Entomological Science (2007) **10**, 245–248 doi:10.1111/j.1479-8298.2007.00220.x

ORIGINAL ARTICLE

Effects of carcass size and male presence on clutch size in *Nicrophorus quadripunctatus* (Coleoptera: Silphidae)

Masahiro NAGANO[1] and Seizi SUZUKI[2]

[1]*Echigo-Matsunoyama Museum of Natural Science, Matsunoyamamatsukuchi, Tokamachi City, Niigata, and* [2]*Center for e-Learning Research and Application, Nagaoka University of Technology, Nagaoka, Niigata, Japan*

Abstract

The effects of carcass size and male presence on clutch size in *Nicrophorus quadripunctatus* were examined. Male presence increased clutch size and improved the female's ability to produce replacement clutches. Clutch size was also related to carcass size. There was a negative correlation between number of clutches and clutch size for most carcass sizes. We conclude that *N. quadripunctatus* is potentially iteroparous and hypothesize that reproductive energy is reserved for brood failure.

Key words: brood failure, clutch size, iteroparity, male presence.

INTRODUCTION

Parental care in insects has evolved independently in many families (Tallamy & Wood 1986). The complex biparental care of burying beetles (Silphidae: *Nicrophorus*) is well known and has received considerable attention (reviewed in Eggert & Müller 1997; Scott 1998). *Nicrophorus* exploits small vertebrate carrion as food for their young. Typically, a male–female pair prepares a carcass by burying it, removing the hair, and rounding it into a ball (Pukowski 1933). Eggs are then laid in the soil adjacent to the carrion ball. After hatching, larvae crawl to the carrion ball, where they are fed via parental regurgitation.

The clutch size of burying beetles is reported to be restricted by carcass mass. The clutch size of *N. vespilloides* is significantly correlated with carcass mass for carcasses less than 10 g in size only (Müller *et al*. 1990). Female burying beetles can produce a replacement clutch when larval mortality is high (Müller 1987) or when intruders kill their initial brood (Trumbo 2006). Since carrion is a nutritionally valuable but limited resource, competition for carrion is intense among congeneric *Nicrophorus* (Eggert & Müller 1997). Larger *Nicrophorus* species have a competitive advantage in interspecific competition (Otronen 1988). Usurpation by intruders often occurs when the species is small and/or a single female is the occupier (Trumbo 1990a). Burying beetles that are frequently usurped from carcasses often fail to reproduce and must attempt reproduction several times. Thus, when the likelihood of brood failure is higher, burying beetles must regulate their clutch size more strictly. We examined whether *Nicrophorus quadripunctatus,* a small species that is common in most of Japan, regulates clutch size and how the number and size of clutches are affected by carcass mass and the presence of a male.

MATERIALS AND METHODS

Nicrophorus quadripunctatus were collected using bait traps from the Tama Forest Science Garden in 2002 between April and early May, which is the beginning of the reproductive season of *N. quadripunctatus* (Nisimura *et al*. 2002; Nagano & Suzuki 2003), when most beetles are expected to be in the pre-reproductive stage. Similar-sized beetles (pronotal width 5.0 ± 0.2 mm, mean ± SD) were selected for experiments. Phoretic mites were removed from the beetles, and then the beetles were placed in plastic boxes and

Correspondence: Seizi Suzuki, Center for e-Learning Research and Application, Nagaoka University of Technology, 1603-1 Kamitomioka, Nagaoka, Niigata, 940-2188 Japan. Email: seizi@oberon.nagaokaut.ac.jp

Received 30 August 2006; accepted 7 March 2007.

allowed to reproduce. Boxes were half-filled with soil, and contained a piece of thawed chicken meat (6 g and 25 g carcasses: 12 cm diameter, 10 cm depth box; 100 g carcasses: 20 cm × 12 cm × 15 cm box). All experiments were conducted in the dark at 20°C. All females were coupled with a male for 12 h prior to the start of the experiment.

Carcasses of three sizes (approximately 6 g, 25 g and 100 g) were used for this experiment. A single female or male–female pair was introduced in a box to confirm the effect of male presence. Each box was checked every 12 h, and when hatched larvae were present on the carcass, the parent(s) were removed and all larvae and eggs were counted. Since this time corresponds to when oviposition has ceased but care has not yet started, the parent(s) have made minimal post-hatching investment. The removed female was then coupled with a male for several hours. We also recorded the time from introduction of the parent to confirmed egg hatching. This was regarded as the time between instances of parental care.

