Evolutionary biology

Opposite differential allocation by males and females of the same species

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Differential allocation (DA)—the adjustment of an individual’s parental investment in relation to its mate’s attractiveness—is increasingly recognized as an important component of sexual selection. However, although DA is expected by both sexes of parents in species with biparental care, DA by males has rarely been investigated. We have previously demonstrated a decrease in the feeding rates of female blue tits Cyanistes caeruleus when their mate’s UV coloration was experimentally reduced (i.e. positive DA). In this study, we used the same experimental protocol in the same population to investigate DA by male blue tits in relation to their female’s UV coloration. Males mated to UV-reduced females had higher feeding rates than those mated to control females (i.e. negative DA). Thus, male and female blue tits display opposite DA for the same component of parental effort (chick provisioning), the first time that this has been reported for any species.

1. Introduction

Differential allocation (DA) is the adjustment of an individual’s parental investment in relation to the attractiveness of its mate [1–4]. Such differential investment is expected when a mate’s sexual attractiveness is a signal of the offspring’s expected reproductive value. For example, sexually attractive males may have ‘good genes’ which they pass on to their offspring [2,4]. In its broadest current use, DA encompasses responses by males, as well as females, to their mate’s attractiveness [4], and may involve either increasing (‘positive DA’) or decreasing (‘negative DA’, ‘reproductive compensation’) parental effort with increasing mate attractiveness [3,4]. However, previous studies have focused on DA by females, for whom there is ample experimental evidence for positive DA in birds [5] and other taxa [2–4], and several examples of negative DA, mostly involving maternal allocation into avian eggs [4]. In contrast, studies of DA by males have rarely been carried out [6,7]. The role that female attractiveness plays in male parental investment decisions in species with biparental care is therefore unclear.

We have studied DA in blue tits (Cyanistes caeruleus), a species with extensive biparental care in the form of parental feeding visits, and UV plumage coloration that is an indicator of sexual attractiveness ([8,9], but see [10]), male [11,12] and female [13] survival, and genetic quality ([11,14], but see [15]). We have previously demonstrated DA by females: when male UV chroma was experimentally reduced, females decreased their feeding rates and growth of the young was reduced [16]. Thus not only was there positive DA by female blue tits, but also an immediate effect on offspring condition. This is consistent with a positive correlation between female feeding rates and male UV chroma in the same population [17]. Intriguingly, our descriptive study revealed a negative correlation between male feeding rates and female UV chroma, raising the possibility of DA of opposite sign in males and females. The aim of this study is to test whether there is indeed a negative causal relationship between male feeding rates and female UV chroma in blue tits by experimentally reducing female UV chroma, and hence determine whether DA occurs in opposite directions in males and females of the same species.
2. Material and methods
To test for a causal relationship between male feeding rates (number of feeding visits per 2 h) and female UV coloration, we conducted an experiment in May and June 2003 in the Hoge Veluwe National Park, The Netherlands, using the same protocol as our previous experiment [16] but manipulating females instead of males. Females' crown feathers were manipulated on days –2 and 7 (where day 0 is the hatching date of a brood), and the feeding behaviour of the adults video-recorded on days 10 and 14.

To minimize maternal effects mediated by egg composition, we cross-fostered whole clutches with similar clutch size and expected hatching date on day –3. We caught females on day –2 (and day 7 when the treatment was reapplied) and allocated them at random to treatment with a mixture of either UV-blocking chemicals and duck preen gland fat (UV-reduced group) or only duck preen gland fat (control group) [18]. This resulted in significantly lower UV-chroma (R<sub>320–400</sub>/R<sub>320–700</sub>) the proportion of reflectance in the UV part of blue tits' visible spectrum (wavelengths of 320–700 nm)) in UV-reduced females (mean UV chroma immediately after treatment: UV-reduced females: 0.194 ± 0.008 (s.e.); control females: 0.258 ± 0.002 (s.e.); change in UV chroma in UV-reduced females: ANOVA, F<sub>1,32</sub> = 31.02, p < 0.0001). On days 10 and 14, we videotaped parental feeding behaviour for 3 h, and scored the number of feeding visits by each parent in the last 2 h of the recording (feeds per 2 h). To assess the effect of treatment on offspring growth, chicks were sexed using DNA analysis [19] of blood samples taken on day 3, and offspring tarsus length and mass measured on day 15.

