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

3  
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9  
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*,

24  
25  
26 Keywords: parental investment, game theory, handicapping, mate removal

29 **Introduction**

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

34 In species showing biparental care, parents have been found to adjust their  
35 level of care facultatively (Westneat & Sargent, 1996). Game theory has been the main  
36 theoretical tool for investigating the evolutionary stability of biparental care (Houston  
37 & McNamara, 1999). In the "negotiation model", parents modify their effort  
38 sequentially in direct response to the prior effort of their mate. The negotiation model  
39 predicts that parents should partially compensate for a reduction in their mate's effort  
40 (Houston & McNamara, 1999). There have been many studies of biparental systems to  
41 investigate behavioral dynamics between the sexes (Harrison et al., 2009; Hinde &  
42 Kilner, 2007; Johnstone & Hinde, 2006; Schwagmeyer et al., 2008, Wright & Cuthill,  
43 1989), and the negotiation model makes clear predictions about facultative adjustments  
44 between caring parents and has been tested empirically. The negotiation model assumes  
45 the response of one parent will occur as an immediate reaction to changes in the other  
46 parent's effort and that total investment is determined by the negotiation.

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

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

60 Biparental care is found in diverse insects (Tallamy, 1994; Suzuki, 2013).  
61 Burying beetles (*Nicrophorus* spp.) present an excellent model for examining  
62 intrafamilial conflict between male and female parents (Suzuki & Nisimura, 2014). The  
63 complex biparental care of burying beetles is well known (reviewed in Eggert & Müller,  
64 1997; Scott, 1998). *Nicrophorus* exploit small vertebrate carrion as food for their young.

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

68 The adjustment of provisioning when a mate is removed has been studied in  
69 several species of *Nicrophorus* (Fetherston et al., 1994; Pilakouta et al., 2015; Rauter &  
70 Moore, 2004; Smiseth & Moore 2004; Smiseth et al., 2006; Suzuki & Nagano, 2009).  
71 Female burying beetles will sometimes adjust provisioning in response to mate removal  
72 (Fetherston et al., 1994) but sometimes do not (Rauter & Moore, 2004; Smiseth et al.,  
73 2005). More recently, handicapping by the attachment of lead weights to one parent has  
74 been used to study negotiation (Suzuki & Nagano, 2009; Creighton et al., 2015; Suzuki,  
75 2016; Ratz & Smiseth, 2018). Other studies have examined the effect of larval begging  
76 on parental provisioning. In burying beetles, larvae beg for food by raising their heads  
77 while waving their legs or touching the parent (Rauter & Moore, 1999; Smiseth &  
78 Moore, 2004). The parents respond to these signals of hunger (Smiseth & Moore, 2004,  
79 Smiseth et al., 2007) by adjusting the allocation of food (Smiseth & Moore, 2002, 2008).  
80 The use of a dead parent as a stimulus to trigger offspring begging has suggested that  
81 the cue for begging is chemical (Smiseth & Parker, 2008; Smiseth et al., 2010; Takata et  
82 al., 2019 but see Suzuki, 2015). If males respond according to the negotiation model,  
83 then males would increase feeding when females decreased feeding, irrespective of  
84 larval begging because males tend to be more responsive to their partner's contribution  
85 to care than females (Royle et al., 2014). If males respond to a change in begging, then  
86 males would increase feeding when larval begging increased, irrespective of mate  
87 behavior. The aim of this study is to examine whether differences in male provisioning  
88 in *Nicrophorus quadripunctatus* can be better explained by their mate's level of  
89 provisioning (negotiation) or by the level of larval begging.

90

## 91 **Materials and methods**

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

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

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

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

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

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

114 I recorded parental behavior 30 min and recorded the following:

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

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

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

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

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

## 135 136 **Results**

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

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

## 148 149 **Discussion**

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

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

209 other directly or indirectly through the begging rates of their offspring (Hinde & Kilner,  
210 2007; Creighton et al., 2014). Direct monitoring of partner care has been proposed in  
211 some bird species (Johnstone & Hinde, 2006; Hinde & Kilner, 2007; Schwagmeyer, et al.,  
212 2008), while indirect monitoring through behavior of young has been observed in fewer  
213 cases (Wright & Cuthill, 1989). In this study, approach to feeding of males changed  
214 neither with female removal nor female handicapped. In contrast, larvae changed their  
215 begging to fathers when their mother was removed but not when the mother was  
216 handicapped. The present study suggested that neither males nor larvae reacted to the  
217 decrease of female provisioning but only reacted to female removal. Though it needs  
218 further investigation, this study suggests the possibility that indirect monitoring  
219 through larval begging determines the level of male provisioning.

