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Do Ornaments Effect Parental Investment?

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Zusammenfassung

Es ist wenig bekannt über über den evolutiven Ursprung von weiblichen Gefiederornamenten. Bei einigen Vogelarten entwickeln Weibchen ähnlich prächtiges Gefieder wie Männchen. Während in älteren Studien diese Ausprägung durch genetische Korrelation mit männlichen Gefiederornamenten erklärt wird, so wird zunehmend intrasexuelle und intersexuelle Selektion als treibende Kraft für die Evolution von Gefiederornamenten bei Weibchen gesehen. Zieht man in Betracht, dass bei vielen Vogelarten beide Elternteile an der Aufzucht der Jungvögel beteilig sind und für Männchen dadurch Kosten enstehen, sollten diese hoch qualitative Weibchen wählen. Dies tritt vor allem dann auf, wenn das männliche Investment in die Brut hoch ist und der reproduktive Erfolg von der Fitness des Weibchens abhängig ist. Intersexuelle Selektion findet zu verschiedenen Zeitpunkten des reproduktiven Zyklus statt, nicht nur während der Phase der Partnerwahl sondern auch während der Zeit der Eiablage und Jungenaufzucht.

Unsere Studie befasst sich mit der „Differential Allocation Hypothese (DAH)“. Diese besagt, dass Individuen eine Entscheidung über den Aufwand in derzeitige und zukünftigen Reproduktionsmöglichkeiten treffen müssen. Die Konsequenz ist, dass der elterliche Aufwand an die Attraktivität des Partners angepasst werden sollte, sofern diese Aussage über dessen Qualität gibt. Diese Vorgehensweise steht in engem Zusammenhang mit dem zu erwartenden Gesamtfortpflanzungserfolg eines Individuums (life-time reproductive success) und tritt vor allem dann auf, wenn nur hoch qualitativer Nachwuchs Chancen auf späteren Fortpflanzungserfolg hat.

Um zu testen, ob auch Männchen differential allocation als reproduktive Strategie wählen und Gefiederfärbung bei Weibchen ein Produkt intersexueller Selektion ist, wurde von uns im Frühjahr 2009 und 2010 eine Studie an frei lebenden Blaumeisen (*Parus caeruleus*) durchgeführt. Dabei wurde die blaue Kappe von Blaumeisen-Weibchen während der Phase der Jungenaufzucht mit einer Substanz behandelt, die die UV-Reflexion des Kopfgefieders reduziert. UV-Färbung des Gefieders spielt eine wichtige Rolle bei der Partnerwahl und spiegelt die

Qualität eines Individuums wieder, wie bereits in mehreren Studien sowohl für Männchen als auch für Weibchen nachgewiesen wurde. In der vorliegenden Untersuchung wurde die Gruppe von Weibchen mit reduzierter UV-Reflexion des Kopfgefieders (n = 19) mit einer Gruppe von unbehandelten Kontroll-Weibchen verglichen (n = 11), deren Kappe nur mit Bürzeldrüsenfett (huil de canard) behandelt wurde. Nach der Manipulation des Kopfgefieders der Weibchen wurde das Fütterungsverhalten von Männchen und Weibchen am Nest beobachtet. Zudem wurde das Gewicht der Jungvögel erfasst und ein Experiment durchgeführt, das die Bereitschaft der Elterntiere zur Nestverteidigung testete. Dazu wurde die Attrappe eines für das Studiengebiet wichtigen Nesträubers (Äskulapnatter, *Zamenis longissimus*) am Nistkasten exponiert.

