1    **Article title**

2    Control of parental investment changes plastically over time with residual reproductive value

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15    Running title

16    Plastic changes in control

17

18   **Abstract**

19   Evolutionary conflict between parents and offspring over parental resource investment is a significant

20   selective force on the traits of both parents and offspring. Empirical studies have shown that for some

21   species, the amount of parental investment is controlled by the parents, whereas in other species, it is

22   controlled by the offspring. The main difference between these two strategies is the residual reproductive

23   value of the parents or opportunities for future reproduction. Therefore, this could explain the patterns of

24   control of parental investment at the species level. However, the residual reproductive value of the parents

25   will change during their lifetime; therefore, parental influence on the amount of investment can be expected

26   to change plastically. Here, we investigated control of parental investment when parents were young and

27   had a high residual reproductive value, compared to when they were old and had a low residual

28   reproductive value using a cross-fostering experiment in the burying beetle *Nicrophorus quadripunctatus*.

29   We found that parents exert greater control over parental investment when they are young, but parental

30   control is weakened as the parents age. Our results demonstrate that control of parental investment is not

31   fixed, but changes plastically during the parent's lifetime.

32

33   **Keywords**: burying beetle, *Nicrophorus*, parent–offspring conflict, phenotypic plasticity

34

35 **Introduction**

36 The theory of parent–offspring conflict over parental investment is well studied (reviewed by Godfray,

37 1995; Godfray & Johnstone, 2000) and is a significant selective force on parent and offspring traits

38 (reviewed by Kilner & Hinde 2008). In a sexually reproducing species, relatedness between parent and

39 offspring is < 1, so the genes of the offspring benefit from parental investment more than those of the

40 parents (Lazarus & Inglis, 1986). This results in evolutionary conflict, in which the optimal level of

41 parental investment for offspring is higher than that of the parents (Trivers, 1974; Godfray & Johnstone,

42 2000; Bossan *et al.*, 2013).

43      Parent–offspring conflict causes a co-evolutionary arms race between the traits of the parents and

44 their offspring (Lyon *et al.*, 1994; Kilner & Hinde, 2012). For example, it is beneficial for offspring to

45 perform begging behaviour in surplus to obtain high levels of parental investment, whereas parents must

46 change their responsiveness to the begging of their offspring to optimally allocate the investment across the

47 brood (Parker & Macnair, 1979; Hussell, 1988; Kölliker, 2003). Quantitative genetic models predict that

48 when parents control the amount of investment, selection acts on traits in the offspring and there is a

49 positive correlation between the amount of parental resource provisioning and offspring begging intensity.

50 When the offspring control the amount of investment, traits in the parents are under selection and there is a

51 negative correlation between the amount of parental resource provisioning and offspring begging intensity

52 (Kölliker *et al.*, 2005). Empirical studies have shown that for some species, there is a positive correlation

53 between the amount of parental provisioning and offspring begging intensity, suggesting that the amount of

54 parental resource provisioning is controlled by the parents (Kölliker *et al.*, 2000; Hager & Johnstone, 2003;

55 Curley *et al.*, 2004; Lock *et al.*, 2004; Mas *et al.*, 2009; Hinde *et al.*, 2010), whereas in other species, there

56 is a negative correlation, suggesting that it is controlled by the offspring (Agrawal *et al.*, 2001; Kölliker *et*

57 *al.*, 2005).

58      Residual reproductive value may be the ecological factor influencing whether the parent or offspring

59 control parental investment. When residual reproductive value is high, parents have more to lose by being

60 exploited by their young, because the difference in the optimal level of parental investment between parent

61 and offspring is greater. Therefore, higher residual reproductive value may cause stronger selective

62 pressure for parental control of investment. On the other hand, when residual reproductive value is near to

63 zero, parents should give offspring all that they ask for (meaning that offspring control the amount of

64    investment), because the optimal level of parental investment for parent and offspring is almost equal.

