

Partial begging: an empirical model for the early evolution of offspring signalling

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Species where, from birth, the offspring feed themselves in addition to begging for food from the parents can be described as 'partially begging'. Such species provide a unique opportunity to examine the evolution of offspring begging from non-signalling offspring foraging strategies. We used the partially begging burying beetle *Nicrophorus vespilloides* to test specific hypotheses concerning the coexistence of begging and self-feeding. We first tested whether the cessation of larval begging coincided with an increase in the efficiency of self-feeding. As predicted, begging ceased when the efficiency of self-feeding reached the point where the larvae grew just as well without as with access to food provided by the parent. We next tested whether the transition to nutritional independence was under parental or offspring control. The parent did not change its behaviour towards the larvae over time, while the larvae changed their behaviour by reducing the time spent begging in the presence of the parent. Food allocation during the transition to nutritional independence was therefore under offspring control. Our results on partial begging provide a starting point for new theoretical models for the origin of begging. We suggest that these should be constructed as scramble-competition models because the offspring control food allocation.

Keywords: burying beetles; control of resource allocation; honest signalling; offspring foraging strategies; scramble competition

1. INTRODUCTION

During the past decade, the phenomenon of offspring begging for food from their parents has received considerable theoretical and empirical interest as a model of animal communication between signallers and receivers with conflicting interests (Kilner & Johnstone 1997; Godfray & Johnstone 2000; Budden & Wright 2001; Royle *et al.* 2002; Wright & Leonard 2002). Empirical studies, conducted primarily on birds, show that offspring increase their begging as they get hungrier (Kilner & Johnstone 1997; Budden & Wright 2001). This finding has been interpreted as support for honest-signalling models predicting that costly begging is an honest signal of offspring need (Godfray 1991, 1995). These models view begging as a resolution of familial conflicts where resource allocation is under parental control (Godfray 1991, 1995). However, recent scramble-competition models, which also predict that begging reflects need, assume that food allocation is under offspring control (Rodríguez-Gironés *et al.* 2001; Parker *et al.* 2002). Hence, to distinguish between these models, studies of begging need to test whether food allocation is under parental or offspring control.

Most of the current understanding of offspring begging derives from studies of altricial birds (Kilner & Johnstone 1997; Budden & Wright 2001; Wright & Leonard 2002), in which the nestlings cannot provide for themselves and obtain food only by begging from their parents. Because begging by nestling altricial birds is a derived character state, these studies are of limited relevance in understanding the origin and early evolution of begging from non-signalling offspring foraging strategies.

To improve our understanding of how offspring begging might evolve, we require studies of partially begging species, defined as species where the offspring beg for food and feed for themselves immediately after hatching or birth. Such species provide an empirical model representing an intermediate stage in the evolution of begging between species where the offspring are completely self-sufficient and species where the offspring obtain food only from the parents. Partial begging describes an evolutionary transition rather than a developmental change such as occurs after fledging in altricial birds (e.g. Leonard *et al.* 1991). Partially begging species are suitable for addressing hypotheses concerning the coexistence of begging and non-signalling offspring foraging strategies, and may thereby contribute to understanding potential evolutionary pathways for offspring signalling. One group of species in which partial begging occurs is burying beetles, *Nicrophorus* spp. (Smiseth & Moore 2002). Here, we show how these species can be used as an empirical model for the early evolution of begging.

Burying beetles are known for their elaborate post-hatching care, including regurgitation of food to the larvae (Eggert & Müller 1997; Eggert *et al.* 1998; Scott 1998). Existing studies suggest that larval begging reflects need, that parents respond to begging and that the larvae adjust their begging according to the number of competing siblings (Rauter & Moore 1999; Smiseth & Moore 2002). In some species, such as *Nicrophorus vespilloides* and *N. pustulatus*, the larvae can survive in the absence of post-hatching parental care (Eggert *et al.* 1998; Rauter & Moore 2002; but see Trumbo 1992), suggesting that begging and self-feeding coexist as alternative foraging strategies from hatching until the larvae cease begging.