The removed parent(s) were reintroduced into a new box containing a carcass of the same size within 12 h. This procedure was repeated up to six times. If a female died or did not oviposit within 10 days of being introduced into a new box, that trial was terminated.

RESULTS

Paired females were more likely than single females to produce the maximum of six clutches, irrespective of carcass size ($P < 0.01$, log-linear analysis, $R^2 = 0.26$; Table 1). Total clutch size was related to both carcass size and to the presence of a male (Table 2). The time from introduction of the adult(s) to larval hatching was affected by both clutch order (Fig. 1) and carcass size (Table 3).

The relation between clutch size and clutch order was determined using a correlation coefficient weighted using the number of replicates for each individual. With the exception of single females with 6 and 25 g carcasses, all treatments showed a significant negative correlation between clutch order and clutch size ($P < 0.05$, Fig. 2).

DISCUSSION

Several previous studies of burying beetles have suggested that clutch size is affected by carcass size (Müller *et al.* 1990; Trumbo 1990b). For example, for *N. vespilloides* a significant correlation between clutch size and carcass mass was found for carcasses less than 10 g in weight, but no effect was found for larger carcasses (Müller *et al.* 1990). In contrast, in the present study using *N. quadripunctatus* pairs, a significant correlation was found over the entire range of carcass sizes

Table 1 Fraction of single females and pairs of *Nicrophorus quadripunctatus* that produced six clutches in succession

Carcass size (g)	Single females	Pairs
6	5/9	9/9
25	4/8	9/10
100	4/8	10/10

Table 2 Repeated measures ANOVA examining effect on *Nicrophorus quadripunctatus* clutch size

Factor	d.f.	F	*P*
Clutch order	5	66.89	<0.001
Carcass size	2	14.43	<0.001
Male presence	1	7.47	0.007
Error	275		

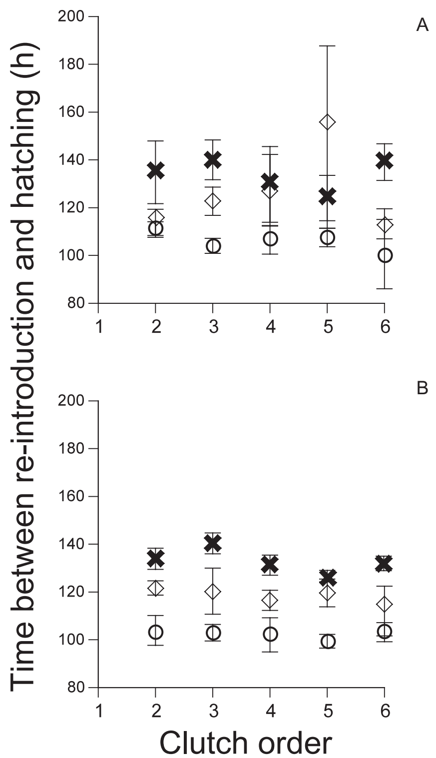

Figure 1 Relation between clutch order and time from beetle re-introduction to larval hatching for three carcass size classes for *Nicrophorus quadripunctatus* (mean ± SE). (A) Single female; (B) pair. ○, 6 g; ◇, 25 g; ×, 100 g.

Table 3 Repeated measures ANOVA examining effect on the time from beetle re-introduction to hatching for *Nicrophorus quadripunctatus*

	d.f.	F	*P*
Clutch order	4	9.71	<0.001
Carcass size	2	68.76	<0.001
Male presence	1	0.62	0.42
Error	223		

