Anne-Katrin Eggert · Scott K. Sakaluk

Female-coerced monogamy in burying beetles

Abstract The reproductive interests of the sexes often do not coincide, and this fundamental conflict is believed to underlie a variety of sex-specific behavioral adaptations. Sexual conflict in burying beetles arises when a male and female secure a carcass that can support more offspring than a single female can produce. In such a situation, any male attracting a second female sires more surviving offspring than he would by remaining monogamous, whereas the female's reproductive success decreases if a rival female is attracted to the carcass. Monogamously paired males on large carcasses do in fact attempt to attract additional females by means of pheromone emission, whereas males on small carcasses do not. Females physically interfere with male polygynous signaling using various behavioral tactics. We demonstrate that such interference leads to a significant decrease in the amount of time that males spend signaling, according females a means by which to impose monogamy on their mates.

Key words Sexual conflict · Burying beetles · *Nicrophorus defodiens* · Monogamy · Pheromones

Introduction

Sexual conflict occurs whenever the reproductive strategy pursued by one sex poses a selective disadvantage to the other, and is believed to be an important selective milieu within which male and female mating strategies have evolved (Parker 1979; Thornhill and Alcock 1983; West-Eberhard et al. 1987). The reproductive interests of males and females may differ with respect to the occurrence and timing of mating, number of mating partners, level of parental investment, and paternity of offspring. Sex-specific adaptations that can be attributed at least in part to sexual conflict include mate guarding, coercive mating, courtship feeding, and facultative polygyny in males, and ejaculate manipulation and facultative polyandry in females (Thornhill and Alcock 1983). In animal species with biparental care, sexual conflict over the form of the breeding association should occur when males benefit through polygynous matings, but when females paired with polygynous males experience a concomitant decrease in the level of paternal investment (Trivers 1972).

Burying beetles (Silphidae: *Nicrophorus*) are one of only a handful of insect taxa exhibiting biparental care (Zeh and Smith 1985). Males and females independently search for small vertebrate carcasses that serve as a food source for the developing young (Pukowski 1933). A male successful at locating a carcass emits a sex pheromone that serves to attract a sexually receptive female (Pukowski 1933; Eggert and Müller 1989). The male and female cooperate in burying the carcass, and actively defend it against conspecific intruders and members of other *Nicrophorus* species (Pukowski 1933; Scott 1990; Trumbo 1990a, 1991). Adults of either sex also make competent single parents that feed the larvae up until the larvae have consumed the carcass and left the brood chamber (Reinking and Müller 1990; Trumbo 1991).

Aggressive interactions between conspecifics are a regular component of burying beetle reproduction (Fabre 1899; Pukowski 1933; Bartlett 1988; Otronen 1988). Since another male's presence on a carcass poses a significant threat to a male's paternity, fights between conspecific males on the same carcass can be intense (Pukowski 1933; Bartlett 1988; Otronen 1988). Reproductive competition among females is also severe, because small carcasses often lack sufficient food with which to support the larvae hatching from even a single female's eggs (Pukowski 1933; Bartlett 1987;

A.-K. Eggert (✉)
Institut für Zoologie der Albert-Ludwigs-Universität, Albertstr. 21 a, D-79104 Freiburg, Germany

S.K. Sakaluk
Ecology Group, Department of Biological Sciences, Illinois State University, Normal, IL 61790–4120, USA

Bartlett and Ashworth 1988). The majority of larvae reared by *N. vespilloides* on small carcasses are the offspring of the dominant male (Bartlett 1988; Eggert 1992) and female (Müller et al. 1990) that ultimately feed and protect the brood.

Interactions between individuals, as well as the composition and reproductive success of breeding associations, are greatly influenced by carcass mass (Eggert and Müller 1992; Trumbo 1992; Trumbo and Wilson 1993). On carcasses that provide more food than a single female's clutch requires, intrasexual aggression is less pronounced and several conspecific females have been found caring for young simultaneously (Eggert and Müller 1992; Trumbo 1992; Trumbo and Wilson 1993). Experimental work has shown that polygynous associations on large carcasses produce a greater total number of surviving young than do single-female groups, but fewer offspring on a per female basis (Eggert and Müller 1992; Trumbo and Wilson 1993; Trumbo and Eggert 1994; Trumbo and Fiore 1994).

