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

Stephen T. Trumbo
David S. Wilson
Department of Biology
State University of New York
Binghamton, NY 13902-6000, USA

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 nestling failure and costs of fighting on cooperation. Burying beetles are known to form monogamous pairs when exploiting small carcasses and form cooperative breeding associations (jointly prepared a carcass and fed young) in N. defodiens, but not N. orbicollis. In N. defodiens, 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. imitans, N. defodiens, N. orbicollis). In N. imitans, 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 was 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 kin selection, have contributed to the evolution of cooperative behavior in this group. In addition, we hypothesize that beetles might initially tolerate congeneric rivals on large carcasses when there is a high likelihood of nestling failure, thereby avoiding potentially costly conflicts. Key words: burying beetles, cooperative breeding, sociality, parental care, aggression, nest mate discrimination, Nicrophorus orbicollis, N. defodiens, N. imitans. [Behav Ecol 4:332-339 (1993)]

Q uasisociality, characterized by cooperative brood care without reproductive cases or overlap in generations (Michener, 1969), is poorly understood. Although often regarded as a state in which conflict prohibits cooperation and interests among reproductive females, the potential conflicts of interest on the behaviour of Nicrophorus defodiens levels of sociality (Michener, 1974), stable, quasi- social associations have been described (Abrahms and Eckworth, 1981; Sakagami and Zacchi, 1978). To understand such systems, it is necessary to explore both the ecological determinants of the breeding system and potential conflicts of interest within the society. Two of these conflicts involve access to reproductive opportunities and care of the young. Burying beetles (Sphindidae: Nicrophorus) are excellent subjects for exploring the 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 (Fahie, 1899; Pokoski, 1933). Females oviposit in the soil away from the carcass, and parents begin brood care after young hatch and make their way to the nest (Pokoski, 1933). Care includes regurgitations to young larva and protection from predators and congeneric intruders (Scott, 1990; Trumbo, 1986b). The dominant male and female are thought to form a monogamous pair (Pokoski, 1933; Trumbo, 1991). Recent work has demonstrated that groups of three or more beetles are sometimes found with brood in the field (Scott and Tramille, 1991; Trumbo, 1992) and that both hostility and parent care can be shared (Egger and Miller, 1992; Scott and Williams, 1989). The degree of shared parent care seems higher than would be expected from brood parasitism (Miller et al., 1990) and satellite male copulatory behavior (Egger et al., 1988). Although group size has been correlated with survival of young in the field (Scott and Tramille, 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 is unknown, and it was not possible to control for differences in natal care 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

S. T. Trumbo is now at the Department of Entomology, University of Illinois, Urbana, IL 61801, USA.
Received 13 April 1992
Revised 9 September 1992
Accepted 28 September 1992

© 1993 International Society for Behavioral Ecology

352 Behavioral Ecology Vol.4 No.4
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 carrion size in two species that differ in competitive ability and the probability of nest failure, and (5) test the prediction that nestmate competition of similar-sex females will be more likely to delay fights by comparing competitive behavior of similar-size and mismatched females.

METHODS

Experiment 1: Cooperative feeding in 
order

We used females from two laboratory strains of N. orbicollis, normal and spotters (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's botanical garden (UBMS), have equivalent fitness in the laboratory, and breed true within the strain (Trumbo and Firet, 1991). We housed beetles as 23°C and kept them on a 15 h light:9 h dark photoperiod. In 62 trials, two females (normal and spotters) were provided a 180-200 g rabbit carcass (Rattus rattus) under a paper towel in a 8 x 15 x 30 cm plastic container that had three-quarter size holes in soil. Females previously had been mated to unrelated males from their strain (a female will use preovulatory accessory gland fluid 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 feed cooperatively. In the first treatment, the females were of similar size (≤ 5% difference in both prosectional width and body mass) and in the other half, females were mismatched (> 10% difference in prosectional width and > 20% difference in body mass). Six days after presentation of the carcass, we checked containers daily until larval 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 setup twice daily for 3 days to verify that the dyad had not formed a communal association. In communal associations, the first 5 rowed feces by each female were removed and reared in separate containers on chicken liver or by N. difficilis foster parents which had their own young removed (removed for smaller N. orbicollis larvae; see Trumbo 1992). The remaining larvae were left on the carcass. We determined the strains of each offspring after emergence as an adult.

