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ORIGINAL ARTICLE

Brood size reduction in *Nicrophorus vespilloides* after usurpation of carrion from *Nicrophorus quadripunctatus* (Coleoptera: Silphidae)

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Abstract

Burying beetles bury small vertebrate carcasses, which become food for their larvae. They sometimes usurp carcasses occupied and buried by other beetles. Brood sizes of intraspecific and interspecific intruders were examined using *Nicrophorus quadripunctatus* as the resident. The brood sizes of usurpers were not reduced relative to control brood sizes when the usurper was conspecific, but were reduced when the usurper was heterospecific (*N. vespilloides*).

Key words: burying beetle, takeover.

INTRODUCTION

Burying beetles, the genus *Nicrophorus* (Coleoptera: Silphidae), occupy a unique ecologic position in their ability to use small vertebrate carcasses as a reproductive resource. Elaborate biparental care of the brood is part of their specialized reproductive strategy. The beetles bury carcasses in the soil as food for their larvae (Pukowski 1933; Scott 1998), rolling the carcass into a ball underground, and removing fur or feathers covering the outer surface of the carcass (Pukowski 1933). The adults remove soil particles that fall on the surface of the carrion ball, and continually moisten it with anal and oral secretions (Pukowski 1933). Eggs are laid in the soil adjacent to the carrion ball. After hatching, larvae crawl to the carrion, and aggregate in a small patch of exposed flesh on the top of the carrion ball that the parents have created. The parents feed on the carrion ball, and later regurgitate predigested carrion to the larvae.

When more than two beetles arrive at the same carcass, there may be a violent fight for possession of the carcass (Pukowski 1933). Through intrasexal competition, the victorious male and female (usually the largest individuals of each sex) remain to bury the resource (Pukowski 1933; Bartlett & Ashworth 1988; Otronen 1988). Fights occur between conspecifics of the same sex as well as between members of different species (Pukowski 1933).

Nicrophorus intruders frequently usurp carcasses even after other beetles have buried them, and competition for carrion is thought to be very intense. These intruders may be conspecifics (Scott 1990; Trumbo 1991; Robertson 1993), or congeners (Trumbo 1990; Scott 1994). Wilson and Knollenberg (1987) reported that many congeners discovered carrion buried by *Nicrophorus defodiens* Mannerheim in Michigan, USA.

Although intraspecific and interspecific competition is an important component of the reproductive ecology of burying beetles, there have been few studies that have dealt with the effects of takeover on reproductive success. I examined the brood size of intruding burying beetles after intraspecific and interspecific takeovers.

MATERIALS AND METHODS

Collection and treatment of beetles

Experiments were conducted in a grove on the campus of Hokkaido University, Sapporo, south-western Hokkaido, in 2001 and 2003. All beetles were caught in the field with hanging traps baited with rotten meat. Beetles

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used for the intraspecific takeover experiment were caught at the Naebo Forest Park in Otaru, near Sapporo, in July; those for interspecific takeover experiments were caught at the Hokkaido University Nakagawa Experiment Forest, northern Hokkaido, northern Japan, in July. Beetles were used for experiments within 2 days of collection. July is the main reproductive season for both *N. quadripunctatus* Kraatz and *N. vespilloides* (Herbst) (Ohkawara *et al.* 1998).

To establish reproductive success after usurpation, a pair of *N. quadripunctatus* was placed in a soil-filled plastic container (81 mm in diameter, 58 mm in depth) with a piece of chicken meat (approximately 20 g) placed on the soil in the center of the container. The container was placed on the forest floor.

Cost of intraspecific takeover

After confirming carrion burial and rolling 2 or 3 days after the introduction of the resident pair, I introduced a female of *N. quadripunctatus*, larger than the resident female, as an intruder ($n = 20$). When she successfully usurped the carcass, I removed the resident female carefully to minimize the effect of handling (after takeover). As a control, data were obtained for broods produced by pairs that were maintained without intruders ($n = 15$). To determine if fighting is costly, I also introduced intruders after having removed resident beetles, and measured the number and the total weight of the brood ($n = 5$). In all experiments, I maintained the container covered until beetle larvae crawled away from the carcass for pupation, at which point I opened the container and measured the number and weight of the brood. Mean larval weight was calculated by dividing total weight with the number of larvae. Because intruders usually kill all larvae present on the carcass (Scott 1990) and destroy eggs present in the soil (Robertson 1993), I considered all of the larvae to be offspring of the intruders.

Cost of interspecific takeover

After confirming burial of the carrion by the resident pair, I introduced a pair of *N. vespilloides* ($n = 13$). When they successfully usurped the carcass, I removed the resident *N. quadripunctatus* pair. As a control, data were obtained for broods produced by pairs of *N. vespilloides* that were not used as intruders ($n = 10$). As with the intraspecific experiment, the removal experiment was conducted by introducing intruders after resident beetles were removed ($n = 5$). The number and weight of the brood was measured after larvae had dispersed for pupation.

Because brood size of burying beetles is not correlated with body size of the mother but is correlated with carrion size in *N. vespilloides* (Müller *et al.* 1990), I regarded brood size to also be independent of mother's body size in this study.

RESULTS

In the intraspecific experiment, 10 of the 20 intruders usurped the carcasses and reproduced successfully (Table 1). Larvae crawled away from the usurped carcasses 10–12 days after the intruder had been introduced. Five broods were excluded: these broods failed due to growth of fungi on the carcasses (Table 1). The average number of larvae, total brood mass, and larval weight were not significantly different between treatments (Table 2).