It is on these large carcasses that the reproductive interests of males and females diverge. Male reproductive success on such carcasses is higher in polygynous breeding associations than in monogamous ones, because the resident male sires the majority of offspring in either case (monogamous associations: Bartlett 1988; Müller and Eggert 1989; Trumbo 1990a; polygynous associations: Scott and Williams 1993). For females, however, the situation is reversed; in a polygynous association, the mean number of offspring produced per female is smaller than the number produced by single females (Eggert and Müller 1992; Trumbo and Eggert 1994; Trumbo and Fiore 1994). Sexual conflict thus arises from the fact that different kinds of breeding associations maximize the reproductive success of males and females. This conflict manifests itself as a specific behavioral conflict when one male and female are present on a large carcass. Males in this situation often emit the sex pheromone although a mate is already present. Females appear to attempt to physically deter pheromone transmission by mounting males, biting them, undercutting them, or displacing them from the perches from which they emit the pheromone (Trumbo and Eggert 1994). Males, in apparent response to such interference, often relinquish the pheromone-emission posture, secure another signaling perch, or cease pheromone emission altogether. In this study, we manipulated the ability of female *N. defodiens* to interfere with male pheromone emission to determine its effectiveness in thwarting male polygynous signaling.

Methods

Effectiveness of female interference

Beetles were captured in pitfall traps baited with pieces of pig's lung between 5 and 29 June 1993 in a tract of boreal forest near Wolfe Lake in northern Ontario, Canada (46°02′N, 79°32′W). They were maintained under ambient photoperiod and temperature conditions in a field laboratory located at the study site and fed small (< 1 g) pieces of chicken liver every 3 days. Observations of beetles in the experiment were carried out between 5 June and 7 July 1993. We observed the behavior of a total of 35 male-female pairs of beetles on carcasses in two different experimental situations: in one treatment, the female was tethered to reduce her ability to interfere with male sexual signaling, and in the other treatment, the female was free to interact with the male. The female of each pair was subjected to both treatments, with an interval of two days between successive observations. Treatment order was reversed for every other pair.

Experiments were carried out on previously frozen carcasses of laboratory rats (35–60 g) that had been allowed to thaw for approximately 5 h at room temperature. Each carcass was fresh when thawed for the first observation of a given pair, was re-frozen immediately following the first observation, and re-thawed the day of the second observation. Thus, each pair was observed in both experimental situations on the same carcass. Tails were removed from carcasses before pairs were established on them because tethers tended to get tangled up in them, leading to complete immobilization of females. Carcasses of this size and quality, as well as the smaller mouse carcasses used for control trials (see below), are routinely utilized by *N. defodiens* for reproduction in the field (Trumbo 1992).

At 1400 hours EST, each experimental female was equipped with a leash, consisting of a 20-cm section of dental floss, the end of which was tied around her "waist" behind the pronotum, i.e., at the junction of her pro- and mesothorax. To ensure rapid detection of the carcass, each female and her assigned mate were placed on the carcass in a small transparent plastic container (diameter 8 cm, height 7 cm). At 1700 hours, each pair of beetles and their respective carcass were carefully transferred to a larger plastic observation chamber ($16.5 \times 30.5 \times 8.5$ cm), the bottom of which was covered with a 2-cm layer of soil. The carcass was placed at one end of the cage, and a fist-sized rock, to be used by the males as a signaling perch, was placed at the other. In "tethered" trials, the dental-floss leash was used to tether the female so that she could move freely around the carcass but no further. The dental floss was secured to the lid of the observation chamber on the side of the chamber that contained the carcass. The other half of the chamber, which contained the signaling perch, was beyond the female's reach. In the second treatment, i.e., in "untethered" trials, the female's dental-floss leash was cut to a length of approximately 2 cm, allowing the female unimpeded movement about the entire cage.

