
Do honest signalling models of offspring solicitation apply to insects?

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Honest signalling models predict that the intensity of solicitation by offspring influences the level of provisioning provided by parents and reflects offspring need. The empirical evidence supporting these predictions primarily comes from studies of birds or mammals. Thus, although parental care of altricial offspring is taxonomically widespread, the generality of these models is not well known. To investigate whether honest signalling models apply to insects, we manipulated parent and offspring behaviour in the burying beetle *Nicrophorus orbicollis*, a species with advanced parental care. First, within biparental care, we manipulated the brood size to alter the parents' perception of offspring need. We measured the care giving behaviour of male and female parents to examine whether either adjusts its level of care according to offspring need. In the second experiment, because two parents together provision the brood more often than single parents, we manipulated the number of care givers (uniparental and biparental care) and measured offspring solicitation to assess whether offspring change their behaviour in response to need. Our results show that parent behaviour is broadly consistent with the first prediction of the models; both sexes provisioned larger broods more often than smaller broods. Larval solicitation was also consistent with the second prediction; larvae that were provisioned less often begged more. Our results provide evidence that honest signalling models can be applied to insects as well as vertebrates, although there are also subtle differences in care giving behaviour that may be important.

Keywords: begging; burying beetle; *Nicrophorus orbicollis*; offspring solicitation; parental care; parent-offspring conflict

1. INTRODUCTION

Solicitation of food from parents by offspring is a widespread phenomenon, particularly when parents provide altricial offspring with resources that are necessary for development (e.g. Matura & Yamane 1984; Clutton-Brock 1991; Mock & Parker 1997). Solicitation is expected to evolve because of the conflict between parent and offspring over allocation of resources (Kilner & Johnstone 1997; Mock & Parker 1997; Bradbury & Vehrencamp 1998). Parents are equally related to all their offspring; hence, they should prefer to allocate resources evenly among all offspring. Each offspring, however, should try to obtain more food from the parents than its siblings, because it is not genetically identical to its siblings (Trivers 1974; Clutton-Brock 1991; Mock & Parker 1997; Bradbury & Vehrencamp 1998). This conflict over the allocation of resources leads to attempts by offspring to bias provisioning by its parents towards itself through solicitation. Considerable theoretical effort has been directed towards understanding when and how offspring should signal need and when and how parents should respond to the signals of their offspring (Mock & Parker 1997).

Honest signalling models of offspring solicitation (Godfray 1991, 1995) assume that (i) offspring vary in

their condition but the parents are unable to assess offspring condition directly, (ii) parents receive greater fitness benefits by provisioning offspring in poor condition than by provisioning offspring in good condition, (iii) solicitation signals offspring need, allowing parents to distribute resources in such a way that parental fitness benefits are maximized, and (iv) the begging signal itself has to be costly if it is to be maintained as an honest signal (but see Maynard Smith 1994; Bergstrom & Lachmann 1998; Johnstone 1998). Based on these assumptions, three main predictions have been derived: (i) parents adjust their level of provisioning to solicitation intensity, (ii) solicitation intensity reflects offspring need, and (iii) solicitation is costly to offspring. There is some empirical evidence supporting these predictions (Kilner & Johnstone 1997). Empirical studies, however, have been conducted primarily with altricial birds and, to a minor extent, mammals (Kilner & Johnstone 1997; Bradbury & Vehrencamp 1998; Jensen *et al.* 1998). Thus, it is not known how well honest signalling models of offspring solicitation apply to other organisms with advanced parental care.

Parental care is not limited to birds and mammals or even to vertebrates. Many insects, including Hymenoptera, Isoptera and Coleoptera, provision hatched offspring with food continuously (Wilson 1971; Clutton-Brock 1991). Unfortunately, insect parent-offspring interactions have not been well studied and the few empirical data collected on insects have not been applied to models

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of parent–offspring interactions (Wilson 1971; Clutton-Brock 1991; Bradbury & Vehrencamp 1998). For example, although begging signals of larvae have been documented for several insect species (Pukowski 1933; Matsura & Yamane 1984; Hölldobler & Wilson 1990), it is unknown whether these begging signals vary in accordance with offspring need. Still, there is some experimental evidence that adult insects can respond to larval food demand in honey bees (*Apis mellifera*) (Huang & Otis 1991) and an ant (*Pheidole morrisi*) (Brown & Traniello 1998).

