Nesting failure in burying beetles and the origin of communal associations

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Summary

Information on reproductive success and the probability of nest failure was gathered from 11 recent studies of *Nicrophorus defodiens*, which readily forms communal breeding associations and *Nicrophorus orbicollis*, which rarely tolerates consexuals in the nest. *Nicrophorus defodiens* was subject to a high rate of nest failure on larger carcasses and consequently, is expected to achieve little reproductive benefit by excluding a rival during nest initiation. *Nicrophorus orbicollis*, on the other hand, was successful on a higher proportion of carcasses of all sizes and is predicted to gain substantial benefits by excluding a rival. These findings support the hypothesis that high rates of nest failure can promote the evolution of tolerance and incipient communality among unrelated adults, even in the absence of immediate reproductive gains.

Keywords: communal breeding; cooperation; agonistic encounters; nest failure; cost of fighting; burying beetles

Introduction

Nesting behaviour is thought to be an important prerequisite for the evolution of sociality in insects (Hansell, 1987; Seger, 1991), in part because a nest provides a focal point for social interactions. There are a variety of possible benefits that individuals might obtain by forming associations on nests, including improved defence (Lin and Michener, 1972) or ergonomic specialization (Rissing and Pollock, 1986). The substantial investment that must be made in a nest and the possibility of nest failure, in themselves, are also thought to promote cooperative associations. A young adult may do better by participating immediately in reproduction (directly or indirectly) at an established nest of a relative rather than initiating a nest on its own (Queller, 1989). Larger groups also may simply be more competent in preventing nest failure or in rebuilding after a nest is destroyed (Strassmann *et al.*, 1988). In many cases, such benefits depend upon an established association or coordinated responses of individuals and, thus, presupposes prior selection for tolerance of a potential rival. Cost–benefit analyses of derived social adaptations are adequate for understanding the maintenance of social behaviour but may not address the question of why a simple social trait, such as tolerance of a co-foundress, originated.

Because the reproductive value of a nest changes as it is constructed, a nest differs from a resource which can be exploited in the short term. The expected benefits at the time a nest is initiated may be low, but this expectation increases as the nest is elaborated and the time needed to escape nest failure (prior to a pay-off) decreases. Models of contests which assume rapid assessment of a resource that does not change in value predict that contests for resources of low value should be settled by brief, low-intensity contests (Davies, 1978; Parker and Rubenstein, 1981). At the time of nest initiation, however, low-intensity contests might not effectively exclude rivals for an extended period of time from a site which rivals have the incentive to monitor (in order to usurp the resource or to be a brood parasite at a favourable time). Rather, I argue that

Table 1. Mean '($\pm$SD)[a] number of young produced per success (P) and proportion of successful nests (S) by individual male-female pairs.

Carcass size	Number of young per successful nest(P)[b]	Proportion of nests that were successful (S)[b]
N. defondiens		
Small (5–15 g)	13.1 ± 4.9 (4)	0.74 ± 0.08 (3)
Medium (16–35 g)	23.8 ± 2.6 (8)	0.16 ± 0.08 (3)
Large (40–90 g)	34.1 ± 6.0 (6)	0.04 ± 0.07 (2)
N. orbicollis		
Small (8–20 g)	8.0 ± 3.0 (5)	0.83 ± 0.04 (3)
Medium (21–35 g)	14.7 ± 3.0 (17)	0.66 ± 0.11 (3)
Large (40–90 g)	39.7 ± 1.5 (3)	0.41 ± 0.01 (2)

[a] Calculated using the mean of each set of trials as a single data point.
[b] The number of sets of trials used to calculate means is shown in parentheses. Each set of trials represents a minimum sample of 20 (probability of a nesting success) or eight (brood production). Data were from the following studies: Wilson and Fudge (1984), Wilson *et al.* (1984), Scott (1989), Trumbo (1990, 1991, 1992, 1993), Scott and Traniello (1990), Trumbo and Fiore (1991), Scott and Gladstein (1993) and Trumbo and Wilson (1993)

nest failure can promote tolerance and incipient communality among unrelated adults in the absence of benefits from cooperation. This might occur when a nest has a low value at initiation, a highly unpredictable pay-off and must be contested over an extended time period.

