

Original Article

Differentiating among alternative models for the resolution of parent–offspring conflict

Clare P. Andrews and Per T. Smiseth

Institute of Evolutionary Biology, University of Edinburgh, King's Buildings, West Mains Road, Edinburgh EH9 3JT, UK

Received 15 November 2012; revised 2 May 2013; accepted 2 May 2013; Advance Access publication 10 June 2013.

Understanding the behavioral mechanisms mediating the resolution of parent–offspring conflict is an important challenge given that the resolution of this conflict shapes the transfer of resources from parents to offspring. Three alternative models suggest that offspring begging provides an important behavioral mechanism for conflict resolution: honest signaling, scramble competition, and cost-free signaling models. However, there has so far been little progress in testing between these models because they share the same predictions. Here, we test between these models by focusing on their contrasting assumptions concerning who controls resource allocation and whether begging is costly in 2 experiments conducted on the burying beetle *Nicrophorus vespilloides*. In Experiment 1, we manipulated the degree to which offspring and parents can control resource allocation by presenting broods with age-based competitive asymmetries with a live or a dead female parent. We found that seniors (i.e., older larvae) gained more access to the parent's mouthparts than juniors only when presented with a live parent. In Experiment 2, we provided parents with broods of 60 newly hatched larvae and found that larvae were more likely to become a target of filial cannibalism when begging than would be expected if parents targeted larvae irrespective of their behavior. These findings suggest that offspring begging increases the parents' influence over food allocation and that begging is costly by increasing the offspring's risk of being a target of filial cannibalism. Our results support the assumptions of honest signaling models for the resolution of parent–offspring conflict.

Key words: costly begging, honest signaling, *Nicrophorus vespilloides*, parent–offspring conflict, scramble competition.

INTRODUCTION

Parents and offspring have conflicting interests over the amount and distribution of parental resources due to asymmetries in their relatedness, with offspring being selected to demand more resources from their parents than parents are selected to provide (Trivers 1974). Understanding the resolution of this conflict is an important challenge because it shapes the transfer of resources from parents to offspring, thereby determining both the parents' future reproductive prospects and the offspring's recruitment into the population. Across many taxa, offspring perform elaborate and conspicuous begging displays (Kilner and Johnstone 1997), which theoretical work suggests have evolved as a mechanism for resolving parent–offspring conflict by communicating information about offspring to parents (Godfray 1991, 1995; Maynard Smith 1991, 1994; Parker et al. 2002). Three distinct classes of such model have been proposed. Initial models viewed the allocation of parental resources to offspring as a form of scramble competition among offspring for access to the resources provided by parents (Macnair

and Parker 1979; Parker et al. 2002). Subsequently, honest signaling models (Godfray 1991, 1995; Johnstone 1996) argued that parents benefit from monitoring offspring begging because such displays provide the parent with information on the nutritional need of the offspring, which would otherwise be cryptic to parents, with honesty being maintained by a cost of begging. Finally, cost-free models (Maynard Smith 1991, 1994; Bergstrom and Lachmann 1998) proposed that honest parent–offspring communication could be evolutionarily stable even if begging was not costly, provided that parents and offspring shared some overlapping interests.

There remains considerable debate over how offspring begging evolved as a mechanism of conflict resolution due to the fundamental challenge of distinguishing between these models (Kilner and Johnstone 1997; Royle et al. 2002). This challenge arises because these models share the same empirically well-supported predictions; that begging reflects offspring need/quality and that parents allocate resources in response to begging (Royle et al. 2002; Mock et al. 2011). However, the 3 models make contrasting assumptions regarding which generation gains control over resource allocation and whether begging is costly to offspring. Concerning control, honest signaling and cost-free models assume that parents respond to offspring begging to obtain honest information about offspring's needs and/or quality (Mock et al. 2011; Boncoraglio et al. 2012),

Address correspondence to P.T. Smiseth. E-mail: per.t.smiseth@ed.ac.uk.
C.P.A. Coauthor is now at the Queen's Medical Research Institute, University of Edinburgh, 47 Little France Crescent, Edinburgh EH16 4TJ, UK.

thereby providing parents with increased control over resource allocation (Godfray 1991, 1995). By contrast, scramble competition models assume that begging is a form of sibling competition where by parents passively allocate resources based on begging, thus providing offspring with increased control over resource allocation (Parker et al. 2002). Although these theoretical models define control at opposing ends of a continuum, natural systems may occupy any position along this power continuum (Royle et al. 2002). Thus, to allow for more realistic intermediate scenarios, we define control operationally as the degree to which a given trait of interest (in this case, offspring begging) increases the parents' or the offspring's ability to influence resource allocation. This trait-based operational definition does not imply that either parents or offspring exercise complete control over resource allocation, nor does it imply that the realized allocation of resources corresponds to the optimum of either generation (i.e., either "wins" the evolutionary conflict). Concerning costs, both honest signaling and scramble competition models assume that begging incurs a cost to offspring (Godfray 1991, 1995; Parker et al. 2002), whereas cost-free models assume that begging incurs no such costs (Maynard Smith 1991, 1994). Empirical studies to date, conducted mainly on altricial birds, provide mixed evidence as to whether parent-offspring communication provides parents or offspring with increased control over resource allocation (Kilner 1995; Royle et al. 2002; Smiseth et al. 2003; Hinde et al. 2010; Mock et al. 2011) and whether begging is costly (Kilner 2001; Rodríguez-Gironés et al. 2001; Chappell and Bachman 2002; Haskell 2002; Noguera et al. 2010).