Experiment 2: Cooperation and reproduction

We collected N. orbicollis and N. difficilis in June and July 1991 at UBMS in pitfall traps baited with ripe carrot. We kept them in cages in mixed-sex groups at ambient room temperature, under natural photoperiod for 3–10 days before the experiments and continuously supplied them with small pieces of chicken liver. All beetles were checked for injures to legs and antennae.

Six experimental treatments were established us-
ing N. difficilis (N = 10–12/treatment). We pro-
vided one or two females (similar-sized or mismatched dyads) a small (15–25 g, Mus musculus) or large (56–90 g, Rattus rattus) carcass in a container as described above. We kept breeding containers un-
der a red light and checked them daily beginning on day 4. After larvae were established on the car-
cass, we made two observations (10 min) each day to determine whether females fed young. Females feeding young were removed and replaced with a nonsexed parent. When a female was absent from the carcass for > 4 consecutive days, we removed her and checked her again for injuries (severance of legs or antennae). In this way, dyads with dyads, female pairs were scored as "cooperative" 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 pre-
semination until arrival of larvae).

Cooperative breeding attempts in which both N. difficilis females remained with the brood until day 18 after larval arrival were employed in nest-mate discrimination tests. We chose one of the two fe-
nales randomly, removed her from the carcass, and placed her in a smaller cup (8 cm diameter). We then placed the nest mate or a non-mate introducer female (well-fed but not in possession of a carcass) into the cup for 6 min to record the number of attacks (attacking attempts). Nest mates were then placed back on the carcass, and 1–2 h later the female was tested with a female from the alternative treatments. 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-sized or mismatched dyads) on small and large carcasses were established using N. orbicollis (N = 12–18/treatment). The procedure was as described for N. difficilis except that daily checks began on day 5, small carcasses were 23– 30 g, large carcasses were 180–90 g, and nest-
mate discrimination tests were not performed be-
cause few dyads stayed on the carcass together for
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 (Trumbo, 1992, for maximal reproductive output by single females of different size species).

**Experiment 5: Body size and cooperation in N. tenuicollis**

To examine the ontogeny of potentially cooperative relationships, *N. tenuicollis* females (similar-size or mismatched dyads) were established on intermediate-size carcasses (53–59 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 *p* 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. tenuicollis*. 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 spotted female fed young jointly (both females on the carcass and feeding young) in 8 of 42 trials, with no indication that partenogenetic feedings toward their own offspring. Of 34 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 (55% normal, *N* = 179, *p* = 0.02, *p* > 0.05). Similarly, 62% of 21 young fed by spotted females were normal (*G* = 0.59, *p* > 0.05, 0.03 as females with a smaller-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* (RHR versus ZPH, *G* = 8.45, *p* < 0.01, *N* = 20, 26 for *N. defodiens* and *N. orbicollis*, respectively).

The relative body size of *N. tenuicollis* females did not affect the probability that they would both be on the carcass 1 day after larval arrived (*G* = 0.60, *p* > 0.05) nor the length of their association (Figure 2). The most extreme difference (on day 4) was not significant (*G* = 2.81, *p* > 0.05) 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. tenuicollis* (*p* = 0.05, one-tailed binomial test) and in six of seven trials for *N. defodiens* (*p* = 0.05).

**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. tenuicollis*). In each species, the total number of beetles injured was greater in similar-size dyads (*N. tenuicollis*: *G* = 6.85, *p* < 0.05; *N. defodiens*: *G* = 15.50, *p* < 0.005; *N. orbicollis*: *G* = 16.16, *p* < 0.001). *N* is twice the variance reported in Figure 5). In *N. tenuicollis*, 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%). 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 at large carcasses, but these tests did not approach significance (*p* > 0.15).
Because the proportion of cooperative to noncooperative 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.