Direct observations were made at dusk, at which time pheromone emission normally occurs (Trumbo and Eggert 1994). During 30-min observation periods (2030–2100 hours), we observed whether the male and female exhibited at least some of the behaviours typical of burying beetles reproducing on a carcass: palpitating the carcass, feeding on it, running around it with moving antennae, removing fur from it, feeding on it, and exploring the surrounding soil. Attempts to fly or avoid the carcass altogether, as well as total inactivity before and during the observation period were considered clear indications of disinterest, and led to exclusion of the respective trials. Our analyses include only those pairs ($n = 24$) in which the activities of both beetles on the carcass during the observation period in both treatments indicated their reproductive readiness. We also recorded the mating frequency, the total amount of time each male spent emitting the pheromone, and the number and kind of female interference behaviours during the 30-min observation periods.

There is clear-cut experimental evidence for chemical attraction of females by males (Eggert and Müller 1989), but only when the males assume the typical "sterzeln" posture (Pukowski 1933): a "headstand" with the head held down and the fully extended abdomen pointing upwards, exposing the last abdominal segment which is normally concealed inside the abdomen. Pheromones

appear to be produced in, and released from, this segment, which is equipped with a multitude of cuticular pores and lined with specialized epithelial gland cells (J.K. Müller, C. Gack, A.-K. Eggert, unpublished data). Therefore, we scored males as pheromone-emitting whenever they extruded their last segment and raised their abdomen well off the substrate. Such occurred when males assumed the above headstand posture, hung upside down from a perch with the abdomen directed downwards, or walked slowly about the arena maintaining a posture closely resembling the "headstand".

All statistical analyses were carried out using nonparametric test procedures because of strong deviations of all measured variables from a normal distribution in the entire sample or in subsets of the sample (Shapiro-Wilks tests: mating frequency in tethered trials $W = 0.761$, $P < 0.0001$; in untethered trials $W = 0.715$, $P < 0.0001$; number of interference attempts in tethered trials $W = 0.682$, $P < 0.0001$; in untethered trials, $W = 0.878$, $P = 0.007$; duration of pheromone emission in tethered trials $W = 0.851$, $P = 0.002$, in untethered trials $W = 0.639$, $P < 0.0001$.

When females are tethered, their reduced mobility might cause males to reject them as suitable mates, thereby leading to higher pheromone emission rates in the tethered treatment. To control for this possibility, we established a separate series of control trials ($n = 13$) in which males and tethered females were provided with small laboratory-mouse carcasses (< 20 g). If males accept tethered females as mates, they should not emit pheromone under these conditions (Trumbo and Eggert 1994). These control observations and the experimental ones were carried out simultaneously.

Attraction of females and competitors to male signals

To assess the costs and benefits of male signaling, we compared the number of females and potential competitors captured in pitfall traps baited either with carrion or a signaling male *N. defodiens*. Each pitfall trap had a diameter of 15.5 cm and was about 20 cm deep. A large can whose top and bottom had been removed was buried with its top rim flush with the soil surface to form the outer wall of the trap. A small trapping container (diameter 8 cm, height 7 cm) with a circular hole in its lid was placed at the bottom of the trap. A large plastic funnel, whose upper margin fit tightly against the inner wall of the trap, was positioned about 5 cm below the soil surface, with its spout directed through the opening in the lid of the trapping container. The bait was placed in a small can suspended from a scaffold erected above the center of the trap. Beetles approaching the bait fall into the opening of the trap, slide down the smooth walls of the funnel, and are caught in the trapping container from which they cannot escape. For collection of captured beetles, the trapping container is easily accessible by reaching into the trap and removing both the funnel and container (for details of trap design see Müller 1984).

Ten traps were placed in the forest on 28 May 1993, with a minimum distance of 50 m between adjacent traps. Each trap was baited with three pieces of decomposing pig's lung (each weighing c. 10 g) in a small can covered with a tea strainer to prevent attracted insects from gaining access to the bait. Captured beetles were removed at 3-day intervals. Whenever a trap was emptied, a new piece of lung was added and one of the old ones discarded. Trapping with carrion continued until 29 June.