Here, we test these 2 critical assumptions using 2 separate experiments in a single model system: the burying beetle *Nicrophorus vespilloides*. In this and related species in the same genus, larvae beg for food by touching the parent's mouthparts with their legs (Rauter and Moore 1999). As predicted by all 3 models, larval begging reflects offspring needs (Rauter and Moore 1999; Smiseth and Moore 2004a), and parents respond to begging by adjusting their provisioning of resources. Brood-size manipulations suggest that parents respond to long-term changes in brood levels of begging by adjusting the amount of resources they provide to the brood (Rauter and Moore 1999), and within-brood manipulation of offspring needs suggests that parents respond to short-term changes in begging by adjusting the way they distribute resources within the brood (Smiseth and Moore 2004a). In Experiment 1, we test the contrasting assumptions concerning which generation gains an increased degree of control over resource allocation by simultaneously manipulating the offspring's and the parent's ability to influence resource allocation. We manipulated the offspring's ability to do so by creating asynchronous broods with controlled age-based competitive asymmetries. We manipulated the parent's ability by presenting broods with either a live or a dead female parent. Conveniently, *N. vespilloides* larvae continue to beg to dead parents at consistent levels for at least 2 h (Smiseth and Parker 2008). This unique design avoids potential cryptic confounding effects due to parental behavior, thus differing from previous studies manipulating only offspring ability to influence resource allocation (Kilner 1995). If parent-offspring communication provides parents with increased control over resource allocation, we predict that the relative begging success of different-aged larvae (i.e., their success at gaining access to the parents' mouthparts while begging) would depend on whether they were presented with a dead parent, who for obvious reasons cannot influence resource allocation, or a live parent who has the potential to do so. Conversely, if begging provides offspring increased control over resource allocation, we predict that the relative success of different-aged larvae at accessing the parents'

mouthparts would remain similar irrespective of whether the larvae were begging toward a parent that was dead or alive. In Experiment 2, we test the contrasting assumptions concerning whether begging is costly or not. A previous study on *N. vespilloides* suggests that the energetic costs of begging are negligible, as are opportunity costs due to the loss of time that larvae otherwise could have spent feeding themselves directly (Smiseth and Parker 2008). However, a potential cost of begging that so far has been neglected is that begging larvae may be at increased risk of becoming a target when parents reduce the brood size after hatching through filial cannibalism (Bartlett 1987). We tested this hypothesis by providing parents with an experimental brood of 60 newly hatched larvae. If there were a parent-induced cost of begging, we predict that the number of larvae that were cannibalized while begging would exceed the number expected if the parent targeted larvae regardless of whether they were begging or not.

METHODS

Study species and general methods

The burying beetle *N. vespilloides* breeds on carcasses of small vertebrates (Eggert and Müller 1997). Females lay eggs in the soil surrounding the carcass and the larvae hatch asynchronously (hatching starts after a mean of 81 ± 3 h following provision of a carcass, with hatching spread from the first to the last larva in a brood ranging from 16 to 56 h; Smiseth et al. 2006). One or both parents provide care for the larvae by burying, defending, and maintaining the carcass and creating an opening (crater) in the carcass within which larvae can self-feed. Parents also directly provision larvae by regurgitating predigested carrion (Smiseth and Moore 2002), which enhances larval growth and speeds development (Lock et al. 2004). We bred pairs of non-sibling virgin beetles from an outbred laboratory population (caught at Kennel Vale, Cornwall, UK) in plastic boxes ($17 \times 12 \times 6$ cm) containing 1–2 cm moist soil and a mouse carcass (Livefoods Direct Ltd, Sheffield, UK; mass range 14–30 g in Experiment 1 and 10–15 g in Experiment 2) under constant light at 20 °C, following established procedures (Smiseth and Moore 2004a). Prior to breeding, virgin adults were housed individually in boxes and fed ad libitum twice weekly with small pieces of organic beef. Before eggs hatched, we transferred the female and carcass to another box. We removed the male at this stage because male involvement with care is highly variable and male provisioning assistance has no detectable effect on larval growth or survival under laboratory conditions (Eggert et al. 1998; Smiseth et al. 2005). When eggs hatched, we used the larvae to establish standardized broods of mixed parentage (see below). We provided females with broods only after their own eggs started hatching, because females will then accept related as well as unrelated larvae (Müller and Eggert 1990).

Experiment 1: Who gains more control over resource allocation?

In this experiment, we examined who gains control over resource allocation by simultaneously manipulating the offspring's and the parent's ability to influence resource allocation. To this end, we first manipulated the offspring's ability to control resources by creating asynchronous broods with controlled age-based competitive asymmetries and then the parent's ability to do so by presenting the broods with either a dead or a live female parent (the latter treatment acting as control). We conducted observations on larval

begging and access to the parent's mouthparts when seniors were 48 h old and juniors were 24 h old, which corresponds to the time at which there is a peak in begging rates (Smiseth et al. 2003, 2007).

