

Female blue tits adjust parental effort to manipulated male UV attractiveness

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The differential allocation hypothesis predicts that parents should adjust their current investment in relation to perceived mate attractiveness if this affects offspring fitness. It should be selectively advantageous to risk more of their future reproductive success by investing heavily in current offspring of high reproductive value but to decrease investment if offspring value is low. If the benefits of mate attractiveness are limited to a particular offspring sex we would instead expect relative investment in male versus female offspring to vary with mate attractiveness, referred to as ‘differential sex allocation’. We present strong evidence for differential allocation of parental feeding effort in the wild and show an immediate effect on a component of offspring fitness. By experimentally reducing male UV crown coloration, a trait known to indicate attractiveness and viability in wild-breeding blue tits (*Parus caeruleus*), we show that females, but not males, reduce parental feeding rates and that this reduces the skeletal growth of offspring. However, differential sex allocation does not occur. We conclude that blue tit females use male UV coloration as an indicator of expected offspring fitness and adjust their investment accordingly.

Keywords: differential allocation; differential sex allocation; parental effort; blue tit; UV coloration; mate attractiveness

1. INTRODUCTION

Parents face a trade-off between their current and future reproduction because any investment to increase the fitness of current offspring evokes costs in terms of their own future survival and reproduction (Trivers 1972). To maximize its lifetime reproductive success a parent should therefore adjust its level of parental investment to the value of the current offspring in each breeding attempt in relation to the expected value of future breeding attempts. One potential factor indicating the value of offspring is the attractiveness of the current mate. Attractive mates might provide either indirect benefits for offspring fitness by passing on ‘good genes’ for attractiveness or viability, or direct benefits by environmental correlates of attractiveness (Andersson 1994). Assuming that the current mate is attractive and there is sufficient variation in the attractiveness of future mates, the value of current offspring will be higher than the expected value of future offspring with different, probably less attractive mates. Mate attractiveness would thus affect the trade-off between current and future reproduction (Sheldon 2000) and we would expect differential allocation to occur (Burley 1986*b*). If the ‘differential allocation hypothesis’ (Burley 1986*b*; Sheldon 2000) is correct, individual parents are expected to adjust their investment to the perceived sexual attractiveness of their mates and, as a consequence, the higher investment in offspring of attractive mates should lead to increased offspring fitness, and equally, reduced investment in offspring of less attractive mates should lead to decreased offspring fitness.

The same logic applies if the benefits indicated by mate attractiveness for offspring fitness are sex-limited, but then increased investment should be restricted to the offspring sex affected (Charnov 1982). For instance, the future reproductive success of male offspring might be more strongly correlated to parental attractiveness than that of female offspring. In this case, the fitness of male offspring would vary strongly with parental attractiveness and we would expect that relative investment in male and female offspring should be adjusted to mate attractiveness. We refer to this as ‘differential sex allocation’.

However, differential allocation requires, by definition, that parents adjust their investment to the attractiveness *per se* of their mates and not to environmental correlates of attractiveness, but attractive individuals might provide some direct benefits, such as food-rich territories, that enable their mates to show higher levels of parental investment. Thus, to establish a causal link between individual investment and mate attractiveness experimental testing is required to eliminate such confounding variables (Sheldon 2000).

Recent experimental tests of differential allocation have primarily focused on aspects of primary reproductive effort (egg number and quality). Parents adjusted clutch size and egg size or quality to manipulated mate attractiveness in various species, such as birds (Gil *et al.* 1999; Cunningham & Russell 2000), fishes (Kolm 2001), amphibians (Reyer *et al.* 1999) and insects (Simmons 1987; Thornhill 1983). Equally, there is evidence for differential sex allocation in primary reproductive effort; that is, females adjusted brood sex ratio in relation to manipulated mate attractiveness (Burley 1986*a*; Sheldon *et al.* 1999).

