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ARTICLE

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Changing dominant–subordinate relationships during carcass preparation between burying beetle species (*Nicrophorus*: Silphidae: Coleoptera)

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Abstract I studied the influence of carrion burial on the interaction between *Nicrophorus quadripunctatus* and *Nicrophorus vespilloides*. In the preburial phase, *N. quadripunctatus*, the smaller species, occupied more carcasses than *N. vespilloides*, the larger species, when both species were allowed to compete for mouse carcasses. However, after carcasses were buried, *N. vespilloides* was more successful in protecting those it had buried, and more successful in intruding on carcasses buried by *N. quadripunctatus*. Direct observation supported these findings. These results may suggest that *N. vespilloides* is cleptoparasitic on *N. quadripunctatus* for carrion burial.

Key words Burying beetle · *Nicrophorus* · Carrion burial · Competition

Introduction

Burying beetles (*Nicrophorus* spp.) are attracted to the carcasses of small vertebrates, which they use as food for their young. Through intrasexal competition, victorious male and female (usually the largest of each sex) remain to bury the resource (Pukowski 1933; Wilson and Fudge 1984; Bartlett and Ashworth 1988; Otronen 1988). The buried carcass is rolled into a ball, and the fur or feathers are removed. The pair use the ball as food for larvae (Milne and Milne 1976; Scott 1989).

Carcasses are frequently usurped by *Nicrophorus* intruders even after beetles bury carcasses, and securing carrion suitable for offspring production is thought to be difficult. These intruders may be conspecifics (Trumbo 1991; Robertson 1993; Scott 1994) or congeners (Scott 1994; Trumbo 1990). Wilson et al. (1984) reported that many congeners discovered carrion buried by *N. defodiens*. Trumbo (1994) has shown that the carcasses treated by *N. defodiens* attracted many other beetles, mostly larger *Nicrophorus* species, and suggested that resident burying beetles may prevent discovery through the efficient burial and maintenance of carcasses. Aggressive interaction is thought to be typical behavior for obtaining carcasses by burying beetles (Pukowski 1933; Bartlett and Ashworth 1988; Otronen 1988), and larger *Nicrophorus* species are usually superior to smaller ones in conflict in both preburial (Otronen 1988) and postburial phases (Scott 1994; Trumbo 1990). Dominant–subordinate relationships are constant in the preburial and postburial phases. In the present study, however, I report that dominant–subordinate relationships on carcasses between *N. quadripunctatus*, a smaller species, and *N. vespilloides*, a larger species, change between preburial and postburial phases; *N. quadripunctatus* is dominant in the preburial phase, while *N. vespilloides* is dominant in the postburial phase. I also report on behavioral changes of the two species before and after carcass burial.

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Materials and methods

Study site

The present study was conducted in the Hokkaido University Nakagawa Experimental Forest, northern Hokkaido, northern Japan, where five *Nicrophorus* species (*N. maculifrons*, *N. quadripunctatus*, *N. vespilloides*, *N. tenuipes*, and *N. investigator*) are known to occur (Katakura and Fukuda 1975).

Material

I chose *N. vespilloides* and *N. quadripunctatus* for the present study. In the study area, these two species are common and do not show apparent spatiotemporal segregation (Katakura and Fukuda 1975; Ohkawara et al. 1998). Both

species live primarily in natural mixed forests and reproduce from July to mid-August, actively searching for carcasses from 1800 to 2200 (Ohkawara et al. 1998). Hence, intense competition for carcasses is expected between the two species. All beetles were caught with hanging pitfall traps in the field. Beetles were used for experiments on the day of or the day after collection. Because most beetles caught from July to mid-August buried carcasses within 24 h under laboratory condition (S. Suzuki, personal observation), I regarded most *N. vespilloides* and *N. quadripunctatus* caught in this period as ready to reproduce.

Previously frozen mouse carcasses were provided from the Centre for Experimental Plants and Animals, Hokkaido University. Mouse carcasses were thawed at room temperature at least one night before use in experiments.

Experimental analysis of competitive interactions

I conducted two types of experiments to understand the effect of burial on competitions for carcasses. Unglazed flower pots (20-cm diameter) were used for these experiments. The pot was filled with soil, and a mouse carcass (18–25 g) was placed in the center of the pot. The experiments were conducted from July to early August, 1996. The pronotal widths of *N. quadripunctatus* were significantly smaller than those of *N. vespilloides* ($n = 74$; *N. vespilloides* male, 5.1 ± 0.4 mm; *N. quadripunctatus* male, 4.6 ± 0.4 mm; $P < 0.001$, $U = 1012.5$; *N. vespilloides* female, 5.1 ± 0.3 mm; *N. quadripunctatus* female, 4.7 ± 0.4 mm; $P < 0.001$, $U = 983.5$, Mann–Whitney *U*-test). The beetles were free of injury before experiments.

