
Short Communication

Sizing Up the Competition: Do Burying Beetles Weigh or Measure Their Opponents?

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INTRODUCTION

Limited resources, like food, space, and mates, set the stage for intraspecific competition in many species. These conflicts are usually settled through the assessment of various asymmetries, or differences, between the competitors. In conflicts there are three basic asymmetries: (1) resource holding potential (RHP), determined by the fighting ability; (2) pay-off, or the cost–benefit ratio for each individual; and (3) an uncorrelated asymmetry, such as ownership, which is not affected by the other two (Maynard Smith and Parker, 1976; Hammerstein, 1981). However, the importance of each asymmetry differs among species. For example, in the grass snake, *Natrix natrix*, RHP is the determining factor (Luiselli, 1996), but in the speckled wood butterfly, *Pararge aegeria*, ownership is crucial (Davies, 1978).

Burying beetles (*Nicrophorus* spp.) compete fiercely for possession of a small carcass, a valuable and unpredictable resource. A mating pair buries the carcass, mates, and raises the young using the carcass as a food source. Reproductive success is based on finding and possessing a carcass, thus setting the stage for intrasexual competition. Same-sex burying beetles compete when they meet at a carcass (the limited

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resource). The winners stay to breed and prepare the carcass by forming it into a ball, shaving the skin, and spreading secretions to delay decomposition (Pukowski, 1933; Eggert and Müller, 1997; Scott, 1998). The losers are chased away but often stay nearby, males to sneak copulations (Wilson and Fudge, 1984; Bartlett, 1988) or females to parasitize the brood (Müller *et al.*, 1990; Trumbo, 1994).

In these competitions RHP asymmetries seem to determine the outcome of the conflict. When determining dominance in many species, size is an obvious cue to assess fighting ability (Huntingford and Turner, 1987). *Nicrophorus* studies have shown that the "larger" male is usually dominant (Pukowski, 1933; Wilson and Fudge, 1984; Bartlett, 1988; Otronen, 1988; Trumbo, 1994). In most studies, "larger" is designated by the width of the pronotum (Müller *et al.*, 1990; Trumbo, 1992) or the elytra length (Otronen, 1988). "Size" could also be measured by mass and this measure has been used in studies of competition within and between *Nicrophorus* species (Otronen, 1988; Otronen, 1990). However, two beetles with the same pronotal width might have different mass. This study addresses whether mass or pronotal width is the better predictor of the outcome of competition between male burying beetles.

METHODS

Beetles (*N. orbicollis*) were reared in the laboratory at 14:10 L:D, and fed mealworms *ad libitum*. Maximum pronotal width and mass were measured and recorded for each sexually mature male. About one week before they were used, they were moved to individual containers with a damp paper towel and fed mealworms, or kidney (the preferred food), to create a wider variance in mass. Beetles were examined daily to see if the mealworm had been eaten. Males were used when they had gained enough mass to be matched with an appropriate competitor.

The beetles were matched for competitions in two ways. In the first group, males with the same mass (less than 10% difference, mean 5.4% difference) and different pronotal widths (greater than 10% difference, mean 12.1% difference) were matched against each other (pronotal-width asymmetry, $N = 16$). The second group matched beetles with different mass (greater than 10% difference, mean 18.7% difference) and the same pronotal widths (less than 10% difference, mean 3.1% difference) (mass asymmetry, $N = 18$). The level of asymmetry (mean % difference) in both contests were similar; therefore, the results should be indicative of the relative importance of the asymmetries (Brandt, 1999). In each pairing, one beetle was marked with yellow enamel paint for identification. The

beetles were examined closely before and after the experiment for any injuries or missing legs; only healthy intact beetles were used.

Containers ($19 \times 14 \times 10$ cm) were prepared with approximately three inches of damp soil, a 25–30 g mouse carcass, and a female burying beetle. The mouse and female were placed at one end of the container. After approximately 15 min, the two competing males were introduced at the end of the container opposite the mouse and female. We aimed to promote the simultaneous discovery of the carcass.

Beetles were left undisturbed for three days and then the carcasses were exhumed. The male present in the burial chamber was identified and designated the “winner” or dominant male. The “loser,” or subordinate, was the male farthest from the carcass or dead. Injuries were recorded and each surviving male was weighed. In two cases, all three beetles were still present with the carcass after three days. These carcasses were replaced and checked again the following day. In one case dominance had been determined on the fourth day. The other case was considered “cooperating” because all three beetles were present in the burial chamber for a week. This latter case was excluded from statistical analysis.