To manipulate the offspring's ability to control resources, we used newly hatched larvae (see above) to generate 79 mixed-parentage broods each comprising 10 senior and 10 junior larvae, with juniors being placed on the carcass 24 h after seniors (Smiseth et al. 2007). This design was chosen to ensure that the experimental broods were close to the mean brood size 24–48 h after hatching (mean \pm standard error [SE]: 21.2 ± 1.0 larvae; range: 2–47 larvae; Smiseth and Moore 2002) and also within the natural range of hatching spread for the species (mean \pm SE: 30 ± 3 h; range: 16–56 h; Smiseth et al. 2006). Larvae of both age classes beg at moderate to high rates (begging rates peak when larvae are around 24 h old and decline by the age of 48 h), yet the 2 age classes are easily distinguished at these ages based on differences in size owing to their extremely rapid growth (Smiseth et al. 2003, 2007).

When juniors were 24 h and seniors 48 h old, we allocated broods alternately to the dead or live parent treatment. In the dead parent treatment, we killed the female by placing her in a -20°C freezer 30 min prior to behavioral observation. After thawing for 5 min, we pinned the female to the carcass adjacent to the crater containing the larvae for which she previously cared, her head protruding, and forelegs oriented toward the crater. Prior work shows that larvae beg to dead parents at consistent and high levels for at least 2 h (Smiseth and Parker 2008), that larval begging is triggered by chemical cues from the parent (Smiseth et al. 2010), and that disturbance caused by handling has no detectable effect on larval begging behavior (Smiseth and Moore 2004a). We obviously acknowledge that dead parents will differ in other respects from live parents, especially with respect to whether they interact with their larvae. However, this difference was the precise rationale behind our dead parent treatment as it provides a unique means for manipulating parental influences on interactions among larvae, while at the same ensuring that larvae continue begging at consistent and high levels. We note that our design resembles established practices in experimental work on birds where offspring begging routinely is measured in response to a standardized stimulus provided by the experimenter (e.g., Lotem 1998; Kilner 2001). In the live parent treatment, we left the female undisturbed given that previous work suggests that handling of larvae might affect parental provisioning behavior (Smiseth and Moore 2007).

Following established protocols (Smiseth and Moore 2002, 2007; Smiseth et al. 2003; Lock et al. 2004), we used instantaneous sampling every 1 min over a period of 30 min to record the number of senior and junior larvae that were begging and that were potentially feeding from the parent. We considered a larva to be begging when raising its head toward the parent while waving its legs or touching the parent and to be potentially feeding when it made mouth-to-mouth contact with the parent (Rauter and Moore 1999). Because larvae beg only when a parent is close, we noted the number of scans in which the female and larvae were in close proximity (P), defined as a distance of less than the female's pronotum width (the approximate distance from the parent at which larvae start begging; Rauter and Moore 1999). We counted the number of senior or junior larvae (L) in each brood after the observations.

For seniors and juniors separately, we calculated the average percentage time spent begging by each larva in the brood as $b = (\Sigma b/L) (100/P)$, where Σb is the total number of begging and feeding events and L and P are defined as above. This measure quantifies larval begging effort largely independently of

variation in parental behavior toward the larvae (Smiseth and Moore 2004b). We calculated the average proportional begging success of each larva in a brood for seniors and juniors separately as $s = \Sigma f/\Sigma b$, where Σb is defined above and Σf is the number of feeding events. We excluded from analysis 3 broods containing less than 4 surviving seniors or juniors, 22 broods in which either seniors or juniors did not beg, and 9 broods due to obstruction of the observer's view (i.e., the female's body blocking the observer's view of the larvae, or the female interacting with the larvae deep within the crater in the carcass), female desertion during observation, or additional eggs being laid after transfer. We analyzed data from 23 dead and 22 live parent treatment broods (mean \pm SE: L juniors = 8.13 ± 0.22 larvae, L seniors = 8.16 ± 0.24 larvae, $P = 22.09 \pm 1.40$ scans in live and 23.30 ± 1.32 scans in dead parent treatment).

Experiment 2: Is begging costly?

In this experiment, we examined whether begging is costly in terms of increasing the risk that a larva becomes a target when parents reduce the brood size after hatching through filial cannibalism (Bartlett 1987). To this end, we provided parents with an experimental brood of 60 newly hatched larvae. We then conducted observations on filial cannibalism immediately after placing the larvae on the carcass, which corresponds to the time at which brood reduction normally takes place (Bartlett 1987).

To obtain data on the effects of begging on the risk that a larva becomes the target of filial cannibalism, we generated 22 broods each comprising 60 newly hatched larvae of mixed parentage. This design was chosen to ensure that the broods were large enough to provide a sufficiently high probability of observing filial cannibalism (a rare event) and that the brood size remained within the natural range of clutch size at the time of hatching (mean \pm SE: 41.3 ± 1.9 eggs; range: 23–53 eggs; Smiseth and Moore 2002; maximum: 78 eggs; Smiseth PT, unpublished data). Females in the wild may encounter even larger clutch sizes due to brood parasitism (Müller et al. 1990). Behavioral observation began immediately once larvae were placed on the carcass, because brood reduction by filial cannibalism occurs mainly within the first 24 h of development (Bartlett 1987). We observed the female continuously for 2 sessions of 1.5 h, separated by a 1-h interval to prevent observer fatigue. When a larva was seen to be cannibalized by the female, we classified the behavior of the larva immediately before it was targeted as begging, feeding from the parent (both defined as for Experiment 1), not begging, already dead (not moving), or undetermined (due to the view being obscured). Concurrently, we used instantaneous sampling every 1 min to count the number of larvae begging and feeding from the parent, and whether the female was in close proximity to the larvae, as described for Experiment 1. We calculated the average percentage time that a larva in the brood spent begging as in Experiment 1 and the percentage of larvae that were cannibalized while begging. We discarded scans in which the observer's view was obscured. We excluded 8 broods in which more than 10% of scans were discarded. In 4 broods, no cannibalism was observed, in 1 brood only dead larvae were cannibalized (2 larvae), and in 1 brood the behavior of the single larva seen cannibalized was undetermined.

