

# Brood discrimination, nest mate discrimination, and determinants of social behavior in facultatively quasisocial beetles (*Nicrophorus* spp.)

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In this study we investigated ecological determinants of sociality in burying beetles (*Nicrophorus* spp.), potential conflicts of interest among reproductive females, and the effects of nesting failure and costs of fighting on cooperation. Burying beetles are known to form monogamous pairs when exploiting small vertebrate carcasses. More complex social behavior in this group is poorly understood. We conducted experiments in which one or two females (*N. defodiens*, *N. orbicollis*) were provided small or large carcasses on which to breed. On large but not on small carcasses, two females often formed cooperative breeding associations (jointly prepared a carcass and fed young). In *N. defodiens*, but not *N. orbicollis*, two females produced a larger brood than single females on large carcasses. In both species, the reproductive output per female was less for two than for one female. The presence of a second female did not decrease the preparation time of a carcass (discovery of resource to egg hatch). Conflict was evident between females. Trials employing females of similar size were more likely to result in injury than trials using females of dissimilar size (*N. tomentosus*, *N. defodiens*, *N. orbicollis*). In *N. tomentosus*, those associations that persisted the longest resulted in the fewest injuries. After care of young was initiated, conflict among familiar nest mates was not observed. There was no evidence that breeding females could discriminate between brood; use of a genetic marker (*N. orbicollis*) demonstrated that females fed related and unrelated young alike. Females of similar size (high potential cost of fighting for the dominant individual) were not more likely to form cooperative breeding associations than females of dissimilar size (low cost of fighting for dominant). Females of a species subject to a high rate of nest failure (*N. defodiens*) were more likely to cooperate than females of a species with a low rate of nest failure (*N. orbicollis*). It is argued that limited reproductive opportunities, difficulty in controlling rivals' access to a large carcass, and the superabundant larval food supply represented by a large carcass, but not kin selection, have contributed to the evolution of cooperative behavior in this group. In addition, we hypothesize that beetles might initially tolerate consensual rivals on large carcasses when there is a high likelihood of nesting failure, thereby avoiding potentially costly conflicts. **Key words:** burying beetles, cooperative breeding, sociality, parental care, aggression, nest mate discrimination, *Nicrophorus orbicollis*, *N. defodiens*, *N. tomentosus*. [*Behav Ecol* 4:332–339 (1993)]

Quasisociality, characterized by cooperative brood care without reproductive castes or overlap in generations (Michener, 1969), is poorly understood. Although often regarded as a state in which conflict predominates over cooperation and as an ontogenetic transition to higher levels of sociality (Michener, 1974), stable quasisocial associations have been described (Abrams and Eickwort, 1981; Sakagami and Zucchi, 1978). To understand such systems, it is necessary to explore both the physical determinants of the breeding system and potential conflicts of interest within the society. Two foci of conflicts involve access to reproductive opportunities and care of the young. Burying beetles (Silphidae: *Nicrophorus*) are excellent subjects for examining environmental determinants of sociality and conflicts of interest because they exhibit both intraspecific plasticity and interspecific variation in their behavior and are amenable to experimental manipulation.

Burying beetles locate, bury, and prepare vertebrate carcasses as a food source for their brood (Fabre, 1899; Pukowski, 1933). Females oviposit in the soil away from the carcass, and parent(s) begin brood care after young hatch out and make their

way to the nest (Pukowski, 1933). Care includes regurgitations to younger larvae and protection from predators and congeneric intruders (Scott, 1990; Trumbo, 1990b). The dominant male and female are thought to form a monogamous pair (Pukowski, 1933; Trumbo, 1991). Recent work has demonstrated that groups of three or more beetles are sometimes found with brood in the field (Scott and Traniello, 1991; Trumbo, 1992) and that both maternity and paternity can be shared (Eggert and Müller, 1992; Scott and Williams, 1993). The degree of shared parentage seems higher than would be expected from brood parasitic (Müller et al., 1990) and satellite male copulatory behavior (Bartlett, 1988). Although group size has been correlated with carcass size in the field (Scott and Traniello, 1991; Trumbo, 1992), it is not clear how behavioral interactions affect group size and what level of sociality has been attained (i.e., the breeding status of group members was unknown, and it was not possible to control for differences in discovery rates of small and large carcasses).