Our goal was to address specific hypotheses concerning the coexistence of begging and self-feeding in a partially begging species to improve our understanding of the

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evolution of begging from non-signalling offspring foraging strategies. Using the burying beetle *N. vespilloides*, we first tested whether larval begging was affected by changes in the efficiency of self-feeding during larval development. We defined the efficiency of self-feeding as the growth of larvae foraging through self-feeding alone (i.e. with the parent removed) relative to the growth of larvae with access to food provisioned directly by the parent. We predicted that the larvae would cease begging when they grew just as well without as with access to food provided by the parent. We then tested the critical assumption distinguishing honest-signalling (Godfray 1991, 1995) from scramble-competition models (Rodríguez-Gironés *et al.* 2001; Parker *et al.* 2002): that is, whether food allocation is under the behavioural control of the parent or the offspring. The parent could control the transition to nutritional independence by changing its behaviour towards the larvae. Burying beetle larvae beg only when the parent is nearby (Rauter & Moore 1999; Smiseth & Moore 2002). Thus, the parent could exercise control by reducing (i) the time they spend near the larvae or (ii) the frequency with which it responded to begging attempts with regurgitation. If the larvae control the transition to nutritional independence, we would expect the larvae to change their behaviour towards the parent and to cease begging at the time predicted from the relative efficiency of self-feeding, despite having ample access to beg for food.

2. METHODS

(a) *General procedures*

The beetles used in this experiment were from an outbred laboratory population (see Smiseth & Moore 2002). Adults were housed individually in clear plastic containers (17 cm × 12 cm and 6 cm high) one-third filled with peat, at 20 ± 2 °C under a 15 L : 9 D photoperiod. Non-breeding adults were fed decapitated mealworms (*Tenebrio* spp.) *ad libitum* twice a week.

For these experiments, we used pairs of non-sibling virgin female and male beetles. Each pair was placed in a new transparent container (17 cm × 12 cm and 6 cm high) provided with previously frozen mouse carcasses (supplied from Livefoods Direct Ltd, Sheffield, UK). Two days after the females initiated egg-laying, and before the eggs hatched, the female and the carcass were transferred to a new container filled with 2 cm of moist soil. The male was removed because male care is redundant under laboratory conditions (e.g. Scott 1989; Trumbo & Fernandez 1995; Müller *et al.* 1998). The soil of the old container was searched for eggs, which were transferred to a moist filter paper placed in a Petri dish. The Petri dishes were checked for the presence of newly hatched larvae four times a day. We provided each reproducing female with a brood of 10 newly hatched larvae of mixed maternity. Because females kill larvae arriving before the hatching of their own brood (Müller & Eggert 1990; Trumbo & Fernandez 1995), we provided females with broods only after their own eggs had started hatching.

(b) *Efficiency of self-feeding and begging*

The aim of the first experiment was to identify the age at which the efficiency of self-feeding rose to the point where the larvae grew just as well without as with access to food provided by the parent. We did this by removing the female at specific times during larval development and comparing the growth of

the brood over the next 24 h with the growth of control broods. The broods were randomly assigned to five different treatments: a control group, where the female remained with the brood until they dispersed (defined as all larvae leaving the crypt surrounding the carcass), and four experimental groups. For the experimental groups, the female was removed: (i) at hatching (i.e. as the brood was placed on the carcass); or (ii) 24 h (± 15 min); (iii) 48 h (range of ± 15 min); or (iv) 72 h (± 15 min) after hatching. All broods were weighed to the nearest 0.001 g at hatching and subsequently at 24 h intervals (± 15 min) until dispersal. We set up broods until reaching a sample size of 20 in each group.

