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Source: Zoological Science, 18(7) : 975-979

Published By: Zoological Society of Japan

URL: https://doi.org/10.2108/zsj.18.975

ZOOLOGICAL SCIENCE **18**: 975–979(2001)

Cost and Necessity of Parental Care in the Burying Beetle *Nicrophorus quadripunctatus*

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ABSTRACT—The physiological cost of parental care and the necessity of parental care for larval growth were examined in the burying beetle, *Nicrophorus quadripunctatus*, by removing adult pairs during the first reproduction and allowing them to reproduce again. When the reproduction was interrupted after hatching of the first clutch, the number and mass of the second clutch did not decrease as the interruption was performed later. These results demonstrated that the physiological cost of parental care was relatively small. The parental care for one day or less after hatching was necessary for the growth of progeny larvae. Parental care later than one day after hatching influenced neither survival nor growth of progeny larvae. Moreover, progeny larvae grew normally with either a male or female parent. Nevertheless, all parental females and most males stayed with their progeny until the larvae finished feeding. The evolution of parental care in *N. quadripunctatus* will be discussed along with both its cost and benefit.

INTRODUCTION

The burying beetles of the genus *Nicrophorus* have evolved the most advanced form of parental care in the Coleoptera (Wilson, 1971). When a pair of adults find a carcass of a small vertebrate, they bury and prepare it as food for their progeny. The parents take care of their progeny by feeding with regurgitated food from their mouths (Milne and Milne, 1976). The parental care has been suggested to be important or indispensable for survival and growth of progeny in several burying beetles (Trumbo, 1992).

It is likely that the effort that parents dedicate to the production and growth of their progeny is at the expense of future survival or fecundity. This ‘cost of reproduction’ reflects a trade-off between current and future reproduction (Williams, 1966). Individuals must decide to allocate resources between current and future reproduction. If they consume all the resources for the first reproduction, the subsequent survival rate must be close to zero and they would not obtain progeny in a second or later reproduction. On the other hand, if they reproduce repeatedly, the allocation of resources among repetitions becomes a serious problem. The cost of reproduction can be measured as decrease in the number and/or weight of progeny of later reproduction.

The cost of reproduction can be divided into physiological and ecological origins. Ecological origins of costs may be the result of the increased use of hazardous environments, for instance to collect food to provision a brood. Physiological costs may result when energy is shunted to egg production rather than growth or maintenance (Calow, 1979). In the present study, we examined the physiological cost and the necessity of parental care in *Nicrophorus quadripunctatus*. Reproduction was interrupted at various stages, and immediately a resource was given again to the parents. The cost of reproduction was determined by the decrease in number and weight of progeny in the second reproduction. The contribution of parental care was estimated by the decrease in the number and weight of progeny in the first reproduction interrupted at various stages.

Bartlett (1988) demonstrated that there was no significant difference between male and female feeding efforts in *Nicrophorus vespilloides*. Moreover, male presence did not affect the number or weight of progeny larvae in *N. vespilloides* and *N. orbicollis* when potential competitors were excluded (Bartlett, 1988; Trumbo, 1991). We examined whether care by only the male or female resulted in similar production of progeny in *N. quadripunctatus* in the absence of competitors.

MATERIALS AND METHODS

Insects

Adults of *N. quadripunctatus* were captured in hanging pitfall traps baited with chicken and installed 1.5 m above the ground on tree trunks in Iwakura, Kyoto city, in early May and early September 1998. Each male and female pair was reared in a plastic pot (11.5 cm in diameter, 11.0 cm in depth) quarter-filled with soil, and provided with a piece of chicken for reproduction at 20±1°C under LD 12:12. As female burying beetles regulate the clutch size depending on the size of the carcass (Müller *et al*., 1990), the weight of chicken for repro-

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duction was kept stable at about 25 g. The chicken was wrapped in a piece of tissue paper to imitate a small vertebrate carcass. Phoretic mites of burying beetles sometimes influence the reproduction of beetles by consuming and/or damaging host eggs (Beninger, 1993), and *Poecilochirus davydovae* was shown to be a specialist predator of beetle eggs (Blackman, 1997). Therefore, phoretic mites were carefully removed from the progeny larvae with a fine paint brush when the larvae finished feeding and started to disperse into the soil for pupation, and then the larvae were transferred into a different plastic pot (14.8 cm in diameter, 9.0 cm in depth), half-filled with soil. They pupated in the soil, and new adults emerged on the soil after about 25 days. Thus, adults free from mites were obtained.