To address possible cooperative breeding in this group, we propose a delayed fighting hypothesis, which states that intense fights are postponed until

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individuals obtain information that a resource is likely to support a brood. Tolerance of rivals and eventual cooperative brood care should be more likely to occur when the costs of fighting are high relative to reproductive benefits. In burying beetles, for instance, reproductive output on a large carcass is quite unpredictable, and the expected output is low (Trumbo, 1992), despite the fact that it is a potential superabundant resource for larvae. We predict that (1) burying beetles will be more likely to cooperate when the nest failure rate is high, as occurs when a competitively inferior species colonizes the resource (*N. defodiens*, for example, is often displaced from carcasses by the larger *N. orbicollis*; Trumbo 1991a, 1992; Wilson and Knollenberg, 1984) and (2) competitors of similar fighting ability will be more likely to delay fights and cooperate than mismatched individuals because of the greater costs of fighting.

In this study we (1) determine whether female burying beetles feed young cooperatively, (2) examine the ability of females to discriminate adult nest mates from non-nest mates, (3) compare the reproductive performance (brood number, total brood mass, and preparation time of the carcass) of single females to two females, (4) make an initial test of the prediction that beetles will cooperate when nest failure rate is high by manipulating carcass size in two species that differ in competitive ability and the probability of nest failure, and (5) test the prediction that competitors of similar fighting ability will be more likely to delay fights by comparing cooperative behavior of similar-size and mismatched females.

## METHODS

### Experiment 1: Cooperative feeding in *N. orbicollis*

We used females from two laboratory strains of *N. orbicollis*, normal and spotless (missing the basal two spots on the elytra), to examine possible cooperative feeding of young. Both strains were derived from a natural population at the University of Michigan Biological Station (UMBS), have equivalent fitness in the laboratory, and breed true within the strain (Trumbo and Fiore, 1991). We housed beetles at 23°C and kept them on a 15 h light : 9 h dark photoperiod. In 42 trials, two females (normal and spotless) were provided a 180–250 g rat carcass (*Rattus rattus*) under a paper towel in a 8 × 15 × 30-cm plastic container that was three-quarters filled with soil. Females previously had been mated to unrelated males from their strain (a female will use stored sperm to fertilize eggs and will care for young on her own if a male fails to discover the carcass; Eggert, 1992; Eggert and Müller, 1989). We divided female dyads into two treatments to examine the effect of relative body size on the tendency to form cooperative associations. In half of the trials, the females were of similar size (less than 5% difference in both pronotal width and body mass) and in the other half, females were mismatched (>10% difference in pronotal width and >20% difference in body mass). Six days after presentation of the carcass, we checked containers daily until larvae had made their way to the carcass. On the second day after arrival of larvae, 2-h observations were

made under red light. If both females were not on the carcass, we checked the set-up twice daily for 3 days to verify that the dyad had not formed a communal association. In communal associations, the first 3 young fed by each female were removed and reared in separate containers on chicken liver or by *N. defodiens* foster parents which had their own young removed (necessary for smaller *N. orbicollis* larvae; see Trumbo 1992). The remaining larvae were left on the carcass with the two females. We determined the strain of each offspring after emergence as an adult.

### Experiment 2: Cooperation and reproductive success

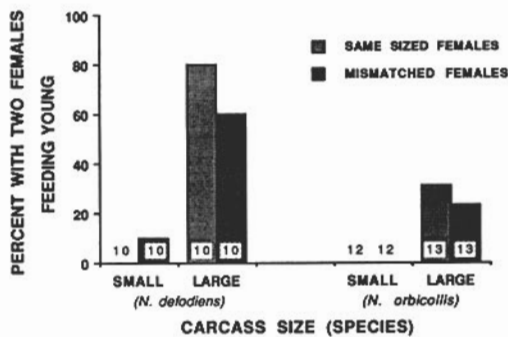
We collected *N. orbicollis* and *N. defodiens* in June and July 1991 at UMBS in pitfall traps baited with ripe carrion. We kept the beetles in mixed-sex groups at ambient room temperature, under natural photoperiod for 5–10 days before the experiments and continuously supplied them with small pieces of chicken liver. All beetles were checked for injuries to legs and antennae.

Six experimental treatments were established using *N. defodiens* ( $N = 10\text{--}12/\text{treatment}$ ). We provided one or two females (similar or mismatched dyads) a small (15–25 g, *Mus musculus*) or large (50–90 g, *Rattus rattus*) carcass in a container as described above. We kept breeding containers under a red light and checked them daily beginning on day 4. After larvae were established on the carcass, we made two observations (10 min) each day to determine whether females fed young. Females feeding young were marked on the elytra with a nontoxic paint. When a female was absent from the carcass for 3 consecutive days, we removed her and checked her again for injuries (severance of legs or antennae). In trials with dyads, females were scored as “cooperative feeders” if both fed at least two larvae. Measures of reproductive performance were number of larvae, total brood mass at dispersal, and preparation time of the carcass (time from presentation until arrival of larvae).

