

**Biparental Burying Beetles, *Nicrophorus quadripunctatus*
(Coleoptera, Silphidae),
Do Not Show a Division of Labor
in Their Carrion-burial Behavior**

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Abstract The burying beetle, *Nicrophorus* spp., buries carrion biparentally. Whether there is a difference in the frequency of burying behavior in *Nicrophorus quadripunctatus* between single females and pairs was examined. Males were observed to spend less time in burying behavior than females, and whether males were present or not, the frequency of female burying behavior did not differ. These results suggest that burying beetle pairs do not cooperate in carrion burial.

Introduction

Parents rearing offspring commonly face competition with conspecifics and other species for the resources they wish to devote to their young (CLUTTON-BROCK, 1991). Carrion is nutritionally rich, but small, distinct and ephemeral, and thus animals attracted to it must have specialized themselves to rapidly exploit this resource. Of these carrion-consuming organisms, burying beetles of the genus *Nicrophorus* (Coleoptera: Silphidae) occupy a unique position by their specialization in small vertebrate carcasses and elaborate parental care. They exclusively bury vertebrate carcasses in the soil as food for their larvae. They roll the carcass up into a ball underground, and remove fur or small feathers covering the outer surface (PUKOWSKI, 1933). The adults remove any soil particles that fall on the surface of the carrion ball, and continually treat it with anal and oral secretions. Eggs are laid in the soil adjacent to the carrion ball. After hatching, the larvae crawl to the carrion ball. The parents feed on the carrion ball, and later regurgitate predigested carrion to the larvae (SCOTT, 1998).

Intruder burying beetles often kill resident larvae, and such infanticide is a regular occurrence in the wild (SCOTT, 1990; KOULIANOS & SCHWARZ, 2000). TRUMBO (1994) postulated that burying beetles adopt two strategies to compete against the congeners: preventing discovery by efficient burial and maintenance, and repelling individuals that manage to discover the resource. In fact, carrion burial and treatment by the burying beetle has several effects such as reducing discovery by other burying beetles (SUZUKI, 1999, 2000). If parents bury and treat carcasses cooperatively soon after discovery, then discovery by other beetles is expected to be reduced. Although the time of burial did not differ between the presence and absence of a male (SCOTT, 1990), this result does not confirm that there is no division of labor. It is necessary to clarify whether 1) males participate in burial in less time, or 2) females of pairs work less time than single females because of the division of labor. In this study, the frequency of burying behavior in each sex was examined with instantaneous sampling using a network camera.

Materials and Methods

Field-caught adults of *Nicrophorus quadripunctatus* were used in the experiments. All beetles were collected from mid June to early July, 2009 when this species actively reproduce (NAGANO & SUZUKI, 2003), and maintained two to four days under constant dark, 20°C, no food condition before observation. Chicken meat (15 grams) was placed into a polyethylene container (15×15×9 cm) that was half filled with soil. A pair or a female was introduced into the container. All beetles were marked individually with lacquer paint. Using an AXIS® 221 Network Camera, their behavior was recorded every 30 seconds for eight hours (YOKOYAMA *et al.*, 2008). All observations were conducted under a dim red light, 20°C. When the beetles contacted the carcass, they were regarded as showing “burying behavior.” When the carcasses were buried completely (all of the carcasses were concealed with soil) in less than eight hours, the time was recorded, and the frequency of burying behavior was corrected as the number of burying behaviors×8 hours/the time required for burial hours.

Results

The frequency of burying behavior is shown in Fig. 1. Whether a male was present or not, the frequency of female burying behavior was not different ($P=0.9$, $U=116.0$, U-test). The frequency of male burying behavior was significantly smaller than that of females in pairs ($P=0.003$, $t=3.0$, Wilcoxon signed-rank test). The rate of complete burial within eight hours was not different between pairs and single females (Table 1, $P=0.6$, Fisher’s exact test).