In the interspecific study, beetle reproduction was successful in all of the experiments, and 10 out of 13 carcasses were usurped by *N. vespilloides* (Table 1). Although the average number of larvae and mean larval weight were not significantly different, total brood mass was significantly different between treatments (Table 3). In addition, total brood mass in both of the after takeover and removal experiments was smaller than that of the control (posthoc test, Scheffe's method; $P < 0.01$).

DISCUSSION

Larger burying beetles usually prevail in intraspecific and interspecific competition (Bartlett & Ashworth 1988; Otronen 1988). One of the results of this study was that many larger females successfully usurped carrion in the intraspecific experiment (Table 1). The interspecific experiment also showed that *N. vespilloides* was a successful usurper. The body size of *N. vespilloides* tends to be larger than *N. quadripunctatus* (Suzuki 2000), and it has previously been shown that

Table 1 Fate of carcasses buried by *Nicrophorus quadripunctatus* after introduction of intruder

	Intraspecific intruder	Interspecific intruder
Usurped by intruder and brood success	10	10
Held by resident	3	2
Owner not determined	2	1
Brood failure	5	0
Total	20	13

Table 2 Number of larvae and brood mass produced on the carcasses under control and experimental conditions (intraspecific takeover)

	After takeover ($n = 10$)	Resident removal ($n = 5$)	Control ($n = 15$)	F	P
Number of larvae (mean ± SE)	8.1 ± 1.6	9.4 ± 1.6	9.8 ± 0.7	0.39	0.68
Total brood mass (g; mean ± SE)	1.18 ± 0.24	1.40 ± 0.32	1.71 ± 0.15	1.23	0.30
Mean weight of larva (g; mean ± SE)	0.15 ± 0.01	0.14 ± 0.02	0.16 ± 0.01	1.74	0.19

F- and *P*-values were obtained by one-way ANOVA.

Table 3 Number of larvae and brood mass produced on the carcasses under control and experimental conditions (interspecific takeover)

	After takeover ($n = 10$)	Resident removal ($n = 5$)	Control ($n = 10$)	F	P
Number of larvae (mean ± SE)	10.6 ± 1.3	10.6 ± 2.5	16.4 ± 2.4	2.79	0.08
Total brood mass (g; mean ± SE)	1.50 ± 0.19	1.25 ± 0.29	2.61 ± 0.32	6.88	0.005
Mean weight of larva (g; mean ± SE)	0.15 ± 0.01	0.14 ± 0.01	0.17 ± 0.01	3.23	0.06

F- and *P*-values were obtained by one-way ANOVA.

N. vespilloides is successful in intruding on carcasses buried by *N. quadripunctatus* (Suzuki 2000).

The total brood mass was not different between intraspecific experiments (Table 2); intraspecific carrion takeover by *N. quadripunctatus* appears to have little or no cost to the fitness of intruders.

In contrast, the total brood mass was different between interspecific experiments. Although brood size was not measured when *N. vespilloides* usurp conspecific carrion, brood size reduction after intraspecific takeover will not occur, because brood size reduction in intraspecific takeover by *N. quadripunctatus* was not seen. Thus brood size reduction in *N. vespilloides* can only occur in interspecific takeover. Both the number of larvae and the mean larval weight of after takeover were smaller than those in the control group, although this difference was not statistically significant (Table 3). The cost of takeover may affect both the number and the mass of larvae.

Competition for carrion is usually very intense, and much of the carrion buried by burying beetles is usurped by intraspecific and interspecific intruders (Trumbo 1990; Eggert & Sakaluk 2000). Therefore, reproduction opportunities are limited. In addition, smaller species of burying beetles tend to search for carrion more efficiently (Wilson *et al*. 1984; Trumbo & Bloch 2002), and *N. quadripunctatus* is a dominant species (Ohkawara *et al*. 1998). Therefore, *N. vespilloides* have a lot of opportunities for finding carrion buried by *N. quadripunctatus*.

Suzuki (2000) reported that *N. quadripunctatus* was superior to *N. vespilloides* in preburial conflicts, but after carcasses were buried, *N. vespilloides* was more successful in protecting the carcasses it had buried, and more successful in intruding on carcasses buried by *N. quadripunctatus*. Thus, Suzuki (2000) suggested that *N. vespilloides* is cleptoparasitic on *N. quadripunctatus*. Smith *et al*. (2000) reported that the brood size of *N. investigator* Zetterstedt pairs that had reproduced in ready-made holes was not different from the brood size of *N. investigator* pairs that had reproduced in holes prepared by parents. It seems that carrion burial itself has little or no cost to the reproduction of burying beetles. In addition, as demonstrated in this study, a beetle pair's brood size is smaller when a carcass usurped from another species is used.

There are two explanations why brood size would be smaller after usurpation by a different species: cost due to fighting and cost of using carrion used by another species. The cost of fighting is expected to be small in interspecific competition because the injury rate after competition is very low (Suzuki 2000). In addition, because the total brood mass was not significantly different between after takeover and removal experiments, the cost of using carrion used by another species appears to have a greater effect.

The carcasses that burying beetles bury are eaten by parents and treated with oral and anal secretions. These secretions are thought to reduce the growth of fungi by their chemical effects (Suzuki 2001). It is possible that carcass mass reduction due to parental feeding and/or the application of secretions may have negative effects on the reproduction of congeneric intruders.

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