The second experiment was designed to identify the age at which the larvae ceased begging. We conducted experiments on changes over time in the efficiency of self-feeding and begging on different broods, to avoid disturbances to larval or parental behaviour caused by handling. We conducted behavioural observations on the day of hatching and at 24 h, 48 h, 72 h and 96 h of age (range of ± 15 min). On the day of hatching, the observations were conducted 1 h after the broods were placed on the carcass to avoid the effects of disturbance. We used instantaneous scan sampling (Martin & Bateson 1986) every 1 min for 30 min, and counted, at each scan, the number of larvae that were begging. A larva was considered to be begging when raising its head towards the parent while waving its legs or touching the parent with their feet (Rauter & Moore 1999; Smiseth & Moore 2002). For use in the analyses, we calculated the average percentage of time spent begging by each larva in the brood, b_i , as $b_i = \Sigma b/L \times 100/30$, where Σb is the total number of begging events occurring during the 30 scans in an observation session and L is the brood size at the time of observation (Smiseth & Moore 2002). We set up broods until reaching a sample size of 20 broods in each observation group. Broods were dismissed from statistical analyses if the female showed obvious responses to disturbance, such as hiding under the carcass or temporarily abandoning the brood.

(c) *Behavioural control of food allocation*

Behavioural observations also provided information on the behavioural control over the transition to nutritional independence. Because begging occurs only when parents are near the larvae (Rauter & Moore 1999; Smiseth & Moore 2002), we tested whether females exercised control by moving away from or not approaching the larvae. We did this by noting the number of scans where a female was in near proximity to the larvae, defined as within a distance of less than the width of its pronotum from the larvae. This is approximately the distance to the parent at which the larvae start begging (Rauter & Moore 1999). From this, we calculated the percentage time that females spent near the larvae.

The parent could also control the transition to nutritional independence by reducing the frequency of responding to begging attempts with regurgitation. We assessed whether females became less likely to respond to begging over time by counting the number of larvae that were fed during each scan, defined as the number of larvae in mouth-to-mouth contact with the female. We calculated a female's likelihood of provisioning in response to begging, p_i , as $p_i = \Sigma m/\Sigma b \times 100$, where Σb is defined as in § 2b and Σm is the total number of mouth-to-mouth contacts during the observation session.

Near proximity to the parent is a necessary but not sufficient condition for begging to occur. If the transition to nutritional independence is under offspring control, we predict that the larvae should cease begging despite having ample opportunities to

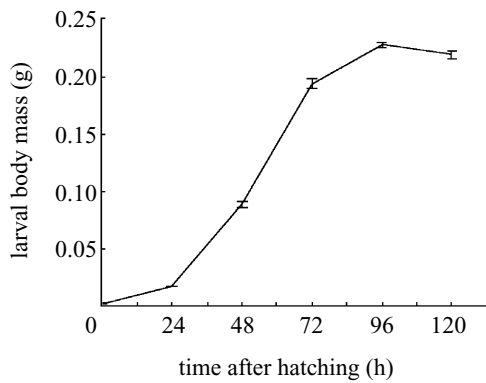


Figure 1. Growth of *Nicrophorus vespilloides* larvae in control broods, which were cared for by the female parent throughout development, from hatching to 120 h after hatching. Error bars indicate ± 1 s.e.

beg for food from the female. To test for this, we calculated the average percentage time spent begging by each larva in the brood in near proximity to the female, bp_i , as $bp_i = \Sigma b/L \times 100/p$, where Σb and L are as in § 2b and p is the number of scans during which the female was near the larvae.

(d) Statistical analyses

All variables used in the statistical analyses were normally distributed or transformed to achieve normal distribution. The data were analysed using SYSTAT v. 10. All tests were two tailed. First, t -tests were used to compare broods with and without parents on a given day. Comparisons were made within days, as we were interested in identifying the days on which there was an effect of the removal of a parent. Next, one-sample t -tests were used to test for begging greater than zero for each day. Finally, analysis of variance (ANOVA) was used to examine how female and larval behaviour changed over time.

