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Article title

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

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Running title

Plastic changes in control

Abstract

Evolutionary conflict between parents and offspring over parental resource investment is a significant selective force on the traits of both parents and offspring. Empirical studies have shown that for some species, the amount of parental investment is controlled by the parents, whereas in other species, it is controlled by the offspring. The main difference between these two strategies is the residual reproductive value of the parents or opportunities for future reproduction. Therefore, this could explain the patterns of control of parental investment at the species level. However, the residual reproductive value of the parents will change during their lifetime; therefore, parental influence on the amount of investment can be expected to change plastically. Here, we investigated control of parental investment when parents were young and had a high residual reproductive value, compared to when they were old and had a low residual reproductive value using a cross-fostering experiment in the burying beetle *Nicrophorus quadripunctatus*. We found that parents exert greater control over parental investment when they are young, but parental control is weakened as the parents age. Our results demonstrate that control of parental investment is not fixed, but changes plastically during the parent's lifetime.

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

Introduction

The theory of parent–offspring conflict over parental investment is well studied (reviewed by Godfray, 1995; Godfray & Johnstone, 2000) and is a significant selective force on parent and offspring traits (reviewed by Kilner & Hinde 2008). In a sexually reproducing species, relatedness between parent and offspring is < 1, so the genes of the offspring benefit from parental investment more than those of the parents (Lazarus & Inglis, 1986). This results in evolutionary conflict, in which the optimal level of parental investment for offspring is higher than that of the parents (Trivers, 1974; Godfray & Johnstone, 2000; Bossan *et al.*, 2013).

Parent–offspring conflict causes a co-evolutionary arms race between the traits of the parents and their offspring (Lyon *et al.*, 1994; Kilner & Hinde, 2012). For example, it is beneficial for offspring to perform begging behaviour in surplus to obtain high levels of parental investment, whereas parents must change their responsiveness to the begging of their offspring to optimally allocate the investment across the brood (Parker & Macnair, 1979; Hussell, 1988; Kölliker, 2003). Quantitative genetic models predict that when parents control the amount of investment, selection acts on traits in the offspring and there is a positive correlation between the amount of parental resource provisioning and offspring begging intensity. When the offspring control the amount of investment, traits in the parents are under selection and there is a negative correlation between the amount of parental resource provisioning and offspring begging intensity (Kölliker *et al.*, 2005). Empirical studies have shown that for some species, there is a positive correlation between the amount of parental provisioning and offspring begging intensity, suggesting that the amount of parental resource provisioning is controlled by the parents (Kölliker *et al.*, 2000; Hager & Johnstone, 2003; Curley *et al.*, 2004; Lock *et al.*, 2004; Mas *et al.*, 2009; Hinde *et al.*, 2010), whereas in other species, there is a negative correlation, suggesting that it is controlled by the offspring (Agrawal *et al.*, 2001; Kölliker *et al.*, 2005).

Residual reproductive value may be the ecological factor influencing whether the parent or offspring control parental investment. When residual reproductive value is high, parents have more to lose by being exploited by their young, because the difference in the optimal level of parental investment between parent and offspring is greater. Therefore, higher residual reproductive value may cause stronger selective pressure for parental control of investment. On the other hand, when residual reproductive value is near to zero, parents should give offspring all that they ask for (meaning that offspring control the amount of investment), because the optimal level of parental investment for parent and offspring is almost equal. Previous studies support this theory. In species where the parents control the amount of investment (e.g. mice *Mus musculus*, Hager & Johnstone, 2003; Curley *et al.*, 2004, earwigs *Forficula auricularia*, Mas *et al.*, 2009, burying beetles *Nicrophorus vespilloides*, Lock *et al.*, 2004, great tits *Parus major*, Kölliker *et al.*, 2000, and canaries *Serinus canaria*, Hinde *et al.*, 2010), parents typically produce more than two offspring per breeding attempt and have more than two reproductive bouts during their lifetime. In species where the offspring control the amount of investment (e.g. sheep, macaques *Macaca mulatta*, Kölliker *et al.*, 2005, and burrower bugs *Sehirus cincta*, Agrawal *et al.*, 2001), parents typically produce one or two offspring per breeding attempt, and/or have one or two reproductive bouts during their lifetime. The main difference between these two strategies in these groups of species is their residual reproductive value or the opportunity for future reproduction. These data suggest that differences in the residual reproductive value of parents explain the patterns of control of parental investment (reviewed by Kilner & Hinde, 2012). However, the residual reproductive value of the parents will change during their lifetime; therefore, parental influence on the amount of investment can also be expected to change during their lifetime (Thorogood *et al.*, 2011).