65    Previous studies support this theory. In species where the parents control the amount of investment (e.g.

66    mice *Mus musculus*, Hager & Johnstone, 2003; Curley *et al.*, 2004, earwigs *Forficula auricularia*, Mas *et*

67    *al.*, 2009, burying beetles *Nicrophorus vespilloides*, Lock *et al.*, 2004, great tits *Parus major*, Kölliker *et al.*,

68    2000, and canaries *Serinus canaria*, Hinde *et al.*, 2010), parents typically produce more than two offspring

69    per breeding attempt and have more than two reproductive bouts during their lifetime. In species where the

70    offspring control the amount of investment (e.g. sheep, macaques *Macaca mulatta*, Kölliker *et al.*, 2005,

71    and burrower bugs *Sehirus cincta*, Agrawal *et al.*, 2001), parents typically produce one or two offspring per

72    breeding attempt, and/or have one or two reproductive bouts during their lifetime. The main difference

73    between these two strategies in these groups of species is their residual reproductive value or the

74    opportunity for future reproduction. These data suggest that differences in the residual reproductive value

75    of parents explain the patterns of control of parental investment (reviewed by Kilner & Hinde, 2012).

76    However, the residual reproductive value of the parents will change during their lifetime; therefore,

77    parental influence on the amount of investment can also be expected to change during their lifetime

78    (Thorogood *et al.*, 2011).

79          Recent models show cross-fostering experiments provide experimental evidence on control of

80    parental provisioning (Hinde *et al.*, 2010). When parental supply and offspring demand are co-adapted,

81    there are genetic correlations between parent and offspring traits. Experimental approaches using a

82    cross-fostering treatment to exchange the young break these genetic correlations. Under the parental control

83    model, exchanging young is predicted to have a negative effect on offspring fitness, but not parental fitness.

84    In contrast, under the offspring control model, exchanging young is predicted to have a negative effect on

85    parental fitness, but not offspring fitness.

86          Here, we investigated whether control of parental provisioning changes plastically over time in the

87    burying beetle *Nicrophorus quadripunctatus*, which has elaborate parental care. The burying beetle *N.*

88    *quadripunctatus* uses the carcasses of small vertebrates (2–100 g) as a food resource for their larvae. *N.*

89    *quadripunctatus* can produce more than six clutches (Nagano & Suzuki, 2007) and reproduce multiple

90    times under laboratory conditions, although it is not known how many times burying beetles breed in the

91    field. After hatching, larvae obtain food by begging for predigested carrion from their parents or by directly

92    feeding from the carcass themselves (in *N. vespilloides*, Smiseth & Moore, 2002; Smiseth *et al.*, 2003; in *N.*

93    *quadripunctatus*, Takata, unpublished data). Although parental food provisioning is not necessary for larval

94    survival, it improves offspring survival and body size dramatically (in *N. vespilloides*, Eggert *et al.*, 1998;

95    Smiseth *et al.*, 2003; in *N. quadripunctatus*, Takata, unpublished data). In the burying beetles, parental

96    supply and offspring demand are co-adapted and the amount of parental investment is controlled by the

97    parents (in *N. vespilloides*, Lock *et al.*, 2004; in *N. quadripunctatus*, Takata, unpublished data), when the

98    parents are young. However, a recent study showed that residual reproductive value decreases with age

99    (Cotter *et al.*, 2011). Therefore, control of parental investment may change plastically over time in response

100   to the residual reproductive value of parents. In this study, we investigated whether control of parental

101   provisioning changes in response to residual reproductive value. We predict that parents will control

102   parental investment when parents are young and have high residual reproductive value, but offspring will

103   control parental investment when parents are old and have low residual reproductive value.

104

105   **Materials and methods**

106   **Origin and maintenance of the beetles**

107   The beetles used in this experiment were first-generation offspring of over 200 wild-caught adult

108   *Nicrophorus quadripunctatus* Kraatz collected by baited pitfall traps in June 2014 in Tokyo, Japan. Adult

109   body size, taken by measuring thoracic width, was $5.2 \pm 0.5$ mm (mean ± SD) in this population. The

110   beetles were maintained individually in small transparent plastic cups (height 4 cm, diameter 6 cm) at $20 \pm$

111   $1 \,°C$ under a 14 : 10 h light: dark cycle. After they emerged as adults, they were fed 200 mg of freshly

112   killed mealworms (*Zophobas atratus*) three times a week.