To investigate whether honest signalling models apply to insects, we tested the predictions regarding levels of parental provisioning and offspring solicitation in the burying beetle *Nicrophorus orbicollis*. Specifically, we addressed whether this burying beetle provisions its offspring in relation to solicitation intensity and whether the solicitation intensity of larvae reflects their need. *N. orbicollis*, like all burying beetles investigated, has elaborate parental care (Pukowski 1933; Eggert & Müller 1997; Scott 1998). There is some empirical evidence that the parental provisioning rate is correlated with brood size (Fetherston *et al.* 1990). Further, in *N. orbicollis*, parental care is necessary for offspring development (Trumbo 1992). Although biparental care is common in this beetle, uniparental care can also result in successful broods. Single female care is fairly common but single male care is rare (Wilson & Fudge 1984; Trumbo 1991; Scott 1998). Therefore, *N. orbicollis* provides an invertebrate model for testing honest signalling models.

Burying beetles reproduce on small dead animals from which they provision their offspring (Pukowski 1933; Eggert & Müller 1997; Scott 1998). After the carrion is buried, skinned and worked into a ball and eggs are laid nearby, the parents make a small crater on top of the ball. After hatching, the larvae crawl to the carrion and gather within this crater. When the adult beetle approaches the crater, the larvae crawl towards the parent and push their heads to the mouth parts of the parent. The parent responds by regurgitation of digested carrion. In addition to regurgitation of carrion directly to the larvae, parents also provide offspring with an additional food source from which the offspring can feed by themselves. Parent beetles produce this additional food resource by consuming carrion within the crater and regurgitation of droplets of partly digested carrion back into the crater. Larvae then feed on the pre-digested food.

Our tests of the honest signalling models used manipulations of offspring and parental behaviour similar to those performed by Von Haartman (1953) on pied flycatchers. Making the same assumptions as Von Haartman (1953), we tested the prediction that burying beetles provision food in relation to their perceived larval need by manipulating the intensity of larval begging through alteration of brood size. Because biparental care results in more regurgitations to larvae than uniparental care (C. M. Rauter and A. J. Moore, unpublished data), we also manipulated the number of care givers to test the prediction that larvae solicit regurgitations in relation to their need. We then compared the begging frequency of larvae that received care from two parents compared to the begging frequency of larvae that received care from only one parent. Thus, in this study, we tested the first

two predictions of honest signalling models of offspring solicitation.

2. METHODS

(a) *Origin and rearing methods of the beetles*

All adult *N. orbicollis* beetles used in this study were first generation offspring of field-caught beetles collected in the Research Forest of Berea College, Kentucky, USA. Before the experiment beetles were housed individually in plastic containers (15 cm × 10 cm × 5 cm) filled to two-thirds with moist peat and fed dead mealworms twice a week. The beetles were maintained in a room at a temperature of 20–23 °C and under a reversed 15 L : 9 D cycle.

(b) *Parental response to offspring solicitation*

We manipulated the begging intensity of larvae by altering the brood size to assess the effect of offspring solicitation on the provisioning behaviour of adult beetles. All offspring were reared with two parents. Each pair of parents was subjected to three brood size treatments: five larvae (small brood), 15 larvae (medium brood) and 25 larvae (large brood).

The first generation, laboratory-born offspring used in this study were generated by placing a virgin male and a virgin female, both chosen at random from our stock colonies, into a clear plastic container (15 cm × 10 cm × 5 cm) with a 2 cm layer of moist peat on the bottom and a previously frozen mouse (30–39 g). We checked twice a day for eggs. We transferred the beetles and the mouse to a new container the day after the first appearance of eggs and searched the peat of the old container for eggs. We put these eggs on a moistened paper towel in a Petri dish and checked these Petri dishes three times a day for newly hatched larvae. Once the larvae hatched, we again transferred the parent beetles and the mouse to a new container. This second transfer ensured that larvae hatched from eggs after the first transfer to a new container did not interfere with the brood size manipulations. We put the newly hatched larvae on top of the mouse one hour after the transfer.

