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Beyond monogamy: territory quality influences sexual advertisement in male burying beetles

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Abstract. Burying beetles, *Nicrophorus defodiens*, reproduce on vertebrate carcasses, and the number of beetles of either sex on a carcass is known to be highly variable. Field and laboratory studies were conducted to examine how sexual advertisement by males is affected by resource quality and number of mates, and to determine the reproductive output of males in different breeding associations. Carcass size had a strong influence on the reproductive benefits of polygyny to males, and on male sexual advertisement. In the field, polygynous groups produced more young and a greater brood mass than monogamous or polyandrous groups when using a large carcass (40–60 g). On a small carcass (15–18 g), however, no differences in reproductive output between the three breeding associations were found. In light of these findings, advertisement for mates was monitored when males were provided: (1) a small carcass and one female; (2) a large carcass and one female; and (3) a large carcass and four females. Most males that were paired with a female on a large carcass released pheromone even after copulating with the resident female. Pheromone emission was rare, however, in males that were paired with a single female on a small carcass, or in males that were given access to four females. Male *N. defodiens* thus assess both resource quality and number of mates when deciding whether to emit pheromone, and this decision appears to agree with the reproductive interests of males but not necessarily that of resident females.

Males are generally expected to maximize the number or quality of mates (Bateman 1948; Thornhill & Alcock 1983; Davies 1991). When males defend territories, the number of females that are attracted to a territory is thought to be dependent, in a large part, on the qualities of the male and his territory (Verner & Willson 1966; Searcy & Yasukawa 1989). There are no unequivocal examples, however, in which male advertisement varies such that monogamy is favoured on territories with few resources, and polygyny is favoured when more resources are available.

Species with a variable breeding system (monogamous, polygynous, polyandrous or polygynandrous outcomes) such as dunnocks, *Prunella modularis* (Davies & Houston 1986), saddle-back tamarins, *Sanguinus fuscicollis* (Terborgh & Goldizen 1985) and burying beetles, *Nicrophorus* spp. (Eggert & Müller 1992; Trumbo 1992; Scott & Williams 1993) are excellent for examining the reproductive consequences of individuals' decisions. In burying beetles, territory quality is easily measured as the size of the critical resource, a small vertebrate carcass. In this study we examine how sexual advertisement by males is affected by both resource quality and number of mates. We also determine the reproductive output of males in different breeding associations (monogamy, polygyny, polyandry), and conclude that there is apparent congruence between male advertisement behaviour and his reproductive interest.

Burying beetles prepare vertebrate carrion as a food source for their young. Suitable carcasses are very scarce relative to the number of potential breeders (Wilson & Fudge 1984; Trumbo 1992), and beetles will accept a broad size range of carcasses (e.g. *N. defodiens* breeds on carcasses from 3 to 100+g: Trumbo 1990a, 1992). On a small carcass, intra-sexual fights reduce the resident population to a dominant male–female pair (Pukowski 1933). On large carcasses, however, the

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mating system is quite variable. Consexual adults often tolerate each other and even feed each other's young (quasisociality: Scott & Traniello 1990; Eggert & Müller 1992; Trumbo 1992; Scott & Williams 1993; Trumbo & Wilson, 1993). Male burying beetles advertise for mates by adopting a handstand 'sterzeln' posture (Pukowski 1933; see cover of *Behavioral Ecology*, 1992, 3) and releasing a pheromone that attracts females (Bartlett 1987a; Eggert & Müller 1989a, b). Pheromone is emitted only during the few hours each day that correspond to a portion of the species' activity period (Müller & Eggert 1987). Males are known to release pheromone when they are the first to arrive at a small carcass, or as an alternative mating tactic when they are unable to locate a carcass (Eggert & Müller 1989b). Sexual advertisement from a large carcass has not been investigated previously.