113

114   **Experimental procedure**

115   Firstly, we measured the thoracic width of female parents as a proxy for body size using an electronic

116   vernier caliper (Mitutoyo Corp., Kanagawa, Japan) to an accuracy of 0.1 mm. Then, the females were

117   randomly assigned to following 4 experimental groups. There was no statistically significant difference in

118   the body size of female parents between experimental groups ($P > 0.05$, t-test with Bonferroni correction).

119   Pairs of nonsibling, same-aged male and female beetles were randomly selected, and each pair was placed

120   in a plastic cup (height 8 cm, diameter 15 cm) with moist peat. They were provided with $4.0 \pm 0.5$ g of a

121   whole body mouse carcass supplied by Cyber Cricket, Shiga, Japan. In our pilot study, they bred $3.2 \pm 0.8$

122   larvae (mean ± SD) on this size of carcass. The beetles in the plastic cups were kept in a dark incubator at

123   20 ± 1 °C for 72 h. During this period, female beetles laid eggs in the soil near the carcass. Then, the

124   female and the carcass were transferred to a second, new plastic cup with moist peat. The male beetles were

125   removed from the original plastic cup at this stage because parental care by male parents has no effect on

126   larval growth or survival under laboratory conditions (Smiseth *et al.*, 2005). The eggs were left to hatch in

127   the original plastic cup. Hatching of larvae was checked at 2 hourly intervals, and newly hatched larvae

128   were used for experiments.

129

130   **Who controls the amount of provisioning when parents were young or old?**

131   Two different age groups of *N. quadripunctatus* parents reproduced twice in this experiment. Young

132   parents were 2 weeks old and old parents were 6 weeks old, from the date of eclosion. Breeding longevity

133   is approximately 12 weeks in *N. quadripunctatus*. The beetles in this study had not bred previously. The

134   first breeding attempt investigated the fitness cost incurred by offspring due to being raised by a foster

135   parent. One larva was transferred to a carcass with its natal mother (natal group), and a sibling was

136   transferred to a carcass with a foster mother (foster group). The ages of foster parents were the same as

137   natal parents. Then, larval body weight was measured 120 h after being transferred onto the carcass,

138   because larvae disperse away from the carcass at 120 h (Takata *et al.*, 2013). Immediately after the first

139   breeding attempt, female parents of natal and foster groups were transferred in small transparent plastic

140   cups (height 4 cm, diameter 6 cm) and kept at 20 ± 1 °C under a 14 : 10 h light: dark cycle. They were fed

141   200 mg of freshly killed mealworms on the day and 2 days later.

142       The second breeding attempt investigated the fitness cost incurred by parents due to caring for foster

143   offspring in the first breeding attempt. The second breeding attempt started 3 days after the end of the first

144   breeding attempt. The same pairs of females and males used in the first breeding attempt bred again, using

145   the same experimental procedure as the first breeding attempt. In this breeding attempt, a larva was

146   transferred to a carcass with its natal mother in both experimental groups. Therefore, mothers of natal and

147   foster groups cared their own offspring in this breeding attempt. Then, larval body weight was measured

148   after 120 h.

149

150 **Statistical analysis**

151 Generalized linear models (GLM) were used to investigate the fitness cost of cross-fostering experiment for

152 parents and offspring. To investigate the difference in larval body weight between natal and foster

153 experimental groups, the larval body weight at 120 h old was treated as a response variable assuming a

154 Gaussian distribution, and the experimental groups and ID of the genetic parent of the larva were treated as

155 explanatory variables. Data were analysed separately for the first and second breeding attempt and old and

156 young experimental groups. The influence of female body size on larval body weight was excluded from

157 this analysis, because it did not have a significant effect in the foster experimental groups.

158       To investigate the influence of parental age on the amount of parental investment, we analysed the

159 difference in body weight between larvae raised by young or old parents in the first breeding attempt. Data

160 were analysed separately for natal and fostered experimental groups. Firstly, larval body weight at 120 h

161 old was treated as a response variable assuming a Gaussian distribution, and parental age and thoracic

162 width of female parents and its interaction were treated as explanatory variables. Then, the interaction term

163 was excluded from this analysis, because it did not have a significant effect. All GLMs were conducted

164 using R 3.1.1 GUI 1.65 (http://cran.r-project.org). *P*-values were calculated using the likelihood ratio test.