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In species with prolonged parental care, however, offspring provisioning is the major component of parental investment and should therefore be adjusted to mate attractiveness, but unequivocal experimental evidence from wild populations is lacking. Most experimental studies have not demonstrated differential allocation in provisioning rate (Rohde *et al.* 1999; Sanz 2001; Mazuc *et al.* 2003; Pilastro *et al.* 2003). Of the two studies that provide some support, Burley's (1988) pioneering study on zebra finches (*Taeniopygia guttata*) with artificial ornaments, was carried out on captive birds, and the other on barn swallows (*Hirundo rustica*; De Lope & Møller 1993) cannot be unambiguously interpreted as differential allocation. This is because males with experimentally elongated tails (attractive males) reduced their feeding effort and the observed increase in female feeding rate may have been a response to this rather than the male's tail length (Witte 1995, but see also Møller & De Lope 1995). We know of no experimental study that has measured feeding effort in the two sexes of offspring in relation to mate attractiveness, so differential sex allocation in feeding effort has not previously been investigated.

Structural UV coloration in blue tits (*Parus caeruleus*) offers an ideal study system to experimentally test whether females differentially allocate parental feeding effort. Blue tits are sexually dimorphic in the UV spectrum, with males having brighter UV coloration with a peak at shorter wavelengths than females (Andersson *et al.* 1998; Hunt *et al.* 1998). UV crown coloration indicates sexual attractiveness in both sexes (Hunt *et al.* 1999) and male viability (Sheldon *et al.* 1999; Griffith *et al.* 2003). Male UV coloration might thus act as an indicator of the expected value of current offspring and females adjust their feeding effort accordingly (i.e. show differential allocation). In addition, because of high levels of extra-pair paternity, sexual selection is likely to act more strongly in males than females (Kempnaers *et al.* 1992). The expected reproductive success of male offspring may therefore be more dependent on parental attractiveness than that of female offspring, favouring differential sex allocation. Moreover, the experimental test showing that female blue tits modify the sex ratio of the offspring that they produce in relation to manipulated male attractiveness (Sheldon *et al.* 1999) also implies that differential sex allocation in feeding rates would be selectively advantageous. Lastly, we have found (unpublished data) a correlation between female feeding rate and male UV coloration, but an experimental test is needed to determine whether this involves differential allocation.

The aim of this study was therefore to experimentally test whether female blue tits show either differential allocation or differential sex allocation in relation to male UV coloration. We also examined whether any differential allocation had apparent fitness costs for the female parent or fitness benefits for the offspring.

2. MATERIAL AND METHODS

(a) *General description of the experiment*

The experiment was performed in May and June 2002 on a Dutch blue tit population breeding in nest-boxes in the Hoge Veluwe National Park. To study the influence of male sexual attractiveness on parental investment we manipulated the UV coloration of males' crown feathers shortly before hatching and again during

the nestling stage, and video-recorded the feeding behaviour of the adults on days 10 and 14 (where day 0 is the hatching date).

To minimize maternal effects mediated by egg composition (Schwabl 1993) we cross-fostered whole clutches on the estimated day -3 between nests with similar clutch sizes (± 2 eggs) and predicted hatching dates (± 2 days). We caught males on the following day in a random order independent of the cross-fostering, sequentially assigned them to a UV-reduced or control group and applied the respective treatment (see § 2b). As a result, there should be no bias in egg quality with respect to experimental treatment. Moreover, the two treatment groups did not differ in hatching date ($F_{1,23} = 0.31$, $p = 0.58$) or clutch size ($F_{1,23} = 0.01$, $p = 0.94$) after cross-fostering.

On day 3, we individually marked all young and took 10 μ l blood samples, which were used to identify offspring sex by using a molecular technique (Griffiths *et al.* 1998). On day 7, both parents were caught and weighed (to the nearest 0.1 g) and the UV-reduced or control treatment was reapplied to males. Offspring mass (to the nearest 0.1 g) and tarsus length (to the nearest 0.1 mm) were measured on day 15, shortly before the chicks fledge from day 16 onwards.