Männchen, die mit UV-reduzierten Partnerinnen konfrontiert wurden, fütterten ihre Jungen signifikant weniger als jene mit einem Weibchen aus der Kontrollgruppe. Sowohl die Futtermenge als auch die Futterflüge pro Jungvogel variierten signifikant zwischen den beiden Versuchsgruppen. Der Räuberversuch ließ keinen signifikanten Unterschied in der Verteidigungsbereitschaft (Zeit bis zur Ankunft des Elterntieres am Nest, Attacken, Abwehrverhalten) erkennen. Auch das Gewicht der Jungvögel änderte sich nicht aufgrund der UV-Manipulation. Die Weibchen selbst unterschieden sich weder in ihrem Fütterungsverhalten, noch ihrem Abwehrverhalten gegen die Räuberattrappe. Die Ergebnisse, im Bezug auf das männliche Fütterungsverhalten, sind weitgehend in Übereinstimmung mit der DAH, die eine Reduktion des elterlichen Aufwandes voraus sagt, wenn ein Merkmal eine geringere Qualität des Partners anzeigt. Entgegen unserer Erwartung und der ursprünglichen Idee der DAH wurde keine Kompensation des reduzierten männlichen Fütterungsverhalten durch die Weibchen beobachtet. Dies führen wir darauf zurück, dass Weibchen meist den Maximalaufwand zeigen, der im Wesentlichen durch Nahrungsressourcen limitiert ist. Des Weiteren blieb ein messbarer Effekt der UV-Reduktion auf das Abwehrverhalten der Vögel aus.

Diese Studie ist einer von wenigen Versuchen sich mit „Differential Allocation“ als Fortpflanzungsstrategie von Männchen zu beschäftigen und dessen Rolle tatsächlich nachzuweisen. Unsere Ergebnisse legen nahe, dass UV-Färbung des

Kopfgefieders von Blaumeisen-Weibchen ein Merkmal ist, dessen Entwicklung durch intrasexuelle Selektion beeinflusst wird.

Abstract

Differential allocation hypothesis (DAH) predicts that individuals will invest in parental care to the offspring of the current reproduction according to their own and their current mate’s quality. This applies to females in most cases, but also to males at least in cases in which female quality is crucial for offspring survival and the males’ parental investment is high. Male differential allocation may at least partly explain why females of several species are ornamented. However, male differential allocation has been tested in only very few experimental studies, revealing contradictory results. We conducted a field experiment to test whether male blue tits (*Parus caeruleus*) allocate their parental effort in relation to female ornamentation (ultraviolet coloration of the blue crown plumage), as predicted by the DAH. We reduced the UV-reflectance in a sample of females and compared the parental care (feeding investment, nest defence intensity) of their mates with the parental care of males paired to females, which were manipulated with avian preen gland fat. Our results revealed a significant effect of female treatment on male feeding trips and food load provided per nestling. As predicted by the DAH our results demonstrate that males invested less in parental effort when paired to UV-reduced females than to control females. Tests of the male nest defence behaviour did not indicate differences between the two female groups; furthermore we did not find differences in nestling body mass between the two female groups. However, to our knowledge, this is one of the first studies providing support for male differential allocation as response to female ornamentation.

Keywords: male allocation, female ornamentation, ultraviolet colouration, blue tits

Introduction

Females frequently choose males on the basis of traits signalling individual quality (Darwin 1871; (reviewed in Andersson 1994). In consequence they gain direct benefits, e.g. through high quality territories and paternal investment, or indirect benefits, because attractive mates may provide good genes for passing viability and attractiveness to offspring (reviewed in Andersson 1994). On the other side there is little knowledge, why in several species also females elaborate showy traits (reviewed in Amundsen 2000). For a long time the presence of ornaments in females was interpreted as consequence of genetic correlation with males' ornamentation (reviewed in Amundsen 2000; Lande 1980). However, recent studies suggested that female ornaments play a role in female-female competition (intrasexual selection) (Griggio et al. 2010b; Jones & Hunter 1999) or are sexually selected by males (intersexual selection) (Amundsen et al. 1997; Doutrelant et al. 2008; Griggio et al. 2009a; Griggio et al. 2005; Smiseth & Amundsen 2000). In species with biparental care males may gain benefits from choosing high quality females and adjust their parental investment in relation to female quality. This may happen if female mate quality variance is high, crucial for offspring survival and the male´ s parental investment is high (reviewed in Amundsen 2000).