Statistical analysis

We analyzed data from Experiment 1 using repeated-measures analysis of variance (ANOVA) (senior and junior partial broods constitute repeated measures of the same brood) with time spent begging (arcsine square root transformed to achieve normality) or begging success

(untransformed) as dependent variable, larval age (senior or junior) as within-subjects factor, parental treatment (dead or live) as between-subjects factor, and their interaction. For begging success, the distribution of model residuals diverged from normality even after attempted data transformations. Thus, to confirm that our results were robust, we employed a multinomial mixed model (Faraway 2006) based on complimentary limitations accounting for dependency between correlated data on behavior. In this analysis, the status of each larva (begging, not begging, or feeding) at each scan was treated as a categorical response with feeding as the baseline status. Parental treatment, larval age, and their interaction were fitted as fixed effects for each of the 2 contrasts (i.e., begging vs. feeding and not begging vs. feeding). The effects of brood and scan (nested within brood) were fitted as random effects, with specific variances and a covariance for each contrast. We fitted multinomial models using a Bayesian Markov chain Monte Carlo approach implemented in MCMCglmm (Hadfield 2010). In Experiment 2, we compared the percentage of larvae cannibalized which were begging to that expected under the null hypothesis that parents cannibalize at random with respect to larval behavior (i.e., the mean percentage time spent begging in the brood) using a Wilcoxon signed-rank test. Statistical tests were 2 tailed with $\alpha = 0.05$. Data were analyzed using SPSS 18.0 (SPSS for Macintosh) and R (R Core Team 2013).

RESULTS

Experiment 1: Who gains more control over resource allocation?

Junior larvae spent significantly more time begging overall than seniors (repeated-measures Anova: larval age $F_{1,43} = 70.88$, $P < 0.001$). However, there was no significant difference in the amount of larval begging toward live and dead parents (repeated-measures Anova: parental treatment $F_{1,43} < 0.001$, $P = 0.99$), and there was no significant difference between seniors and juniors with respect to the extent to which they reduced the time they spent begging when presented with a dead parent as opposed to one that was alive (Figure 1a; repeated-measures Anova: larval age \times parental treatment $F_{1,43} = 2.52$, $P = 0.12$).

Both senior and junior larvae had higher begging success when presented with a live parent compared with when presented with one that was dead (Figure 1b; repeated-measures Anova, larval age \times parental treatment $F_{1,43} = 9.10$, $P = 0.004$). The relative begging success of senior compared with junior larvae depended on whether or not they were begging toward a live parent that could potentially influence resource allocation: begging success was almost twice as high for senior as for junior larvae when the parent was alive, whereas there was no difference when the parent was dead (Figure 1b). Because the residuals of this model were not normally distributed, we confirmed that this result was robust using a multinomial mixed model. This analysis confirmed that the contrast between seniors and juniors with respect to time spent gaining access to the parent's mouthparts relative to time spent begging was greater when larvae were presented with a live parent than with a dead one (credible interval does not overlap 0; posterior mode = -0.859 [95% CI = -1.569 to -0.351]).

Experiment 2: Is begging costly?

Of the 60 larvae initially present in the brood, $4.6 \pm 1.5\%$ (mean \pm SE, $N = 14$ broods) were seen to be cannibalized by the parent during a 3-h observation period. As predicted if begging increased the risk that larvae would fall victim to filial cannibalism, the proportion of the cannibalized larvae that were begging when they