Recent models show cross-fostering experiments provide experimental evidence on control of parental provisioning (Hinde *et al.*, 2010). When parental supply and offspring demand are co-adapted, there are genetic correlations between parent and offspring traits. Experimental approaches using a cross-fostering treatment to exchange the young break these genetic correlations. Under the parental control model, exchanging young is predicted to have a negative effect on offspring fitness, but not parental fitness. In contrast, under the offspring control model, exchanging young is predicted to have a negative effect on parental fitness, but not offspring fitness.

Here, we investigated whether control of parental provisioning changes plastically over time in the burying beetle *Nicrophorus quadripunctatus*, which has elaborate parental care. The burying beetle *N. quadripunctatus* uses the carcasses of small vertebrates (2–100 g) as a food resource for their larvae. *N. quadripunctatus* can produce more than six clutches (Nagano & Suzuki, 2007) and reproduce multiple times under laboratory conditions, although it is not known how many times burying beetles breed in the field. After hatching, larvae obtain food by begging for predigested carrion from their parents or by directly feeding from the carcass themselves (in *N. vespilloides*, Smiseth & Moore, 2002; Smiseth *et al.*, 2003; in *N.*

quadripunctatus, Takata, unpublished data). Although parental food provisioning is not necessary for larval survival, it improves offspring survival and body size dramatically (in *N. vespilloides*, Eggert *et al.*, 1998; Smiseth *et al.*, 2003; in *N. quadripunctatus*, Takata, unpublished data). In the burying beetles, parental supply and offspring demand are co-adapted and the amount of parental investment is controlled by the parents (in *N. vespilloides*, Lock *et al.*, 2004; in *N. quadripunctatus*, Takata, unpublished data), when the parents are young. However, a recent study showed that residual reproductive value decreases with age (Cotter *et al.*, 2011). Therefore, control of parental investment may change plastically over time in response to the residual reproductive value of parents. In this study, we investigated whether control of parental provisioning changes in response to residual reproductive value. We predict that parents will control parental investment when parents are young and have high residual reproductive value, but offspring will control parental investment when parents are old and have low residual reproductive value.

Materials and methods

Origin and maintenance of the beetles

The beetles used in this experiment were first-generation offspring of over 200 wild-caught adult *Nicrophorus quadripunctatus* Kraatz collected by baited pitfall traps in June 2014 in Tokyo, Japan. Adult body size, taken by measuring thoracic width, was 5.2 ± 0.5 mm (mean ± SD) in this population. The beetles were maintained individually in small transparent plastic cups (height 4 cm, diameter 6 cm) at 20 ± 1 °C under a 14 : 10 h light: dark cycle. After they emerged as adults, they were fed 200 mg of freshly killed mealworms (*Zophobas atratus*) three times a week.

Experimental procedure

Firstly, we measured the thoracic width of female parents as a proxy for body size using an electronic vernier caliper (Mitutoyo Corp., Kanagawa, Japan) to an accuracy of 0.1 mm. Then, the females were randomly assigned to following 4 experimental groups. There was no statistically significant difference in the body size of female parents between experimental groups ($P > 0.05$, t-test with Bonferroni correction). Pairs of nonsibling, same-aged male and female beetles were randomly selected, and each pair was placed in a plastic cup (height 8 cm, diameter 15 cm) with moist peat. They were provided with 4.0 ± 0.5 g of a whole body mouse carcass supplied by Cyber Cricket, Shiga, Japan. In our pilot study, they bred 3.2 ± 0.8

larvae (mean ± SD) on this size of carcass. The beetles in the plastic cups were kept in a dark incubator at 20 ± 1 °C for 72 h. During this period, female beetles laid eggs in the soil near the carcass. Then, the female and the carcass were transferred to a second, new plastic cup with moist peat. The male beetles were removed from the original plastic cup at this stage because parental care by male parents has no effect on larval growth or survival under laboratory conditions (Smiseth *et al.*, 2005). The eggs were left to hatch in the original plastic cup. Hatching of larvae was checked at 2 hourly intervals, and newly hatched larvae were used for experiments.