The idea of adjusting parental effort in accordance to partners' ornamentation is known as Differential Allocation Hypothesis (DAH). Differential allocation is found whenever individuals face a trade-off between current and future reproduction and reproductive values are connected to attractiveness of the mate (Burley 1986). Several previous studies experimentally tested the DAH, with different results, on a number of species and showed two general pathways (Evans et al. 2010; Head et al. 2006; Oksanen et al. 1999; Sheldon 2000). Positive Differential Allocation (PDA) theory predicts that individuals are willing to pay higher costs when mated to an attractive partner (Burley, 1986). In contrast, Compensatory Investment (CI) theory (Gowaty et al. 2007) suggests that individuals paired to lower quality mates need to increase their parental effort (reviewed in Ratikainen & Kokko 2010). PDA and CI have been basically tested for females' parental effort during different stages of the breeding cycle, starting from egg deposition and egg quality to feeding investment (Cunningham & Russell 2000; D'Alba et al. 2010; Johnsen et al. 2005; Kingma et al. 2009; Ligon & Hill 2010). Considering that female traits can indicate quality (Amundsen et al. 1997; Doutrelant et al. 2008; Griggio et al. 2010b; Roulin 2004), males may allocate parental investment in respect to female ornaments (Matessi et al. 2009; Pilastro et al. 2003). Some studies have explored the importance of female ornaments through mate choice and female quality but very few through male parental investment (Burley 1988; Matessi et al. 2009; Pilastro et al. 2003; reviewed in Ratikainen & Kokko 2010).

The blue crown feathers of the blue tit reflect ultraviolet light (UV) due to interactions between light waves and nanometer-scale physical structures, which result mostly from combinations of keratin and pigment structures (Prum 2006). Variation in UV reflectance is caused by deviations from regularity and precision of the nanometer-scale structure. To achieve and maintain a high UV reflectance is a physiological costly process (Shawkey et al. 2003). Previous studies demonstrated a decrease of UV reflectance in worn feathers and due to dust accumulation (Griggio et al. 2010a; Griggio et al. 2011; Örnborg et al. 2002; Zampiga et al. 2004). Furthermore, removing ectoparasites and dirt from feathers results in a trade-off between preening and activities like foraging (Cucco & Malacarne 1997; Redpath 1988; Walther & Clayton 2005). According to the hypothesis that producing feathers is a costly physiological process and preening behaviour faces a trade-off, individuals in poorer condition cannot afford plumage with high UV-reflectance. This theory meets the results from studies indicating that UV-reflectance of the crown reflects male and female quality (Delhey et al. 2006; Griffith et al. 2003; Griggio et al. 2009b; Sheldon et al. 1999; Szigeti et al. 2007). In order to investigate if males allocate their parental effort in response to female attractiveness we conducted a field experiment on ultraviolet/blue crown colouration of blue tits (*Parus caeruleus*). Blue tits mate assortatively with respect to UV-reflectance of the crown and its importance for mate-choice is confirmed by several studies (Andersson et al. 1998; Hunt et al. 1999). Previous experiments indicated that females allocate egg quality, feeding and nest defence behaviour in relation to crown colouration and ultraviolet reflectance of mates (Hadfield et al. 2006; Johnsen et al. 2005; Limbourg et al. 2004; Szigeti et al. 2007).

The purpose of this work is to relate variation in parental care of males to females' attractiveness. For this reason we captured breeding females, which were assigned to two groups with unchanged and decreased UV reflectance of the blue crown plumage, respectively (control and UV reduced group). We recorded parental effort by conducting behavioural observations and measurements of nestlings' condition. We expected that in line with the DAH (Burley 1986; reviewed in Sheldon 2000) males should allocate more parental care when mated to high quality mates as these are expected to produce higher quality offspring.

Methods

General Methods

The study area is located in Pressbaum (48° 18´ N, 16° 8´ E; about 320 m asl), near Vienna. Our experiment was conducted during spring 2009 and 2010, from the year 2008 approximately 250 nestboxes were installed, which were controlled every 3 days from beginning of March until mid of June.