Over the period from 1 July to 21 July, each pitfall trap was baited with a sexually mature male, held in a small can that was filled with moist soil and covered with a tea strainer to prevent the male from leaving the can. Five pairs of traps were used, with a distance of 1.5 m between the traps of each pair and a distance of 50 m or more between pairs; this alteration in the spatial arrangement of traps was necessitated by a mate-choice experiment, the results of which will be reported elsewhere. Traps were emptied at intervals of two or three days, and the males used as baits were replaced at 5-day intervals. *N. defodiens* captured in carrion- or male-baited traps were not released back into the forest until the experiments were completed.

Results

Effectiveness of female interference

The behavior of males in the control trials demonstrated that they accept tethered females as adequate mates despite their reduced mobility. When males and tethered females were provided with small carcasses only, males never emitted pheromone. Male acceptance of tethered females is also supported by the finding that mating frequency on large carcasses was not significantly different between tethered and untethered trials (median = 1.0, interquartile range = 1.0–2.0 for both treatments; Wilcoxon MPSR test, $z = 0.30$, $P = 0.98$), i.e., males did not mate less with females that were restricted in their ability to move about the arena.

In 18 of the 24 experimental pairs included in the analysis, the male emitted pheromone in the course of one or both 30-min observation periods. Pheromone emission occurred at various locations in the observation chamber: on the carcass, on the rock, on the soil covering the bottom of the container, and from the walls or lid of the container. Females often attempted to interfere with male pheromone emission. The interference behavior observed most frequently was mounting of the male by the female, but we also observed the female pushing the male, undercutting him, or pinching his abdomen with her mandibles. Female mounts accounted for more than half (62.3%) of all interference events observed ($n = 263$), varying in duration from about a second to more than a minute. While female mounts may be attempts to incite mating attempts by the male, they are not mating attempts per se, since it is the male that has to mount the female for mating to occur.

Tethering effectively reduced the median number of female interference attempts by almost 90% (Fig. 1). In tethered trials, the movement of females around the carcass often led to further restriction of their mobility such that some females were unable to move away from the carcass at all. Nonetheless, because males frequently emitted pheromones directly on the carcass, some of these females were still able to interfere with male signaling.

Males emitted pheromone for significantly longer periods when their mates were tethered, than when females were free to interfere with pheromone emission (Fig. 2). The order in which a pair experienced the two treatments had no significant effect on pheromone-emission durations, mating frequencies, or number of interference events (Mann-Whitney tests, all $n_1 = n_2 = 12$: pheromone-emission duration in untethered treatments: $U = 56.5$, $z = -0.956$, $P = 0.34$; in tethered treatments, $U = 40$, $z = -1.862$, $P = 0.06$; mating frequency in untethered treatments, $U = 67.5$, $z = -0.311$, $P = 0.76$; in tethered treatments: $U = 44.5$, $z = -1.766$, $P = 0.08$; number of interference
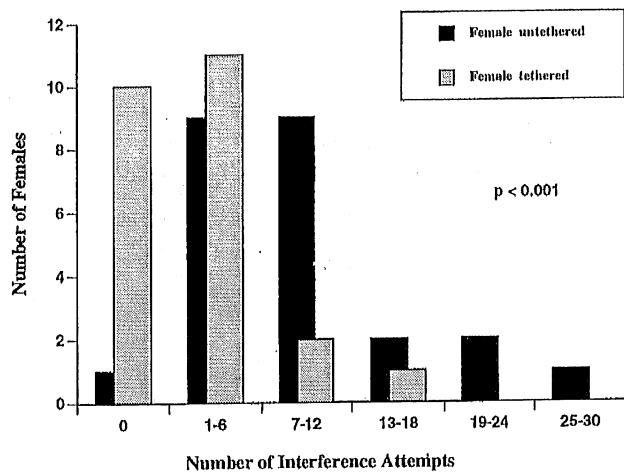
Fig. 1 Frequency distribution of the number of female attempts to interfere with male pheromone emission in 30-min observations of *Nicrophorus defodiens* pairs. When females were tethered, they interfered with male signaling less often (median = 1 interference attempt) than when they were free to move about the observation container (median = 8 interference attempts; Wilcoxon matched pairs-signed ranks test, $P < 0.001$)
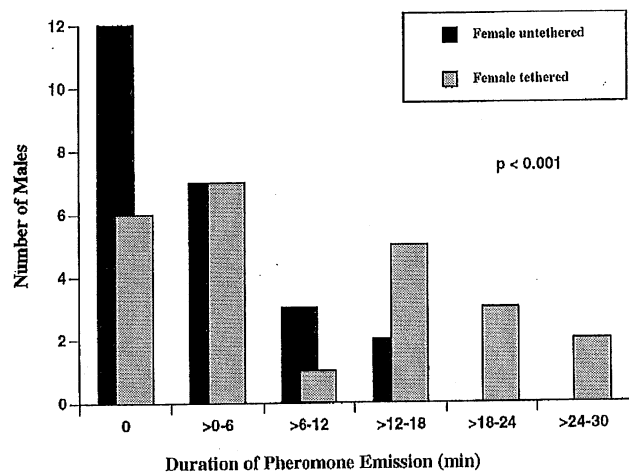