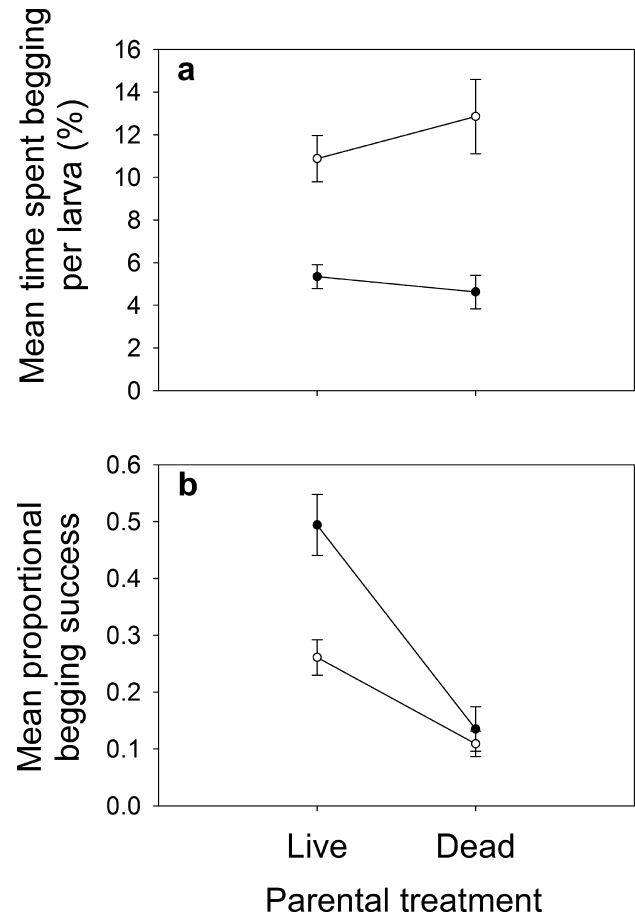


Figure 1

Begging behavior of senior (●) and junior (○) *Nicrophorus vespilloides* larvae within a brood when presented with a live or dead female parent: (a) mean (\pm SE) time spent begging (%) per larva and (b) mean (\pm SE) begging success, measured as the proportion of the total number of begging events in which larvae made mouth-to-mouth contact with the parent. Seniors were 48 h and juniors 24 h old. $N = 23$ dead and 22 live parent treatment broods.

were targeted was significantly greater than that expected from the proportion of time that the larvae spent begging (mean \pm SE percentage of live larvae that were cannibalized while begging = $52.3 \pm 12.7\%$, mean time spent begging \pm SE = $3.8 \pm 0.4\%$, Wilcoxon signed-rank test, $Z = -2.38$, $P = 0.017$, $N = 8$ broods). Thus, the risk that a begging larva fell victim to cannibalism was more than 13 times greater than expected if parents targeted larvae irrespective of their behavior.

DISCUSSION

Our study sought to distinguish between 3 alternative models for the evolution of offspring begging, and hence the role of begging as a behavioral mechanism mediating the resolution of parent-offspring conflict, by testing the contrasting underlying assumptions of these models. The main findings of our study were that 1) seniors were more successful in gaining access to the parent's mouthparts than juniors when presented with a live parent, but not when presented with a dead parent, and 2) begging increased the probability that a larva fell victim to cannibalism during brood reduction. Our findings suggest that offspring begging affords parents with an increased degree of control over resource allocation and that

begging is costly, and taken together, they provide support for the assumptions of honest signaling models for the evolution of begging and the resolution of parent–offspring conflict. Our findings contrast with previous work on canaries (the only other species for which both assumptions have been tested), which suggest that offspring appear to control within-brood allocation (Kilner 1995) and that begging incurs a growth cost (Kilner 2001), thus supporting the assumptions of scramble competition models. However, because the parents' ability to influence resource allocation was not manipulated in canaries, potential cryptic confounding effects due to parental behavior cannot be excluded in that species. Below, we discuss the implications of our findings for our understanding of intrafamilial conflict and its resolution.

The first main aim of our study was to test the assumption that parent–offspring communication affords either parents or offspring with an increased degree of control over resource allocation. In support of the assumption that offspring begging affords parents with an increased degree of control over resource allocation (as assumed by honest signaling and cost-free models), we found that there was a difference in begging success of different-aged larvae when presented with a dead or a live parent. Specifically, seniors were more successful in gaining access to the parent's mouthparts than juniors when interacting with a live parent, whereas there was no difference in the success of seniors and juniors when presented with a dead parent. This latter finding is important as it suggests that the greater begging success of seniors is not driven by direct competitive interactions among larvae but instead is mediated through an interaction with a live parent whose actions have the effect of biasing resource allocation toward seniors. An alternative explanation for this finding is that seniors were better able to detect that a parent was dead than were junior larvae. However, our results provide no evidence in support of this explanation because it would predict that seniors should reduce their begging effort toward the dead parent compared with the live parent to a greater extent than juniors. In contrast, we found no evidence of an effect of the interaction between larval age and parental treatment on the time offspring spent begging. Given that our results show that the actions of live parents somehow bias the relative begging success of senior and junior larvae, we conclude that offspring begging affords parents with an increased degree of control over resource allocation in *N. vespilloides*.

Although our finding that senior larvae had a higher begging success than juniors when presented with a live parent suggests that offspring begging provides parents with increased control over food allocation, our findings should not be taken as evidence that parents have complete control over resource allocation, nor that the allocation achieved matches the parental optimum. Indeed, the allocation of resources may be influenced by many parental and offspring traits besides offspring begging, including asynchronous hatching, asymmetric sibling competition, and offspring self-feeding. The full implications of the complexity due to multiple parental and offspring traits influencing resource allocation are yet to be tackled in theoretical and empirical work on the resolution of parent–offspring conflict, and this is therefore an important priority in future work in this field. Furthermore, because our results were conducted at a specific time window during development (i.e., when seniors were 48 h old and juniors were 24 h old), they provide no insights into how the degree of control exerted by parents and offspring varies over the course of offspring development (Royle et al. 2002). It is noteworthy that even though our findings suggest that begging affords parents increased control over within-brood resource

allocation in burying beetles, previous studies suggest that larvae have a high degree of control over the duration of the parental care period (Smiseth et al. 2003; Leigh and Smiseth 2012). Interestingly, the converse pattern appears to occur in canaries, with offspring controlling within-brood resource allocation and parents controlling the duration of the parental care period (Kilner 1995; Hinde et al. 2010). A future theoretical and empirical challenge will be to investigate potential factors driving variation in the degree to which parents or offspring control the allocation of resources.