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

Two different age groups of *N. quadripunctatus* parents reproduced twice in this experiment. Young parents were 2 weeks old and old parents were 6 weeks old, from the date of eclosion. Breeding longevity is approximately 12 weeks in *N. quadripunctatus*. The beetles in this study had not bred previously. The first breeding attempt investigated the fitness cost incurred by offspring due to being raised by a foster parent. One larva was transferred to a carcass with its natal mother (natal group), and a sibling was transferred to a carcass with a foster mother (foster group). The ages of foster parents were the same as natal parents. Then, larval body weight was measured 120 h after being transferred onto the carcass, because larvae disperse away from the carcass at 120 h (Takata *et al.*, 2013). Immediately after the first breeding attempt, female parents of natal and foster groups were transferred in small transparent plastic cups (height 4 cm, diameter 6 cm) and kept at 20 ± 1 °C under a 14 : 10 h light: dark cycle. They were fed 200 mg of freshly killed mealworms on the day and 2 days later.

The second breeding attempt investigated the fitness cost incurred by parents due to caring for foster offspring in the first breeding attempt. The second breeding attempt started 3 days after the end of the first breeding attempt. The same pairs of females and males used in the first breeding attempt bred again, using the same experimental procedure as the first breeding attempt. In this breeding attempt, a larva was transferred to a carcass with its natal mother in both experimental groups. Therefore, mothers of natal and foster groups cared their own offspring in this breeding attempt. Then, larval body weight was measured after 120 h.

Statistical analysis

Generalized linear models (GLM) were used to investigate the fitness cost of cross-fostering experiment for parents and offspring. To investigate the difference in larval body weight between natal and foster experimental groups, the larval body weight at 120 h old was treated as a response variable assuming a Gaussian distribution, and the experimental groups and ID of the genetic parent of the larva were treated as explanatory variables. Data were analysed separately for the first and second breeding attempt and old and young experimental groups. The influence of female body size on larval body weight was excluded from this analysis, because it did not have a significant effect in the foster experimental groups.

To investigate the influence of parental age on the amount of parental investment, we analysed the difference in body weight between larvae raised by young or old parents in the first breeding attempt. Data were analysed separately for natal and fostered experimental groups. Firstly, larval body weight at 120 h old was treated as a response variable assuming a Gaussian distribution, and parental age and thoracic width of female parents and its interaction were treated as explanatory variables. Then, the interaction term was excluded from this analysis, because it did not have a significant effect. All GLMs were conducted using R 3.1.1 GUI 1.65 (http://cran.r-project.org). *P*-values were calculated using the likelihood ratio test.

Results

Who controls the amount of provisioning when parents were young?

The body weight of the cross-fostered larvae was lower than the larvae raised by natal parents when parents were young and had a high residual reproductive value (GLM: estimate = -18.774, χ^2 = -5463.300, d.f. = 1,61, $P = 0.024$, Fig. 1a). In contrast, there was no statistically significant difference in offspring body weight between experimental groups in the second breeding attempt where the larvae were reared by natal mother (GLM: estimate = 2.875, χ^2 = -99.188, d.f. = 1,54, $P = 0.794$, Fig. 1a).

Who controls the amount of provisioning when parents were old?

There was no statistically significant difference between the body weight of offspring raised by natal or foster female parents when parents were old and had a low residual reproductive value (GLM: estimate = 1.419, χ^2 = -31.226, d.f. = 1,61, $P = 0.856$, Fig. 1b). There was no statistically significant difference in offspring body weight between experimental groups in the second breeding attempt where the larvae were reared by their natal mother (GLM: estimate = 5.958, χ^2 = -426.020, d.f. = 1,53, P = 0.456, Fig. 1b).

The influence of parental age on the amount of parental investment

In the natal experimental groups, the body weight of offspring raised by young parents was significantly heavier than those raised by old parents (GLM: estimate = 22.567, χ^2 = -7561.600, d.f. = 1,60, P = 0.002, Fig. 2a). Furthermore, parental body size had a significant positive effect on offspring body weight (GLM: estimate = 52.973, χ^2 = -30147.000, d.f. = 1,60, $P < 0.001$, Fig. 2a). There was no significant interaction between parental age and body size, on offspring body weight (GLM: estimate = -24.630, χ^2 = -1496.200, d.f. = 1,61, P = 0.174).

In the foster experimental groups, neither parental age (GLM: estimate = -3.209, χ^2 = -153.670, d.f. = 1,60, P = 0.789, Fig. 2b) nor body size (GLM: estimate = 22.173, χ^2 = -5386.600, d.f. = 1,60, P = 0.112, Fig. 2b) had a significant positive effect on offspring body weight. There was no significant interaction between parental age and body size on offspring body weight (GLM: estimate = 5.689, χ^2 = -88.174, d.f. = 1,61, P = 0.840).