Experiment 1. Carrion occupation in preburial phase: I released a pair of *N. vespilloides* and a pair of *N. quadripunctatus* simultaneously in the pot. The pot then was covered by a plastic plate to prevent escape. After the carcass was buried by the beetles, I exhumed it, identified the beetles that held the carcass, and checked legs and antennae for injuries. I carried out 20 replicates.

Experiment 2. Carrion occupation in postburial phase: I released either a pair of *N. vespilloides* ($n = 29$) or a pair of *N. quadripunctatus* ($n = 25$) in the pot and allowed them to bury a mouse carcass. After confirming that the carcass was buried (1 day after the first pair was released), I released a pair of heterospecific beetles in the pot. On the next day, I exhumed the carcass and identified the beetles occupying it, and checked for injuries.

Direct observation of behavioral interactions

To study behavioral changes of burying beetles before and after the burial of carcasses, I conducted direct observations of burying beetle behavior under two different conditions, using glass cages (200 × 250 × 25 mm) filled with soil on which a carcass was placed. The cage was made of two glass plates and a narrow wood frame, which formed the bottom and two sides of the cage, allowing the observation of behavior with the buried carcasses. These cages were placed in a large plastic container, and were kept constantly in the dark. Beetles were released on top of the soil of the edge of containers carefully to minimize handling effects. The following observations were conducted from July to early August, 1997.

Experiment 3. Observation of preburial phase behavior: at least 6 h before observation, I released a pair of *N. quadripunctatus* and a pair of *N. vespilloides* in a glass cage. All the beetles were individually marked with lacquer paint on elytra to discriminate individuals. After sunset (usually 1830), I placed a mouse carcass (10–17 g) in the cage and started the observation. I checked the carcasses through a glass plate every 5 min under red light. I recorded whether beetles were witnessed on the carcass. When both *N. vespilloides* and *N. quadripunctatus* were found on the carcass, I recorded subsequent behaviors. The observation was discontinued when more than half of the carcass was buried. There were 16 replicates.

Experiment 4. Observation of postburial phase behavior: I released either a pair of *N. vespilloides* ($n = 15$) or *N. quadripunctatus* ($n = 8$) in the cage with a mouse carcass (10–17 g) and allowed them to bury the carcass. One day after the carcass burial was confirmed, I released a pair of the heterospecifics at sunset and observed behavior. The observation procedure was the same as experiment 3, except that the observation periods were 3 h long, from 1830 to 2130.

Results

Experiment 1

All carcasses were buried by either *N. vespilloides* or *N. quadripunctatus*; 75% (15/20) of the carcasses were occupied by *N. quadripunctatus*, a significant greater percentage than *N. vespilloides* ($P = 0.02$, binomial test). Seventeen males and 17 females of the *N. vespilloides* were larger than their *N. quadripunctatus* companions, and even if *N. vespilloides* were smaller, most of them did not occupy carcasses.

The legs or antennae of some beetles were injured, but the rates were very low. Only 2/40 (2 females) of *N. vespilloides* and 1/40 (1 female) of *N. quadripunctatus* were injured.

Experiment 2

The results are summarized in Table 1. Most *N. vespilloides* (28/29 carcasses were buried by *N. vespilloides*, and 25/25 by *N. quadripunctatus*) were larger than the companion of *N. quadripunctatus*. A majority of carcasses (72%) originally buried by *N. vespilloides* were held by *N. vespilloides* after 24 h, whereas only about half (52%) of the carcasses originally buried by *N. quadripunctatus* were held by *N.*

quadripunctatus, although this difference was not significant ($P = 0.16$, Fisher's exact test).

Injury rates were again very low: 3/58 (2 males and 1 female) of *N. vespilloides* and 4/58 (3 males and 1 female) of *N. quadripunctatus* were injured when carcasses were buried by *N. vespilloides*, and 3/50 (1 male and 2 females) of *N. vespilloides* and no *N. quadripunctatus* were injured when carcasses were buried by *N. quadripunctatus*.

Experiment 3

Nicrophorus quadripunctatus were found more frequently on the carcasses left on the ground than *N. vespilloides* (male, $P = 0.002$; female, $P = 0.029$; Fisher's exact test; Table 2). All *N. quadripunctatus* individuals except one male were witnessed at least once on the exposed carcasses, whereas only a few *N. vespilloides* (females in all cases) were on the carcasses (Table 2).