(b) *Measurements and manipulation of male UV reflectance*

The UV component of male coloration was reduced using a previously developed method (Andersson & Amundsen 1997; Sheldon *et al.* 1999) in which a mixture of UV blocking chemicals (Parsol 1789 and MCX) and duck preen-gland fat was smeared on the males' crown feathers. Control males were treated with the duck preen-gland fat only. Before and after the treatments we took five replicate crown reflectance measures using an USB2000 Spectrometer with a DH2000 deuterium-halogen lamp as light source (both Avantes) illuminating and measuring perpendicularly to the feathers. The reflectance measurements were used to derive the previously identified (Sheldon *et al.* 1999) main predictor of male attractiveness, 'UV chroma' ($R_{320-400}/R_{320-700}$, the proportion of reflectance in the blue tits' visible spectrum (between wavelengths 320 and 700 nm) occurring in the UV (between wavelengths 320 and 400 nm)). This is a measure of the purity of UV coloration. The treatment was successful in producing a difference in the UV chroma of UV-reduced males compared with control males (mean UV chroma in the UV-reduced group = 0.258 ± 0.005 s.e.m.; mean UV chroma in the control group = 0.345 ± 0.004 s.e.m.; ANOVA, $F_{1,35} = 185.03$, $p < 0.0001$). To ensure that males were UV-reduced throughout the nestling period we re-applied the experimental and control treatments on day 7. Within the UV-reduced group the blocking effect was diminished but still significant (comparison with pre-treatment chroma: paired $t = -2.44$, $n = 14$, $p = 0.03$) whereas the UV chromas of control males did not differ from pre-treatment chroma (paired $t = -1.47$, $n = 16$, $p = 0.162$). The second application resulted in similar UV chromas to the first treatment. A small sample of UV-reduced males caught for a third time (mean days post-hatching: 15.2) showed a similar diminished but significant blocking effect (comparison with pre-treatment chroma: paired $t = -3.58$, $n = 5$, $p = 0.023$). In summary, we reduced the UV chroma of UV-reduced males throughout the nestling period although the level of reduction varied considerably.

(c) *Parental feeding effort*

To measure parental investment, we made 3 h infrared video recordings within the nest-boxes on days 10 and 14 and scored the last 2 h of each recording. Chicks had been individually marked

Table 1. Hierarchical mixed model of the number of male and female feeding visits on 10 ($n = 19$) and 14 days ($n = 23$) post hatching in relation to UV treatment (11 UV-reduced pairs, 13 control pairs).

(‘UV treatment’ tests the difference between males in the UV-reduced and control group. ‘Parental sex’ tests the difference between males and females in the control group.)

	Z	d.f.	p
variables included in model			
parental sex	-1.22	1	0.224
UV treatment	0.17	1	0.869
parental sex \times UV treatment ^a	-2.35	1	0.019
brood size	1.84	1	0.066
brood size \times parental sex	4.49	1	< 0.0001
variables not included in model (all $p > 0.05$)			
brood size \times UV treatment			
male UV chroma			
male UV chroma \times parental sex			
male UV chroma \times UV treatment			
male UV chroma \times UV treatment \times parental sex			
chick age			
chick age \times parental sex			
chick age \times UV treatment			

^a The final model was overdispersed (deviance = 234.14 with 78 d.f., $p < 0.001$), but the ‘parental sex \times UV treatment’ interaction remained significant in a scaled-likelihood ratio test (scaled change in deviance = 5.07 with 1 d.f., $p < 0.05$).

with paint spots on their crown and the sex of the parent and the identity of the fed chick was recorded for each feeding visit. Parental loads are normally (93% of visits) given to a single chick but when parents distributed the prey among more than one chick we estimated the proportion that each chick received. Videos were not scored if one of the parents did not enter the nest-box in the first 90 min of the video recording (UV-reduced group: two males, two females on day 10; one control female on days 10 and 14) or if females showed extensive (more than 20 min) brooding behaviour (due to cold or wet weather) during the scoring period (one control each on days 10 and 14).