Cooperative breeding attempts in which both *N. defodiens* females remained with the brood until day 3 after larvae arrived were employed in nest-mate discrimination tests. We chose one of the two females randomly, removed her from the carcass, and placed her in a small cup (8-cm diam). We then placed the nest mate or a non-nest mate intruder female (well-fed but not in possession of a carcass) into the cup for 6 min and recorded the number of attacks (biting attempts). Nest mate(s) were then placed back on the carcass, and 6–12 h later the female was tested with a female from the alternative treatment. In five cases we presented the nest mate first, and in four cases we presented the non-nest mate first.

The same six experimental treatments [one or two females (similar sizes or mismatched dyads) on small and large carcasses] were established using *N. orbicollis* ( $N = 12\text{--}13/\text{treatment}$ ). The procedure was as described for *N. defodiens* except that daily checks began on day 5, small carcasses were 25–30 g, large carcasses were 180–300 g, and nest-mate discrimination tests were not performed because few dyads stayed on the carcass together for

**Figure 1**  
Percentage of carcasses on which two females fed young. Log-linear analysis of  $2 \times 2 \times 2$  contingency tables [*N. defodiens*: carcass size (CSIZ)  $\times$  cooperative feeding (CF),  $G = 16.98, p < .001$ ; relative body size (RBS)  $\times$  CF,  $G = 0.16, p > .20$ ; CSIZ  $\times$  RBS  $\times$  CF,  $G = 1.85, p > .10$ ; *N. orbicollis*: CSIZ  $\times$  CF,  $G = 7.54, p < .01$ ; RBS  $\times$  CF,  $G = 0.00, p > .20$ ; CSIZ  $\times$  RBS  $\times$  CF,  $G = .20, p > .20$ ; each test had 1 df]. Sample sizes are shown at the base of each bar.



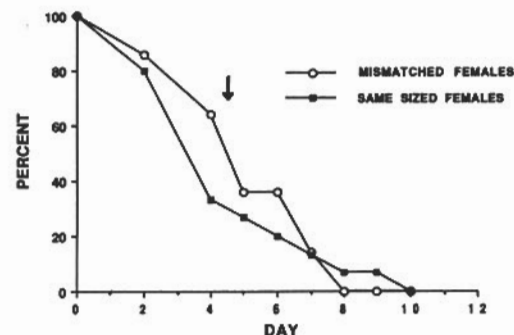
an extended period. We scaled large carcasses in the *N. defodiens* and *N. orbicollis* experiments to body size of the beetle such that the carcass mass was 2–3 times that required to raise a single maximal brood (see Trumbo, 1992, for maximal reproductive output by single females of different size species).

### Experiment 3: Body size and cooperation in *N. tomentosus*

To examine the ontogeny of potentially cooperative relationships, *N. tomentosus* females (similar size or mismatched dyads) were established on intermediate-size carcasses (33–39 g) (beetles were collected at UMBS during July, 1992). We checked nests briefly on days 2 and 4 and each day thereafter to determine the location of both females. As in experiment 2, we removed any female that was away from the carcass for 3 consecutive days and noted any injuries. Reproductive measurements were taken as in experiment 2.

### Statistical analysis

Unless otherwise specified, continuous dependent variables were analyzed using one-way or two-way ANOVA (Wilkinson, 1989), and discrete variables were analyzed using hierarchical log-linear techniques for two- or three-factor contingency tables (all reported  $G$  values were adjusted using William's correction; Sokal and Rohlf, 1981).



**Figure 2**  
Percentage of carcasses with two females remaining in the nest as a function of time in *N. tomentosus*. The arrow represents the mean time at which larvae were first seen on the carcass.

## RESULTS

### Experiment 1: Cooperative feeding in *N. orbicollis*

The normal and spotless female fed young jointly (both females on the carcass and feeding young) in 8 of 42 trials, with no indication that parents biased feedings toward their own offspring. Of 24 larvae fed by normal females (removed and raised separately), 54% were normally marked. This was not significantly different from the proportion of normal offspring in the total population of offspring (53% normal,  $N = 179, G = 0.02, p > .20$ ). Similarly, 62% of 21 young fed by spotless females were normal ( $G = 0.59, p > .20$ ; 3 offspring failed to reach the adult stage). Females in mismatched dyads were just as likely to feed young jointly (19%,  $G = 0.00, p > .20$ ) as females with a similar-size partner.

