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1 Biparental negotiation or larval begging? Determinant of male provisioning in a
2 burying beetle (*Nicrophorus quadripunctatus*)

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10 Summary

11 In species showing biparental care, parents often adjust their level of care facultatively.
12 Partners can potentially monitor each other directly (modify their effort sequentially in
13 direct response to the prior effort of their mate) or indirectly (parents modify their effort
14 through the begging rates of their offspring). This study examined whether partner
15 negotiation or begging by larvae best explains male provisioning in *Nicrophorus*
16 *quadripunctatus*. The frequency of males approaching larvae to feed did not increase
17 with either female removal or female handicapping. However, larval begging toward
18 males increased with female removal, but not with female handicapping. This suggests
19 that larvae are not affected by the change of female investment in care but larvae
20 reacted to the absence of a female parent. Although larvae begged more towards the
21 male when the female was removed, my findings show that males did not respond by
22 increasing their care, which suggests that males are insensitive to variation in their
23 partner's state or offspring behavior in *N. quadripunctatus*,
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26 Keywords: parental investment, game theory, handicapping, mate removal
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Introduction

The main benefit of biparental care is an increase in the number of offspring that can be reared (Clutton-Brock, 1991). In systems with biparental care, an individual's optimal parental investment will depend, in part, on the amount of investment provided by the cooperating partner (Trivers, 1972).

In species showing biparental care, parents have been found to adjust their level of care facultatively (Westneat & Sargent, 1996). Game theory has been the main theoretical tool for investigating the evolutionary stability of biparental care (Houston & McNamara, 1999). In the "negotiation model", parents modify their effort sequentially in direct response to the prior effort of their mate. The negotiation model predicts that parents should partially compensate for a reduction in their mate's effort (Houston & McNamara, 1999). There have been many studies of biparental systems to investigate behavioral dynamics between the sexes (Harrison et al., 2009; Hinde & Kilner, 2007; Johnstone & Hinde, 2006; Schwagmeyer et al., 2008, Wright & Cuthill, 1989), and the negotiation model makes clear predictions about facultative adjustments between caring parents and has been tested empirically. The negotiation model assumes the response of one parent will occur as an immediate reaction to changes in the other parent's effort and that total investment is determined by the negotiation.

In addition, offspring begging for food from their parents has received considerable theoretical and empirical interest as a model of animal communication between signalers and receivers with conflicting interests (Kilner & Johnstone, 1997; Royle et al., 2002). When parents take care of their offspring after hatching, the offspring have the potential to influence the duration and amount of costly care (Kilner & Johnstone 1997; Royle et al., 2002). Several game strategy models have been developed to explain parent-offspring interactions, especially the behavior of begging for food (Godfray, 1995; Parker et al., 2002).

While the amount of care may be influenced both by negotiation between parents and by begging of young, previous studies have not considered the case of both effects simultaneously (Hinde & Kilner, 2007; Kölliker et al., 1998). Determining the relative importance of these two effects will help understand the resolution of intrafamilial conflict of biparental care.

Biparental care is found in diverse insects (Tallamy, 1994; Suzuki, 2013). Burying beetles (*Nicrophorus* spp.) present an excellent model for examining intrafamilial conflict between male and female parents (Suzuki & Nisimura, 2014). The complex biparental care of burying beetles is well known (reviewed in Eggert & Müller, 1997; Scott, 1998). *Nicrophorus* exploit small vertebrate carrion as food for their young.

Typically, a male-female pair prepares a carcass by burying it, removing hair, and rounding it into a ball. Eggs are laid in the soil adjacent to the carrion ball. After hatching, larvae crawl to the carrion ball where they are fed by parental regurgitations.

The adjustment of provisioning when a mate is removed has been studied in several species of *Nicrophorus* (Fetherston et al., 1994; Pilakouta et al., 2015; Rauter & Moore, 2004; Smiseth & Moore 2004; Smiseth et al., 2006; Suzuki & Nagano, 2009). Female burying beetles will sometimes adjust provisioning in response to mate removal (Fetherston et al., 1994) but sometimes do not (Rauter & Moore, 2004; Smiseth et al., 2005). More recently, handicapping by the attachment of lead weights to one parent has been used to study negotiation (Suzuki & Nagano, 2009; Creighton et al., 2015; Suzuki, 2016; Ratz & Smiseth, 2018). Other studies have examined the effect of larval begging on parental provisioning. In burying beetles, larvae beg for food by raising their heads while waving their legs or touching the parent (Rauter & Moore, 1999; Smiseth & Moore, 2004). The parents respond to these signals of hunger (Smiseth & Moore, 2004, Smiseth et al., 2007) by adjusting the allocation of food (Smiseth & Moore, 2002, 2008). The use of a dead parent as a stimulus to trigger offspring begging has suggested that the cue for begging is chemical (Smiseth & Parker, 2008; Smiseth et al., 2010; Takata et al., 2019 but see Suzuki, 2015). If males respond according to the negotiation model, then males would increase feeding when females decreased feeding, irrespective of larval begging because males tend to be more responsive to their partner's contribution to care than females (Royle et al., 2014). If males respond to a change in begging, then males would increase feeding when larval begging increased, irrespective of mate behavior. The aim of this study is to examine whether differences in male provisioning in *Nicrophorus quadripunctatus* can be better explained by their mate's level of provisioning (negotiation) or by the level of larval begging.