New adults of the first and second laboratory generations were kept on larvae of the blow fly, *Protophormia terraenovae*, for 12 days. Then, their body weight was measured. As the size of adults sometimes affects reproductive success in burying beetles (Wilson and Fudge, 1984; Bartlett and Ashworth, 1988), only adults of which body weight was between 0.22 and 0.32 g were used for experiments.

Experimental procedures

Male and female pairs were provided with chicken as described for field-collected adults, and the first reproduction of these pairs was interrupted at one of the following six stages: Stage I, 1 day after the pair started reproduction, when the female had not laid eggs; stage II: 2 days after eggs were first observed through the wall of the pot, when no larvae were seen on the chicken; stage III, the day when larvae were first observed on the chicken; stage IV, 1 day after stage III; stage V, 2 days after stage III; stage VI, the day when the larvae finished feeding and at least one burrowed into the soil for pupation.

Immediately after interruption of the first reproduction, the adult pairs were placed on new pots with chicken for the second reproduction, and the pots with larvae of the first reproduction were maintained without parents. In the first and second reproduction, the numbers of larvae were counted at stage VI, and their total weight was measured for each parent pair. These parameters were regarded as the gain of the pair. They were also used to calculate the mean larval weight. When no larvae were observed during 12 days after the pair started reproduction, or all larvae died during the feeding stage, the pair was regarded as gaining no larvae.

As a control, adult pairs were left to continue reproduction without interruption. Some of these pairs were observed twice a day, i. e., immediately and 6 h after lights-on, to examine whether one or both of the parents had deserted their progeny before stage VI.

To determine the necessity of parental care by each sex, male and female pairs were provided with chicken, and either the female or male parent was removed at stage II. The number and total weight of post-feeding larvae were measured at stage VI.

RESULTS

Cost of parental care

Fig. 1 shows the number and mean weight of post-feeding larvae obtained in the second reproduction after interruption at various stages of the first reproduction. Interruption of the first reproduction before oviposition (stage I) showed no effect on the number of post-feeding larvae obtained in the second reproduction (Fig. 1A). When the first reproduction was interrupted 2 days after oviposition (stage II), however, the number of post-feeding larvae obtained in the second reproduction was significantly less than that in the control group (Fig. 1A). When the first reproduction was interrupted at later stages, the number of post-feeding larvae obtained in the second reproduction was less than that in the control group, but the differences were not statistically significant (Fig. 1A). There were no significant differences in the mean larval weight in the second reproduction among all experimental series (Fig. 1B).

