitors have not been excluded.

The high rate of nest failure on large carcasses (placed on intact forest soil and presented to beetles after 1-½ days of fly oviposition) is evidence that *Nicrophorus defodiens* sometimes has difficulty using these resources under natural conditions. Similarly, Springett (1968) and Wilson (1983) also reported a high rate of nest failure by burying beetle pairs in competition with carrion flies. Nest failure on similar-sized carcasses in the laboratory rarely occurs (Trumbo, 1992; Eggert and Müller, 1992; Scott and Williams, 1993; Trumbo and Wilson, 1993).

On 90–100 g carcasses (a resource size near the limit that *Nicrophorus defodiens* will accept), groups with two females produced broods 80% larger than those of pairs in the field, a greater difference than recorded in any previous study. Even so, consideration of all experimental manipulations to date (Table 2), suggests that reproductive output per female in multiple-female groups is generally less, and can only approach that of single-female groups. Females seem to have higher fitness if each is able to secure its own resource. Therefore, other factors such as a shortage of available resources, difficulty in controlling access to a large resource, or reducing the costs of contests (Eggert and Müller, 1992; Trumbo and Wilson, 1993; Scott and Williams, 1993), are likely to be important in the formation of communal breeding associations by burying beetles on large carcasses.

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