The finding that seniors were more effective at securing food by begging to a live parent than juniors is consistent with findings of previous studies on burying beetles and many birds (Kilner 1995; Lotem 1998; Cotton et al. 1999; Smiseth et al. 2003, 2007; Smiseth and Moore 2007). For example, Smiseth et al. (2007) found that seniors grew faster than juniors in the presence of parents, whereas growth rates were similar in their absence. Our finding suggests that parents often preferentially allocate food to senior larvae, as predicted on the basis that seniors often have a higher reproductive value than juniors (Jeon 2008). There is some evidence this might be the case in *N. vespilloides* as seniors achieve a larger mass at dispersal (Smiseth et al. 2007), which in turn determines adult size and success in competition for limited resources (Müller et al. 1990; Lock et al. 2004). The finding that seniors have greater begging success than juniors appears to contradict the prediction of initial honest signaling models that parents should provision food in proportion to offspring begging effort alone (Godfray 1991). Our result suggests that parental allocation of resources is influenced by additional unmeasured attributes of the tactile begging display that are difficult to quantify, such as tactile pressure, or by other aspects of larvae, such as their body size. Later versions of honest signaling models have allowed for noncryptic differences between offspring, such as position in the size hierarchy, that can be perceived directly by the parent in addition to cryptic differences between offspring with respect to their needs (Godfray 1995). Such models predict that parents should favor senior offspring if the function describing how the amount of resources that offspring obtain translates into their fitness is less steep for seniors than for juniors (Godfray 1995). Currently, there is no information on the shape of this function for burying beetles or any other species, and it is therefore unclear whether this model accounts for why seniors are more successful at begging than juniors.

The second main aim of our study was to investigate the contrasting assumptions concerning whether begging is costly or cost-free. In support of the assumption that begging is costly (as assumed by honest signaling and scramble competition models), we found that begging increased the probability that a larva would fall victim to cannibalism during brood reduction. This finding demonstrates that begging incurs a significant fitness cost to offspring, which is induced by the parents' response to begging in terms of filial cannibalism. Our finding that begging offspring incurred a higher risk of mortality due to becoming a target of filial cannibalism provides evidence for a previously unconsidered form of signaling cost that is induced by the parent's response to begging. It is noteworthy that the observed rate of filial cannibalism in our experiment is similar to that reported in a previous laboratory study on burying beetles (Bartlett 1987), although it is unclear how these estimates compare with filial cannibalism in the wild where there may be predation of eggs or larvae. The parent-induced cost that we have documented is distinct and independent of the parent's feeding response to begging, as the latter determines the benefit of begging to offspring. Furthermore,

the parent-induced cost differs from the energetic, predation, or opportunity costs of begging reported in previous studies on birds (Kilner 2001; Rodríguez-Gironés et al. 2001; Chappell and Bachman 2002; Haskell 2002) in the sense that the parent-induced cost is not inherent in the production or expression of the signal itself but is instead imposed by the parent through its response to the signal. Existing honest signaling models do not specifically mention parent-induced costs, but we see no logical reason why a parent-induced cost cannot act to stabilize the honesty of begging in a similar manner as energetic and predation costs. The reason for this is that the fundamental assumption on which honest signaling models rest is that an increase in the level of begging by an individual offspring incurs a significant fitness cost to that individual, an assumption which is clearly met for a parent-induced cost of begging.

Parental aggression and infanticide are well documented in some birds and mammals in which offspring beg for food from their parents (Horsfall 1984; Leonard et al. 1988, 1991; Clutton-Brock and Parker 1995; Lummaa et al. 1998; Kilner and Drummond 2007; Raihani and Ridley 2008; Moreno 2012), suggesting that similar parent-induced costs of begging could also be important in these species. However, at the present time, there is no evidence from studies on other species that begging increases an offspring's risk of becoming a target of parental aggression and/or infanticide. For example, in Eurasian coots, where parents frequently touse chicks during the parental care period, only 5% of observed instances of tousing occurred immediately after the victim had begged for food (8.5% if "pestering" also be considered a begging display), whereas 44% occurred immediately after the parent had fed the victim (Horsfall 1984). Thus, in this species, begging might be associated with a decrease in the risk of becoming a target of parental aggression. Furthermore, in black-capped chickadees, fledglings are more likely to be attacked (or chased) when they are following a parent (Leonard et al. 1991), but it is unclear whether parental aggression qualifies as a parent-induced cost of begging as the study did not compare parental aggression when fledglings were begging or not. In humans, evidence suggests that parental aggression may be triggered in response to the elevated levels of "abnormal" crying by sick infants (Soltis 2004). On the other hand, there is evidence that crying may reduce the likelihood of infanticide by signaling good condition or that aggressive parental responses to crying may reflect nonadaptive outcomes of evolutionarily novel modern childcare practices (Lummaa et al. 1998). In summary, evidence from humans argues against a parent-induced cost of begging (crying), whereas evidence from studies on birds is inconclusive due to the lack of a formal test of such a cost. A formal test would require data that would allow us to compare the risk of parental aggression associated with begging against the null expectation if parental aggression is randomly directed with respect to the offspring's behavior. Thus, we believe that our study provides the first demonstration of a parent-induced cost of begging and its fitness consequences.