Nicrophprus vespilloides were driven away by *N. quadripunctatus* in all eight encounters observed (all females), even if they arrived at the carcasses sooner. Through these encounters, I identified an interference behavior, "touch," in which two beetles meet on a carcass, one touches the other with its antennae, and one of them runs away.

Experiment 4

Behavior on buried carcasses was different from the behavior on exposed carcasses (Table 2). Except for one female *N. vespilloides* and one male *N. quadripunctatus*, all individuals of both species were confirmed on carcasses that they had buried. Moreover, heterospecifics were observed on 4 of 15 carcasses buried by *N. vespilloides* and 4 of 8 carcasses buried by *N. quadripunctatus*. All *N. quadripunctatus* (5 males and 2 females) found on the carcasses buried by *N. vespilloides* were driven away by the owners. A total of four individuals of *N. vespilloides* (1 male, 3 females) were found on carcasses buried by *N. quadripunctatus*. Of these, one male and one female were driven away by the owners, but two females won the conflict and drove away *N. quadripunctatus* from the carcasses they had buried.

I identified two kinds of interference, "touch" and "grapple." Grapple behavior is said to occur when one beetle rides on the body of another beetle. Only the touch behavior was observed on carcasses buried by *N. quadripunctatus*. Both touch and grapple behaviors were observed on carcasses buried by *N. vespilloides*. The grapple behavior was observed in two of seven encounters, between *N. quadripunctatus* females and *N. vespilloides* males, and between *N. quadripunctatus* females and *N. vespilloides* females.

Table 1. Numbers of mouse carcasses taken over by heterospecific *Nicrophorus* intruders in experiment 2 (carrion occupation in postburial phase)

Carcasses buried by	Carcasses held by:		*n*
	Residents	Heterospecifics	
N. vespilloides	21	8	29
N. quadripunctatus	13	12	25

Discussion

Bonanza resources (Wilson 1971), such as carrion, attract many organisms, many of which are specialized to exploit the resources rapidly before competitors become established. Burying beetles bury carcasses underground, and then eliminate microbial and dipteran competitors (Pukowski 1933). It has been suggested that burying beetles compete for carcasses through interference competition (Trumbo 1990, 1994; Wilson et al. 1984).

Generally, larger species tend to be dominant in interspecific competition, especially during interference competition (Persson 1985; Schoener 1983). It has been reported that larger *Nicrophorus* species are dominant in conflict in preburial (Otronen 1988) and postburial conditions (Scott 1994). There are no reports of smaller *Nicrophorus* species being superior to larger ones.

However, the results presented here follow a different pattern. In experiment 1, *N. quadripunctatus*, the smaller species, tended to occupy more carcasses than *N.*

Table 2. Percentage ratio of beetles that were witnessed at least once in experiments 3 and 4

	Buried by	Number of replicates	Beetles witnessed (%)			
			N. quadripunctatus		*N.vespilloides*	
			♂	♀	♂	♀
Experiment 3	–	16	93.7	100	0	25
Experiment 4	*N. vespilloides*	15	26.7	13.3	100	93.3
	N. quadripunctatus	8	87.5	100	50	50

Data for males and females are given separately. In experiment 3, one pair each of *N. vespilloides* and *N. quadripunctatus* were simultaneously introduced to a cage and allowed to compete for a carcass. In experiment 4, a pair of either *N. vespilloides* or *N. quadripunctatus* was introduced into a cage after a carcass was buried by a pair of heterospecifics

vespilloides, the larger species, in the preburial phase. Furthermore, at a glance, the dominant–subordinate relationship between *N. vespilloides* and *N. quadripunctatus* seemed to be reversed before and after the burial of carrion. In experiment 2, *N. vespilloides* occupied about half the carcasses buried by *N. quadripunctatus*, whereas *N. quadripunctatus* occupied a smaller number of carcasses buried by *N. vespilloides* (see Table 1). The results of experiments 3 and 4 support these findings.

Two questions then arise. First, is it really true that *N. quadripunctatus*, the smaller species, was dominant over *N. vespilloides*, the larger species? Second, why was the dominant–subordinate relationship reversed after burial?

