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Short Communication

Facultative Adjustment of the Duration of Parental Care by Burying Beetles

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INTRODUCTION

Organisms face a trade-off of investing in current versus future reproduction. In species for which offspring benefit from parental care, parents continue to provide care at the expense of departing to search for additional breeding opportunities (Trivers, 1972). Many factors may influence the decision to remain or leave: the probability that the mate will remain, the effect on offspring survival and growth, the probability of finding another breeding opportunity, the costs of searching, the effect on fecundity, and the level of intrasexual competition for mates or breeding opportunities (Pianka and Parker, 1975; Maynard Smith, 1977; Zeh and Smith, 1985; Alcock, 1994). Thus relatively available breeding opportunities and low search costs, relatively little intrasexual competition, and good competitive ability may all select for an earlier departure. As the probability of future reproduction decreases, individuals may be selected to provide longer parental care. Because male fitness is more likely to be limited by mating opportunities than female fitness (Trivers, 1972), males are expected to invest less in current offspring than females and perhaps to be more responsive to social and environmental factors that affect the duration of care.

Male and female burying beetles (*Nicrophorus orbicollis*) provide extended parental care (Pukowski, 1933). They bury and prepare small vertebrate carcasses as food for their young. Eggs are laid in the soil nearby 24–60 h after the carcass is discovered. These hatch 3–4 days later into altricial larvae that are fed by both parents. Although the young of some species, including *N. orbicollis*, fail to develop without some parental feeding (Trumbo, 1992),

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larvae can feed directly from the carcass and dependence on parental feeding decreases with age. Females of all species typically remain longer than males, often staying until larval development is complete, 6–8 days after hatching (Scott and Traniello, 1990; Trumbo, 1991). The duration of paternal care is more variable, both within and among species, and male *N. orbicollis* leave, on average, when the larvae are 3–4 days old.

The major benefit of biparental care is that the presence of two adults greatly reduces the probability that a conspecific competitor will usurp the carcass and kill the young (Scott, 1990; Trumbo, 1991). As the carcass becomes depleted during larval development, this threat is reduced (Scott and Gladstein, 1993). By remaining until larval development is complete rather than leaving when the male does, the female rears significantly heavier larvae (Scott and Traniello, 1990).

A dynamic optimization model to predict the duration of paternal care (Scott and Gladstein, 1993) examined how fitness is predicted to be affected by the probability of finding another carcass (availability of breeding opportunities) and the probability that their current carcass would be discovered and usurped (population density and intensity of competition) if males left their current brood to search for another carcass and mate. The model predicted that the duration of care would increase as competition increases and decrease as the probability of finding another carcass increases (Scott and Gladstein, 1993). This paper examines the duration of care by both males and females when contact among beetles (the expected level of competition) and the timing of first breeding (probability of finding additional breeding opportunities) are experimentally manipulated. It also examines the impact of reduced residual reproductive value late in the breeding season on the duration of care.

METHODS

All beetles were derived from individuals captured in southern New Hampshire between 1989 and 1994. They were maintained at 20°C with a 14:10 L:D period, fed mealworms, and bred in the laboratory in plastic boxes of soil, 19 × 14 × 10 cm. Some were reared with no contact with other beetles by isolating them immediately after the completion of larval development and maintaining them individually in plastic boxes, 11 × 11 × 4 cm, until use. They were fed and cleaned either outside or in an air current and handled in a manner to reduce olfactory cues from other beetles. Beetles reared in contact with others pupated in the soil with the others of their brood and were removed at eclosion and maintained with two or three like-sex beetles until use. Maximum pronotal width was used as the measure of beetle size.

To measure the duration of parental care, all work was conducted outside in natural temperature and light. A male and female were placed in a covered pot of soil 20 cm high and 22 cm in diameter with a previously frozen 25- to 35-g mouse. After 24 h this pot was uncovered and placed inside a larger pot that was covered with Plexiglas. When adults left the brood chamber, they fell into the larger pots, which were checked every morning. The next evening, these deserters were transferred in a dark tube to a covered Plexiglas, double-walled arena into which the original pot fit (Scott and Traniello, 1990). Beetles could make a choice of returning to the brood chamber or taking flight, whereupon they flew over the inner, short wall and were captured between the inner and the outer walls. Few beetles returned to the brood chamber and stayed; those that returned but departed again the next night were scored as having left on the first departure.