METHODS

We collected *N. defodiens* from Pellston, Michigan and Moran, Wyoming in baited pitfall traps during June and July, and held them for 5–12 days prior to experimental trials. We tested males from the Michigan population for their tendency to adopt the pheromone-emitting posture in three situations. We placed each male in a small glass aquarium (35 × 15 × 20 cm) half filled with soil. A paper towel was placed over most of the soil surface and a small rock perch was set on top of the paper towel (males often release pheromone from on top of small objects: Pukowski 1933). The treatments were: small carcass, one female (treatment 1, $N=16$); large carcass, one female (treatment 2, $N=31$); and, large carcass, four females (treatment 3, $N=16$). During a 2-h period prior to sunset, we scanned aquaria seven different times (10 min each) under natural light supplemented by red light. If a male was seen in the 'sterzeln' posture on at least one occasion, we scored him as a pheromone-emitter. We made brief observations of pheromone-emitting males in treatment 2 to confirm that the male and female interacted. After the first evening, we divided pheromone-emitting males from treatment 2 into two groups. We provided half of the males with three additional females (treatment 2A) and we left half of the males with their original female (treatment 2B). We observed these males a second evening, as before. To estimate reproductive success we measured number of larvae and total brood mass within 24 h of larvae crawling away from the carcass.

Using *N. defodiens* from the Wyoming population, we placed 17 male–female pairs individually into an observation chamber containing 1·27 cm of moist soil at 1000 hours. Thirty minutes later, we provided either a small (10–15 g) or large (45–60 g) carcass. We recorded behaviour using a Panasonic video-recorder from 1030 hours until 0100 hours the next morning. We placed eight additional male–female pairs individually on 45–60 g carcasses and transported them to a nearby field site. To exclude vertebrate scavengers while allowing beetles to exit and re-enter the experimental set-up, we placed a beetle pair and a carcass into a soil-filled container that was covered by a wire mesh cage (1·3-cm mesh) and buried flush with the soil surface. We checked each trial every 30 min between 1800 and 2100 hours.

To examine reproductive output of different breeding associations on small and large resources independently, we separated beetles from the Michigan population into monogamous (one male, one female), polygynous (one male, two females) or polyandrous (two males, one female) groups. Plugs of soil were dug from the forest floor and trimmed to fit snugly into plastic containers (8 × 15 × 30 cm). We placed a breeding group and a small (15–18 g) or large (40–60 g) carcass into the container, covering the beetles with loose soil. To prevent larger insects from entering the container we covered it with a wire screen (0·32-cm mesh) and then placed the set-up into the hole created by digging (wire screening also excludes congeners that sometimes attempt to take over the resource: see Scott 1990; Trumbo 1990a, b). After 6 days, we brought the containers to the laboratory and removed the wire screening, allowing adults to disperse from the carcass. We counted and weighed young within 24 h of larvae crawling away from the carcass.

RESULTS

Carcass size and the number of females present significantly affected pheromone emission by *N. defodiens* males. Only one male (6%) released pheromone from a small carcass while 22 (71%)

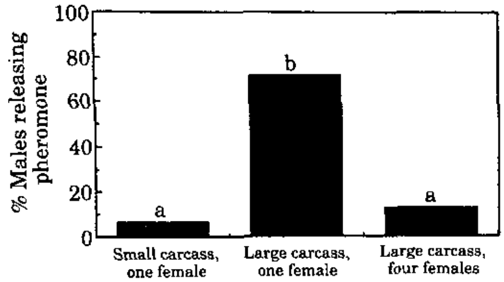

Figure 1. Percentage of males observed in the pheromone-releasing posture in three experimental treatments. Different letters above bars indicate statistically significant differences between treatments ($P<0{\cdot}025$, Fisher's exact tests).

emitted pheromone from a large carcass in the presence of a single resident female ($P<0{\cdot}001$, Fig. 1). In treatment 2, 20 of the 22 pheromone-emitting males were observed to release pheromone on two or more occasions and 21 males copulated with the female. All 21 of these males adopted the 'sterzeln' posture after copulation, a behaviour that has never been recorded previously on a carcass. It is therefore clear that in all but perhaps one case, males were not emitting pheromone because they failed to encounter the female. Only two males (13%) released pheromone from a large carcass when four females were present, a significantly lower percentage than in treatment 2 ($P<0{\cdot}001$).