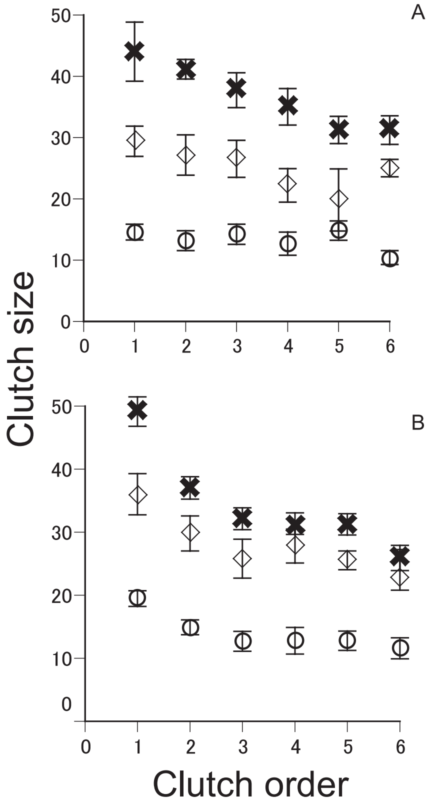

Figure 2 Relation between clutch size and clutch order for three carcass size classes for *Nicrophorus quadripunctatus* (mean ± SE). (A) Single female; (B) pair. ○, 6 g; ◇, 25 g; ×, 100 g.

(6–100 g). Brood size regulation in burying beetles is thought to consist of two phases, clutch size regulation and then infanticide by parents (Trumbo 1990c). The latter method is required because of superfluous oviposition. *Nicrophorus quadripunctatus* appears to be most reliant on clutch size regulation, which is the more efficient of the two approaches.

Females of *N. tomentosus* cannot produce a third brood (Trumbo 1990b), and in *N. orbicollis* the size of the second clutch is smaller than that of the first (Scott & Traniello 1990). Notably, Müller (1987), who used an experimental procedure similar to ours, reported that the second clutch of *N. vespilloides* is much smaller than the first clutch. These studies suggest that burying beetles are iteroparous but that the number of reproductive attempts possible is rather small. Our study indicates that *N. quadripunctatus* can produce more than six clutches with only a moderate decrease in clutch size. Since the sixth clutches on the 100 g carcasses were still rather large, we expect that *N. quadripunctatus* could produce still more clutches. In addition, the time from introduction to hatching decreased slightly as clutch order (i.e. the number of clutches laid) increased. These results indicate that *N. quadripunctatus* reserves its energy for producing a secondary clutch.

Burying beetles are often displaced from carcasses by conspecifics and congeners (Scott 1990; Trumbo 1990b; Eggert & Sakaluk 2000). The likelihood of brood failure is high, and displaced beetles attempt to produce another brood (Bartlett 1988; Trumbo 1990c). Thus, they must have available some energy for reproduction in case of brood failure. Although opportunities for reproduction are expected to be limited because of competition (Eggert & Müller 1997), it is unclear how many times burying beetles reproduce in field conditions. *Nicrophorus quadripunctatus* may be particularly susceptible to usurpation (Suzuki 2000), being abundant and small in size (Ohkawara *et al.* 1998; Nagano & Suzuki 2003). In other burying beetles, a male presence does not increase brood size or mass (Müller *et al.* 1998), but does decrease the possibility of takeover (Trumbo 1990a). In addition, a male presence increases the subsequent brood size of a paired female (Jenkins *et al.* 2000). A male presence clearly decreases the reproductive costs for females. In the present study, the size of the first clutch was larger for pairs than for single females, suggesting that females adjust clutch size in response to the risk of reproductive failure. *Nicrophorus quadripunctatus* can produce more clutches than other species of *Nicrophorus* as an adaptation to a higher rate of brood failure.

In conclusion, *N. quadripunctatus* can produce multiple clutches and regulate clutch size in response to carcass size, and paired females produce larger clutches than single females. We hypothesize that females save energy in case of brood failure. The cost of maternal provisioning was excluded in this experiment because females were removed immediately after larval hatching. Most takeovers of carrion by usurping burying beetles occur before larvae hatch (Robertson 1993; Suzuki

1999); brood failure after hatching is rare. Like other care-giving insect species (Tallamy & Brown 1999), *N. quadripunctatus* invests considerable amounts of energy in parental behaviors after larvae hatch.

ACKNOWLEDGMENTS

We would like to thank Dr S. T. Trumbo, Dr N. Kaneko and Dr M. Ito for providing valuable advice. Our cordial thanks also go to Dr K. Niijima and Mrs M. Nagano for their kind help with field and laboratory experiments.