3. RESULTS

(a) Larval growth

The larvae in the control broods, which were cared for by the single female parent throughout development, grew very rapidly, attaining a peak body mass 96 h after hatching (figure 1). The larvae increased nearly 90-fold in body mass from 0.0026 g at hatching to 0.23 g after 96 h (figure 1). The relative increase in body mass, measured over the following 24 h, decreased over time from 580% at hatching to 18% at 96 h after hatching (figure 2a).

(b) Efficiency of self-feeding and begging

The experimental removal of the female during the early stages of development significantly reduced larval growth during the following 24 h compared with the control broods (figure 2a). This was the case for broods where the female was removed at hatching ($t_{40} = 11.66$, $p < 0.0001$) and at 24 h ($t_{38} = 6.41$, $p < 0.0001$) and 48 h after hatching ($t_{38} = 3.62$, $p = 0.0009$). By contrast, there was no significant reduction in larval growth rate compared with control broods when the female was removed 72 h after hatching, ($t_{40} = 1.34$, $p = 0.19$). Thus, the efficiency of self-feeding increased during larval development such that larval growth rates were similar for larvae with and without access to their parents after 72 h (figure 2a).

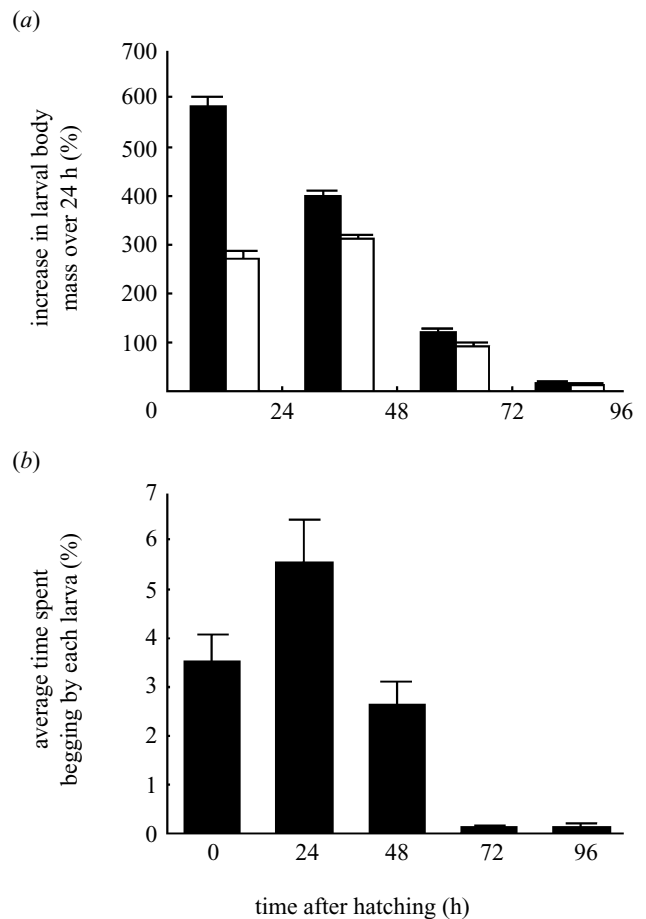


Figure 2. Changes in the efficiency of self-feeding and time spent begging during the development of *Nicrophorus vespilloides* larvae. (a) The efficiency of self-feeding (defined as the growth of larvae foraging through self-feeding alone relative to that of larvae with access to food provisioned directly by the parents) increased over time such that the larval growth rates were similar for larvae with (filled bars) and without (open bars) access to food provided directly by the parent 72 h after hatching. (b) The time spent begging by the larvae declined to very low levels, being confined to a minority of larvae in a minority of broods, from 72 h after hatching. Error bars indicate ± 1 s.e.