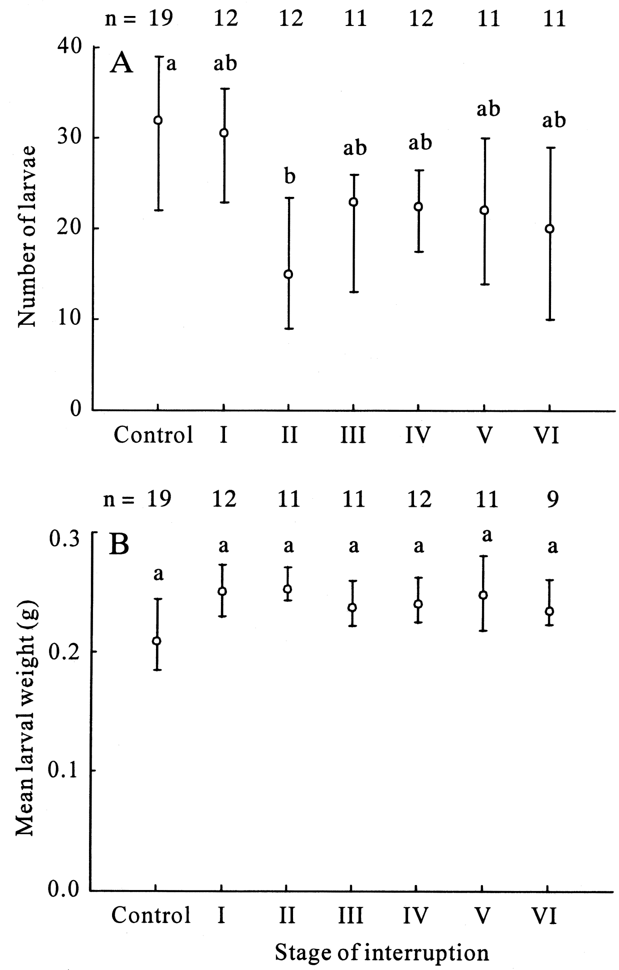

Fig. 1. The number (A) and mean weight (B) of post-feeding *Nicrophorus quadripunctatus* larvae in the second reproduction after interruption of the first reproduction at various stages. Circles and bars show medians and interquartiles, respectively. Values with the same letter are not significantly different ($P>0.05$, nonparametric multiple comparisons [Zar, 1999, pp. 223–226]). Results without interruption are shown as a control.

No apparent difference was observed in the timetable of parental care between the first and second reproduction. Larvae were first observed on the chicken after 5.4±0.9 (mean± SD) days in the control group and 5.5±1.3 days in the second reproduction of the group in which the first reproduction was interrupted at Stage II; there was no significant difference between them ($P > 0.05$, Student t-test).

Necessity of parental care

In 8 pairs in the control group, whether the parents deserted their progeny before stage VI was examined. All the females stayed with their progeny until stage VI, although 3 males disserted in stage II, IV and between stage VI and V.

Fig. 2 shows the number and body weight of post-feeding larvae obtained in the first reproduction with parents

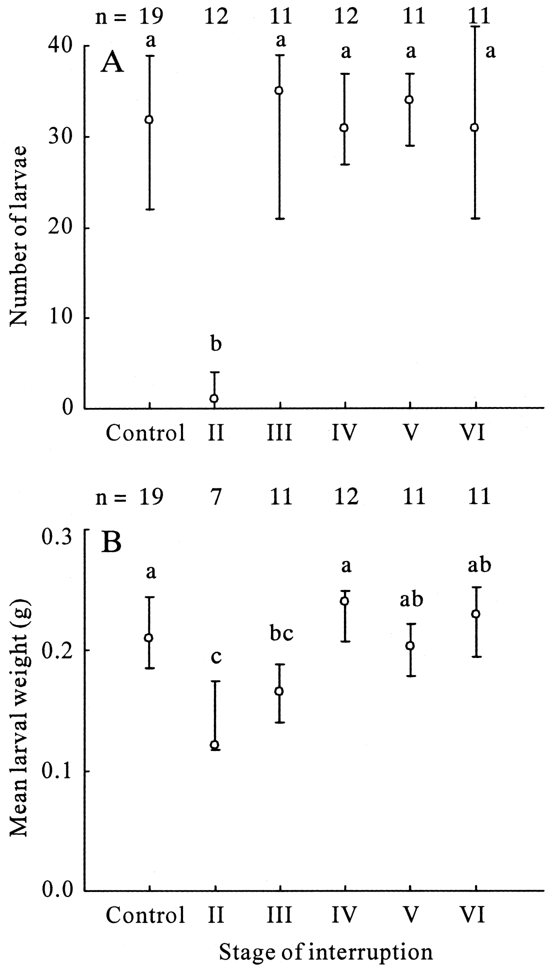

Fig. 2. The number (A) and mean weight (B) of post-feeding *Nicrophorus quadripunctatus* larvae with interruption of reproduction at various stages. Circles and bars show medians and interquartiles, respectively. Values with the same letter are not significantly different (P>0.05, nonparametric multiple comparisons [Zar, 1999, pp. 223–226]). Results without interruption are shown as a control (the same data as in Fig. 1).