(d) Statistical analysis

We analysed parental feeding effort (the number of feeds during 2 h), relative investment in offspring sex and offspring tarsus length and mass using hierarchical mixed models in SAS (SAS Institute Inc. 1996). We fitted UV-treatment and its interactions with parental sex (analysis of parental feeding effort), offspring sex (analysis of offspring tarsus length and mass) or both parental sex and offspring sex (analysis of relative investment in offspring sex). We tested additional variables and their interactions as appropriate (see tables 1 and 2) to control for their potential effects. These additional variables and their interactions were removed if they were not significant, but the variables of specific interest (parental and offspring sex, UV treatment) were always retained in the model. Interactions were removed first followed by the main effects. Parental feeding effort was treated as a Poisson-distributed variable using PROC GENMOD with nest as a subject with repeated measurements, UV treatment and brood size as between-subject variables, and parental sex and chick age as within-subject variables. The number of feeds to offspring of each sex were divided by the number of young of that sex and analysed using PROC MIXED assuming a normal distribution, with nest as a repeated measure subject, UV treatment and brood size as

between-subject variables, and parental sex, offspring sex and chick age as within-subject variables. Offspring tarsus length and mass were analysed using PROC MIXED assuming a normal distribution, with individual offspring nested within broods. UV treatment and brood size were fitted as between-nest, and offspring sex as within-nest variables. For offspring mass, we additionally fitted offspring tarsus length as a within-nest variable and the time of weighing as a between-nest variable.

3. RESULTS

Females of UV-reduced males fed at a significantly lower rate than females in control pairs (figure 1). By contrast, UV-reduced males did not differ in feeding rate from control males (figure 1). There was no difference between control parents in feeding rates (figure 1). In our mixed model (table 1), these results are seen as a significant interaction between parental sex and UV treatment, whereas both of these main effects (effectively the sex difference in control pairs and the effect of experimental treatment in males) are non-significant (table 1).

In contrast to the differential allocation in the feeding effort of females, we found no evidence for differential sex allocation. Our treatment did not affect relative investment in male and female offspring (offspring sex \times UV treatment, $F_{1,21} < 0.01$, $p = 0.95$; one brood contained sons only and was excluded from the analysis), and male and female parents did not differ in the number of feeds per offspring sex in relation to our treatment (offspring sex \times UV treatment \times parental sex, $F_{1,21} = 2.52$, $p = 0.127$).

Young, in broods of UV-reduced males had significantly shorter tarsi compared with young in the control group (figure 2; table 2). However, we found no difference in mass between the two groups (figure 2; table 2).

Parental mass taken on day 7 did not differ between the UV-reduced and control group in females (ANOVA, $F_{1,23} = 0.79$, $p = 0.39$) or males (ANOVA, $F_{1,23} = 0.58$, $p = 0.46$).

4. DISCUSSION

Our experiment demonstrates differential allocation in maternal feeding rates in a wild blue tit population. We reduced the sexual attractiveness of males by reducing their UV crown coloration throughout the nestling period; females of those males had lower feeding rates compared with females of non-UV-reduced control males. Because the only difference between the two groups was in the amount of male UV coloration, and mate choice occurred before manipulation, our experimental approach demonstrates that females reduced feeding effort in response to reduced male UV coloration and not to phenotypic or environmental correlates. The interpretation of our results further benefits from the fact that males of both groups did not differ in feeding rates. This avoids the problems of interpretation faced by the earlier experiment on barn swallows (De Lope & Møller 1993; Witte 1995).

