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Cooperative defence of brood in *Nicrophorus quadripunctatus* (Coleoptera: Silphidae)

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Abstract. A positive correlation between the parental effort of a male and female should promote stable biparental care. In order to prevent infanticide male and female burying beetles are said to guard against intruders cooperatively and the presence of a male partner is said to increase the probability of successful defence. However, this hypothesis is supported only by indirect evidence. In this study this hypothesis is tested by direct observation. Whether the intruder was male or female, contests between the same and the opposite sex occurred, although there were few contests between resident females and intruding males. In addition, resident pairs tended to win irrespective of the sex of the intruder, although it is reported that among burying beetles large beetles usually win intra-sexual contests. In the presence of a partner, a small resident can defend a carcass against a large con-sexual intruder. These results suggest that by means of biparental cooperation burying beetles can repel stronger intruders and supports the hypothesis that the threat of infanticide is the primary explanation for extended biparental care in these beetles.

INTRODUCTION

Biparental care occurs in many species of vertebrate (Clutton-Brock, 1991) and some insect species (Costa, 2006). The major functions of biparental care are assumed to be the provision of food to the young and defence against potentially infanticidal intruders (Clutton-Brock, 1991). Resident parents risk losing both resources and offspring through infanticide. If a male in guarding against infanticidal intruders can increase the probability of success from low to moderate, risk-taking by the female might be expected to increase (Trumbo, 2006a). Infanticide is a cost for both parents and if guarding can increase the probability of success then this will strongly favour biparental cooperation.

The complex parental behaviour of burying beetles (Silphidae: Nicrophorinae: *Nicrophorus*) is well studied (reviewed in Eggert & Müller, 1997; Scott, 1998). *Nicrophorus* feeds small vertebrate carrion to its young. Typically, a male and female beetle co-operate in preparing a carcass by burying it, removing its hair and rounding it into a ball. Eggs are laid in the soil adjacent to the ball of carrion. After hatching, the larvae crawl to the carrion ball, where their parents feed them by regurgitating partially digested food.

Nicrophorus is generally monogamous (Trumbo, 1992; Trumbo & Eggert, 1994; Eggert & Sakaluk, 2000) and both sexes display intense intra-sexual competition (Otronen, 1988; Suzuki et al., 2005). Two or more individuals of both sexes often locate the same carcass but usually only a single dominant pair eventually occupies the carcass. Inferior individuals occasionally remain close to the carcass as satellite males (Müller & Eggert, 1989) and brood parasites (Müller et al., 2007). The larger individuals are usually the winners in contests among conspecifics (Otronen, 1988; Müller et al., 1990). In *Nicrophorus* spp., even after oviposition and hatching, infanticidal takeovers by intruding individuals occur regularly in the field (Scott, 1990; Koulianos & Schwarz, 2000). Intruders kill the eggs and larvae of the residents and reproduce on the carcass (Trumbo, 1990b).

Since infanticide reduces the reproductive success of the resident parents it is advantageous for both parents to reduce the possibility of infanticide. The relationship between biparental care and infanticide in burying beetles is well studied (Trumbo, 1990a). Both males and females cooperatively defend carcasses and broods against intruders even after the larvae hatch (Scott, 1990; Robertson, 1993; Trumbo, 1994, 2006a). However, the notion of biparental cooperation against infanticidal intruders is based on indirect evidence such as a higher probability of reproductive success and higher rates of injury when there are intruders (Otronen, 1988; Trumbo, 1990a). The aim of this study is to determine by observing the behaviour of the beetles whether defensive behaviour against infanticidal intruders involves the cooperation of the sexes.

MATERIAL AND METHODS

All beetles were caught in the field using hanging traps baited with rotten meat. For the experiments, *N. quadripunctatus* individuals were sorted into large (pronotal width 5.5–5.0 mm) and small (4.5–4.0 mm) classes. A pair of differently sized individuals (large male and small female or small male and large female) of *N. quadripunctatus* and 15 g of chicken meat were placed in a polyethylene container (15 × 15 × 9 cm) that was half full of soil. All containers were kept at 20°C in constant darkness. Each container was checked daily and after oviposition the soil covering the carcass was removed.