The time spent begging by the larvae also changed over time (figure 2b). Begging was significantly higher than a hypothesized mean of no begging at hatching (one-sample t -test: $t_{19} = 7.86$, $p < 0.0001$) and at 24 h (one-sample t -test: $t_{19} = 9.42$, $p < 0.0001$) and 48 h after hatching (one-sample t -test: $t_{19} = 7.95$, $p < 0.0001$). At 72 h and 96 h after hatching, larval begging was confined to a minority of broods, thereby violating the assumptions of parametric statistics. However, as is evident from figure 2b, begging declined to very low levels from 72 h after hatching, occurring sporadically, rather than regularly as was the case up to 48 h after hatching. Hence, as predicted, the timing of the cessation of begging coincided with the increased efficiency of self-feeding at 72 h after hatching.

(c) Behavioural control of food allocation

The females did not reduce the percentage of time they spent near the larvae ($F_{4,96} = 0.751$, $p = 0.560$; figure 3a) or the frequency with which they responded to begging attempts ($F_{4,57} = 2.018$, $p = 0.103$; figure 3b) over time.

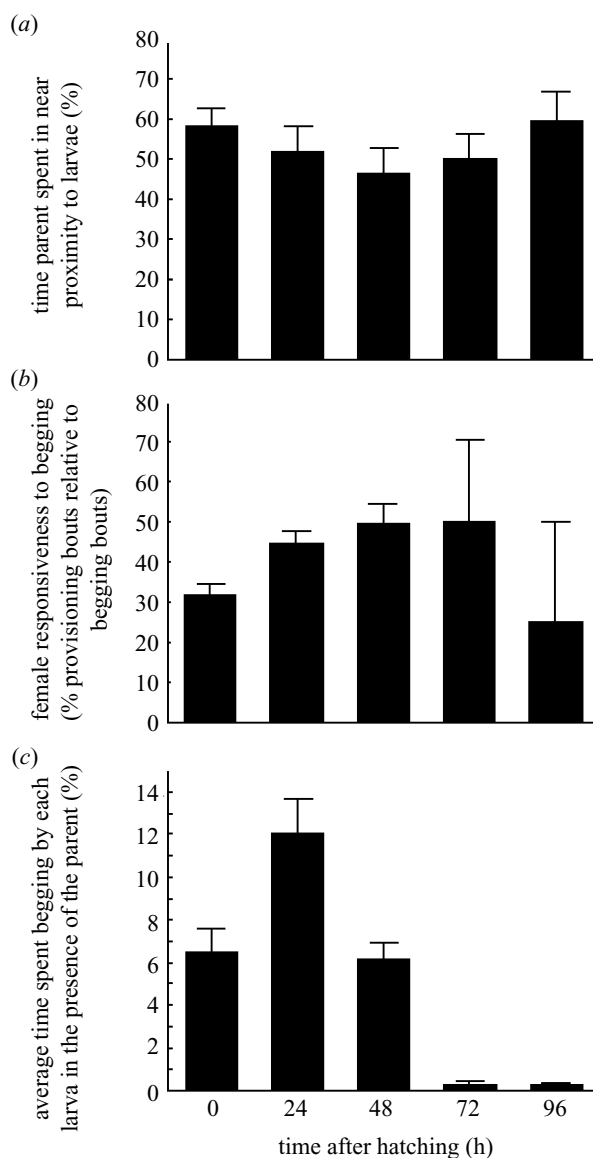


Figure 3. Parental versus offspring control over the transition to nutritional independence in *Nicrophorus vespilloides*. (a) Time spent in near proximity to the larvae by the female parent. (b) The frequency with which the female responded to larval begging, defined as the percentage of provisioning bouts relative to begging bouts for a brood. (c) Time spent begging by the larvae when the parent was in near proximity to the larvae. Error bars indicate +1 s.e.