### Experiments 2 and 3: Cooperative associations

For both *N. defodiens* and *N. orbicollis*, females in dyads were much more likely to feed young jointly on large than on small carcasses. The tendency of females to cooperatively feed young, however, was not dependent on whether females were of similar size or mismatched (Figure 1). Females of the smaller species, *N. defodiens*, were much more likely to feed young cooperatively on large carcasses than females of *N. orbicollis* (70% versus 27%,  $G = 8.43, p < .005, N = 20, 26$  for *N. defodiens* and *N. orbicollis*, respectively).

The relative body size of *N. tomentosus* females did not affect the probability that they would both be on the carcass 1 day after larvae arrived ( $G = 0.80, p > .20$ ) nor the length of their association (Figure 2). The most extreme difference (on day 4) was not significant ( $G = 2.81, .05 < p < .10$ ) and was in the opposite direction of that predicted. When mismatched females jointly fed larvae, the larger female stayed with the brood longer in seven of eight trials for *N. tomentosus* ( $p = .035$ , one-tailed binomial test) and in six of seven trials for *N. defodiens* ( $p = .06$ ).

### Injuries

The first female to leave the carcass was injured more often in similar-size rather than in mismatched dyads in all three species, as expected if closely matched opponents engaged in more intense conflicts (Figure 3; this result was not significant for *N. tomentosus*). In each species, the total number of beetles injured was greater in similar-size dyads (*N. tomentosus*:  $G = 4.36, p < .05$ ; *N. defodiens*:  $G = 10.50, p < .005$ ; *N. orbicollis*:  $G = 16.16, p < .001$ ;  $N =$  twice the values reported in Figure 3). In *N. tomentosus*, the longest associations produced the fewest injuries. The first female to leave the carcass was more likely to be injured when associations between females lasted less than 4 days (60%) than when associations lasted 4 or more days (21%,  $G = 4.31, p < .05$ ). For both *N. defodiens* and *N. orbicollis*, there was a trend toward fewer injuries when cooperative feeding occurred rather than when it did not occur on large carcasses, but these tests did not approach significance ( $p > .15$ ).

Because the proportion of cooperative to non-cooperative trials was quite unbalanced in these two species, the statistical test was less powerful. In all three species, no aggressive interactions were recorded during observations of joint care of young by two females.

### Nest-mate discrimination

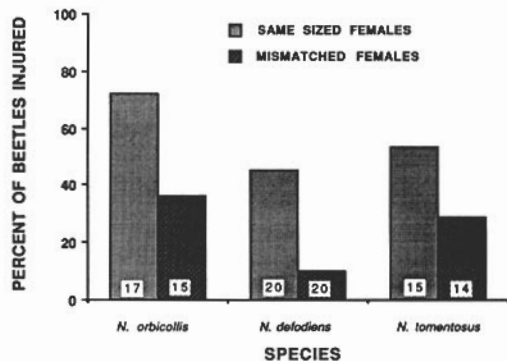
There were 14 trials in which *N. defodiens* females jointly fed young. Of these, the nine in which both females remained on the carcass until day 3 after the arrival of larvae were used in nest-mate discrimination tests. The resident female never attacked its nest mate. In contrast, the resident attacked the unfamiliar female in seven of nine trials ( $p < .01$ , Fisher's Exact test) with a mean ( $\pm$ SE) of 5.0 ( $\pm 1.9$ ) attacks per 6-min trial. Fighting was always initiated by the resident female; the intruder never attempted to bite unless the resident had gripped the intruder with its mandibles.

### Preparation time of the carcass

The presence of a second female does not shorten the preparation time of the carcass (time of discovery until larvae arrive on the carcass). When *N. defodiens* exploited a large carcass, preparation time was slightly longer in trials with two females rather than one ( $p = .03$ ,  $N_1 = 12$ ,  $N_2 = 20$ , Mann-Whitney *U* test), but no effect was seen on small carcasses ( $p = .23$ ,  $N_1 = 12$ ,  $N_2 = 20$ ). For *N. orbicollis*, preparation time was longer in trials with two females on small carcasses ( $p = .01$ ,  $N_1 = 12$ ,  $N_2 = 24$ ), but there was no effect on larger carcasses ( $p = .17$ ,  $N_1 = 12$ ,  $N_2 = 26$ ). In *N. tomentosus*, neither relative body size of females in dyads ( $G = 0.32$ ,  $p > .20$ ) nor the duration of association (longer or shorter than 4 days) affected preparation time of the carcass ( $G = 1.58$ ,  $p > .20$ ;  $2 \times 2 \times 2$  contingency test).

