



Paternal attractiveness and the effects of differential allocation of parental investment



Kathryn E. Arnold^{a,*}, Lucy Gilbert^b, Helen E. Gorman^c, Kate J. Griffiths^c, Aileen Adam^c, Ruedi G. Nager^c

^a Environment Department, University of York, York, U.K.

^b Ecological Sciences Group, The James Hutton Institute, Craigiebuckler, Aberdeen, U.K.

^c Institute of Biodiversity, Animal Health and Comparative Medicine, School of Life Sciences, College of Medical, Veterinary and Life Sciences, University of Glasgow, Glasgow, U.K.

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The differential allocation hypothesis (DAH) predicts that an individual should vary its reproductive investment according to the attractiveness of its mate. A recently revised version of the DAH makes explicit that investment can be positive, i.e. higher for the offspring of attractive males which should be of higher quality, or negative, i.e. higher for offspring of unattractive males, for example compensating for inheriting poor paternal genes. Moreover, investment can be made by the father and the mother. Here, we tested whether experimental manipulation of male attractiveness affected parental investment at different reproductive stages and thus influenced fitness-related traits in offspring. In two aviaries, all male zebra finches, *Taeniopygia guttata*, were given red leg rings to increase attractiveness and in two aviaries all males received green leg rings to decrease attractiveness. This controlled for assortative mating between treatments. Ring colour was merely an experimental manipulation of male attractiveness, not paternal quality, so we might expect additional investment to elevate offspring quality. Eggs were cross-fostered between and within treatments to allow differentiation of effects of investment in eggs and nestlings. Clutch and brood sizes were standardized. Both positive and negative investment were observed: Eggs from red-ringed fathers had higher yolk to albumen ratios than eggs from green-ringed fathers. Nestlings from eggs laid and incubated by parents in the red-ringed group had higher hatching masses than those in the green-ringed group. Both parents in the green-ringed group fed nestlings more frequently than red-ringed parents. Offspring performance was influenced by the treatment of both foster and biological parents, but combined effects of these different investment patterns on fitness-related traits were ambiguous. Male attractiveness appeared to affect patterns of reproductive investment but not consistently across all forms of reproductive investment suggesting that the costs and benefits of differential allocation vary among individuals and across contexts.

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The classic differential allocation hypothesis (DAH) predicted that females should invest more in offspring of attractive than unattractive males to maintain the current and future pair bond with an attractive mate (Burley, 1986a, 1988). This has subsequently been expanded to the rationale that if male attractiveness is indicative of genetic quality or resource availability, then a reproductive event with an attractive mate represents a higher value reproductive event than one with an unattractive male (Sheldon, 2000). Therefore, since females have a limited amount of

resources to invest in reproduction, they would benefit from investing relative to the value of a particular event (Trivers & Willard, 1973; but see Jones, Nakagawa, & Sheldon, 2009). However, positive differential allocation may also occur if, for example, the females mated to attractive males increase their investment in order to compensate for attractive males investing less in offspring feeding than unattractive males (e.g. Witte, 1995). While the result of this is a pattern of positive differential allocation by the female, this is because of compensatory investment rather than maximizing the value of high-quality offspring. Data on investment by both parents at both egg and nestling stages are therefore needed to identify the underlying causation, at least in species with biparental care (Montoya & Torres, 2015). More recently it has been

* Correspondence: K. Arnold, Environment Department, University of York, Heslington, York YO10 5DD, U.K.

E-mail address: Kathryn.Arnold@york.ac.uk (K. E. Arnold).

recommended that the DAH is generalized such that the investment could be allocated by the father as well as the mother. Moreover, differential allocation could also be negative, i.e. parents may invest more in offspring of unattractive than attractive mates (Ratikainen & Kokko, 2010). Thus, parents may invest more to compensate for a poor situation such as low genetic quality of their offspring due to a poor quality mate, i.e. 'making the best of a bad job'.

The impacts on offspring fitness of differential allocation are difficult to predict, particularly in socially monogamous species with biparental care. If, for example, attractive males contribute less paternal care than less attractive males (e.g. Mazuc, Chastel, & Sorci, 2003; Sanz, 2001; Witte, 1995) then offspring with attractive fathers might benefit from good genes but suffer from reduced paternal care, if mothers are unable to fully compensate. Under negative differential allocation, if mothers invest heavily in offspring of unattractive fathers then offspring may receive an overall benefit from having an unattractive father (Byers & Waits, 2006; Griffith & Buchanan, 2010). Theoretical models have predicted that a positive relationship between mate attractiveness and reproductive investment should be the more common pattern of differential allocation (Harris & Uller, 2009; but see Ratikainen & Kokko, 2010). This appears to be supported by empirical studies of investment in the prehatching (Cunningham & Russell, 2000; Gilbert, Williamson, Hazon, & Graves, 2006; Rutstein, Gilbert, Slater, & Graves, 2004; Saino et al., 2002; Uller, Eklof, & Andersson, 2005; but see Horvathova, Nakagawa, & Uller, 2012) and posthatching stages (e.g. Burley, 1988; Gorman, Arnold, & Nager, 2005; Hasegawa, Arai, Watanabe, & Nakamura, 2012; Limbourg, Mateman, Andersson, & Lessells, 2004; Maguire & Safran, 2010). For offspring, such positive levels of investment can affect growth and development (Gilbert et al., 2006) and have positive effects on fecundity and other fitness-related traits (Bowers et al., 2013; Cunningham & Russell, 2000; Gilbert, Williamson, & Graves, 2012; Gilbert et al., 2006).