We manipulated brood size by the following procedure. We removed all larvae when they were one day old and had moulted to the second instar. We used only second instar larvae, because parental provisioning peaks at this larval stage (Fetherston *et al.* 1990, 1994). After removing the larvae from their parents, we mixed the larvae from same-age broods and redistributed them randomly among the parents, while adjusting the brood size. We distributed the larvae at random to control for individual differences between families. Two hours later we observed the behaviour of each parent. This procedure (i.e. adjusting the brood size by removing and redistributing the larvae, followed by behavioural observation) was performed for each pair of parents three times consecutively for the three different brood sizes. The order of brood size experienced by the parents was chosen randomly.

We scored parental behaviour as occurring or not (yes or no), i.e. using instantaneous sampling (Martin & Bateson 1993). We recorded the behaviour of both the male and female of each pair of parents separately every minute for 30 min. We scored three categories of parental behaviour: regurgitation to larvae (mouth-to-mouth contact between parent beetle and larvae), processing carrion (parent beetle stands still in or at the edge of the crater and treats carrion with mouth parts) and ‘other’ (e.g. walking and self-preening). The frequency of regurgitating and carrion processing were analysed separately by a repeated-measure

ANOVA (Winer *et al.* 1991) with one within-factor (brood size) and one grouping factor (sex of parent). We used SYSTAT 7.0 for Windows (SYSTAT 1996) to perform the statistical analyses.

(c) *Offspring solicitation in relation to need*

We analysed offspring solicitation by manipulating the number and sex of the care givers: biparental care, uniparental female care and uniparental male care. In this experiment we standardized all broods to 15 larvae, which is the average brood size for this species on carrion weighing 30–35 g (Wilson & Fudge 1984; Scott & Traniello 1990; Trumbo 1991). The mates of the beetles subject to the uniparental care treatments were removed 12 h after adding the newly hatched larvae to the carrion (mouse of 30–39 g). We did not remove the mates earlier because males tend to desert the brood when the female is removed prior to this (C. M. Rauter, personal observation). In all other respects beetles, eggs and larvae were treated in the same way as in the previous experiment. As above, larvae from different broods were mixed to control for variation between families and individual differences in larval behaviour. Observations were again made when the larvae had moulted to the second instar.

Biparental care results in greater offspring provisioning than uniparental care (C. M. Rauter and A. J. Moore, unpublished data) assuming that a lower frequency of parental regurgitation and processing carrion results in a lower food intake by larvae. We therefore made the *a priori* prediction that the uniparental care treatment should result in greater larval begging than in the biparental care treatment. We tested our prediction using one-way ANOVA with parental care as the three-level factor (biparental care, uniparental female care and uniparental male care) followed by an *a priori* pairwise contrast of biparental and uniparental care. We analysed the data using SYSTAT 7.0 for Windows (SYSTAT 1996).

We recorded larval behaviour using the same instantaneous sampling regime as in the previous experiment. We scored three categories of larval behaviour. Because larvae show distinct begging behaviour only when a parent is close (C. M. Rauter, personal observation), we scored larval behaviour as ‘undetermined’ when no parent was within a distance of less than the width of its pronotum from the larvae. When at least one parent met this distance criterion, we scored larvae as ‘begging’ when one or more larvae pressed its mouth parts against the parent’s head or one or more larvae crawled straight towards the parent’s head. If the parent and offspring were within a pronotum width but larvae did not beg, we scored them as ‘not begging’. Because larvae begged only in the presence of a parent, we scored the intensity of larval begging as the proportion of encounters between larvae and either parent where one or more larvae begged to the total number of encounters between larvae and either parent (i.e. the frequency of larval begging).