To address the possible relationship between nesting failure, resource value and the origin of tolerance behaviour, I examined the choice of adult female burying beetles (*Nicrophorus* spp.) to either fight or tolerate another female on the day a carcass is discovered. Information regarding the probability of nesting success and reproductive output for two species which are known to differ in social behaviour was taken from 11 previously published studies of male–female pairs (see Table 1). These data were then used to estimate the reproductive value of a carcass on the day of its discovery for females breeding in one- or two-female groups and to determine at what cost of fighting a female would be indifferent to the 'fight–tolerate' decision.

Study animal

Adult burying beetles inter a vertebrate carcass which provides a food resource for their offspring. Parents maintain an underground nest, protect the vulnerable brood from predators and regurgitate liquified carrion to young larvae (Pukowski, 1933). The male parent remains in the nest for 5–12 days and the female parent for 10–15 days (Scott and Traniello, 1990; Trumbo, 1991). Carrion nests are highly attractive to competitors. Breeding failures can be caused by heavy exploitation of the resource by carrion flies or ants, scavenging by vertebrates or takeovers by congeners which can occur throughout the nesting cycle (Scott, 1990; Trumbo, 1990, 1993). During the breeding season there is an extreme shortage of available carcasses relative to the number of breeders (Wilson and Fudge, 1984; Wilson *et al.*, 1984; Trumbo, 1992) and the consequent fights over possession often result in injury (Pukowski, 1933; Otronen, 1988). Burying beetles have a relatively simple level of social organization (facultatively quasisocial), which is not well developed (groups with multiple females are slower to produce a brood than single females) and in which kin associations are not important (Eggert and Müller, 1992; Scott and Williams, 1993; Trumbo and Eggert, 1993; Trumbo and Wilson, 1993).

Results

In burying beetles, the reproductive success of a presumptive dominant female (the larger of two females) can be estimated as $P \times S \times M$ where P is the production of young per nesting success, S is the probability of nesting success and M is the proportion of young in a nest that can be attributed to the dominant female (maternity). The subscripts t and f will be used to refer to a tolerate or fight decision. P and S on small, medium and large carcasses can be estimated for *Nicrophorus defodiens* and *Nicrophorus orbicollis* from data on reproductive output by individual male-female pairs (Table 1). Mean values from each study were used as single data points to calculate grand means. There were two clear trends. In successful nests, a greater number of offspring were produced on larger carcasses in both *N. defodiens* and *N. orbicollis* (one-way ANOVAs, $p < 0.01$). This is a straightforward consequence of more resources (Wilson and Fudge, 1984). In addition, the probability of nesting success declines as carcass size is increased, reflecting the greater difficulty of handling a larger resource which is more attractive to carrion competitors (Trumbo, 1992). Note that *N. defodiens* faces a higher risk of nest failure, especially on large carcasses, compared to *N. orbicollis* (two-way ANOVA, $F_{carcass\ size'\ (2,12)} = 26.30$, $p < 0.001$; $F_{species\ (1,\ 12)} = 25.56$, $p < 0.001$). This occurs primarily because *N. defodiens* (among the smallest species of burying beetle in North America) is the victim of a high rate of takeovers throughout the nesting cycle by larger congeners (Wilson *et al.*, 1984; Trumbo, 1990, 1992).