Materials and methods

I trapped *N. quadripunctatus* in the field by baiting with rotten meat. Similar-sized *N. quadripunctatus* beetles (pronotal width 4.5–5.0 mm) were selected for experiments. A pair of *N. quadripunctatus* and 15 g of chicken meat were introduced into a polyethylene container (15 × 15 × 9 cm) that was half-filled with soil. All containers were kept at 20 °C in constant darkness.

Containers were checked daily. Approximately 24–36 h after hatched larvae reached the carcass, the carcass was exposed by removing soil from above. Each trial was randomly assigned to a treatment and parental behavior was recorded 1–2 h after each treatment.

Handicapped treatment (N=12): I experimentally handicapped a female by attaching a small metal weight (about 0.2g) with aronalpha® to their pronotum. This weight is about 40% of the wet weight of *N. quadripunctatus* for the size range used in this experiment. The details of the handicapping method are shown in Suzuki & Nagano (2009). If the weight became detached from the beetle before the observation period was finished, the trial was excluded from the analysis (only successful trial was shown as sample size) .

Removal treatment (N=12): The female parent was removed.

Control treatment (N=12): Neither parent was removed or handicapped

All observations were recorded using a video camera (Sony Handicam HDR-CX680) under dim light. Video recording was focused 2-4 diameter around the brood to observe larval behavior. To minimize the effect of brood size, larvae of different stage (large and small) were removed to leave 10 medium-sized larvae per container.

I recorded parental behavior 30 min and recorded the following:

1) Number of times that parents approached the young to feed (approach to feeding). When a parent walked near to larvae and made mouth-to-mouth contact to a larva, the behavior was scored. The score was recorded as "one" even if multiple larvae were fed or were fed for long time.

2) Feeding frequency was recorded whether father feed young or not using instantaneous sampling every 30 second for 30 min. The score was recorded as "two" if parents continued to feed young for 30s.

3) Number of larvae showing begging behavior when parents approached and made mouth-to-mouth contact to a larva (number of begging larvae).

“Approach to feeding” was used to indicate motivation to feed because this behavior is an essential component of provisioning, and “number of begging larvae” was used to indicate larval behavior.

“Approach to feeding” and "Feeding frequency" were assessed using the Steel–Dwass test, which is a non-parametric pairwise multiple comparison test ($p < 0.05$) because of its robustness even if it is not ordered to normal distribution. The statistical analyses of “number of begging larvae” to males were conducted by GLM using REML analyses with each broods as a random factor. When there were significant differences among treatments ($p < 0.05$), paired comparisons were conducted using Holm's method. All analysis was performed in JMP version 9.0 (SAS Institute Inc., Cary, NC, USA).

Results

The number of times that fathers approached young to feed did not differ among treatments ($q=2.72$, $P>0.05$, Fig. 1). The number of times female parents to feed young were reduced when females were handicapped ($q=1.96$, $P<0.05$). Total activity of male behavior (feeding and other behavior) on the upper side of carcass were not also different among treatment but feeding frequency was different in removal treatment ($q=2.34$, $P<0.05$, Fig 2).

The number of larvae showing begging behavior also did not change when females were handicapped but changed when females were removed ($F_{2,33}=48.3$, $P<0.001$, Fig. 3). Although handicapped females approached to feed the young less frequently than control females, larvae still begged more from females than males. Only when females were removed did begging toward males increase.

Discussion

The aim of this study was to examine the effect of female parental effort and larval begging on male parental behavior. The use of handicapping demonstrated that although female provisioning did decrease, larval begging toward males did not increase. This findings indicate that, although handicapped females effectively reduced their provisioning to the young, males did not alter their provisioning to the young in response to female handicapping. In contrast, although "approach to feed" by father did not change among treatments but feeding frequency increased in female removal. This suggests that not male feeding times but the duration of feeding was increased, then once feeding by fathers began feeding to young took longer time but the frequency that fathers tried to feed was not increased in mate removal.