Thus, there was no evidence that female parents changed their behaviour towards the larvae over time, which would be expected if females controlled food allocation. By contrast, the time spent begging by the larvae in the presence of the parent changed significantly over time ($F_{4,59} = 18.675$, $p < 0.001$) and was lowest from 72 h after hatching (figure 3c) when the larvae grew just as well without access to food provisioned by the parent. This test could be performed only on nests in which at least one larva begged, thereby underestimating the decrease in begging with age because begging occurred in a minority of broods from 72 h after hatching. Thus, the larvae ceased begging at the time predicted from the relative efficiency of self-feeding despite having ample opportunities to beg for food from their parents, suggesting that food allocation

during the transition to nutritional independence was under offspring control.

4. DISCUSSION

Because begging is not obligate, we suggest that the burying beetle *N. vespilloides* can serve as an empirical model for the origin and early evolution of begging. We illustrate this by examining changes in begging, efficiency of self-feeding and control of food allocation during the transition to nutritional independence. The efficiency of self-feeding increased with larval age. As predicted, we found that the larvae ceased begging when they grew just as well without as with access to food provided by the parent 72 h after hatching. Thus, our results suggest that offspring begging changed over time as a consequence of the increased efficiency of self-feeding. We then tested the distinguishing assumption between honest-signalling (Godfray 1991, 1995) and scramble-competition models (Rodríguez-Gironés *et al.* 2001; Parker *et al.* 2002): that is, whether food allocation is under parental or offspring control. We found no evidence that the female parent changed its behaviour towards the larvae over time, whereas the larvae changed their behaviour towards the parent by reducing the time spent begging when in proximity to the parent. These findings suggest that the transition to nutritional independence was under the behavioural control of the offspring.

Recent theoretical models of begging, which have been developed primarily for birds (Godfray & Johnstone 2000; Wright & Leonard 2002), have largely ignored questions concerning the origin and early evolution of begging. A notable exception are the models by Rodríguez-Gironés *et al.* (1996, 1998), which extended Godfray's honest-signalling models by including the potential for a non-signalling equilibrium at which parents provide food at a fixed rate in the absence of begging. Rodríguez-Gironés *et al.* (1996, 1998) suggested that, because the expected fitness returns to both parents and offspring were higher at the non-signalling equilibrium than at the signalling equilibrium, begging could evolve from a non-signalling origin only through direct sibling competition in multiple-offspring broods. Rodríguez-Gironés *et al.*'s models, developed to investigate the origin of begging in birds, have little relevance to burying beetles where the larvae can feed directly from the carcass independently of parental provisioning (Smiseth & Moore 2002). Thus, there is a need for new theoretical models, fitted to extant partially begging species, that include begging and self-feeding offspring foraging strategies.

Our results suggest that, because food allocation is under offspring control, theoretical models for partial begging should be based on scramble competition (e.g. Rodríguez-Gironés *et al.* 2001; Parker *et al.* 2002) rather than honest signalling (e.g. Godfray 1991, 1995). Our study, which focused on the behavioural control of food allocation during the transition to nutritional independence, should be followed up by studies on the control of food allocation before nutritional independence. This could be accomplished by introducing competitive asymmetries among siblings. Such competitive asymmetries arise from hatching asynchrony may lead to profound variation in size within broods (P. T. Smiseth, personal

observation). If the larvae have behavioural control, senior larvae would be predicted to outcompete juniors for access to food provided by the parents. By contrast, if the parents are in control, they would be predicted to feed juniors preferentially because they have a lower efficiency of self-feeding than seniors.

In conclusion, our study provides evidence that changes in the efficiency of self-feeding affect begging in partially begging species, and that the transition to nutritional independence is under offspring control. Partially begging species, such as burying beetles and some semi-precocial birds (e.g. rallids; Leonard *et al.* 1988), provide a unique model system for the origin and early evolution of begging from non-signalling offspring foraging strategies. We therefore encourage further empirical research on partially begging species accompanied by the development of appropriate theoretical models.

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