The experiment shows that differential allocation by females occurred, but not whether the females responded to the reduced coloration *per se* or to the rapid fluctuations in the UV coloration due to our treatment. Changes in attractiveness might indicate a drop in health status, pointing to a low genetic quality of males (e.g. in disease resistance; Hamilton 1982; Westneat & Birkhead 1998) or a

Table 2. Hierarchical mixed model (type III tests) of tarsus length and mass of male and female fledglings (11 UV-reduced nests, 13 control nests).

	tarsus length (mm)			mass (g)		
	<i>F</i>	d.f.	<i>p</i>	<i>F</i>	d.f.	<i>p</i>
variables included in model						
offspring sex	14.97	1,200	0.0001	53.55	1,189	< 0.0001
UV treatment	6.58	1,17.8	0.0196	0.04	1,22	0.838
offspring sex × UV treatment	0.07	1,200	0.793	1.03	1,189	0.311
variables not included in model (all <i>p</i> > 0.05)						
brood size						
brood size × UV treatment						
brood size × offspring sex						
brood size × UV treatment × offspring sex						
tarsus length ^a						
time of weighing ^a						

^a Tarsus length and time of weighing were used only for the analysis of offspring mass.

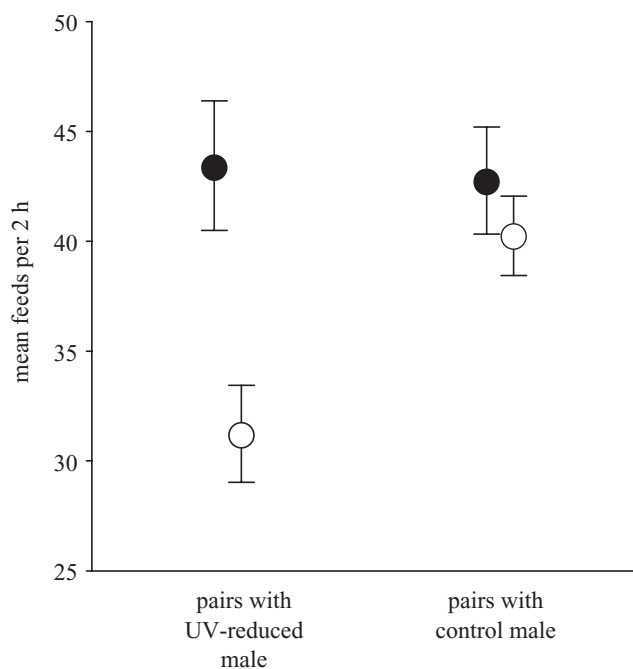


Figure 1. Feeding visits by male and female parents in pairs where the male's UV crown coloration was reduced or subjected to a control treatment. The number of feeding visits by males (filled circles) and females (open circles) was scored from 2 h of video recordings made 10 ($n = 19$) and 14 days ($n = 23$) post hatching from a total of 24 nests. Points shown are the mean (\pm s.e.m.) number of feeding visits estimated from the mean brood size from a hierarchical mixed model (see table 1).

reduced ability to invest in the brood (Møller & Thornhill 1998).

We found no evidence for differential sex allocation in maternal feeding rates, as might have been expected from the previous study on blue-tit sex ratio (Sheldon *et al.* 1999). However, our negative result does not allow us to conclude that the offspring fitness benefits related to differential allocation are not limited to male offspring because parents may simply be constrained by an inability to identify offspring sex, for instance because of the relative darkness inside the nest cavity (Hunt *et al.* 2003).