It appears that there was little interference competition between the two species during the preburial phase. As demonstrated by experiment 3, most *N. quadripunctatus* released in the cages, both males and females, were witnessed on the exposed carcasses and buried them. On the other hand, no males and only 25% of females of *N. vespilloides* were witnessed on the exposed carcasses during experiment 3. These experiments were conducted in small containers, so the possibility that beetles could not find the carcass can be eliminated. Further, when the two species met on a carcass, *N. vespilloides* avoided *N. quadripunctatus* without apparent aggression (only "touch" behavior was observed). Moreover, the injury rates of both species were very low in experiment 1, and direct conflict was rare in experiment 3. Trumbo (1994) reported the frequent occurrence of injuries in both sexes in contest between *N. orbicollis* and *N. pustulatus*. Thus, I can conclude that conflicts over carcasses between *N. vespilloides* and *N. quadripunctatus* rarely occurred, at least during the preburial phase. For unknown reasons, *N. vespilloides* seemed to be less eager to bury carcasses than *N. quadripunctatus*. After a carcass was buried, *N. vespilloides* seemed to be dominant over *N. quadripunctatus*, as demonstrated by experiments 2 and 4. Injury rates were also low in experiment 2, indicating that dominance was usually established without intense fighting.

Nicrophorus vespilloides might not become immediately aggressive when they discover carcasses on which *N. quadripunctatus* are present, but became aggressive when carcasses were buried by other beetles. If this interpretation is correct, *N. vespilloides* might be cleptoparasitic on *N. quadripunctatus*. If carrion burial is costly compared to carrion takeover by *N. quadripunctatus*, *N. vespilloides* would prefer to be cleptoparasitic on *N. quadripunctatus*. However, there is little direct evidence of cleptoparasitism by *N. vespilloides*. Trumbo (1994) reported that *N. pustulatus* can be cleptoparasitic on *N. orbicollis*. However, parasitism of *N. pustulatus* is brood parasitism, and is quite different from that of *N. vespilloides* postulated here. *Nicrophorus vespilloides* is known to bury carcasses and care for their brood by themselves (Bartlett 1988; Eggert 1992), so cleptoparasitism, if it exists, is facultative. Nevertheless, we must pay attention to plasticity in reproductive histories to understand the complicated interspecific interactions of burying beetles.

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References

Barlett J, Ashworth CM (1988) Brood size and fitness in *Nicrophorus vespilloides* (Coleoptera: Silphidae). Behav Ecol Sociobiol 22:429–434

Bartlett J (1988) Male mating success and parental care in *Nicrophorus vespilloides* (Coleoptera: Silphidae). Behav Ecol Sociobiol 23:297–303

Eggert AK (1992) Alternative male mate-finding tactics in burying beetles. Behav Ecol 3:243–254

Katakura H, Fukuda H (1975) Faunal makeup of ground and carrion beetles in Kamiotoineppu, Hokkaido University Nakagawa Experiment Forest, Northern Japan, with some notes on related problems. Res Bull Coll Exp For Fac Agric Hokkaido Univ 1:75–92

Milne LJ, Milne M (1976) The social behaviour of burying beetles. Sci Am 235:84–90

Ohkawara K, Suzuki S, Katakura H (1998) Competitive interaction and niche differentiation among burying beetles (Silphidae, *Nicrophorus*) in Northern Japan. Entomol Sci 1:551–559

Otronen M (1988) The effect of body size on the outcome of fights in burying beetles (*Nicrophorus*). Ann Zool Fenn 25:191–201

Persson L (1985) Asymmetrical competition: are larger animals competitively superior? Am Nat 126:261–265

Pukowski E (1933) Okologische untersuchungen an *Necrophorus* F. Z Morphol Oekol Tiere 27:518–586

Robertson IC (1993) Nest intrusions infanticide, and parental care in the burying beetle, *Nicrophorus orbicollis* (Coleoptara: Silphidae). J Zool Lond 231:583–593

Schoener TW (1983) Field experiments on interspecific competition. Am Nat 122:240–285

Scott MP (1989) Male parental care and reproductive success in the burying beetle, *Nicrophorus orbicollis*. J Insect Behav 2:133–137

Scott MP (1994) The benefit of parental assistance in intra- and interspecific competition for the burying beetle, *Nicrophorus defodien*s. Ethol Ecol Evol 6:537–543

Trumbo ST (1990) Interference competition among burying beetles (Silphidae, *Nicrophorus*). Ecol Entomol 15:347–355

Trumbo ST (1991) Reproductive benefits and the duration of parental care in a biparental burying beetle, *Necrophorus orbicollis*. Behaviour 117:82–105

Trumbo ST (1994) Interspecific competition, brood parasitism and the evolution of biparental cooperation in burying beetles. Oikos 69: 241–249

Wilson DS, Fudge J (1984) Burying beetles: intraspecific interactions and reproductive success in the field. Ecol Entomol 9:195–203

Wilson DS, Knollenberg WG, Fudge J (1984) Species packing and temperature dependent competition among burying beetles (Silphidae, *Nicrophorus*). Ecol Entomol 9:205–216

Wilson EO (1971) The insect societies. Harvard University Press, Cambridge