The negotiation model predicts that parental effort of the male parent should increase when the female decreases feeding (Houston & McNamara, 1999). This idea assumes that a parent indirectly assessed its partner's parental ability by monitoring its partner's workload. The present study did not find support for this prediction because male beetles did not adjust their parental behavior by the change of female workloads. In addition, larval begging toward males was not increased by female handicapping but was by female removal. Smiseth & Moore (2004), using path analysis, found that males directly respond to changes in female effort in *N. vespilloides*. Suzuki & Nagano (2009) concluded that *N. quadripunctatus* parents were sensitive to their partner's presence but not their level of effort because compensation was observed following mate removal but not following handicapping. However, Suzuki (2016) found that provisioning times of males increased when a handicap was attached before larvae hatched but not after, suggesting that adjustments in the male care in *N.*

173 *quadripunctatus* involve a time lag for several days to adjust. At least, we can say that
174 both male parents and larva did not react to the workload of the current provisioning by
175 female parents in handicapped conditions.

176 Previous studies of burying beetles suggested that offspring prefer the parent
177 from which they would obtain the greatest returns on begging (Suzuki 2015; Paquet et
178 al., 2017). Not only growth cost of larval begging has previously been detected (Takata
179 et al., 2019), but also begging did affect the probability that a larva would fall victim to
180 cannibalism by its mother during brood reduction (Andrews & Smiseth, 2013). It is
181 expected that begging to a parent that is not motivated towards food provision entails a
182 large cost for larva. In *Nicrophorus*, larvae usually spent more time begging towards
183 females than towards males regardless of their level of hunger (Suzuki, 2015; Paquet et
184 al., 2017). Previous work suggests that larval begging in *N. vespilloides* is triggered by
185 parental CHC profiles and that these differ between breeding and nonbreeding adults
186 (Smiseth et al., 2010). It was still unclear whether this key to begging can explain the
187 larval preference for the mother (Suzuki, 2015; Paquet et al., 2017), however, larvae
188 prefer to beg to the mother in usual conditions.

189 It has been reported that parental care improves larval fitness (brood size,
190 survival, and growth rate) in *Nicrophorus* spp. (Eggert et al., 1998). However, many
191 studies have shown that a second parent provides no additional benefit (Trumbo &
192 Fernandez, 1995; Sakaluk et al., 1998; Smiseth et al., 2005; Trumbo, 2006) and
193 Pilakouta et al (2018) showed that biparental care in *N. vespilloides* improved the larval
194 mass but males provided less care when working with a partner. Why males provide
195 care to their young in burying beetles is still unknown. Suzuki (2013) hypothesized that
196 a primary benefit of male attendance during care is preventing extra-pair copulations to
197 increase his confidence in paternity. Intersexual conflict plays an important role in
198 determining the level of parental care during carcass preparation (Creighton et al.,
199 2014) because male behavior during this phase improves his mating success. As larval
200 provisioning will not improve the confidence of paternity, there appears to be a limited
201 selection for males to provision unless the female parent is absent (Eggert et al., 1998;
202 Rauter & Moore, 2004; Smiseth & Moore, 2004). Plasticity in caregiving (Royle et al.,
203 2014) has been found for both maternal feeding and offspring begging in *N. vespilloides*
204 (Lock et al., 2004). Because females provide far more care than males, it is said that
205 reduced male-offspring contact might limit the potential for coadaptation between
206 fathers and their offspring (Head et al., 2014).

207 The negotiation model assumes that parents can monitor the efforts of their
208 partner and adjust their level of care accordingly. Partners can potentially monitor each

other directly or indirectly through the begging rates of their offspring (Hinde & Kilner, 2007; Creighton et al., 2014). Direct monitoring of partner care has been proposed in some bird species (Johnstone & Hinde, 2006; Hinde & Kilner, 2007; Schwagmeyer, et al., 2008), while indirect monitoring through behavior of young has been observed in fewer cases (Wright & Cuthill, 1989). In this study, approach to feeding of males changed neither with female removal nor female handicapped. In contrast, larvae changed their begging to fathers when their mother was removed but not when the mother was handicapped. The present study suggested that neither males nor larvae reacted to the decrease of female provisioning but only reacted to female removal. Though it needs further investigation, this study suggests the possibility that indirect monitoring through larval begging determines the level of male provisioning.

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Fig.1

The difference among treatments (female handicapped, female removed, and control) on the number of times that parents approached young to feed in 30 min. Data are presented as mean + SE. The same letter above the bars indicates that the responses are not significantly different (Steel–Dwass test, $p > 0.05$).

Fig.2

The difference among treatments (female handicapped, female removed, and control) on time spent by male parent. White bars showed total behavior spent near young (feeding and other behaviors), hatched bars showed feeding behavior. Data are presented as mean+SE. The same letters above the bars on each graph indicate that they are not significantly different (Steel–Dwass test, $p > 0.05$).

Fig3

The number of larvae showing begging behavior when parents approached at the different treatments (female handicapped, female removed, and control). Data are presented as mean + SE. The same letters above the bars on each graph indicate that the responses are not significantly different (GLM using REML analyses, Holm's method, $p > 0.05$).