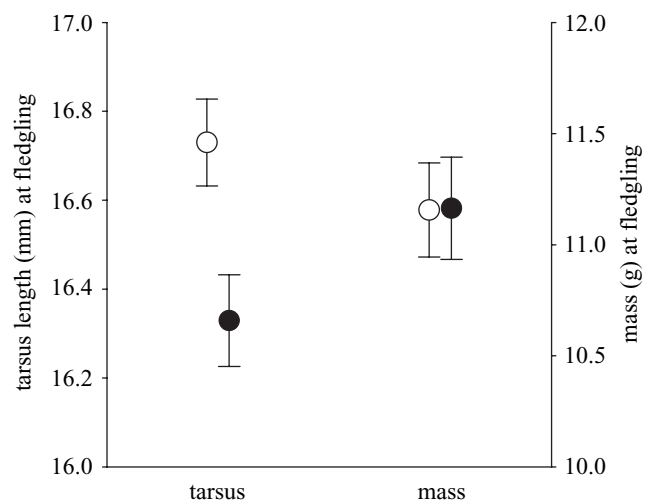


Figure 2. Fledgling tarsus length and mass of chicks with UV-reduced (filled circles, $n = 11$) and control male parents (open circles, $n = 13$). Points shown are the mean (\pm s.e.m.) estimated from hierarchical mixed models (see table 2).

The differential allocation hypothesis suggests that females adjust parental investment to male attractiveness to trade off their own future fitness with current offspring fitness. Consistent with this, we found that reduced investment of females in the UV-reduced group was accompanied by detrimental effects on nestling growth. Young in the UV-reduced group had shorter tarsi than young in the control group but there was no difference in body mass. The different effects on these two body measures might be due to different trajectories for skeletal growth and the accumulation of fat reserves (Kunz & Ekman 2000). To our knowledge, this is the first time that decreased feeding effort in relation to manipulated mate attractiveness in birds has been shown to result in detrimental effects for the offspring. Small body size is known to have adverse effects on offspring survival post fledging and competitive ability later in life (Garnett 1981; Alatalo & Lundberg 1986), so reduced tarsus length is likely to result in reduced offspring fitness. Decreased provisioning might have further costs for the offspring if it hampers the

development of sexually attractive traits. Indicator traits, including blue tit UV coloration, are thought to be condition dependent (Rowe & Houle 1996; Keyser & Hill 1999) and good condition at fledging might be necessary to sufficiently develop attractive UV coloration as adults (Ohlsson *et al.* 2002). A recent study of blue tits showed that fledgling coloration (structural and carotenoid-based colours) is condition dependent (Johnsen *et al.* 2003) and a similar effect of early condition on adult coloration might exist.

The shorter tarsus length of offspring in the UV-reduced group compared with the control group seems to be attributable to the lower feeding rates of females of UV-reduced males. Our experiment therefore shows that the benefits the offspring gain by being sired by a male with an indicator trait of high value may not necessarily be due to 'good genes' for viability passed on from fathers to their offspring. Instead, differences in offspring viability between males could thus be driven purely by male genes for attractiveness, mediated by differential investment of their females.

We could show adverse effects on offspring growth but decreased female investment should also lead to benefits in terms of their own future reproduction (Sheldon 2000). We found no difference between the UV-reduced and control group in female mass on day 7, but females do not provision young extensively before that age, and other variables might well have revealed costs to females. Female blue tits with experimentally enlarged broods had reduced survival (Dhondt 2001), most probably because of an increase in feeding effort. We expect the decreased feeding rates of females of UV-reduced males to have the opposite effect.

We have experimentally demonstrated differential allocation in a wild blue tit population and that this affected offspring growth. Our result supports the idea that fitness benefits of attractive males are not only mediated by advantages in mate choice but also by differential maternal effects (Mousseau & Fox 1998) such as the differential allocation we have demonstrated. Attractive individuals might therefore gain a double benefit: first, through mate choice advantages and second because their mates show increased investment in their offspring. UV coloration has been recognized as a ubiquitous signal across avian families (Eaton & Lanyon 2003) and our finding underlines the importance of UV coloration to sexual selection in birds. Our study, in combination with a previous experimental study showing that female blue tits modified sex ratio in relation to male UV coloration (Sheldon *et al.* 1999), demonstrates that female blue tits may adjust their parental investment in multiple ways to mate attractiveness, and makes blue tit UV coloration one of the best understood signals of sexual attractiveness.

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