Discussion

In this study, we investigated whether control of parental investment changes plastically over time in response to the residual reproductive value of the parents in *N. quadripunctatus*. When parents were young, the cross-fostering treatment had a negative effect on offspring fitness components, but not on parental fitness components. These results correspond to the predictions of the parental control model. However, when parents were old, the cross-fostering treatment did not have a negative effect on either offspring or parental fitness components. Therefore, neither parents nor offspring exert greater control over parental investment when the residual reproductive value of the parents is decreased. Our study demonstrates that control of parental investment is not consistent, but changes plastically during the parent's lifetime.

This study showed that parents exert greater control over parental investment when they are young and have high residual reproductive value, but parental control is weakened as the parents age and their residual reproductive value lowers. Our results correspond with patterns at the species level reported in previous studies (Kölliker *et al.*, 2000, 2005; Agrawal *et al.*, 2001; Hager & Johnstone, 2003; Curley *et al.*, 2004; Lock *et al.*, 2004; Mas *et al.*, 2009; Hinde *et al.*, 2010, see Kilner & Hinde 2012 for review). Residual reproductive value of parents can explain the patterns in controls on parental investment not only at the species level, but also at the parental condition level. Large number of studies on life-history strategy theory showed that the amount of parental investment for the current brood is limited by the high residual reproductive value of the parents (Reviewed by Lessells 1991; Stearns 1992; Székely *et al.* 1996). For example, in *Nicrophorus* spp., parental investment is limited by ageing (Creighton *et al.*, 2009; Cotter *et al.*, 2011, but see Trumbo, 2009) and previous investment (Ward *et al.*, 2009). Selective pressure for parental life-history strategy may influence control of parental investment.

Maternal effects may cause the plastic changes in control of parental investment, because maternal effects influence offspring behaviour by controlling the physiological condition of offspring. Previous studies showed that maternal effects transmit information about the condition of parents to their offspring, such as the residual reproductive value (in the bird species hihi *Notiomystis cincta*, Thorogood *et al.* 2011) and parent age (in *N. vespilloides*, Lock *et al.* 2007), and in the cross-fostering experimental groups, offspring body weight is maximized when offspring information and the condition of the caretaker matched. We also observed a significant correlation between parental body size and offspring body weight when offspring information about body size of parents and that of the caretaker matched, but it was not observed when mismatched (Fig. 2a, b). A recent study revealed that maternal effects link and match with offspring begging intensity and parental responsiveness to it (Hinde *et al.*, 2010). These results suggest maternal effects contribute to match the phenotypes of the offspring and parent. In this study, control of parental investment changes plastically in response to parent age, suggesting that maternal effects influence the condition-dependent power balance between parent and offspring by transmitting information about the parent (e.g. residual reproductive value of parents) to their offspring. Juvenile hormone (JH) may play a key role in mediating this plastic changes, because in a congeneric burying beetle to our study species, JH levels are related to caring behaviour of female parents (in *N. orbicollis*, Trumbo, 1992; Scott & Panaitof, 2004) and offspring begging (in *N. vespilloides*, Crook *et al.*, 2008). Furthermore, in the burying beetle, there are changes in egg investment with parental age (in *N. vespilloides*, Lock *et al.*, 2007; in *N. orbicolis*, Trumbo, 2012). This might serve as maternal effect and up-regulate the JH levels in offspring; however, whether JH levels in parent and offspring change with parental age and the amount of egg investment remain to be determined in future work.

In this study, we investigated plasticity of control of parental investment by using a rather unusual brood size (1 larva) in *N. quadripunctatus*, although on a 4 g carcass, this brood size is within the range naturally seen in this species. This brood size enables us to compare the amount of parental investment obtained by each offspring even if the relationship between the amount of parental investment and offspring body mass gain is nonlinear. However, we cannot discuss how sibling competition and cooperation influence control of parental investment and its plasticity over time. Further studies are needed to reveal this influence by using broods with more than one offspring.

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Author's contributions

M.T. conceived and designed the experiments, collected data, produced figures and wrote the paper. H.D. collected data. C.E.T. co-wrote the paper. S.K. analysed the data and co-wrote the paper.

Competing interest

We have no competing interests.