A large male was introduced into the container as an intruder when the resident pair was composed of a small male and a

large female, and a large female was introduced when the resident pair was composed of a large male and a small female. The behavioural interactions between the residents and the intruder were recorded for 1 h under dim red light. Since soil prevented confirmation of the exact results of a contest, only the participants in the contest were recorded; the results of the contest were not recorded. After recording the behaviour, the beetles present near the carcass were deemed the winners.

RESULTS

Whether the intruder was male (N = 17) or female (N = 17), both intra- and inter-sexual contests were observed, although there were fewer instances of contests between resident females and male intruders (Table 1). In addition, the resident pair tended to win irrespective of the sex of the intruder (Table 2).

TABLE 1. Number of contests (mean ± SD) between residents and intruders.

Sex of intruder	Intra-sexual contests	Inter-sexual contests	t	P
Male	3.3 ± 3.2	2.1 ± 1.7	2.3	0.04
Female	3.1 ± 2.5	3.2 ± 2.2	0.3	0.77

Paired t-test

TABLE 2. Winner of contests between residents and intruders recorded one hour after intrusion.

Sex of intruder	Resident wins	Intruder wins
Male	11	6
Female	11	6

DISCUSSION

Biparental cooperation usually results in an increase in the number of young that are successfully reared (Clutton-Brock, 1991). Although in burying beetles both parents are involved in caring for the young, most male care does not enhance reproductive success. For example, a male does not affect burial speed (Scott, 1990; Suzuki, 2011) and does not increase brood size or brood mass (Scott & Gladstein, 1993; Trumbo & Fernandez, 1995; Trumbo, 2006b). In contrast, a male is important in repelling intruders, irrespective of the sex of the intruders (Trumbo, 2006a). Although contests occur only intra-sexually before carrion is buried (Suzuki, 2000; Suzuki et al., 2005), many inter-sexual contests occurred in this study after burial. Many resident pairs win against intruders after burial (Scott, 1990; Trumbo, 1990, 2006b). In addition, resident males attacked intruder females more frequently than resident females. This supports the notion that males specialize in guarding.

The body size of burying beetles is a good indicator of their resource-holding ability in intra-sexual contests; large individuals usually repel small individuals of the same sex (Otronen, 1988; Suzuki et al., 2005). In contrast, in this study many small residents stayed after intrusion by large beetles of the same sex. Since the difference in the body-size between intruders and residents of the opposite sex was small in this experiment, small residents were able to win when they had a cooperating partner. This result suggests that burying beetle pairs guard carcasses cooperatively and that by means of biparental cooperation they can repel stronger intruders.

For females, losing a defensive fight carries a high cost because the consequence of a loss is infanticide, but even when females successfully defend their broods, they have lower reproductive output (Trumbo, 2006a). Thus, defending females pay a high cost whether they win or lose against an intruder. Trumbo (2006b) reports a low rate of injury among defending females in the absence of a male partner when the intruder is male. Not only infanticide but also injury is costly in terms of female reproductive success, so females must determine the chances of being injured in defending her brood.

Regardless of the intruder's sex, resident males were more likely to be injured than resident females (Trumbo, 2006b). Male burying beetles have both a greater tendency to guard (more time spent guarding: Fetherston et al., 1990, 1994) and a better ability to guard the brood. Resident females can produce replacement clutches after infanticide by intruding males whereas the loss of the resident male results in the loss of both brood and carrion. In addition, the replacement clutches produced by intruding females are smaller than the original clutches (Trumbo & Valetta, 2007). Irrespective of the sex of the residents, infanticide has a large cost for both parents because it limits their opportunity to reproduce. Because it is very difficult to find carrion, the expectation is that parents should invest most heavily in their most recent offspring. In addition, males and females both sustain fecundity costs as a consequence of caring for larvae (Ward et al., 2009). Thus, males defend the brood irrespective of the sex of the intruder because by doing so prevents a reduction in the number of offspring they are currently attempting to rear. Although burying beetles care for their young there are very few reports of biparental cooperation or a division of labour (Smiseth & Moore, 2004; Cotter & Kilner, 2010). This suggests that the advantage of biparental cooperation is that it results in a more effective defence against conspecific intruders. In addition, though infanticide was not observed in the current experiments, its occurrence supports the hypothesis that the threat of infanticide is the primary explanation for extended biparental care in burying beetles (Trumbo, 2006a).

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