REFERENCES

Bartlett J (1988) Male mating success and paternal care in *Nicrophorus vespilloides* (Coleoptera: Silphidae). *Behavioral Ecology and Sociobiology* **23**, 297–303.

Eggert AK, Müller JK (1997) Biparental care and social evolution in burying beetles: lessons from the larder. In: Choe JC, Crespi BJ (eds) *The Evolution of Social Behavior in Insects and Arachnids*, pp 216–236. Cambridge University Press, Cambridge.

Eggert AK, Sakaluk SK (2000) Benefits of communal breeding in burying beetles: a field experiment. *Ecological Entomology* **25**, 262–266.

Jenkins EV, Morris C, Blackman S (2000) Delayed benefits of paternal care in the burying beetle *Nicrophorus vespilloides*. *Animal Behaviour* **60**, 443–451.

Müller JK (1987) Replacement of a lost clutch: a strategy for optimal resource utilization in *Necrophorus vespilloides* (Coleoptera: Silphidae). *Ethology* **76**, 74–80.

Müller JK, Eggart AK, Furlkröger E (1990) Clutch size regulation in the burying beetle *Nicrophorus vespilloides* Herbst (Coleoptera: Silphidae). *Journal of Insect Behavior* **3**, 265–270.

Müller JK, Eggert AK, Sakaluk SK (1998) Carcass maintenance and biparental brood care in burying beetles: are males redundant? *Ecological Entomology* **23**, 195–200.

Nagano M, Suzuki S (2003) Phenology and habitat use among Nicrophorine beetles of the genus *Nicrophorus* and *Ptomascopus* (Coleoptera: Silphidae). *Edaphologia* **73**, 1–9.

Nisimura T, Kon M, Numata H (2002) Bimodal life cycle of the burying beetle *Nicrophorus quadripunctatus* in relation to its summer reproductive diapause. *Ecological Entomology* **27**, 220–228.

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

Otronen M (1988) The effect of body size on the outcome of fights in burying beetles (*Nicrophorus*). *Annales Zoologici Fennici* **25**, 191–201.

Pukowski E (1933) Ökologische untersuchungen an *Necrophorus* F. *Zeitschrift Morphologie und Oekologie der Tiere* **27**, 518–586.

Robertson IC (1993) Nest intrusions, infanticide, and parental care in the burying beetle, *Nicrophorus orbicollis* (Coleoptara: Silphidae). *Journal of Zoology, London* **231**, 583–593.

Scott MP (1990) Brood guarding and the evolution of male parental care in burying beetles. *Behavioral Ecology and Sociobiology* **26**, 31–39.

Scott MP (1998) The ecology and behavior of burying beetles. *Annual Review of Entomology* **43**, 595–618.

Scott MP, Traniello JFA (1990) Behavioral and ecological correlates of male and female parental care and reproductive success in burying beetles (*Nicrophorus* spp.). *Animal Behaviour* **39**, 274–283.

Suzuki S (1999) Does carrion-burial by *Nicrophorus vespilloides* (Silphidae: Coleoptera) prevent discovery by other burying beetles? *Entomological Science* **2**, 205–208.

Suzuki S (2000) Changing dominant-subordinate relationships during carcass preparation between burying beetle species (*Nicrophorus*: Silphidae: Coleoptera). *Journal of Ethology* **18**, 25–28.

Tallamy DW, Brown WP (1999) Semelparity and the evolution of maternal care in insects. *Animal Behaviour* **57**, 727–730.

Tallamy DW, Wood TK (1986) Convergence patterns in subsocial insects. *Annual Review of Entomology* **31**, 369–390.

Trumbo ST (1990a) Interference competition among burying beetles (Silphidae, Nicrophorus). *Ecological Entomology* **15**, 347–355.

Trumbo ST (1990b) Regulation of brood size in a burying beetle, *Nicrophorus tomentosus* (Silphidae). *Journal of Insect Behaviour* **3**, 491–500.

Trumbo ST (1990c) Reproductive benefits of infanticide in biparental burying beetle *Nicrophorus orbicollis*. *Behavioral Ecology and Sociobiology* **27**, 269–273.

Trumbo ST (2006) Infanticide, sexual selection and task specialization in biparental burying beetles. *Animal Behaviour* **72**, 1159–1167.