Founding

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Author notes

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Figures

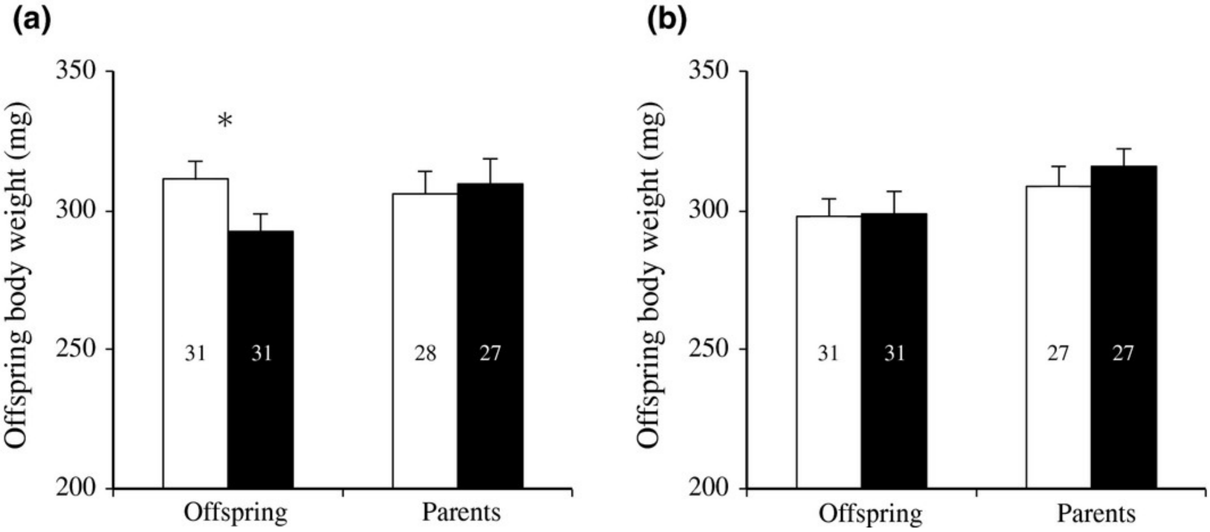

Figure 1 The average effect of cross-fostering on fitness components of offspring and parent when parents are young (a) or old (b). White bars show fitness components of offspring and parents in natal groups. Black bars show those in foster groups. Data are presented as mean + SE. The numbers in the bars show sample sizes. The asterisk indicates a significant difference at $P < 0.05$.

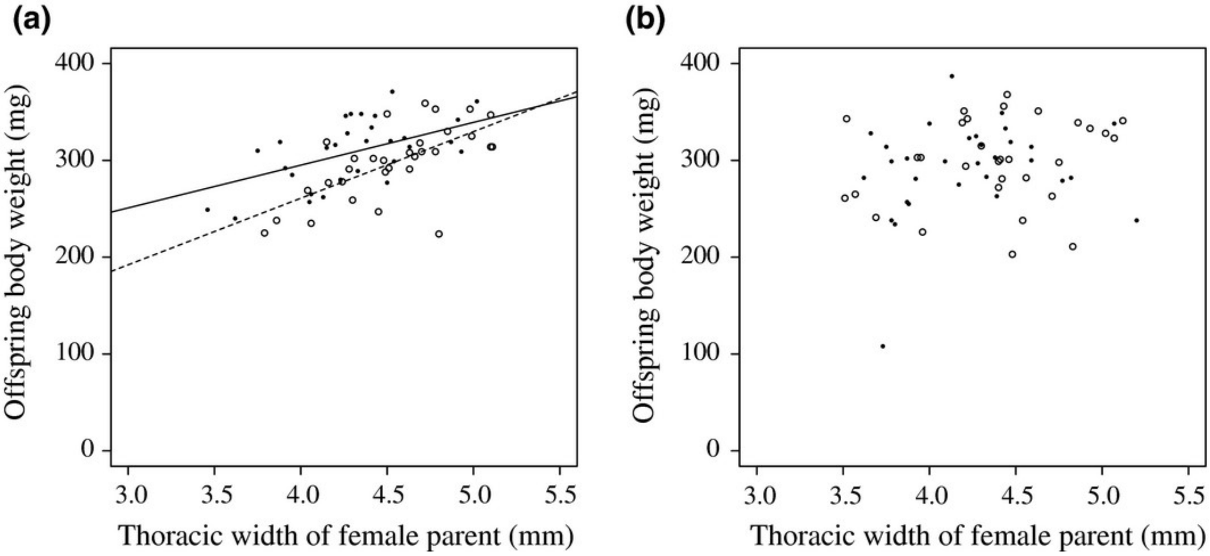

Figure 2 The effect of female body size on offspring body weight when offspring were cared for by natal (a) or foster parents (b). Solid and open plots show the results from young and old parents respectively. Solid and dashed lines show the regression line for young and old parents respectively.