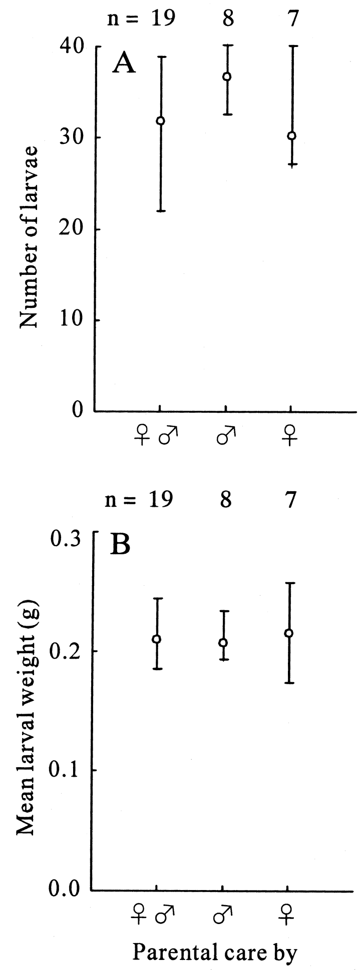

Fig. 3. The number (A) and mean weight (B) of post-feeding *Nicrophorus quadripunctatus* larvae with removal of either parent before hatching. Circles and bars show medians and interquartiles, respectively. Results without removal are shown as a control (the same data as in Fig. 1). No significant differences were observed among the three groups (P> 0.05, Kruskal-Wallis test).

removed at various stages. In 5 of 12 pairs in which parents were removed before larval hatching (stage II), no larvae survived to the post-feeding stage. In the remaining 7 pairs, only a small number of post-feeding larvae were obtained, and their weight was significantly less than that in the control group (Fig. 2B). Because each female adult laid eggs synchronously in a day and hatching of larvae was confirmed, it is evident that all or most larvae died by removing their parents. When parents were removed within 1 day after larvae reached to the chicken (stage III), the number of post-feeding larvae was similar to that in the control group (Fig. 2A), although the mean larval weight was significantly less than that in the control group (Fig. 2B). There were no significant differences in the number or mean larval weight among the three groups in which parents were removed at later stages (IV–VI) and the control group (Fig. 2AB).

Even when the male or female parent was removed 2 days after oviposition (stage II), neither the number nor the mean weight of post-feeding larvae was significantly decreased compared with those in the control group (Fig. 3AB).

DISCUSSION

Physiological cost of parental care

In *N. quadripunctatus*, when the first reproduction was interrupted at any stage, the mean weight of progeny larvae in the second reproduction was not significantly different from that in the control group (Fig. 1B). However, when the first reproduction was interrupted after oviposition, the number of post-feeding larvae obtained in the second reproduction was less than that in the control group, although the difference was statistically significant only when the first reproduction was interrupted 2 days after oviposition (Fig. 1A). This decrease in number of progeny was probably due to the cost of oviposition. Moreover, it is suggested that 2 days after the first oviposition yolk has not been accumulated sufficiently for the second reproduction, and therefore the decrease was more conspicuous when the first reproduction was interrupted within this period.

If the adults were exhausted during the care of their young, the number or mass of progeny in the second reproduction would decrease as the interruption of the first reproduction was delayed. However, no significant differences were observed in the number or mass of progeny of the second reproduction among experimental series in which the first reproduction was interrupted (Fig. 1). These results demonstrated that the physiological cost of parental care was relatively small in *N. quadripunctatus*.