Fig. 2 Frequency distribution of the total duration of male pheromone emission in 30-min observations of *N. defodiens* pairs. Males emitted pheromone for longer periods when females were tethered (median = 4.59 min), than when females were free to move about the observation container (median = 0.03 min; Wilcoxon MPSR test, $P < 0.001$)

events in untethered treatments: $U = 68$, $z = -0.232$, $P = 0.82$; in tethered treatments: $U = 70$, $z = -0.120$, $P = 0.90$).

If females attack their mates in response to pheromone emission, the number of attacks by females should covary with the total time spent signaling by males. Indeed, in trials involving untethered females, there was a significant positive correlation between the duration of pheromone emission and the number of female interference attempts (Spearman rank correlation: $n = 24$, $r_s = 0.61$, $P = 0.003$; see Fig. 3). As expected, no such correlation arose in the tethered trials, because females were not permitted to interfere
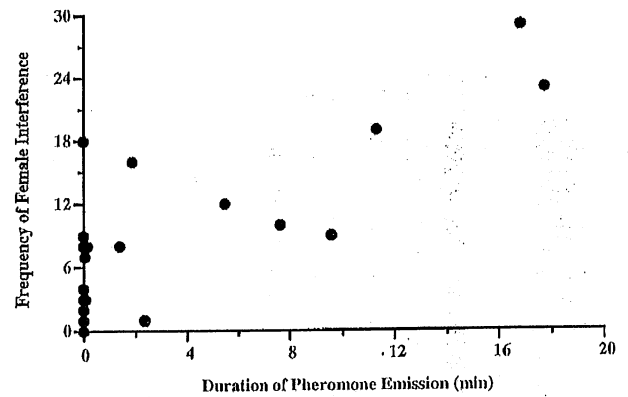

Fig. 3 Time invested in polygynous signaling (pheromone emission) by monogamously paired males and the frequency of physical interference by their untethered mates in 30-min observations of *N. defodiens* pairs

with male pheromone emission ad libitum (Spearman rank correlation, $n = 24$, $r_s = 0.10$, $P = 0.62$). Interference behaviors were also observed, and could be quite abundant, in trials in which males were not scored as pheromone-emitting at all (Fig. 3). Possibly these males never assumed the pheromone-emitting posture in the course of our observations because they had only very limited opportunity to escape the female's attacks. In the field, males often choose less accessible sites at a greater distance from the carcass for polygynous signaling (Trumbo and Eggert 1994).

Attraction of females and competitors to male signals

N. defodiens were first collected from carrion-baited traps on 5 June, and a total of 317 individuals were captured over the period ending 29 June. The sex ratio in these traps was slightly male-biased (181 males: 136 females, $\chi^2 = 6.39$, $P = 0.011$). In the traps baited with sexually mature males, 149 *N. defodiens* were captured over the 3 weeks ending 21 July. The sex ratio in these traps was heavily female-biased (15 males: 134 females, $\chi^2 = 95.04$, $P < 0.0001$), and deviated significantly from the sex ratio observed in carrion-baited traps (log likelihood ratio $\chi^2 = 103.8$; $P < 0.0001$). It is highly unlikely that such a difference was due to seasonal variation in the relative abundance of males and females. None of the *Nicrophorus* species studied to date have exhibited heavily female-biased sex ratios when trapped with carrion baits, whereas trapping with pheromone-emitting males has revealed varying degrees of skew in favor of females in several species (Müller and Eggert 1987).