There also was a significant difference in pheromone emission on the second evening. Males from treatment 2 that were given three additional females (treatment 2A) did not subsequently release pheromone or attempt to climb the perch, while five of 11 males that were not given additional females (treatment 2B) resumed pheromone emission ($P=0{\cdot}035$, Fisher's exact test). Reproductive output of these polygynous associations was much higher than for monogamous associations. A mean ($\pm$ SE) of $70{\cdot}0 \pm 8{\cdot}5$ larvae dispersed from the carcass for treatment 2A breeding groups, while $28{\cdot}2 \pm 5{\cdot}0$ larvae were produced by treatment 2B groups (Mann–Whitney U-test, $U=12$, $P<0{\cdot}001$). Total brood mass in polygynous associations was twice that of monogamous groups ($10{\cdot}89 \pm 1{\cdot}36$ g versus $5{\cdot}44 \pm 1{\cdot}01$ g, $U=18$, $P<0{\cdot}01$).

Pheromone emission in the Wyoming population was not observed on small carcasses ($N=8$) in the laboratory. On large carcasses, however, seven of nine males exhibited pheromone-emitting behaviour ($P=0{\cdot}0023$). In six of these seven trials, the female apparently attempted to interfere by pushing the males, crawling under them or walking back and forth on top of males. A male would often walk away and attempt to re-adopt the 'sterzeln' posture while the female repeatedly pursued him. In the field, four of eight males on large carcasses were observed in the pheromone-emitting posture. Males left the screen-covered containers and emitted pheromone as far as 50 cm away from the carcass using dead wood and nearby bushes as perches. Even at this distance, females in two trials located pheromone-emitting males and proceeded to push and mount them.

Nicrophorus defodiens successfully produced broods in 117 of 120 field trials. Both carcass size (CSIZ) and group composition (GC) affected reproductive output (number of larvae: CSIZ, $F_{1,114}=25{\cdot}35$, $P<0{\cdot}001$; GC, $F_{2,114}=9{\cdot}85$, $P<0{\cdot}001$; CSIZ $\times$ GC, $F_{2,114}=6{\cdot}05$, $P=0{\cdot}003$; total brood mass: CSIZ, $F_{1,114}=26{\cdot}86$, $P<0{\cdot}001$; GC, $F_{2,114}=3{\cdot}85$, $P=0{\cdot}024$; CSIZ $\times$ GC, $F_{2,114}=1{\cdot}95$, $P=0{\cdot}15$; two-way ANOVAs). The significant interaction term for number of larvae suggests that the effect of group composition was not the same on carcasses of different size. One-way comparisons (Fig. 2) make it clear that polygynous groups had more larvae and produced a greater brood mass than other groups on large, but not small, carcasses. On both small and large carcasses, reproductive output per female was less for multiple- than for single-female treatments ($P<0{\cdot}01$, one-way ANOVAs).

DISCUSSION

Most of the variation in reproductive success of a dominant male burying beetle appears to be explained by variation in group reproductive output and not by variation in paternity. Use of three different methods of paternity analysis (phenotypic marker, biochemical marker and sterile-male techniques) has demonstrated that the resident male(s) fathers 85–93% of the brood on small as well as large carcasses, and in single- as well as multiple-female associations (Bartlett 1988; Müller & Eggert, 1989; Trumbo 1990b; Scott & Williams 1993). On a small carcass, a male's reproductive output is not enhanced by attracting a second female (although we would expect the