The information on reproduction in Table 1 is used, along with four assumptions outlined below, to estimate the value of a carcass to a mated female breeding in one- or two-female groups and to determine at what cost of fighting a presumptive dominant would be indifferent to tolerating or contesting a subordinate female. These assumptions are as follows. First, a presumptive dominant either tolerates a subordinate and shares brood production equitably ($M_t = 0.5$; $M = 0.5$ on large carcasses when a second female is not excluded; Eggert and Müller, 1992) or fights a subordinate and thereby produces the majority of the brood ($M_f = 0.9$) in successful nests. A presumptive dominant which decides to fight may not produce 100% of the brood because smaller individuals win a low percentage of fights (0–30%, Bartlett and Ashworth, 1988; Otronen, 1988; Müller *et al.*, 1990) or because the subordinate can sometimes parasitize the brood (3–7% of the brood were attributed to subordinates in studies of contests between two females; Müller *et al.*, 1990; Trumbo, 1990). Second, group size (of more than two individuals) does not affect the rate of nest failure (*N. defodiens*, Trumbo and Fiore, 1993; *N. tomentosus*, M. P. Scott, personal communication). Thus, S_t always equals S_f. Third, group size does not affect the number of young produced on carcasses of less than 35 g ($P_t = P_f$, summary data from four species appear in Trumbo and Fiore (1993) and references therein). Finally, groups with two females produce either the same number of young as a single female on large carcasses ($P_t = P_f$) or 40% more young ($P_t = 1.4P_f$). Groups with two females have been found to produce 20–80% more young than single females (Eggert and Müller, 1992; Scott and Williams, 1993; Trumbo and Fiore, 1991; Trumbo and Fiore, 1993); it is not clear if greater production of brood on large carcasses is simply a consequence of prior selection for tolerance or a contributing factor to the origin of communality. Both assumptions, therefore, were examined.

Information on the costs of injuries sustained during fights is not available for burying beetles, a deficiency common to most studies of contests. Instead, benefits (B) of fighting are calculated as the expected reproductive output from winning a fight minus the expected output from tolerating or $B = P_f S_f M_f - P_t S_t M_t$. Indifference curves are then constructed to represent at what cost of fighting a female would be indifferent to the fight versus tolerate decision (where the costs of fighting equal the calculated benefit (B), Fig. 1) The dissimilarity in the shapes of the indifference curves for *N. orbicollis* and *N. defodiens* is due principally to differences in the rate of nest
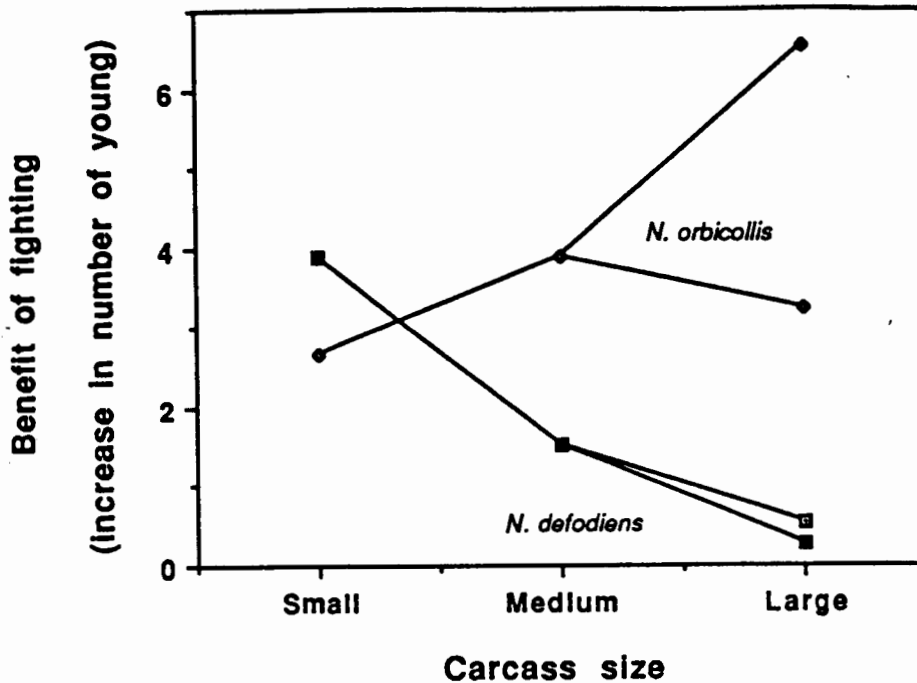
Figure 1. The estimated benefits (B) of fighting for *N. defodiens* and *N. orbicollis* on small, medium and large carcasses ($B = P_f S_f M_f - P_t S_t M_t$; see text for explanation of terms). A dominant female should fight if the expected cost of fighting (as measured by a decrease in the number of young in future reproduction) is below the curve and tolerate a consexual rival if the cost is above the curve. Where curves bifurcate, the lower segment shows the indifference curve based on an assumption of a 40% increase in the total number of young when the subordinate is tolerated on a large carcass ($P_t = 1.4P_f$).