Statistical methods are described in the electronic supplementary material.

3. Results
Males with UV-reduced females had higher feeding rates than males with control females, as shown by the significant UV-treatment effect on male feeding rates (see figure 1a and electronic supplementary material, table S1a), while there was no difference in female feeding rates between groups (see figure 1a and electronic supplementary material, table S1b). We found a similar pattern in our previous experiment [16] manipulating male UV chroma: individuals of the manipulated sex did not change their feeding rates, but their mates did. However, females decreased their feeding rate when mated to UV-reduced males (treatment effect on female feeding rate = −0.255 ± 0.084; unpublished estimate from the analysis in [16]), whereas in the current experiment males increased their feeding rates when mated to UV-reduced females (treatment effect on female feeding rate = 0.153 ± 0.056; t for difference in estimates = 4.041, p = 0.0002).

In addition to the overall effect of the manipulation on male feeding rates, there was also an interaction with hatching date (see the electronic supplementary material, table S1a and figure S1): males in control pairs decreased, and in female UV-reduced pairs increased, their feeding rates as hatching date became later in the season.

Chicks of UV-reduced foster-mothers had marginally non-significantly longer tarsi (see figure 2 and electronic supplementary material, table S2a), but were not significantly heavier (see figure 2 and electronic supplementary material, table S2b).

4. Discussion
Males increased their feeding rates when mated to UV-reduced females. Females were manipulated after pair formation and clutch completion, and UV-reduced females did not alter their own feeding rates, so we can unequivocally interpret the males' response as negative DA [2,16]. In addition, there was also an interaction of treatment with hatching date, such that males mated to control females decreased their feeding rate in relation to hatching date, while those mated to UV-reduced females did the opposite.
One possible explanation is that early breeding males sought additional reproductive opportunities rather than increasing their parental effort when faced with a sudden change in their mate’s appearance. Alternatively, the effect of the UV-treatment may have been dependent on the weather: the first half of the season was dominated by heavy rainfall, and the second half by hot weather (T. Limbourg 2003, personal observation), which could have affected parental foraging. Chicks in the nests of UV-reduced females had (marginally non-significantly) longer tarsi, implying that the negative DA has effects on growth, and hence possibly on offspring fitness [20,21].

In contrast to our results, another recent study found positive DA by male blue tits [22]. This difference could be due to variation between years, study populations or the chick age at which parental effort was measured. Moreover, the other study found a marginally non-significant ($p = 0.05$) interaction between egg-laying date (which would be correlated with hatching date) and treatment. As in our experiment, the relationship was negative in the control group, and positive in the experimental group (M. Griggio 2012, personal communication). Variation in the cross-over point in this interaction relative to the timing of breeding could explain the difference in results between the two studies.

The most striking aspect of our results is that DA in the same component of parental effort to the same indicator of attractiveness is opposite in direction in males (negative) and females (positive). Verbal explanations of DA focus on increasing parental effort when the breeding attempt represents a good investment opportunity [2]. Intuition suggests that ‘good investment opportunity’ equates to high-expected fitness, but it is actually the marginal rate of gain in fitness in relation to investment, and not the total gain, that determines the optimal level of investment ([17], see also [3]). In other words, optimal investment for a parent depends on how mate quality affects the exact shape of the relationship between expected offspring fitness and investment, so it is possible to find opposite DA in the two sexes.

Negative DA by males raises the question why females do not falsely signal low attractiveness. State-dependence of UV coloration might be genetically correlated between the sexes, females gain compensating advantages at other times (e.g. in mate choice), or high UV coloration might be costly in males, but not females. However, UV production seems to be underlain by the same processes, and hence would be expected to incur similar physiological costs, in males and females: UV coloration depends on the precision of nanostructural arrangement [23], and shows similar relationships with fluctuating asymmetry [24], age [25] and time in the season [26], and responses to experimental stressors [27–29].

In conclusion, we have experimentally demonstrated opposite DA in males and females of the same species. Although we are unable to identify the adaptive explanation, our results raise intriguing questions and emphasize the need for more empirical studies investigating DA in both males and females in species with biparental care, and theoretical work identifying the kinds of factors that could explain the pattern of DA that we have found.

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References