Duration of care was measured for beetles with different past social experience. (a) Wild beetles were captured in pitfall traps baited with kidney when they first emerged in mid-June. Within 1–4 days they were given a mate and a carcass to breed and the duration of their care was measured. The duration of care was measured and compared for (b) adults reared in complete isolation and (c) adults maintained in small groups.

The duration of care was also measured for beetles with different reproductive histories. (a) Duration of care for first and subsequent broods was compared for beetles all of which had been reared in isolation. These beetles first reproduced in July, when they were 21–40 days old. After they terminated care for their first broods they were housed alone for 2 or 3 days, then given a new mate and a carcass. Some males produced a third brood but there were too few females and it was too late in the season to continue to test them. (b) Other beetles were reared and maintained in isolation until August, when they were about 60 days old, before they were given a mate and a carcass. The duration of care for first broods started early or late in the season was compared.

RESULTS

Results are presented in Table I. Social history (population density) had a significant effect on parental care. The duration of paternal care on 25- to 35-g carcasses in the field (data from Scott and Traniello, 1990) and by wild-caught males in the laboratory was about 10.7 days. In contrast to wild-caught males, those reared in isolation provided significantly shorter care ($P = 0.01$, Kruskal–Wallis test) and group-reared males provided significantly longer care ($P = 0.002$). The duration of maternal care in the field and for wild-caught females was about 16.7 days. As with males, females reared in isolation provided significantly shorter care than wild-caught females ($P = 0.01$) and females reared in groups, but unlike males, females reared in groups did not provide significantly longer care than wild-caught females ($P = 0.13$).

Reproductive history had a stronger effect on males than on females. Males

Table I. Duration (Means ± SE) of Parental Care on 25- to 35-g Carcasses and Its Correlation with Body Size (Males in Boldface and Females in Regular Typeface)

Broods reared naturally in the field:	**10.7 ± 1.5 days** 16.7 ± 1.1 days	**(*N* = 16)**[a] (*N* = 20)
Wild-caught adults, laboratory broods:	**10.6 ± 0.6 days** 16.7 ± 0.3 days	**(*N* = 20)** (*N* = 23)

Effect of population density

Laboratory-reared isolated	Laboratory-reared together	*P*
9.1 ± 0.7 (*N* = 18)	**14.5 ± 1.1 (*N* = 20)**	**0.001**[b]
15.2 ± 0.8 (*N* = 17)	19.5 ± 1.0 (*N* = 21)	0.001

Effect of number and timing of breeding opportunities (laboratory-reared, isolated beetles)

First broods	Second broods	Third broods	*P*
9.0 ± 0.4 (*N* = 22)	**9.1 ± 0.7 (*N* = 18)**	**11.9 ± 1.6 (*N* = 8)**	**0.05**[c]
15.0 ± 0.9 (*N* = 24)	16.3 ± 0.7 (*N* = 18)	None	0.08[b]

Early first broods (July)	Late first broods (August)	*P*
9.0 ± 0.4 (*N* = 22)	**11.3 ± 0.9 (*N* = 12)**	**0.03**[b]
15.0 ± 0.9 (*N* = 24)	14.9 ± 1.3 (*N* = 10)	0.70

Correlation of body size and duration of parental care

	r	*P*
Wild-caught adults	**+0.05 (*N* = 20)**	**0.83**
	+0.26 (*N* = 23)	0.23
Lab-reared isolated, early breeders	**−0.14 (*N* = 18)**	**0.59**
	+0.22 (*N* = 17)	0.40
Lab-reared together, early breeders	**−0.46 (*N* = 20)**	**0.04**
	−0.06 (*N* = 21)	0.80

[a] Data from Scott and Traniello (1990).
[b] Results from a Kruskal-Wallis test.
[c] Results from an ANOVA.

did not provide longer care for second broods than for first broods but did remain significantly longer with their third broods, which were begun at the end of August. Males that produced their first broods late in the season provided significantly longer care than those first breeding early in the season. Late first broods were begun at the same time in the season, mid-August, as the second broods of the early breeders. The mean duration of maternal care was not significantly different for first and second broods but all individual females provided the same or longer care to their second broods than their first ($N = 18$; Wilcoxon paired signed-ranks test, $P < 0.001$; this test eliminates between-individual variation because each female is paired with herself for statistical comparison).

Body size and duration of care were not correlated in any group of females and were not correlated in wild-caught males or those reared in isolation. They were significantly negatively correlated only in males reared in groups.