failure. It is clear that *N. orbicollis* is expected to risk costlier fights in order to dominate the resource on medium and large carcasses (over the size range of carcasses for which data were available). This occurs because larger carcasses produce more young than smaller carcasses, more than offsetting a higher rate of nest failure. *Nicrophorus defodiens*, on the other hand, should be reluctant to engage in a costly fight on the first day after discovering a large carcass. It is estimated that if as few as 0.55 young are lost in future reproductive attempts as a result of fighting in the present, then a *N. defodiens* female should tolerate a rival on a large carcass (40–90 g). If the larger female can bias maternity somewhat in her favour even when tolerating a subordinate female (M_t greater than the assumed 0.5; Scott and Williams, 1993), then the benefits of fighting are reduced further and tolerance is more likely. When two females breed communally and produce 40% more young than a single female ($P_t = 1.4P_f$), the indifference curves are lowered, suggesting greater selection for tolerance. Adopting one brood production assumption or the other, however, does not change the general shape of the curves, nor greatly alter interspecific predictions resulting from the analysis.

Discussion

Females of *N. defodiens* are far more likely to breed communally on 50–90 g carcasses (60% of two-female associations were communal) than females of *N. orbicollis* on either 30–35 g (0%) or

150–300 g carcasses (20%; Trumbo and Wilson, 1993). I suggest that interspecific differences in tolerance of consexuals are due to differences in the rate of nest failure and the expectation of reproductive success. Several intraspecific comparisons support the assertion that the probability of nesting success affects agonistic encounters. In three different species of burying beetles, associations between two females persist longer (indicating greater tolerance) on larger carcasses which are more·vulnerable to nest failure (Eggert and Müller, 1992; Trumbo and Wilson, 1993). Wilson and Fudge (1984) report differences in tolerance behaviour between two populations of *N. orbicollis*. In northern Michigan, where nesting success is high, there is rarely more than one male or female on a carcass the morning after its discovery by beetles. At a second site where vertebrate scavengers discover a significant proportion of carcasses that are in the process of being buried, however, *N. orbicollis* often tolerated consexuals for a day until the nest was more established and, thus, less vulnerable. Bartlett and Ashworth (1988) noted that *N. vespilloides* males are more likely to tolerate a competitor before the arrival of the first female adult, suggesting that fights are delayed until males obtain information that the carcass is likely to support a beetle brood. Thus, I hypothesize that factors which decrease nesting success, such as a higher probability of a takeover, increased scavenging by vertebrates, exploiting a carcass in poor shape or the temporary absence of a female, should promote tolerance among resident burying beetles.

There is evidence that tolerance can reduce the probability of injury. In *N. tomentosus*, associations between two females which persisted the longest were the least likely to result in injury (Trumbo and Wilson, 1993). Eggert and Müller (1992) and S. T. Trumbo and D. S. Wilson (unpublished) found that females of competitively subordinate species were more likely to tolerate and less likely to injure potential rivals on larger carcasses. This suggests that females which are highly vulnerable to interspecific takeovers are less willing to fight for exclusive access to a resource, despite the potential of producing a larger brood if nesting is successful.

In this paper I have attempted to demonstrate that the time course over which a resource is utilized can be important when examining contest strategies, especially when the expected pay-off for a resource can change markedly as contestants attempt to exploit the resource. Specifically, I hypothesize that a high rate of nest failure (and the consequent low value of a nest at its inception) can select for an initial tolerance of reproductive rivals, irrespective of potential benefits which might result from cooperation. This might be an important mechanism for initiating grouping, thereby facilitating subsequent selection for more complex and coordinated associations.

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