Bartlett (1988) and Trumbo (1991) detected no physiological cost of parental care in male adults of *N. vespilloides* and *N. orbicollis*, although physiological cost of parental care has not been examined in female burying beetles. In the lace bug, *Gargaphia solani*, Tallamy and Denno (1982) measured the physiological cost for allocating energy to maternal care, and reported that maternal care significantly decreased subsequent fecundity and clutch number. In that study, the reproductive success was examined in females that were allowed to reproduce repeatedly until death (Tallamy and Denno, 1982). On the other hand, the physiological cost for maternal care was assumed to be lower in *N. quadripunctatus* examined here. This assumption may be affected by our methods that the reproductive success was measured only in the second reproduction after interruption of the first reproduction. However, our methods seem appropriate for *Nicrophorus*, which does not reproduce repeatedly in the individual life (Trumbo, 1990a).

Necessity of parental care

In *N. quadripunctatus*, parental care was indispensable for larval growth because most progeny larvae did not survive to the post-feeding stage when the parents were removed before hatching (Fig. 2A). Moreover, parental care for 2 days after hatching was necessary to ensure normal growth of the progeny larvae (Fig. 2B). However, parental care by either the female or male was sufficient for normal growth of the progeny larvae (Fig. 3). Parental care is probably nutritionally indispensable for young larvae because parents of burying beetles feed their progeny larvae with regurgitated food (Milne and Milne, 1976). Although pre-oral digestion of phospholipid was demonstrated in *N. marginatus* (Rana *et al*., 1997), the precise role of this regurgitation is unclear.

Notably, a few larvae of *N. quadripunctatus* survived to the post-feeding stage even when their parents were removed before hatching. Parents of burying beetles feed and then regurgitate directly into a small depression at the top of the carrion before larval hatching (Pukowski, 1933). Probably larvae can derive some benefit from this regurgitation on the carrion, and therefore a small proportion of larvae grow without parental care after hatching, as Trumbo (1992) suggested for *N. orbicollis*.

Cost and benefit of parental care

Parental care later than 2 days after hatching influenced neither survival nor growth of progeny larvae in *N. quadripunctatus*. Moreover, progeny larvae grew normally with either a male or female parent. Nevertheless, all parental females and most males stayed with their progeny until the larvae finished feeding. Even if parental care later than 2 days after hatching is physiologically not necessary for the progeny, it can evolve when its cost is small in comparison with its benefit. The present results showed that the physiological cost of parental care was relatively small in *N. quadripunctatus.* Scott (1998) discussed ecological cost of parental care in burying beetles as the potential loss from reduced future fitness if additional reproductive opportunities are lost while providing care, based on field results in some North American species. In *N. orbicollis*, the possibility of finding another carcass by male adults would increase only a little if they deserted their progeny larvae (Scott and Gladstein, 1993). However, ecological cost of parental care has not been determined yet in *N. quadripunctatus*.

The benefit of parental care later than 2 days after hatching in *N. quadripunctatus* is still unclear. In burying beetles, however, ecological significance of parental care has been discussed with regard to competition for vertebrate carcasses. In *N. orbicollis*, the presence of a male on a carcass reduced the probability of takeover by other beetles (Scott, 1990; Trumbo, 1991), although it had no effect on the number or size of larvae (Trumbo, 1991). In this species, infanticide regularly occurs as a consequence of a takeover (Trumbo, 1990b). In *N. vespilloides*, burial and treatment of carcasses with a brown secretion have shown to prevent discovery by other burying beetles and fly infestation in Hokkaido, Japan (Suzuki, 1999, 2000). It is possible that evolution of parental care is also closely related to repelling of intruding congeners in *N. quadripunctatus*. Field observations and experiments are needed to discuss the evolution of parental care based on its physiological and ecological cost and benefit.

ACKNOWLEDGMENTS

We thank Dr. M. Kon, University of Shiga Prefecture for critically reading of the manuscript.

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(Received April 28, 2001 / Accepted June 29, 2001)