165

166 **Results**

167 **Who controls the amount of provisioning when parents were young?**

168 The body weight of the cross-fostered larvae was lower than the larvae raised by natal parents when parents

169 were young and had a high residual reproductive value (GLM: estimate = -18.774, $\chi^2$ = -5463.300, d.f. =

170 1,61, *P* = 0.024, Fig. 1a). In contrast, there was no statistically significant difference in offspring body

171 weight between experimental groups in the second breeding attempt where the larvae were reared by natal

172 mother (GLM: estimate = 2.875, $\chi^2$ = -99.188, d.f. = 1,54, *P* = 0.794, Fig. 1a).

173

174 **Who controls the amount of provisioning when parents were old?**

175 There was no statistically significant difference between the body weight of offspring raised by natal or

176 foster female parents when parents were old and had a low residual reproductive value (GLM: estimate =

177 1.419, $\chi^2$ = -31.226, d.f. = 1,61, *P* = 0.856, Fig. 1b). There was no statistically significant difference in

178    offspring body weight between experimental groups in the second breeding attempt where the larvae were

179    reared by their natal mother (GLM: estimate = 5.958, $\chi^2$ = -426.020, d.f. = 1,53, $P$ = 0.456, Fig. 1b).

180

181    **The influence of parental age on the amount of parental investment**

182    In the natal experimental groups, the body weight of offspring raised by young parents was significantly

183    heavier than those raised by old parents (GLM: estimate = 22.567, $\chi^2$ = -7561.600, d.f. = 1,60, $P$ = 0.002,

184    Fig. 2a). Furthermore, parental body size had a significant positive effect on offspring body weight (GLM:

185    estimate = 52.973, $\chi^2$ = -30147.000, d.f. = 1,60, $P$ < 0.001, Fig. 2a). There was no significant interaction

186    between parental age and body size, on offspring body weight (GLM: estimate = -24.630, $\chi^2$ = -1496.200,

187    d.f. = 1,61, $P$ = 0.174).

188        In the foster experimental groups, neither parental age (GLM: estimate = -3.209, $\chi^2$ = -153.670, d.f.

189    = 1,60, $P$ = 0.789, Fig. 2b) nor body size (GLM: estimate = 22.173, $\chi^2$ = -5386.600, d.f. = 1,60, $P$ = 0.112,

190    Fig. 2b) had a significant positive effect on offspring body weight. There was no significant interaction

191    between parental age and body size on offspring body weight (GLM: estimate = 5.689, $\chi^2$ = -88.174, d.f. =

192    1,61, $P$ = 0.840).

193

194    **Discussion**

195    In this study, we investigated whether control of parental investment changes plastically over time in

196    response to the residual reproductive value of the parents in *N. quadripunctatus*. When parents were young,

197    the cross-fostering treatment had a negative effect on offspring fitness components, but not on parental

198    fitness components. These results correspond to the predictions of the parental control model. However,

199    when parents were old, the cross-fostering treatment did not have a negative effect on either offspring or

200    parental fitness components. Therefore, neither parents nor offspring exert greater control over parental

201    investment when the residual reproductive value of the parents is decreased. Our study demonstrates that

202    control of parental investment is not consistent, but changes plastically during the parent's lifetime.

203        This study showed that parents exert greater control over parental investment when they are young

204    and have high residual reproductive value, but parental control is weakened as the parents age and their

205    residual reproductive value lowers. Our results correspond with patterns at the species level reported in

206    previous studies (Kölliker *et al.*, 2000, 2005; Agrawal *et al.*, 2001; Hager & Johnstone, 2003; Curley *et al.*,

207     2004; Lock *et al.*, 2004; Mas *et al.*, 2009; Hinde *et al.*, 2010, see Kilner & Hinde 2012 for review).