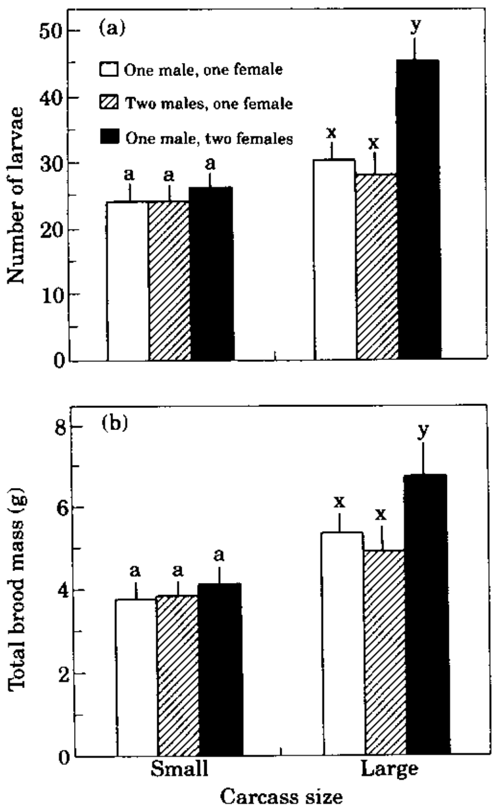

Figure 2. Reproductive output on small and large carcasses by pairs, groups of one male and two females, and groups of two males and one female (N=20/treatment). (a) Mean (+SE) number of larvae. (b) Mean (+SE) total brood mass. Different letters above bars indicate statistically significant differences between treatments (P<0·025, one-way ANOVAs).

male to copulate with any female that discovered the resource). This occurs because a small carcass cannot support the maximum brood of even a single female (Trumbo 1992). Long before a small carcass is exhausted, parents regulate brood size by selective infanticide, ensuring adequate food for surviving young (Bartlett 1987b; Trumbo 1990c). Thus, any reproductive success gained by attracting a second female comes almost exclusively at the expense of the first female (Müller et al. 1990). Groups of more than two individuals are also no better than a pair in preventing take-overs by larger competitors (Trumbo & Fiore, 1994; Michelle Scott, unpublished data).

Without clear reproductive benefits to attracting a second female, males should not risk advertising from a small carcass. Congeners are attracted to carcasses and can respond to pheromone-emitting males (Müller & Eggert 1987). By stopping pheromone emission when other species become active at sunset, *N. defodiens* probably avoids enhancing the attractiveness of a carcass to heterospecific burying beetles (Wilson et al. 1984). Pheromone-emitters, however, cannot avoid the response of conspecific males. In two European species of burying beetle, approximately 20% of conspecifics that are attracted to a pheromone-emitter (in the absence of odour cues from a carcass) are rival males (Müller & Eggert 1987). It is clear from the polyandrous treatment that a male that must share paternity after a consexual discovers the resource is likely to suffer a decrease in reproductive output.

A large carcass is a resource that can support the broods of more than one female (*N. defodiens* females are limited to a maximum clutch of about 40 eggs: Trumbo 1992). A singly mated male might be expected to advertise for a limited number of additional females in this situation. Pheromone release by mated males on large carcasses from two populations of *N. defodiens* (in both the laboratory and field), strongly suggests that this newly described context for sexual advertisement is an integral component of male reproductive behaviour and not the result of an unnatural experimental arrangement. *Nicrophorus defodiens* males are remarkable in that they appear to assess both the quality of the resource and the number of mates present when deciding whether to advertise for females. How this occurs is not understood although similar assessments in burying beetles have already been established. When a carcass is discovered, a beetle makes repeated movements around the periphery and also lifts the carcass from underneath, apparently obtaining information that leads to rejection of very small or large carcasses (Pukowski 1933; Trumbo 1990a). Regulation of brood size, discussed previously, suggests a finer level of assessment of resource potential. During parental care adults tolerate their mate but attack unfamiliar non-nestmates (Pukowski 1933; Trumbo & Wilson, 1993). This ability to discriminate among individual conspecifics is also likely to be important for altering pheromone emission, depending on the number of females encountered on a carcass.

On a small carcass, the interests of the male and female in a monogamous pair largely coincide.

Neither sex would be likely to benefit from a subsequent discovery by an individual of the opposite sex. On a large carcass, however, a male can augment his reproductive output by attracting additional mates, whereas a female would benefit by preventing a male from advertising. Observations of apparent female interference are therefore intriguing; the effectiveness of these behaviour patterns needs to be substantiated.

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