Individuals of a larger congeneric competitor, *N. orbicollis*, were also far more abundant in carrion-baited traps. A total of 219 *N. orbicollis* were captured in carrion-baited traps, whereas only 12 *N. orbicollis* were found in traps baited with *N. defodiens* males. In

carrion-baited traps, the ratio of *N. orbicollis* competitors to female *N. defodiens* (219 *N. orbicollis* vs. 136 female *N. defodiens*), was much higher than in traps baited with *N. defodiens* males (12 *N. orbicollis* vs. 134 female *N. defodiens*; $\chi^2 = 136.0$, $P < 0.0001$). Seasonal effects cannot account for this difference. Although the relative abundance of *N. defodiens* and *N. orbicollis* is influenced by season, such cannot explain the greatly decreased occurrence of *N. orbicollis* in the male-baited traps that were established in early July, because the relative abundance of this species increases in July as the temperature increases (Wilson et al. 1984).

Discussion

A sexual conflict exists between the members of a monogamous *N. defodiens* pair on a large carcass. Male and female interests diverge: female reproductive interests are best served by a monogamous association, but for the male, a polygynous breeding association yields a higher reproductive output (Trumbo and Eggert 1994). Male sexual signaling in this context is directed at changing the breeding system in favor of the male's reproductive interests (Trumbo and Eggert 1994), while female interference appears to be designed to reduce the probability that such a change will occur. The results presented here demonstrate the effectiveness of female interference in thwarting male sexual signaling. Although we did not show directly that female interference leads to a decrease in the number of females detecting the carcass, it appears most likely that a reduction in the time spent signaling would entail a reduction in the number of beetles attracted. Thus, it can be inferred that female interference behaviors reduce the male's ability to alter the breeding association from a monogamous to a polygynous one, and that the female's behavior serves to increase the probability that the breeding association on the carcass will be of a kind commensurate with her reproductive interests.

Male sexual signaling on carcasses that have already been discovered by one female may benefit the male's reproductive success because it increases the probability that an additional mate will discover the carcass, but it also poses a potential threat to the male's reproduction. Pheromone-emitting males risk not only attracting conspecific males, but congeneric competitors as well (Müller and Eggert 1987). When several conspecific males are present on a carcass, clear-cut behavioral roles emerge after the first fights: the dominant male spends most of the time near the carcass, mates more frequently with the resident female(s), and sires the majority of the offspring (a median of about 90%: Eggert 1992 for *N. vespilloides*; Scott and Williams 1993 for *N. tomentosus*), while subordinate males ("satellites") spend most of their time off the car-

cass and attempt surreptitious matings with the female on their occasional brief visits to the carcass. Assuming that the relative paternity of dominant and subordinate males is the same in *N. defodiens* as in *N. vespilloides* and *N. tomentosus*, the attraction of a conspecific rival would at best lead to a slight reduction in a male's paternity (a median of 10%), if the resident male were successful in relegating the intruder to a satellite role. If, on the other hand, the resident were forced to adopt the satellite role, his reproductive success would be severely diminished (by a median of 90%). The consequences of attracting a larger congeneric competitor are even more severe; faced with such competitors, a breeding pair of the smaller species almost invariably forego any reproductive success (Trumbo 1990b). Nonetheless, the risk to a signaling male of attracting a conspecific rival or congeneric competitor is typically much smaller than the probability of attracting a conspecific female (Müller and Eggert 1987). In the present study, male *N. defodiens* had a 9.3% risk of attracting a conspecific male instead of a female, and an additional 7.5% risk of attracting *N. orbicollis*, a larger congeneric competitor.