3. RESULTS

(a) *Parental response to offspring solicitation*

Brood size had a significant effect on regurgitation to larvae by parents (within-factor of repeated-measure ANOVA, $F_{2,92}=34.96$ and $p<0.001$). With increasing brood size, reflecting greater offspring solicitation, parent beetles regurgitated to larvae more often (figure 1). The parental response of regurgitation to offspring solicitation did not depend on the sex of the parent (grouping factor of repeated-measure ANOVA, $F_{1,46}=0.97$ and $p=0.329$).

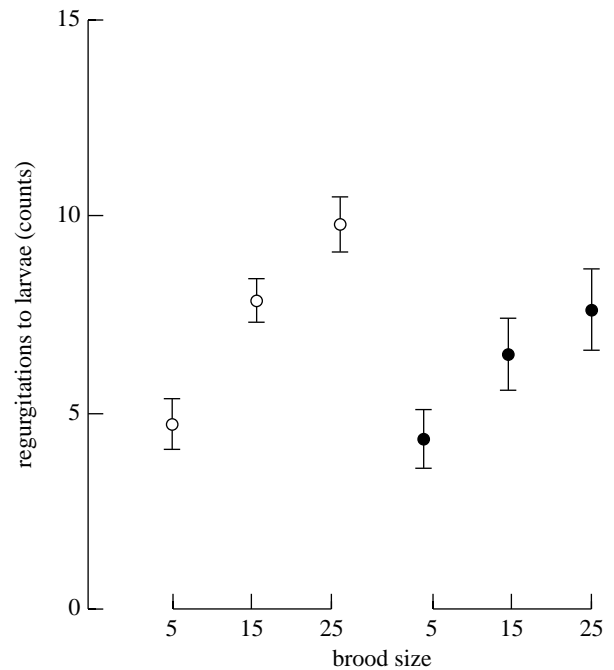


Figure 1. Regurgitation to larvae in relation to brood size and sex of parent ($n=24$ pairs of beetles). The occurrence (yes or no) of regurgitation by parents was recorded every minute for 30 min; thus, the maximum number of occurrences is 30. Means and standard errors are shown. Females, open circles; males, filled circles.

There was no interaction between sex of parent and brood size (repeated-measure ANOVA, $F_{2,92}=0.39$ and $p=0.679$). Both males and females showed a linear increase in their regurgitation response when the brood size increased (polynomial test of order 1 (linear), $F_{1,46}=64.07$ and $p<0.001$; figure 1).

In contrast, brood size did not affect processing carrion by parent beetles (within-factor of repeated-measure ANOVA, $F_{2,92}=0.68$ and $p=0.509$; figure 2). Although males and females did not change their behaviour with respect to processing carrion with increasing brood size, males tended to process carrion less often than females (grouping factor of repeated-measure ANOVA, $F_{1,46}=3.96$ and $p=0.053$). There was no interaction between sex of parent and brood size (repeated-measure ANOVA, $F_{2,92}=1.00$ and $p=0.372$).

(b) *Offspring solicitation in relation to need*

The begging frequency of larvae was strongly related to the number of parents (one-way ANOVA, $F_{2,81}=6.02$ and $p=0.004$). When two parents took care of the larvae, the larvae begged significantly less often than when only one parent provided parental care (specific contrast between biparental care and uniparental care, $F_{1,81}=11.41$ and $p=0.001$; figure 3).

4. DISCUSSION

(a) *Parental response to offspring solicitation*

Our study indicates that parental provisioning and offspring solicitation in the burying beetle *N. orbicollis* generally fit the predictions generated by honest signalling models. Parents regurgitated to larger broods more often