### Number and size of larvae

For *N. defodiens*, there were more young produced and a greater total brood mass on large as opposed to small carcasses. In addition, both measures of reproductive output were significantly greater in trials with two females than trials with a single female (Figure 4). There was a significant interaction between carcass size and number of females, which perhaps can be explained by a positive effect of a second female on number of offspring on large but not small carcasses. This seems to be verified by separate analyses of small and large carcasses: on large carcasses a second female produced a significant increase in number of larvae ( $F_{1,28} = 11.38$ ,  $p < .01$ ) and brood mass ( $F_{1,28} = 9.50$ ,  $p < .01$ ), but no effect was recorded on small carcasses (number of larvae:  $F_{1,30} = 1.11$ ,  $p > .20$ ; brood mass:  $F_{1,30} = 0.26$ ,  $p > .20$ ; one-way ANOVAs). On large carcasses, two females produced 53% more larvae and a 44% greater brood mass than a single female. *N. orbicollis* experienced greater reproductive success on large rather than on small carcasses, but the number of females had no significant effect (Figure 4). In both *N. defodiens* and *N. orbicollis*, the number of larvae and total brood mass per female was significantly lower in trials with two females



**Figure 3**

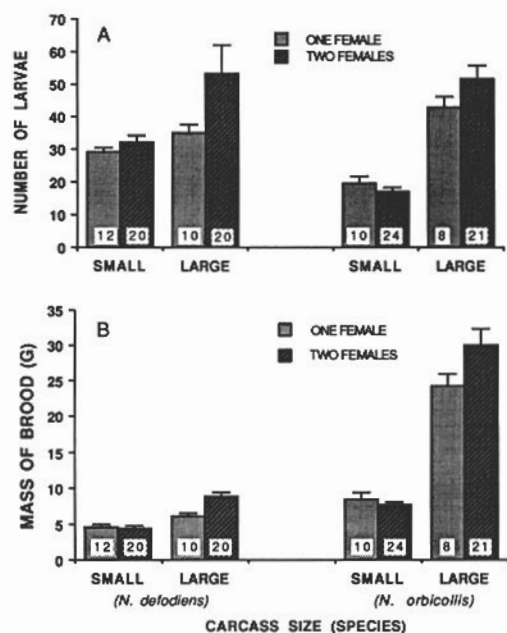
Percentage of first females to leave the carcass that were injured. Log-linear analysis of  $2 \times 2$  table (*N. orbicollis*, effect of relative body size,  $G = 6.11$ ,  $p < .025$ ; *N. defodiens*,  $G = 10.44$ ,  $p < .005$ ; *N. tomentosus*,  $G = 1.78$ ,  $p > .20$ ; each test had 1 df). Sample sizes shown at the base of each bar.

compared to single females for both sizes of carcass (all  $p < .01$ ; one-way ANOVAs).

In *N. defodiens* (trials with two females), neither the number of larvae nor total brood mass was affected by the relative body size (RBS) of the two females [number of larvae: carcass size (CSIZ),  $F_{1,37} = 25.98$ ,  $p < .001$ ; RBS,  $F_{1,37} = .18$ ,  $p > .20$ ; brood mass: CSIZ,  $F_{1,37} = 45.55$ ,  $p < .001$ ; RBS,  $F_{1,37} = .01$ ,  $p > .20$ ; interactions ns]. In *N. orbicollis*, RBS did not affect brood mass (CSIZ,  $F_{1,42} = 101.53$ ,  $p < .001$ ; RBS,  $F_{1,42} = 2.03$ ,  $p = .16$ ), but there was a significant effect on number of larvae (CSIZ,  $F_{1,42} = 80.19$ ,  $p < .001$ ; RBS,  $F_{1,42} = 4.17$ ,  $p = .047$ ). The production of more larvae by similar-size dyads is difficult to interpret and needs further confirmation because relative body size had a marginally significant effect on only one of two measures of reproductive output in just one of three species, and this effect was overwhelmed by a carcass size effect. In *N. tomentosus* the number of larvae and brood mass were not affected by whether females associated for less than 4 days or for 4 or more days ( $F = 0.04$ ,  $0.06$  for number of larvae and brood mass, respectively) or whether females were