RESULTS

If size is not an indicator of the outcome of competition, then it is expected that each beetle has an equal chance of dominance. The results of the competitions with pronotal-width asymmetries (Table I) were compared to the expectation of randomness using Fisher’s Exact Probabilities test. A significant difference was seen ($P = 0.04$, $N = 15$). However, the outcome of competition with mass asymmetries was not different than random (Fisher’s Exact Probabilities, $P = 0.57$, $N = 18$). Thus pronotal width is a better predictor of the outcome of competition between male burying beetles. The injuries incurred by all participants of contests were also compared (Table II). There were significantly fewer injuries from

Table I. Outcomes of Competitions

	Larger winner	Smaller winner	P^a
Pronotal-width asymmetry	13	2	0.04
Mass asymmetry	9	8	0.57

^aProbabilities calculated using Fisher’s Exact tests comparing experimental outcomes to the expectation of randomness.

Table II. Injury Suffered During Competition to Individuals

	No injury	Injury
Pronotal-width asymmetry	22	8
Mass asymmetry	17	17

competitions with pronotal-width asymmetries than from those with mass asymmetries (Fisher's Exact Probability, $P = 0.05$). The elevated probability of injury is a consequence of closely matched fighting ability in the competitions with smaller pronotal-width asymmetries, supporting the notion that pronotal width is an indicator of fighting ability.

DISCUSSION

Many studies have shown that size is an important asymmetry in *Nicrophorus* competition (Pukowski, 1933; Wilson and Fudge, 1984; Bartlett and Ashworth, 1988; Otronen, 1988; Müller *et al.*, 1990; Trumbo, 1994). This examined which aspect of size is more important: pronotal width or mass. The results indicate that pronotal width is a better predictor of the outcome and indicator of size or fighting ability. Larger beetles have a better chance of possessing a carcass and breeding. They also have a better chance of displacing a resident and taking over a buried carcass (Scott, 1990; Trumbo, 1990a, 1990b).

Bartlett and Ashworth (1988) analyzed the relationship between larval weight and adult size. They found that the smaller larvae tend to risk their food reserves to increase their adult size (measured by pronotal width), while heavier larvae do not risk as much of their reserves for added size. Our results stress the importance of sacrificing weight for size: smaller larvae have a better chance of possessing a carcass as adults (and therefore of breeding) if they increase their pronotal width, even if they eclose at a reduced mass.

Conflict appeared to be more intense when beetles were closely matched in pronotal width as suggested by the higher overall level of injury in contests of mass asymmetries. Trumbo (1993) found a similar increase in injury when matching female burying beetles by size, in which case size difference was less than 5% in both mass and pronotal width. In our study, when pronotal width differed, dominance was decided without an intense escalated fight. When RHP in unevenly matched, dominance is usually decided without escalation (Clutton-Brock and Albon, 1979; Crepsi, 1986;

Enquist *et al.*, 1990; Smith *et al.*, 1994). When animals are evenly matched, it may take longer and more intense interactions to determine dominance.

Both beetle groups for which both males were found in the burial chamber on the third day were matched by a mass asymmetry. In both cases the two males might have been very closely matched in fighting ability and unable to determine dominance. If they had proceeded with an escalated fight, the results would most likely have resulted in serious injury to both competitors. Female burying beetles are also more likely to form cooperative breeding association when they are of similar size (Trumbo, 1993). Cooperation is favored when the benefits of being sole owner of the carcass do not outweigh the cost of fighting. Burying beetles are known to cooperate in breeding pairs on larger carcasses, where one pair cannot tend to the carcass efficiently or utilize the entire carcass. The benefit of added help in caring for a large carcass outweighs the cost of sharing the resource. But on smaller carcasses, of the size used in our experiments, communal breeding is uncommon for *N. orbicollis* (Trumbo, 1992; Scott and Traniello, 1990) and the cost of sharing usually outweighs the benefit.

To achieve a wider variance in mass the beetles were fed different diets. If they had been starved instead the results may have differed. Differential feeding most likely only affected fat reserves, not the quality of the muscles. Starvation would cause muscle degradation and therefore poor fighting ability; giving the heavier, better fed beetle the RHP advantage. By keeping the all of the beetles well fed (although on different sources), we were able to eliminate these confounding factors.

Resource holding potential has an effect on male mating success in many species (Garcia *et al.*, 1997; Luiselli, 1996; O'Neill, 1983). But it is important to realize that RHP may be mediated by hormone levels (Kravitz *et al.*, 1983; Röseler *et al.*, 1984) and past fighting experience of winning or losing (Otronen, 1990). Ownership, and many other factors may also affect on the outcome of competition. The data presented here supports the idea that, in the case of burying beetles, pronotal width can be used as an indicator of the outcomes of competition and is also an indicator fighting ability.

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