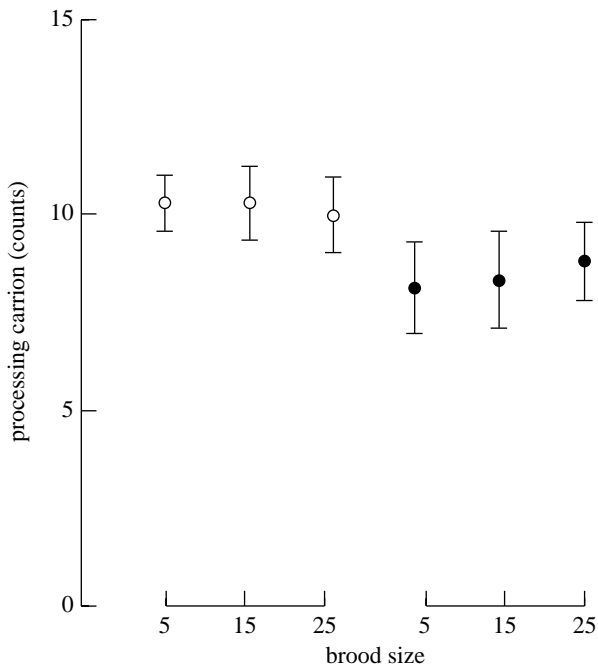


Figure 2. Processing carrion by parents in relation to brood size and sex of parents ($n = 24$ pairs of beetles). The occurrence (yes or no) of processing was recorded every minute for 30 min; thus, the maximum number of occurrences is 30. Means and standard errors are shown. Females, open circles; males, filled circles.

than smaller broods. This result indicates that parents respond to the need of offspring. The prediction that offspring in greater need beg more was supported by the observation that larvae with two parents providing care begged less than larvae with only one parent that regurgitated to the larvae significantly less often than two parents together.

We have assumed that manipulating the brood size manipulates the offspring signal in a manner consistent with changes in offspring need, but this remains an untested assumption within this experiment. Increased regurgitation with increasing brood size could reflect a response to the number of larvae they encounter rather than to changes in the perception of signals of increased needs. However, the preliminary results of an experiment where we manipulated the state of the offspring by starving larvae indicate that parent beetles can respond to the state of larvae. Parents appear to feed hungrier larvae more often than well-fed larvae (C. M. Rauter and A. J. Moore, unpublished data).

An increase in parental provisioning in response to increased needs of larvae has also been seen in social insects. Brown & Traniello (1998) demonstrated that minor and major workers of the ant *P. morrisi* increased their brood care when the need of offspring was manipulated by experimentally doubling the brood size. Honeybee (*A. mellifera*) nurses increased feeding visits when the hunger level of bee larvae was experimentally increased by starvation (Huang & Otis 1991). Thus, it is tempting to suppose that the consistent response of care givers to increased offspring need in a subsocial beetle species and two social hymenopteran species indicates that adjusted parental response to offspring solicitation is

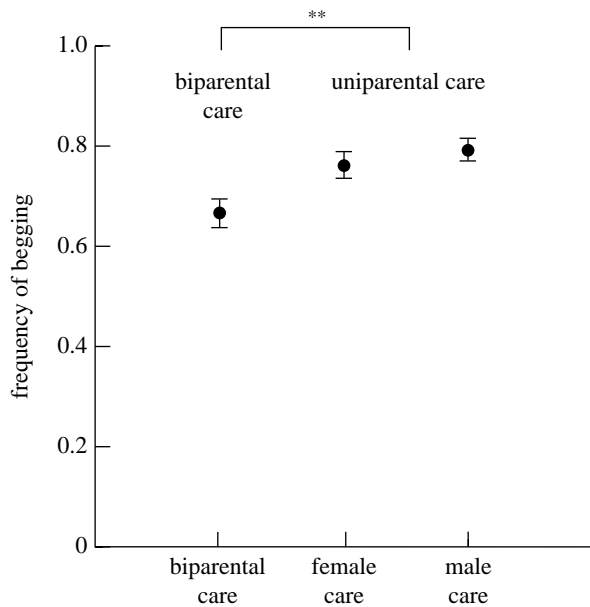


Figure 3. Frequency of begging of larvae (i.e. the number of encounters between larvae and either parent where one or more larvae begged divided by the total number of encounters between larvae and either parent) in relation to biparental care ($n = 24$), uniparental female care ($n = 31$) and uniparental male care ($n = 29$). Means and standard errors are shown. Significance level: $**p = 0.01$.

a general phenomenon in insects. However, relating parent-offspring models to systems such as social Hymenoptera, where the care givers do not reproduce, may be problematic. Non-reproducing care givers may not suffer as large a cost from parental care as parents may; hence, little conflict or even cooperation between offspring and care givers may be the consequence. Thus, in the eusocial species at least, larval signals may be the result of cooperation and not parent-offspring conflict.