**Figure 4**

Mean ( $\pm$ SE) number of larvae (A) and total brood mass at dispersal (B) produced by one and two females. Two-way ANOVAs [*N. defodiens*: (number of larvae), carcass size (CSIZ),  $F_{1,58} = 20.40$ ,  $p < .001$ ; number of females (NF),  $F_{1,58} = 12.91$ ,  $p = .001$ ; CSIZ  $\times$  NF,  $F_{1,58} = 7.04$ ,  $p = .01$ ,  $r^2 = .47$ ; (total brood mass), CSIZ,  $F_{1,58} = 39.33$ ,  $p < .001$ ; NF,  $F_{1,58} = 7.56$ ,  $p < .01$ ; CSIZ  $\times$  NF,  $F_{1,58} = 9.88$ ,  $p < .01$ ,  $r^2 = .56$ ; *N. orbicollis*: (number of larvae), CSIZ,  $F_{1,59} = 71.87$ ,  $p < .001$ ; NF,  $F_{1,59} = 0.83$ ,  $p > .20$ ; CSIZ  $\times$  NF,  $F_{1,59} = 2.59$ ,  $p > .10$ ,  $r^2 = .65$ ; (total brood mass), CSIZ,  $F_{1,59} = 103.52$ ,  $p < .001$ ; NF,  $F_{1,59} = 1.62$ ,  $p > .20$ ; CSIZ  $\times$  NF,  $F_{1,59} = 2.95$ ,  $p = .09$ ,  $r^2 = .72$ ]. Sample sizes are shown at the base of each bar and may not add up to the total number of trials because reproductive failures (9%) were not included in the analysis.



of similar size or mismatched ( $F = 0.14, 0.66$  for number of larvae and brood mass, respectively; all  $p > .20$ ).

## DISCUSSION

This study demonstrates that female burying beetles tolerate consensual nest mates, share maternity, and feed unrelated young under some environmental conditions. Recent evidence for shared maternity is also provided by Eggert and Müller (1992) and Scott and Williams (1993). We believe burying beetles, therefore, should be regarded as facultatively quasisocial (Michener, 1969). Earlier descriptions of quasisociality often emphasized the transitional nature of this level of sociality (Eickwort, 1975; Michener, 1974) and suggested that cooperative brood care among insects in the absence of advanced social characteristics (reproductive castes) is an unstable state and might simply result from occasional provisioning mistakes by parents (Bohart, 1955; Zucchi et al., 1969). There are several reasons why such explanations are inadequate for burying beetles: (1) the quasisocial state is an endpoint (nonreproductive adults never contribute parental care); (2) frequent, nonaggressive interactions among females with larvae suggest that this system has reached a degree of stability; (3) feeding of unrelated young is commonplace; and (4) quasisocial behavior does not occur sporadically but predictably on large carcasses. Thus, burying beetles have reached a level of sociality at least equal to that of many communal bees and wasps in which reproductive females jointly provision nest cells (Abrams and Eickwort, 1981; Brockmann and Dawkins, 1979; Stark et al., 1990).

Previous work suggests that burying beetle adults cannot discriminate between related and unrelated young that arrive on the carcass at the "expected" time (those young that arrive within a window of acceptance that corresponds to the female's oviposition period; Müller and Eggert, 1990; Trumbo, 1993). In this study, use of a genetic marker in undisturbed communal breeding attempts confirms that females do not bias care even when we expect the most intense selection for discrimination (breeding in a group and caring for a mixed brood). Should a discriminatory ability evolve, it would likely spread to fixation and make the quasisocial state unstable. We hypothesize that burying beetles feed any larvae on the carcass to ensure adequate care for their own young. Similarly, when individuals attack unfamiliar intruders, they protect their own as well as unrelated young. A beetle that deserts early risks having inadequate care provided to its offspring. Such cooperative behavior ("byproduct mutualism") can evolve in the absence of kin selection or score-keeping reciprocity (Mesterton-Gibbons, 1991; Wilson, 1990; see Getty, 1987; Mesterton-Gibbons M and Dugatkin LA, in preparation, for discussion of the appropriateness of the term "cooperation" in this context). Although conflicts among breeding females exist (as evidenced by injuries and possible infanticide), we predict that aggression will not be observed once larvae of both females are established on the carcass because of adults' inability to bias care toward their own offspring.