Neat-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 neat-mate discrimination tests. The resident female never attacked her mate. In contrast, the resident attacked the unfamiliar female in seven of nine trials (p < .01, Fisher's exact test) with a mean (±SE) of 3.0 (±1.0) attacks per female 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 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 = 12, N = 20, Mann-Whitney U test), but no effect was seen on small carcasses (p = .23, N = 12, N = 20). For N. oenotherae, preparation time was longer in trials with two females on small carcasses (p = .01, N = 12, N = 24), but there was no effect on larger carcasses (p = .17, N = 12, N = 20). In N. tomentosa, 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 x 2 contingency test).

Number and size of larvae
For N. defodiens, there were more young produced and a greater total brood mass on large than on small carcasses. In addition, both measures of reproductive output were similar in trials with two females than with single females (Figure 4). There was a significant interaction between carcass size and number of females, which could perhaps 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 (p = 1.18, p < .001) and brood mass (p = .01, p < .01), but no effect was recorded on small carcasses (number of larvae: p = 1.1, p > .20; brood mass: p = .20, p > .20, one-way ANOVA). On large carcasses, two females produced 53% more larvae and a 4% greater brood mass than a single female. N. oenotherae 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. oenotherae, the number of larvae and total brood mass per was significantly lower in trials with two females compared to single females for both sizes of carcass (all p < .01; one-way ANOVA).

In N. defodiens (trials with two females), neither the number of larvae nor the total brood mass was affected by the relative body size (RBS) of the two females (number of larvae: carcass size: CSIG, F1,21 = 29.98, p < .001; RBS, F1,21 = .18, p > .20; brood mass: CSIG, F1,21 = 43.55, p < .001; RBS, F1,21 = .01, p > .20; interactions: NS). In N. oenotherae, RBS did not affect brood mass (CSIG, F1,21 = 101.53, p < .001; RBS, F1,21 = 2.03, p > .10), but there was a significant effect on number of larvae (CSIG, F1,21 = 89.19, p < .001; RBS, F1,21 = 4.17, p < .047). The production of more larvae by smaller-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 observed only by a carcass size effect. In N. tomentosa, 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, p > .06) for number of larvae and brood mass, respectively, or whether females were

---

Figure 3

Percentage of first females to leave the carcass that were inquired. Logit analysis of 2 x 2 table (N. oenotherae, effect of relative body size: G = 6.11, p = .015; N. defodiens, G = 10.44, p < .005; N. tomentosa, G = 1.78, p > .20; each test 1 df). Sample sizes shown at the base of each bar.

Figure 4

Mean (±SE) number of larvac (A) and total brood mass at (B) produced by one and two females. Two-way ANOVAs: N. defodiens (number of larvae): CSIG, F1,21 = 29.66, p < .001; number of females (NF), F1,21 = 12.91, p = .001; CSIG x NF, F1,21 = 7.96, p = .01; NF, F1,21 = 5.76, p < .01; CSIG x NF, F1,21 = 9.88, p < .01; 56, N. oenotherae (number of larvae): CSIG, F1,21 = 71.87, p < .001; NF, F1,21 = 8.93, p < .02; CSIG x NF, F1,21 = 7.95, p < .01; r2 = .56; N. oenotherae (number of larvae): CSIG, F1,21 = 10.52, p < .01; NF, F1,21 = 1.62, p > .20; CSIG x NF, F1,21 = 2.55, p < .09; r2 = .22). 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.

Trumbo and Wilson: Sociability of burying beetles
This study demonstrates that female burying beetles tolerate consensual non-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 (Bo- bart, 1955; Zucchi et al., 1969). There are several reasons why such explanations are inadequate for burying beetles: (1) the quasisocial state is an end-point (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 larger 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 next cells (Banks 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, 1992). In this study, use of a genetic marker in unrelated cohorts of young confirms that females do not bias care even when we expect the intense selection for discrimination (burrowing in aspugo and caring for a mixed brood). Should a discriminatory ability evolve, it would likely spread to the quasisocial state unaltered. 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 discovers 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 (Mesersten-Gibbons, 1991;Wilson, 1965; see: Getty, 1987; Mesersten-Gibbons & Daugatkin L.A., in preparation, for discussion of the appropriateness of the term “cooperation” in this context). Although conflicts among breeding females exist (as evidenced by the option to discriminate individual), 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 nestmate recognition as an indirect mechanism of kin recognition (Buckley and Greenberg, 1981; Gaubha et al., 1986; Insinghini et al., 1985; Matthews, 1984), 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 Risling, 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 in 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 (Risling and Pollock, 1987) thus represent the best insect examples to date of nestmate discrimination in the absence of kin selection. The ability to discriminate against non-mate 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 resident females of the opposite sex, and attempt to appropriate the resource for their own reproductive benefit (Scott, 1990; Trumbo, 1996).