Our results fit the broad predictions of the models of honest signalling, but we also see subtle differences that raise questions concerning the type of behaviour and conditions under which a specific behaviour fits these models. Although regurgitation to the offspring increased with increasing offspring need, processing carrion was not affected by brood size. It may be that the beetle parents did adjust their behaviour, but in a way that was not obvious to us. *N. orbicollis* parents could provide additional carrion resources to their offspring by changing other aspects of their behaviour. Because parents consume the same food resource as the offspring, it may be that the parent beetles can accommodate increased offspring need by reducing their own carrion consumption rather than by spending more time processing carrion or by providing bigger drops rather than more frequent drops. We did not measure the quantity of food provided during processing carrion.

An alternative explanation is that regurgitation is experienced by the offspring as shared parental care (*sensu* Lazarus & Inglis 1986), i.e. the benefits of regurgitation must be shared by the offspring. Thus, regurgitation should depend on brood size. In contrast, processing carrion might be an unshared parental care behaviour, because parent beetles regurgitate droplets of digested

carrion resulting in a lake of fluid food on the bottom of the crater available for all larvae. Given that all offspring can profit simultaneously, unshared parental care should not depend on brood size (Lazarus & Inglis 1986).

The effect of brood size on regurgitation suggests that larvae can influence the total amount of parental care, as predicted by honest signalling models (Godfray 1991, 1995). However, the lack of effect of brood size on carrion processing indicates that parents may provide a fixed amount of care and there may be scramble competition among larvae. This is a situation envisaged in models of competitive begging (Mock & Parker 1997). Thus, in contrast to avian systems, within a single species of burying beetle both types of parent-offspring conflict models can be tested.

We also found that male *N. orbicollis* regurgitated to larvae as often as females but males tended to process carrion less often than females. These results are consistent with Fetherston *et al.* (1994). The relative value of different parental care behaviour is not known and the reasons for this sex difference therefore remain unclear. Perhaps females process carrion more often than males because they consume more carrion in preparation for future broods. Equal regurgitation to larvae by both the male and female is, however, consistent with models on biparental cooperation where an equal share of parental care between mates is expected (Winkler 1987).

Males and females both responded in the same way or not at all when we manipulated the brood size. Thus, male and female *N. orbicollis* responses to changes in offspring need are consistent with the prediction from models of biparental care that both parents should respond equally to external factors (Chase 1980; Houston & Davis 1985; Winkler 1987).

(b) *Offspring solicitation in relation to need*

In *N. orbicollis*, larvae that received more food begged significantly less than larvae that received less food. This result suggests that begging level reflects the need of burying beetle larvae and fits with the models of honest signalling. The generality of increased begging with increasing hunger by insect larvae is not clear because the behaviour of insect larvae is not well studied. Acoustical signals indicating hunger have been described for wasp larvae (Matsura & Yamane 1984). Begging of larvae is also reported for some ant species (Hölldobler & Wilson 1990). Whether food solicitation in wasps and ants is related to offspring need, however, is not known. Additional studies on offspring solicitation in other insects are required to show that solicitation of insect larvae generally advertizes larval need.

Despite the great differences between insects, birds and mammals, our study provides evidence that honest signalling models can be applied to insects as well as vertebrates. Beetle parents did adjust their levels of regurgitation to offspring need. Further, the begging of the larvae reflected the level of need in the larvae. Subtle differences from the honest signalling models were also found, but the importance of these is unknown. These differences might be related to the type of parental behaviour (shared or unshared parental care) that was observed. Inherent differences in life history between insects and vertebrates, however, might also account for

some of these differences because honest signalling models have been developed mainly based on bird studies (Kilner & Johnstone 1997). Nevertheless, additional studies examining offspring solicitation and the relationship between solicitation and parental response in other insects with advanced parental care are needed. Finally, the third aspect of the models, whether offspring solicitation in insects is costly or not, remains an open empirical question. Regardless, insects such as the burying beetle *N. orbicollis* provide excellent systems for experimentally addressing questions regarding the evolution of parental care.

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