208     Residual reproductive value of parents can explain the patterns in controls on parental investment not only

209     at the species level, but also at the parental condition level. Large number of studies on life-history strategy

210     theory showed that the amount of parental investment for the current brood is limited by the high residual

211     reproductive value of the parents (Reviewed by Lessells 1991; Stearns 1992; Székely *et al.* 1996). For

212     example, in *Nicrophorus* spp., parental investment is limited by ageing (Creighton *et al.*, 2009; Cotter *et al.*,

213     2011, but see Trumbo, 2009) and previous investment (Ward *et al.*, 2009). Selective pressure for parental

214     life-history strategy may influence control of parental investment.

215             Maternal effects may cause the plastic changes in control of parental investment, because maternal

216     effects influence offspring behaviour by controlling the physiological condition of offspring. Previous

217     studies showed that maternal effects transmit information about the condition of parents to their offspring,

218     such as the residual reproductive value (in the bird species hihi *Notiomystis cincta*, Thorogood *et al.* 2011)

219     and parent age (in *N. vespilloides*, Lock *et al.* 2007), and in the cross-fostering experimental groups,

220     offspring body weight is maximized when offspring information and the condition of the caretaker matched.

221     We also observed a significant correlation between parental body size and offspring body weight when

222     offspring information about body size of parents and that of the caretaker matched, but it was not observed

223     when mismatched (Fig. 2a, b). A recent study revealed that maternal effects link and match with offspring

224     begging intensity and parental responsiveness to it (Hinde *et al.*, 2010). These results suggest maternal

225     effects contribute to match the phenotypes of the offspring and parent. In this study, control of parental

226     investment changes plastically in response to parent age, suggesting that maternal effects influence the

227     condition-dependent power balance between parent and offspring by transmitting information about the

228     parent (e.g. residual reproductive value of parents) to their offspring. Juvenile hormone (JH) may play a

229     key role in mediating this plastic changes, because in a congeneric burying beetle to our study species, JH

230     levels are related to caring behaviour of female parents (in *N. orbicollis*, Trumbo, 1992; Scott & Panaitof,

231     2004) and offspring begging (in *N. vespilloides*, Crook *et al.*, 2008). Furthermore, in the burying beetle,

232     there are changes in egg investment with parental age (in *N. vespilloides*, Lock *et al.*, 2007; in *N. orbicolis*,

233     Trumbo, 2012). This might serve as maternal effect and up-regulate the JH levels in offspring; however,

234     whether JH levels in parent and offspring change with parental age and the amount of egg investment

235     remain to be determined in future work.

236    In this study, we investigated plasticity of control of parental investment by using a rather unusual

237 brood size (1 larva) in *N. quadripunctatus*, although on a 4 g carcass, this brood size is within the range

238 naturally seen in this species. This brood size enables us to compare the amount of parental investment

239 obtained by each offspring even if the relationship between the amount of parental investment and

240 offspring body mass gain is nonlinear. However, we cannot discuss how sibling competition and

241 cooperation influence control of parental investment and its plasticity over time. Further studies are needed

242 to reveal this influence by using broods with more than one offspring.

243

246

247    **Author's contributions**

248 M.T. conceived and designed the experiments, collected data, produced figures and wrote the paper. H.D.

249 collected data. C.E.T. co-wrote the paper. S.K. analysed the data and co-wrote the paper.