220

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225

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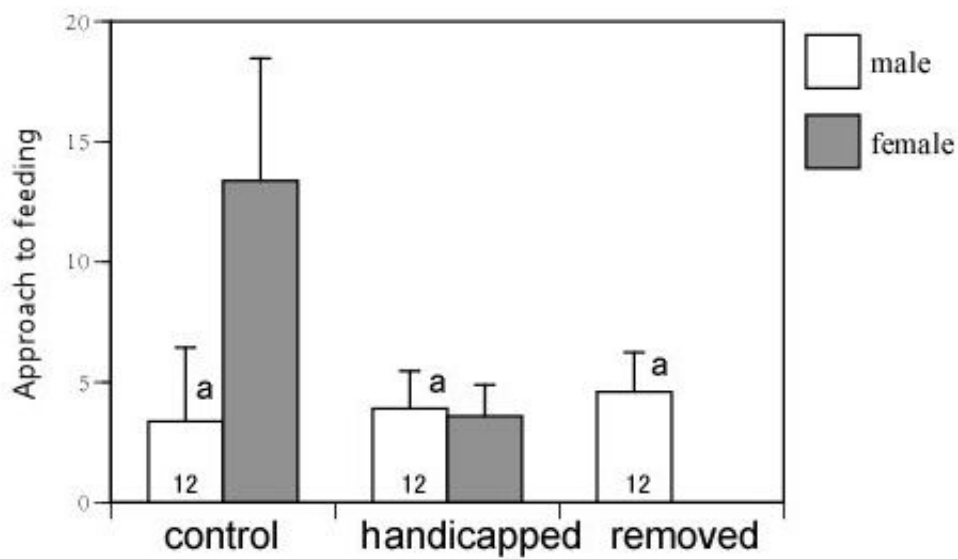
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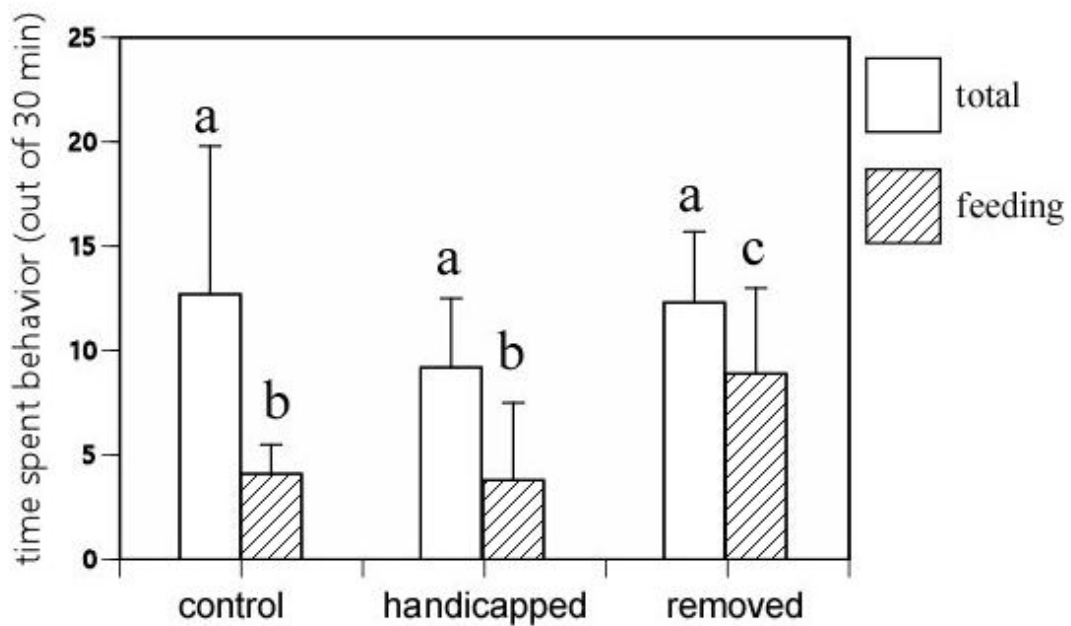
346

347 Fig.1

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

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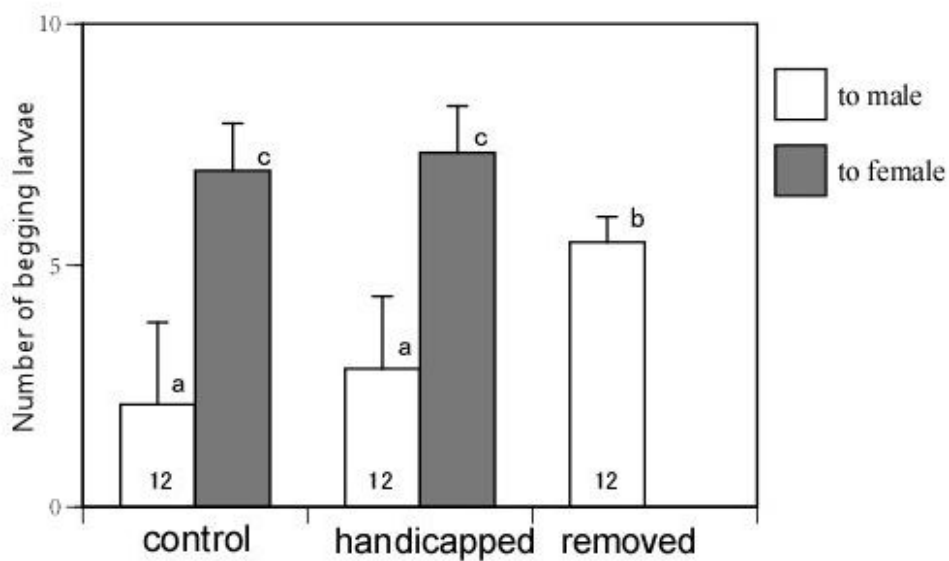
354

355 Fig.2

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

361

362



363

364 Fig3

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