Calculating males? An empirical and theoretical examination of the duration of paternal care in burying beetles

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Summary

Male and female burying beetles (Nicrophorus orbicollis) bury and preserve small carcasses which become food for their young. Typically, females remain with the brood until after larval development is complete, but males leave about 3 days after larvae hatch. In the absence of competitors, the effect of male presence throughout larval development is to reduce the size and weight of the brood on small carcasses, but not on larger ones. However, male assistance greatly reduces the probability that a conspecific competitor will usurp the carcass and kill the brood. A dynamic optimization model of the duration of paternal care is developed and the daily probabilities of discovery by conspecific competitors and of finding a new reproductive opportunity are varied. The model predicts that the duration of care should not be very sensitive to either the intensity of competition or the probability of finding another carcass. For a given probability of discovery by an intruder, the probability of finding a new carcass affects the duration of care in a stepwise fashion such that males should either provide no care or remain 10 days on large carcasses and 9 days on small ones (3 days after larvae hatch, in each case). The model also suggests that by providing an average of 9.5 days of care in nature, males act as if there is a negligible chance of having another brood, i.e. they are maximizing their reproductive success with their current brood.

Keywords: paternal care; beetles; burying

Introduction

Parental investment consists of behaviour that increases the fitness of current offspring at the expense of the ability of the parent to invest in additional or future offspring (Trivers, 1972). Thus, models of parental care and mate desertion must take into account all factors which affect the fitness of current offspring, such as the effects of the different roles of parental care of guarding and feeding and the various factors affecting the potential for additional or future offspring, such as the operational sex ratio, the probability of finding another mate and the time and energy required to produce a new brood (Maynard Smith, 1977; Grafen and Sibley, 1978; Chase, 1980; Lazarus, 1990). Although these models make clear predictions concerning parental investment, it is often the case that important costs or benefits are difficult or impossible to measure empirically. Therefore models, although very important heuristically (Parker and Maynard Smith, 1990), have not often been used to predict or evaluate actual parental decisions (Andersson et al., 1980; Patterson et al., 1980; Regelmann and Curio, 1986; Townsend, 1986).

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Here we use a dynamic optimization model to study paternal care in burying beetles (Coleoptera: Silphidae, Nicrophorus) because of its simplicity; once the consequences of sequential decisions are determined, the model generates the optimum, in our case, of the duration of paternal care. Because the effects of behavioural decisions of the beetles are clearly identified and separate from the optimization process, it is obvious how to incorporate additional factors and complexity. As a consequence of this simplicity, we are able to do more thorough analyses of the model, such as analysing the robustness of optima or sensitivity to (possibly unmeasurable) hypothetical factors (Foulds, 1981; Mangel and Clark, 1988; Gladstein et al., 1991).

Both male and female burying beetles provide lengthy parental care and most of the factors which affect their reproductive ecology can be experimentally manipulated so that the costs and benefits of their parental care can be quantified. A male and female cooperate to bury small vertebrate carrion as food for their larvae, maintain the carcass and regurgitate food to offspring (Pukowski, 1933). On average, male Nicrophorus orbicollis remain with their broods until larvae are about 3–4 days old, 9.5 days after burial of the carcass and female N.orbicollis remain until after larval development is complete, an average of 17.2 days (Scott and Traniello, 1990). Although males perform the same brood-care behaviour as females (Bartlett, 1988; Fetherston et al., 1990), the effect of male presence, if he remains until larval development is complete, may be to decrease the number or weight of the larvae reared (Scott, 1989). However, the male’s presence greatly reduces the probability that the carcass will be discovered and taken over by a conspecific intruder and the brood killed (Scott, 1990; Trumbo, 1990, 1991). Therefore the benefit of paternal care is the difference between these two counteracting effects.

Finding a carcass, not a receptive female, is the limiting resource for males as well as females and both males and females are reproductively capable immediately upon leaving a brood. Thus, the only important factors expected to determine the male’s decision to continue to provide parental investment are the difference in number and weight of young reared with and without male assistance, the probability of being replaced by a conspecific competitor if he remains or leaves and the probability of finding another reproductive opportunity if he leaves. In this study we measure the effect of the duration of male assistance on reproductive success in the laboratory in the absence of competition and on the probability of resisting a takeover in the field. These vary with carcass size and are empirically determined for two sizes. We use a dynamic optimization model to examine the decision of the male to continue to provide care or to desert. We examine the effects of two ecological variables, beetle density, which affects the probability of discovery and takeover by an intruder, and carcass density, which affects the probability of finding another carcass, on the expected duration of male care.

Methods

Male assistance in brood care

In order to determine the effect on reproductive success of male assistance in brood care in the absence of competitors, we set up broods in the laboratory (at 20°C, 14 : 10 L : D). A male and female N.orbicollis, 21–40 days post-eclosion and a previously frozen mouse (20.0–21.9 g or 32.5–34.0 g) were placed in a plastic box (19 × 14 × 10 cm) filled with potting soil. After the carcass was buried, we disturbed the brood chamber to relocate it at the surface and covered it with a paper towel and checked daily. Oviposition usually could be monitored since eggs could be seen through the wall of the plastic boxes. Broods were randomly assigned to one of four treatment groups, each with 20 replicates: (1) males were removed after 24 h, (2) males were removed on the day larvae hatched, (3) males were removed 3 days after larvae hatched, or (4) males