Most insect studies have emphasized nest-mate recognition as an indirect mechanism of kin recognition (Buckle and Greenberg, 1981; Gamboa et al., 1986; Isingrini et al., 1985; Matthews, 1991), even though it is increasingly clear that kin selection is not a requirement for the evolution of cooperative breeding in insects or vertebrates (Pollock and Rissing, 1988; Stacey and Koenig, 1990). Although there are no data on the genetic structure of burying beetle populations, kin selection does not appear to be important to cooperative nest building and communal breeding. Siblings emerge as adults at different times, disperse over large distances in search of a fresh carcass, and have not been observed to fly together in the field or laboratory. Burying beetles and harvester ants (Rissing and Pollock, 1987) thus represent the best insect examples to date of nest-mate discrimination in the absence of kin selection. The ability to discriminate against non-nest mates in burying beetles probably functions to exclude individuals that do not have a genetic interest in any of the brood. Such intruders commonly commit infanticide, mate with residents of the opposite sex, and attempt to appropriate the resource for their own reproductive benefit (Scott, 1990; Trumbo, 1990b).

In field studies, Scott and Traniello (1991) and Trumbo (1992) correlated group size of burying beetles with carcass size. Whether altered behavioral interactions were partly responsible for this correlation was not clear because large carcasses attracted more beetles (Trumbo, 1993). By controlling the discovery rate in the laboratory and by using genetic markers, it is evident that carcass size is a major determinant of this breeding system. In the field, tolerance of consensuals as well as the attractiveness of the resource can account for larger groups on larger carcasses.

When the nesting attempt is considered as a whole, it is unclear whether forming a communal association benefits the adults involved. In the laboratory, two females clearly do not achieve the same reproductive output per female as a female breeding alone even when provided a superabundant resource (see also Eggert and Müller, 1992). One explanation is selective infanticide at the time larvae are coming to the carcass; a female will kill young that arrive outside of her window of acceptance (Müller and Eggert, 1990). It is also apparent that the presence of a second female fails to shorten the time until the production of brood, a benefit recorded for co-founding ants and wasps (Queller et al., 1988; Rissing and Pollock, 1987). Intragroup conflict as evident in burying beetles by a high injury rate, possible selective infanticide, and lower reproductive output per female is a common feature of parasocial and weakly eusocial insects as well as of cooperative breeding vertebrates (Brockmann, 1984; Queller and Strassmann, 1988; Ross and Matthews, 1991; Stacey and Koenig, 1990; Vehrencamp et al., 1988).

Why, then, is a consensual tolerated in the first place? Although habitat saturation (Brown, 1974; Herbers, 1986) may be a necessary condition for communal breeding in this group (there are more beetles than available carcasses; Trumbo, 1992; Wilson and Fudge, 1984), it cannot explain why subordinates are chased away from a small carcass but are often tolerated on a large carcass. Toler-

ating a second female might be beneficial for circumstances in the field present challenges that can be better handled by larger groups. Attempts to demonstrate that larger groups of beetles are more effective in dealing with dipteran competitors (Trumbo ST, unpublished results) or predators (Scott, 1990) have not been successful.

From the first resident's perspective, it might be preferable if the resource was never discovered by a second female. Once the discovery occurs, however, the relevant questions are what is the best behavioral response of both individuals ("making the best of a bad situation," Brockmann, 1984) and is an attempt at expulsion worth the costs? If the costs of fighting are significant, then the stable group size is likely to be larger than the optimal group size. The delayed fighting hypothesis proposes that costly fights are postponed until beetles obtain information that the carcass is likely to support brood.

The prediction that cooperation would be more likely to occur with similar-size females rather than with mismatched females was based on two assumptions. The assumption that fights would be more costly in similar-size dyads was met, as evidenced by a higher proportion of injured individuals. The second assumption was that reproductive benefits would be evenly divided between females irrespective of the relative size of the females. We felt that reproductive dominance should not be pronounced in the absence of kin selection (Strassmann, 1989; Vehrencamp, 1983), especially on an ephemeral resource on which there is little chance of succession. On the other hand, if the larger female obtains considerably more than half of the reproductive benefit, the cost of tolerating a second female is reduced; this might promote tolerance of subordinates among mismatched females, making predictions difficult. The fact that the larger female in mismatched dyads stayed on the carcass for a longer duration, on average, suggests that she expected greater benefits from further parental care. Additional evidence that a disproportionate share of the brood belongs to the larger female is provided by Scott and Williams (1993) and Eggert and Müller (1992). It is possible that the shortage of available carcasses is so severe for burying beetles that considerable reproductive dominance can be maintained in the absence of kin selection.