Evidence of a parent-induced cost of begging has important implications for our understanding of the evolutionary origins of costly and honest begging signals. A key criticism of honest signaling models is that the ancestral nonsignaling state may be evolutionarily stable against costly begging, such that the latter cannot invade due to the costs of signaling (Rodríguez-Gironés et al. 1996). Thus, it has been argued that costly begging could evolve from a nonsignaling origin only if it originated as a form of direct sibling competition (under offspring control of resource

allocation, Rodríguez-Gironés et al. 1996). Our results suggest an alternative scenario in which the evolutionary origin of cost-free begging (under parental control of resource allocation) is followed by the acquisition of a parent-induced cost. The parent-induced costs might originate as a by-product of selection on parents to use begging as a cue about the brood size when they reduce the brood size through filial cannibalism to match it to the amount of resources available for breeding. According to this scenario, begging costs are established secondarily to the origin of begging, leading to a transition from cost-free begging to begging as an honest signal.

FUNDING

This work was supported by a grant from the Natural Environment Research Council (NE/G004293/1 to P.T.S.).

The authors thank J.D. Hadfield for statistical assistance, N. Colgrave, C.A. Hinde, M. Kölliker, D.W. Mock, J. Wright, and 6 anonymous reviewers for helpful comments that improved the manuscript, and A.J. Moore for supplying beetles. The data reported in the paper may be requested from the corresponding author.

Handling editor: Shinichi Nakagawa

REFERENCES

- Bartlett J. 1987. Filial cannibalism in burying beetles. *Behav Ecol Sociobiol.* 21:179–183.
- Bergstrom C.T, Lachmann M. 1998. Signaling among relatives. III. Talk is cheap. *Proc Natl Acad Sci USA.* 95:5100–5105.
- Boncoraglio G, Caprioli M, Saino N. 2012. Solicitation displays reliably reflect oxidative damage in barn swallow nestlings. *Behav Ecol Sociobiol.* 66:539–546.
- Chappell M, Bachman G. 2002. Energetic costs of begging behaviour. In: Wright J, Leonard ML, editors. *The evolution of begging: competition, cooperation and communication.* Dordrecht: Kluwer Academic Publishers. p. 143–162.
- Clutton-Brock TH, Parker GA. 1995. Punishment in animal societies. *Nature.* 373:209–216.
- Cotton PA, Wright J, Kacelnik A. 1999. Chick begging strategies in relation to brood hierarchies and hatching asynchrony. *Am Nat.* 153:412–420.
- Eggert A-K, Müller JK. 1997. Biparental care and social evolution in burying beetles: lessons from the larder. In: Choe JE, Crespi BJ, editors. *The evolution of social behavior in insects and arachnids.* Cambridge: Cambridge University Press. p. 216–236.
- Eggert A-K, Reinking M, Müller JK. 1998. Parental care improves offspring survival and growth in burying beetles. *Anim Behav.* 55:97–107.
- Faraway J. 2006. *Extending the linear model with R: generalized linear, mixed effects and nonparametric regression models.* Boca Raton (FL): CRC Taylor and Francis Group.
- Godfray HCJ. 1991. Signalling of need by offspring to their parents. *Nature.* 352:328–330.
- Godfray HCJ. 1995. Signaling of need between parents and young: parent-offspring conflict and sibling rivalry. *Am Nat.* 146:1–24.
- Hadfield JD. 2010. MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. *J Stat Softw.* 33:1–22.
- Haskell DG. 2002. Begging behaviour and nest predation. In: Wright J, Leonard ML, editors. *The evolution of begging: competition, cooperation and communication.* Dordrecht: Kluwer Academic Publishers. p. 163–172.
- Hinde CA, Johnstone RA, Kilner RM. 2010. Parent-offspring conflict and coadaptation. *Science.* 327:1373–1376.
- Horsfall JA. 1984. Brood reduction and brood division in coots. *Anim Behav.* 32:216–225.
- Jeon J. 2008. Evolution of parental favoritism among different-aged offspring. *Behav Ecol.* 19:344–352.
- Johnstone RA. 1996. Begging signals and parent offspring conflict: do parents always win? *Am Nat.* 263:1677–1681.