250

251    **Competing interest**

252 We have no competing interests.

253

256

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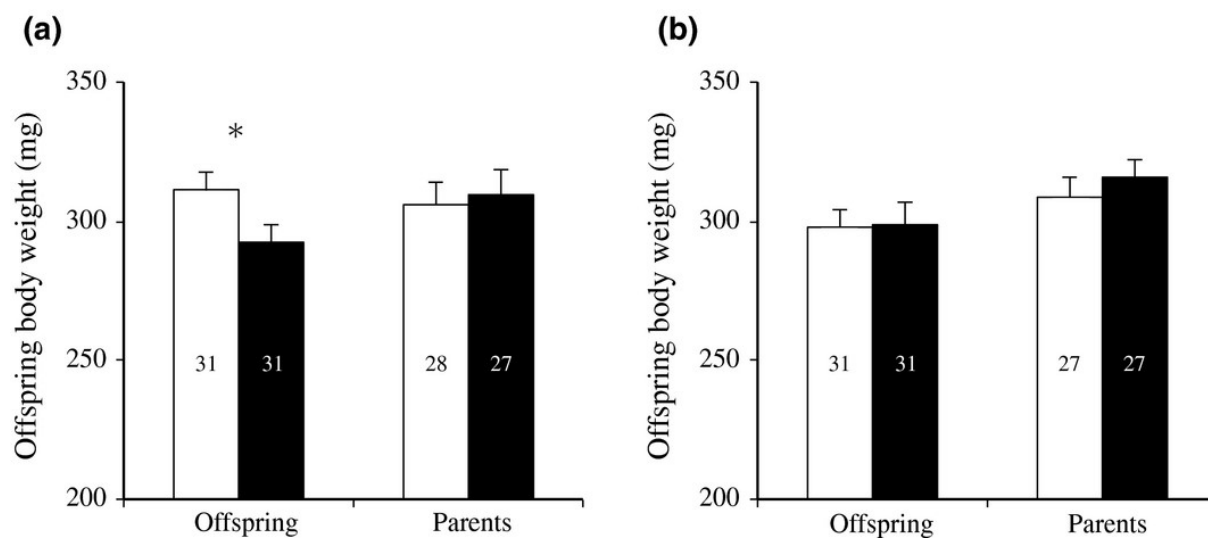
333    **Author notes**

335

336 **Figures**



338 **Figure 1** The average effect of cross-fostering on fitness components of offspring and parent when parents

339 are young (a) or old (b). White bars show fitness components of offspring and parents in natal groups.

340 Black bars show those in foster groups. Data are presented as mean + SE. The numbers in the bars show

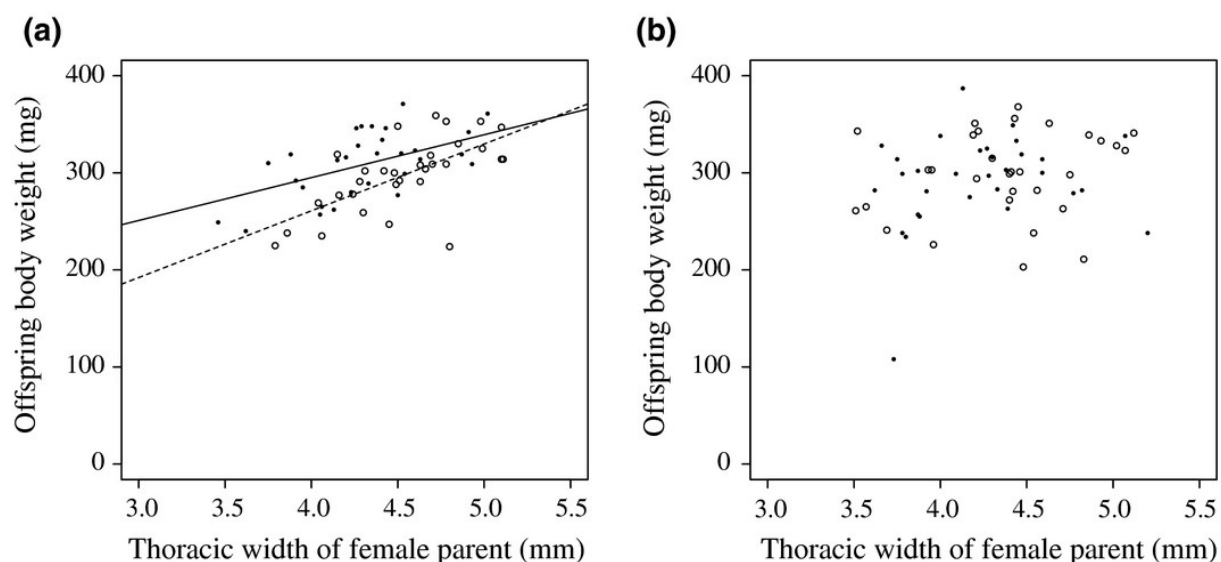341 sample sizes. The asterisk indicates a significant difference at $P < 0.05$.

342



344 **Figure 2** The effect of female body size on offspring body weight when offspring were cared for by natal

345 (a) or foster parents (b). Solid and open plots show the results from young and old parents respectively.

346 Solid and dashed lines show the regression line for young and old parents respectively.