Negative differential allocation has received less attention and, as predicted by models, has been reported less frequently (Harris & Uller, 2009). A number of studies have shown decreased maternal expenditure in egg composition (Bolund, Schielzeth, & Forstmeier, 2009; Michl, Torok, Peczely, Garamszegi, & Schwabl, 2005; Navara, Badyaev, Mendonca, & Hill, 2006; Saino et al., 2002). However, few studies have looked at the investment by both fathers and mothers at both pre- and posthatching stages in the response to male attractiveness (but see Montoya & Torres, 2015; Sheppard, Clark, Devries, & Brasher, 2013). This is important in order to be able to differentiate whether females are allocating investment based on male attractiveness or compensating for reduced parental care by fathers (Witte, 1995). Crucially, even fewer studies have been able to assess the consequences for offspring quality of such allocation decisions. An experimental system with biparental care, in which male attractiveness can be manipulated independently of genetic quality and offspring can be cross-fostered (Montoya & Torres, 2015), is necessary to help us tease apart some of these issues.

In this study, we tested for positive and negative differential allocation (Ratikainen & Kokko, 2010) in egg formation and nestling rearing in response to mate attractiveness in zebra finches, *Taeniopygia guttata*. This is the species used in the original test of the hypothesis by Burley (1988) and male attractiveness can be manipulated using leg rings, with red rings increasing and green rings decreasing attractiveness. Importantly, we also related differential allocation to the phenotype, survival and fecundity of the offspring. Using experimental manipulation of male attractiveness and cross-fostering of the offspring, which allowed us to tease apart the effects of egg investment and nestling-rearing investment, we addressed the following questions. (1) Do females adjust their

investment in eggs based on the ring colour of their mate? (2) Do either males or females provision nestlings differently based on male ring colour? (3) Do the offspring of red- or green-ringed biological or foster fathers differ in their begging behaviour and growth rates? (4) Does the attractiveness of either the biological or foster father influence the adult size, survival and fecundity of offspring?

METHODS

Husbandry

All birds used in this experiment were 9–18 months old, had been housed indoors since birth and had bred at least once with a mate wearing a neutral orange-coloured leg ring. Immediately prior to the experiment, all individuals were housed indoors within single-sex groups of typically four to six birds. At the start of the experiment, these birds were transported to our outside aviary facility and four breeding colonies each consisting of 20 males and 21 females were established in large outdoor aviaries (2.8 × 5.5 m and 2.5 m high) in 2002. No bird was released in the same aviary as its previous breeding partner(s) or with siblings. Birds were fed on a diet of ad libitum seed mix (foreign finch mix supplied by Haith's, Cleethorpes, U.K.), supplemented with an egg food (Haith's egg biscuit) mixed with vitamin supplement (Minavit) three times a week and fresh greens and millet sprays once per week. Fresh drinking water, oystershell grit and cuttlebone were available ad libitum. A calcium supplement (Calciform, Aviform, Wyomondham, U.K.) was added to the water five times per week. From hatching onwards we also provided daily ad libitum soaked seed mix.

Manipulation of Male Attractiveness

A great advantage of the zebra finch for the purposes of experimental design is that there is a well-established technique to manipulate attractiveness by using coloured leg rings. In mate choice trials of both captive and wild-caught zebra finches, females have consistently demonstrated strong preferences for males with red leg rings over males with green leg rings under 'natural' lighting conditions (either outside or inside under UV-rich lighting tubes; Burley, 1986b; Hunt, Cuthill, Swaddle, & Bennett, 1997). It has been suggested that red leg rings enhance the red beak, which in zebra finches is a condition-dependent secondary sexual trait (Blount, Metcalfe, Birkhead, & Surai, 2003). We thus ringed half the males with an individually numbered red or green leg ring at the start of the experiment. Moreover, there is evidence that male zebra finches with red rings sing more and gain more mass suggesting that ring colour alters other male traits as well as female behaviour (Pariser, Mariette & C Griffith, 2010). Red- and green-ringed males were kept in separate aviaries in order to control for potentially assortative mating due to differential access of red-ringed males to high-quality females (Burley, 1986b) which would make it impossible to distinguish between increased female effort due to differential allocation and that due to female quality. However, females were still free to choose their mates within each attractiveness treatment group (Griffith, Pryke, & Buttemer, 2011). Our experiment was performed in four outdoor aviaries, i.e. with a natural UV spectrum (Hunt et al., 1997). All females were ringed with individually numbered orange leg rings, a neutral colour with respect to male mate preference (Burley, 1986b), for identification purposes.

On the day that males and females were released together into the aviaries, all birds were weighed to the nearest 0.1 g and tarsus length measured to the nearest 0.1 mm. There were no differences in either body mass or tarsus length of males and females between

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