It also was predicted that cooperation would be more prevalent when the probability of nest failure is high. Nest failure should be especially relevant on larger carcasses and for species of burying beetles that are commonly victims of takeovers by dominant congeners. For instance, *N. defodiens* was the first species to discover approximately 60% of 50–90-g carcasses at our study site in 1990, but produced larvae on only 2 of 51 carcasses (Trumbo, 1992). Takeovers by larger congeners are the most significant factor in the loss of carcasses by *N. defodiens* (Trumbo, 1990a; Wilson and Knollenberg, 1984). *Nicrophorus defodiens* that fight immediately upon discovering a large carcass will always incur the costs of fighting but only rarely obtain any reproductive benefit by excluding its rival. As predicted, *N. defodiens* was more likely to cooperate than the dominant *N. orbicollis*, even when carcass size was controlled so that a large carcass could support an equivalent number of offspring of either species. The high percentage of trials in which

two *N. tomentosus* females stayed together until after larvae arrived on intermediate-size carcasses gives additional support to the nest failure hypothesis. *Nicrophorus tomentosus*, like *N. defodiens*, is competitively inferior to the larger *N. orbicollis* (Scott MP, personal communication; Wilson and Knollenberg, 1984).

Several additional observations are relevant here. Bartlett (1988) noted that even on small carcasses, *N. vespilloides* males tolerate a competitor before the arrival of the first female adult. This suggests that fights are delayed until males obtain information that the carcass is likely to produce beetle brood. Wilson and Fudge (1984) frequently found more than one male or female *N. defodiens* on a small carcass the day after discovery. At this time there is still a high probability of a takeover by larger congeners (also see Trumbo, 1990a). Interestingly, Wilson and Fudge reported that *N. orbicollis* typically had no more than one male and female on the carcass the first day after discovery in northern Michigan, where they are successful on a very high percentage of discovered carcasses. At a second study site, however, where vertebrate scavengers discover a significant proportion of recently buried carcasses, even *N. orbicollis* tolerated conspecifics for a day until a small carcass could be taken underground. Finally, when a carcass has a low probability of producing beetle brood because it is heavily exploited by dipterans, aggression is almost nonexistent. We have found as many as 15 individuals representing 4 species in feeding aggregations on a carcass in this condition in the field.

Delaying a fight also reduces the effectiveness of an eventual contest in suppressing the reproductive contribution of the loser. If the fight does not occur by the time that larvae are established on the carcass, then the fight can produce no benefit for the winner. The longest associations in *N. tomentosus* produced the fewest injuries, suggesting that one benefit of cooperation is to reduce the costs of fighting. We predict that after larvae are established, associations will break down because of desertion rather than fighting. On larger carcasses, contests also might be less effective in suppressing subordinates' reproductive activity because the carcass is more difficult to patrol, and losers will likely have greater access to the resource.

Selection for delayed fighting can give rise to the grouping of conspecific breeding adults in the absence of clear benefits for group members. Evolutionarily, this mechanism may be important in initiating grouping and thereby allowing selection for more coordinated cooperative behaviors. Unfortunately, models of cooperation rarely incorporate a temporal component (but see Pollock and Rissing, 1988). The shift from cooperation to conflict often occurs at very predictable times. Among co-founding ants and wasps, for instance, conflict often increases just before the production of reproductive eggs (Noonan, 1981; Pollock and Rissing, 1988; Reeve, 1991). In burying beetles, we expect that conflict will be focused around oviposition (when a subordinate female can be excluded from the resource) or just before the arrival of larvae (when a female can be prevented from killing young that arrive outside her window of acceptance).

In this paper we have uncovered several impor-

tant features of the burying beetle breeding system. Breeders feed each other's offspring, residents with young tolerate nest mates and attack non-nest mates, and cooperative care of young is much more likely to occur on a large resource. We believe this group should be characterized as facultatively quasiosocial. Interspecific comparisons of cooperative breeding tendencies gave some support for the delayed fighting hypothesis. Results from reproductive attempts by evenly matched and mismatched females did not support this perspective. Several areas need further attention: genetic markers need to be used in studies of reproductive dominance, observations should be undertaken at critical junctures in the breeding attempt, and field work must be done to more accurately account for the benefits of grouping. The facultative nature of reproductive behavior and the ability to undertake manipulative experiments using genetic markers should make this a rich group for exploring the threshold of sociality.

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