For pheromone emission on large carcasses to benefit the male, the cost incurred through the attraction of rivals has to be more than compensated by the benefit derived from the attraction of additional females. In our trapping study, 83.2% of all beetles attracted to pheromone-emitting males were conspecific females. Field and laboratory studies on *N. defodiens* (reviewed in Trumbo and Fiore 1994) on carcasses over 35 g mass show that broods produced by two females contain between 42 and 78% more offspring than broods produced by single females. Although these data suggest that the benefits of polygynous signalling outweigh the cost (the expected benefit would vary between 35 and 65% of a brood), changes in offspring quality (size) that might well reduce these apparent benefits would need to be measured for a more precise assessment of the tradeoff.

It could be argued that our pitfall-trapping study does not accurately estimate the increased risk experienced by males signaling on carcasses, because the males used as bait were not signaling from a carcass. Our interpretation of these results assumes that there is no synergistic effect between the attractiveness of carrion and pheromones, and that the risk of attracting other males is not increased when males signal instead of burying the carcass. There is evidence to support both of these assumptions. First, field data from Central Europe on the attractiveness of carcasses, single male *N. vespilloides*, and single male *N. vespilloides* provided with carcasses, fail to show any evidence of synergistic interactions. Rather, they indicate that the attractiveness of carrion and male pheromones is purely additive (J.K. Müller and A.-K. Eggert, unpublished work). *N. vespilloides* is considered to be the sister species of *N. defodiens* (Peck and Anderson 1985), and

its European populations experience ecological conditions very similar to those of *N. defodiens*. Secondly, although males cannot participate in carcass burial while emitting pheromone, their participation does not appear to shorten the burial process significantly: pairs do not bury a carcass faster than single females (Scott 1990 for *N. orbicollis*). Consequently, the attractiveness of an unburied carcass to competitors should remain the same regardless of whether the male chooses to emit pheromone. Hence, the number and sex ratio of additional beetles detecting a carcass as a consequence of male signaling is likely to be equal to the number attracted to a signaling male alone, and our methods can be assumed to produce a reliable estimate of the increased risk to the signaler.

On small carcasses, sexual signaling by monogamously mated males does not occur (Trumbo and Eggert 1994; this study), and on these carcasses, male and female interests largely overlap. The number of offspring produced on such carcasses is not significantly different in single-female or two-female associations (Müller et al. 1990; Trumbo and Fiore 1994). Thus, in this situation, male signaling would confer no obvious benefit to the male, while the risk of attracting competitors would still be incurred. Pheromone emission is likely to be unprofitable for monogamously paired males on smaller carcasses. Resource size, or territory quality, is clearly an important determinant of optimal breeding systems for the sexes and alters the tenor of interactions between males and females (Trumbo and Eggert 1994; Eggert and Müller in press).

Due to their elaborate and time-consuming biparental care, burying beetle reproductive behaviours and parental investment patterns resemble those of birds much more than they do those of most insects. In birds, territory quality can also be an important determinant of the breeding system (Verner and Willson 1966; Orians 1969), and sexual conflict over breeding systems has received considerable attention. Male and female dunnocks, for example, each experience their greatest reproductive success in breeding associations that involve multiple opposite-sex individuals, but from which same-sex individuals are absent (Davies 1992). In dunnocks, sexual conflicts arise when males and females attempt to increase their number of mates while restricting their partner's access to additional mates (Davies 1992). This situation parallels the one in *Nicrophorus defodiens*, except that *Nicrophorus* females have nothing to gain from the presence of multiple males on a large carcass (Trumbo and Eggert 1994; Trumbo and Fiore 1994).

We are aware of only one other study that has demonstrated interference with a mate's sexual advertisement in an invertebrate. In the Sierra dome spider, *Liniphia litigosa*, males have been shown to interfere with female sexual signaling (Watson 1986). In this linyphiid spider, females that have not had the opportunity to mate for a few days after sexual maturation start to incorporate a volatile sex pheromone into the silk of their webs. The first male to arrive on the female's web reduces the probability that competing males will be attracted by balling up the strands of silk that carry the pheromone, which greatly reduces the attractiveness of the web to other males (Watson 1986). Sexual conflict may occur in this instance, although it is unclear whether the female spider would derive a benefit from attraction of additional males. We are aware of no other species, however, in which females have been shown to thwart the sexual signals of their mates; moreover, our study is the first empirical demonstration of a sexual conflict over the form of breeding association in a non-vertebrate species.

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