In field studies, Scott and Tran towel (1991) and Trumbo (1992) correlated group size of burying beetles with carcass size. Whether altered behavioral interactions were partly responsible for this correlation is not clear because large carcasses attract 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 consensuality 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, the data indicate that 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 for reproduction (also Eggert and Müller, 1992). One explanation is selective infanticide at the larval stage to the coming 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 to ensure the time until the production of brood, a benefit recorded for co-founding ants and wasps (Queller et al., 1986; Risling 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 (Brockman, 1984; Queller and Strassmann, 1985; Ross and Matthews, 1981; Stacey and Reisinger, 1990; Vehrencamp et al., 1988).

Why, then, is a communal tolerated in the first place? Although habitat saturation (Brawn, 1974; Herbers, 1980) may be a necessary condition for communal breeding in this species (group burrowing is more than available carcasses; Trumbo, 1991; Wilson and Fugate, 1984), it cannot explain why subordinate are chased away from a small carcass. Toler-
being a second female might be beneficial if cir-
cumstances 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 digger competitors (Trumbo TH, unpublished results) or predators (Scott, 1990) have not been successful.

From a first-look perspective, it might be preferable if the resource was never discovered by a second female. Once the discovery occurs, how-
ever, 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 in-
formation 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 as-
sumptions. The assumption that fights would be more costly in similar-size dyads was met, as evi-
denced by a higher proportion of individual

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 (Strass-
mann, 1985; Vehrencamp, 1983), especially on an ephemeral resource on which there is little chance of succession. On the other hand, if the larger fe-
male 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 ex-
gected greater benefits from further parental care.

Additional evidence that a disproportionate share of the brood belongs to the larger female is pro-
vided by Scott and Williams (1995) and Figgert and Willows (1994). The higher proportion of available carcasses is so _were for burying beetles that considerable reproductive dominance can be maintained in the absence of kin selection._

It was also predicted that cooperation would be more prevalent when the probability of a carcass failure is high. Next failure should be especially relevant for larger carcasses and for species of burying bee-
tles that are commonly victims of takeovers by dom-
inant congeners. For instance, _N. fidentia_ was the first species to discover approximately 85% of 50-
90-g carcasses at our study site in 1990, but pro-
duced 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._ de-
fidentia (Trumbo, 1990; Willows and Knollenberg, 1984). _Nemrophora fidentia_ that fight immediately upon discovering a large carcass will always incur the costs of fighting but only rarely obtain any re-
productive benefit by excluding its rival. As pre-
dicted, _N. fidentia_ 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 or ei-
ther species. The high percentage of trials in which two _N. montanum_ females stayed together until after
larvae arrived on intermediate-size carcasses gives additional support to the nest failure hypothesis. _Nemrophora montanum_, like _N. fidentia_, is competit-
inferior to the larger _N. orbicollis_ (Scott MP, per-
sonal communication; Wilson and Knollenberg, 1984).

Several additional observations are relevant here. Bartlett (1988) noted that even on small carcasses, _N. nigripennis_ males tolerate a competitor before the arrival of the first female adult. This suggests that fights are delayed until males obtain infor-
mation that the carcass is likely to produce beetle brood. Wilson and Fudge (1984) frequently found more than one male or female _N. defolians_ 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). Inter-
estingly, Wilson and Fudge reported that _N. orb-
collis_ typically had no more than one male and fe-
male 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 scav-
engers discover a significant proportion of recently buried carcasses, even _N. orbicollis_ tolerated con-

In summary, the data from _N. montanum_ are consistent with the hypothesis that competition for 

We have never uncovered several impor-

Trumbo and Wilson • Sociality of burying beetles 357