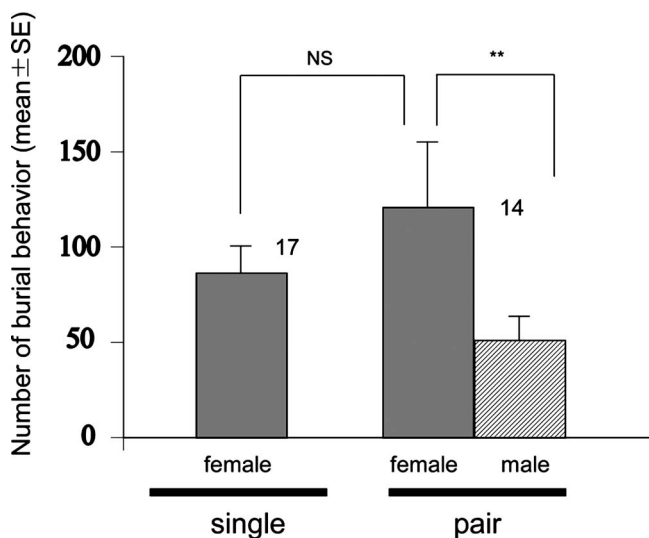


Fig. 1. Frequency of burying behavior (mean±SE). Sample size is shown at the upper part of each bar. Comparison of the behavior between single- and paired females was conducted with U-test, and between paired males and females with the Wilcoxon signed-rank test. **: $P < 0.01$.

Table 1. Rate of complete burial within eight hours.

	Total	Complete burial within 8 hours	<i>P</i>
Single	17	8	0.6
Pair	14	8	

Fisher's exact test

Discussion

This experiment counted the behavior on the carcass. This means that the frequency of burying behavior was over- or underestimated because most of the behavior is conducted under the carcass, which makes it difficult to observe. In addition, some feeding behavior would be counted as burying behavior although apparent difference of feeding behavior was not observed between the case of single females and that of pairs. Nonetheless, this result will be a good indicator of the activity during the carrion-burying period.

Carrion burial and treatment by burying beetles has various effects. Carrion burial prevents fly infestation (SUZUKI, 2000), and treatment prevents both discovery by other burying beetles (SUZUKI, 1999) and fungal development (HOBACK *et al.*, 2007; SUZUKI, 2001). Carcasses easily rot and there is a lot of competition over it, and burying and treating carcasses soon after discovery would improve reproductive success of resident burying beetles. Females can reproduce singly and guard carcasses against enemies. Males, however, must guard not only carrion but females to improve paternity assurance. In fact, females bury carcasses singly but males do not bury carcasses without females (BARTLETT, 1988). This difference may have an influence on the sexual difference in burying behavior.

It is expected that if pairs bury carcasses cooperatively, then 1) the pairs bury carcasses sooner than single females, and 2) the females in the pairs work less time than singles. The present result showed that there was less frequency of burying behavior by males than females, and the frequency of burying behavior by females was independent of male presence. This result does not agree with either expectation. Both sexes of *N. quadripunctatus* provision food and maintain the carcass, although food provisioning by males is performed at a lower rate than by females when care was conducted biparentally (*e.g.* FETHERSTON *et al.*, 1990). Most male care does not improve larvae survival and growth. For example, male presence does not affect burial speed (SCOTT, 1990), and does not increase the brood size or brood mass (SCOTT & GLADSTEIN, 1993; TRUMBO & FERNANDEZ, 1995; SAKALUK *et al.*, 1998; JENKINS *et al.*, 2000; SMISETH *et al.*, 2005; TRUMBO, 2006, 2007). Males cannot increase their rate of provisioning when female provisioning is reduced (SUZUKI & NAGANO, 2009). The adaptive effect of the male presence has been reported only for preventing infanticide (TRUMBO, 2006, 2007). In addition, it has not been confirmed whether burying beetles prevent infanticide cooperatively or not, and there have been no reports of a division of labor between sexes in burying beetles. This study revealed that male burying beetles attend the burying with females, but may not work cooperatively, at least in the burial behavior.

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要 約

鈴木誠治：ヨツボシモンシデムシの雌雄は死体埋葬の際に分業を行わない（コウチュウ目シデムシ科）。——モンシデムシ属は小型脊椎動物の死体を雌雄で地中に埋葬し、育児を行う。ヨツボシモンシデムシを用いて、雌雄ペアの場合とメス単独の場合で埋葬行動の頻度に違いがないか調べた。その結果、オスはメスに比べ埋葬に参加する頻度が低く、メスの参加頻度はオスの有無と無関係だった。一方埋葬にかかる時間はオスの有無に影響されなかった。この結果からヨツボシモンシデムシによる死体埋葬には、雌雄間の協力は無いものと考えられる。

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