DISCUSSION

In the field, male *N. orbicollis* remain with their broods for 9–10 days, until larvae are about 3 days old, and females remain until larval development is complete. This study examines if males or females respond to social and environmental cues to adjust the duration of their parental care adaptively. Males, being the first to leave, may be less constrained and therefore more responsive to such cues. Previous work has shown that males do increase the duration of their care to the average duration of maternal care when their mates are experimentally removed (Trumbo, 1991). Males also adjust the duration of their care to carcass size and remain longer with larvae being reared on relatively large ones (Trumbo, 1991, 1992). Large carcasses are at greater risk of usurpation (Trumbo, 1991; Scott and Gladstein, 1993) and take longer to prepare, delaying oviposition and larval development.

Males must balance the benefit of their assistance in preventing takeovers with the cost of not searching for additional carcasses and, therefore, would gain from being responsive to cues of population density and carcass availability. Results of the current research suggests that they can respond. Males maintained in the laboratory in small groups had different information on population density and thus the expected level of competition and probability of takeovers than those reared in isolation. The frequency of interactions with conspecifics is presumably a mechanism used by beetles to monitor population density. Group-reared males provided significantly longer care and isolated males provided significantly shorter care than wild-caught males. A high population density is correlated with a greater probability of discovery and takeover (Scott, 1990) and thus a greater benefit to male care. Robertson (1993) also investigated if increased competition would be positively correlated with the duration of paternal care. He released potential competitors near the brood chamber but found that resident males did not respond by remaining with their broods longer than unchallenged males. His sample size may have been too small to demonstrate a real difference. Alternatively, the intrusion rate may not have been a sufficient stimulus and the previous experience of the wild-caught beetles used in his experiment could not be influenced experimentally at this stage.

Males also adjusted the duration of their care as predicted in response to carcass availability and provided longer care if their first opportunity to breed did not occur until late in the season. This was not just the effect of reduced time remaining in the breeding season because males producing their second broods at the same time of the season as the late-breeding first-time breeders did not lengthen their care. Presumably beetles use past experience with carcasses to predict future availability. Trumbo (1991), examining the effects of the time in the season of first reproduction on the duration of care by wild-caught males, found no difference in the rate of desertion between males whose first reproduction was delayed and those that had previously bred. The methods and goals of this study and his differed, making comparison of the results difficult. However, since Trumbo tested the late–first-breeding males 3 weeks into the breeding season and I tested them somewhat later, the differences suggest that timing may be a factor in the perception of carcass availability.

The duration of parental care may be more constrained for females than for males. The average duration of maternal care varied little for first or subsequent broods produced early or late in the season. Only the strong reaction of individual females to increase the duration of their care for their second broods suggests that they are responding to their reduced residual reproductive value and that there is no independent effect of the perceived lack of availability of opportunities produced by late primiparity. Reproductive success of females, but not males, diminishes with subsequent broods (Scott and Traniello, 1990; Trumbo, 1991). Females do respond to cues of population density and expected level of competition. Those reared in isolation responded like the males and provided shorter care than wild-caught females and those reared in groups.

Male body size is an important character that is often positively correlated with reproductive opportunities (Thornhill and Alcock, 1983). Greater mating opportunities for large males has been shown to correlate with reduced investment in individual broods by male pine engravers (Reid and Roitberg, 1995). Large size certainly confers a reproductive advantage to burying beetles (Pukowski, 1933; Wilson and Fudge, 1984; Bartlett and Ashworth, 1988; Otronen, 1988) and males, but not females, that are successful in securing a carcass are significantly larger than those of the general population (Scott and Traniello, 1990). However, size has not been shown to have a relationship to the duration of male care in laboratory (Bartlett, 1988) or field (Scott and Traniello, 1990; Trumbo, 1991) studies of burying beetles. In this study duration of care was negatively correlated with body size for group-reared males, which suggests that when males have frequent social contact with others, they get information on their relative size, causing small males to react as if they have a low future mating potential and to provide longer care to their current brood.

In summary, there are few studies of insects that demonstrate that males or females facultatively adjust the duration of their parental care in response to some social or environmental cues. Male and female burying beetles respond to cues of apparent high population density by increasing the duration of their care. In males, but not females, some of this increase might be due to small males with limited future reproductive opportunities having sufficient information about their relative size. In addition, males respond to potential cues of the probability of future reproductive opportunities by providing relatively long care after they have had long delays before breeding.

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