- Kilner R. 1995. When do canary parents respond to nestling signals of need? *Proc R Soc Lond B*. 260:343–348.
- Kilner R, Johnstone RA. 1997. Begging the question: are offspring solicitation behaviours signals of need? *Trends Ecol Evol*. 12:11–15.
- Kilner RM. 2001. A growth cost of begging in captive canary chicks. *Proc Natl Acad Sci USA*. 98:11394–11398.
- Kilner RM, Drummond H. 2007. Parent–offspring conflict in avian families. *J Ornithol*. 148:241–246.
- Leigh D, Smiseth PT. 2012. Parent-offspring conflict over the transition to independence in *Nicrophorus vespilloides*: parental chemical cues and offspring begging. *Ethology*. 118:460–465.
- Leonard ML, Horn AG, Eden SF. 1988. Parent-offspring aggression in moorhens. *Behav Ecol Sociobiol*. 23:265–270.
- Leonard ML, Horn AG, Ratcliffe LM. 1991. Parental aggression in black-capped chickadees. *Behav Ecol*. 2:228–233.
- Lock JE, Smiseth PT, Moore AJ. 2004. Selection, inheritance, and the evolution of parent-offspring interactions. *Am Nat*. 164:13–24.
- Lotem A. 1998. Differences in begging behaviour between barn swallow, *Hirundo rustica*, nestlings. *Anim Behav*. 55:809–818.
- Lummaa V, Vuorisalo T, Barr RG, Lehtonen L. 1998. Why cry? Adaptive significance of intensive crying in human infants. *Evol Human Behav*. 19:193–202.
- Macnair MR, Parker GA. 1979. Models of parent-offspring conflict. III. Intra-brood conflict. *Anim Behav*. 27:1202–1209.
- Maynard Smith J. 1991. Honest signalling: the Philip Sidney game. *Anim Behav*. 42:1034–1035.
- Maynard Smith J. 1994. Must reliable signals always be costly? *Anim Behav*. 47:1115–1120.
- Mock DW, Dugas MB, Strickler SA. 2011. Honest begging: expanding from Signal of Need. *Behav Ecol*. 22:909–917.
- Moreno J. 2012. Parental infanticide in birds through early eviction from the nest: rare or under-reported? *J Avian Biol*. 43:43–49.
- Müller JK, Eggert A-K. 1990. Time-dependent shifts between infanticidal and parental behavior in female burying beetles: a mechanism of indirect mother-offspring recognition. *Behav Ecol Sociobiol*. 27:11–16.
- Müller J, Eggert A-K, Dressel J. 1990. Intraspecific brood parasitism in the burying beetle, *Nicrophorus vespilloides* (Coleoptera: Silphidae). *Anim Behav*. 40:491–499.
- Noguera JC, Morales J, Perez C, Velando A. 2010. On the oxidative cost of begging: antioxidants enhance vocalizations in gull chicks. *Behav Ecol*. 21:479–484.
- Parker GA, Royle NJ, Hartley IR. 2002. Begging scrambles with unequal chicks: interactions between need and competitive ability. *Ecol Lett*. 5:206–215.
- R Core Team. 2013. R: a language and environment for statistical computing [Internet]. Vienna (Austria): R Foundation for Statistical Computing. Available from: <http://www.R-project.org>.
- Raihani NJ, Ridley AR. 2008. Parental aggression against dependent young results in task partitioning in a cooperatively breeding bird. *Biol Lett*. 4:23–26.
- Rauter CM, Moore AJ. 1999. Do honest signalling models of offspring solicitation apply to insects? *Proc R Soc Lond B*. 266:1691–1696.
- Rodríguez-Gironés MA, Cotton PA, Kacelnik A. 1996. The evolution of begging: signaling and sibling competition. *Proc Natl Acad Sci USA*. 93:14637–14641.
- Rodríguez-Gironés MA, Zúñiga JM, Redondo T. 2001. Effects of begging on growth rates of nestling chicks. *Behav Ecol*. 12:269–274.
- Royle NJ, Hartley IR, Parker GA. 2002. Begging for control: when are offspring solicitation behaviours honest? *Trends Ecol Evol*. 17:434–440.
- Smiseth PT, Andrews C, Brown E, Prentice PM. 2010. Chemical stimuli from parents trigger larval begging in burying beetles. *Behav Ecol*. 21:526–531.
- Smiseth PT, Bu RJ, Eikenæs AK, Amundsen T. 2003. Food limitation in asynchronous bluethroat broods: effects on food distribution, nestling begging, and parental provisioning rules. *Behav Ecol*. 14:793–801.
- Smiseth PT, Darwell CT, Moore AJ. 2003. Partial begging: an empirical model for the early evolution of offspring signalling. *Proc R Soc Lond B*. 270:1773–1777.
- Smiseth PT, Dawson C, Varley E, Moore AJ. 2005. How do caring parents respond to mate loss? Differential response by males and females. *Anim Behav*. 69:551–559.
- Smiseth PT, Moore AJ. 2002. Does resource availability affect offspring begging and parental provisioning in a partially begging species? *Anim Behav*. 63:577–585.
- Smiseth PT, Moore AJ. 2004a. Signalling of hunger when offspring forage by both begging and self-feeding. *Anim Behav*. 67:1083–1088.
- Smiseth PT, Moore AJ. 2004b. Behavioral dynamics between caring males and females in a beetle with facultative biparental care. *Behav Ecol*. 15:621–628.
- Smiseth PT, Moore AJ. 2007. Signalling of hunger by senior and junior larvae in asynchronous broods of a burying beetle. *Anim Behav*. 74:699–705.
- Smiseth PT, Parker HJ. 2008. Is there a cost to larval begging in the burying beetle *Nicrophorus vespilloides*? *Behav Ecol*. 19:1111–1115.
- Smiseth PT, Ward RJS, Moore AJ. 2006. Asynchronous hatching in *Nicrophorus vespilloides*, an insect in which parents provide food for their offspring. *Funct Ecol*. 20:151–156.
- Smiseth PT, Ward RJS, Moore AJ. 2007. Parents influence asymmetric sibling competition: experimental evidence with partially dependent young. *Ecology*. 88:3174–3182.
- Soltis J. 2004. The signal functions of early infant crying. *Behav Brain Sci*. 27:443–458.
- Trivers RL. 1974. Parent-offspring conflict. *Am Zool*. 14:249–264.