On day 11 (±1 day) post hatch, parent blue tits were captured from the nest, by closing the entrance hole of the nestbox. Before spectrometric and morphometric measurements and manipulation of the UV reflectance of the crown plumage, sex determination was done by breeding patch, which was still clearly visible. However, sexing was confirmed after breeding season by applying genetic methods (see below). Birds were banded with aluminum rings and a unique combination of darvic colour rings. Furthermore standard measurements of the flattened wing chord length to the nearest 0.5 mm were taken. Weight was recorded to the nearest of 0.1 g (Svensson 1992).

After measurements a blood sample (25 µl) was taken from the brachial vein, from adults as well as from nestlings. The procedure was kept short and below 25 min to ensure nestlings support with food.

Body mass of nestlings was recorded to the nearest of 0.1 g on day 10 and 12 (±1 day) post hatching. Juvenile birds were ringed and measured approximately on day 15 post hatch.

Molecular sexing

Sexing-PCR amplifications were carried out in a total volume of 12.5 µl. Conditions were as follows: 1X PCR Buffer, 2.5 mM M_gCl_2, 200 µM dNTPs, 0.1 uM of each Primer (P2, P8), 2.5 U/µl FirePol, Distilled Water, 2 µl DNA were used for the PCR amplification (Griffith et al. 1998). The PCR was performed in a programmable T1 Thermocycler (Biometra, Göttingen, Germany). Separation was done by gel-electrophoresis for 45-50 min at 9-10 $V{\cdot}cm^{-1}$, in a 2.5% agarose gel (Griffiths et al. 1998).

Treatment and Spectrometry

Crown coloration of captured males and females was measured using a USB-2000 spectrometer and a DHS-2000-FHS deuterium halogen lamp, connected through a bifurcated fiber-optic probe (Ocean Optics, Eerbek, The Netherlands). To exclude disturbance by outer light sources and for keeping standardized distance and angle (90°), a black rubber cylinder was fitted on the top of the probe. Before each measurement the spectrophotometer was recalibrated with a standard white (Avantes, Eerbek, The Netherlands), for calibration of black the probe was removed from the light source and the cap of the plug closed. For quantification of colours standard descriptors of reflectance spectra were used (Hill & McGraw 2006). Measurements were taken from 5 spots of the crown plumage (Fig. 1). Further calculations were carried out using the average of the values we received through the five measurements.

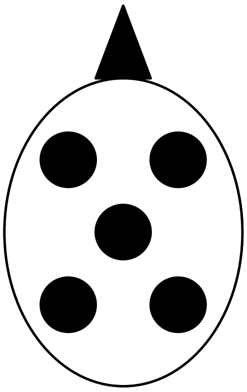

Fig. 1: Dorsal view of a blue tit head showing the 5 spots (indicated by black points) at which UV reflectance of the blue crown plumage was measured.

Calculations were carried out for reflectance in the 300-700 nm range. To quantify UV-reflectance of the blue crown plumage we chose the variable UV-Chroma, which is defined as proportion of UV-reflectance on total reflectance ($R_{300} – R_{400}/R_{300} – R_{700}$) (Delhey et al. 2006; Griggio et al. 2009b; Griggio et al. 2010c; Roberts et al. 2009).

Couples (2009: n = 17, 2010: n = 13) were randomly divided into UV-reduced or control groups (control: n = 11, UV-reduced: n = 19) by altering between two UV-reducing and one control treatment. UV-reflectance of crown plumage was decreased in the UV-reduced group by using a mixture of UV-blocking chemicals (Parsol 1989 and MCX, Roche Switzerland) and duck preen gland fat. Birds of the control group were treated with only duck preen gland fat.

After feathers dried, measurements of reflectance of crown plumage were repeated the same way as before. The chemicals we used are a common method for reducing UV-reflectance in bird’s plumage and were ensured to have no negative effect on bird’s health and behavior (Korsten et al. 2006; Korsten et al. 2007).

Feeding Investment Observations

On day 13 (± 1) post hatching, after the colour manipulation of the female, nests were observed with a spotting telescope for 1 h, either between 6-11 am or 15-17 pm when feeding rates were highest (own observation). The observer was blind to the group (treatment/control) and in about 20 m distance to the nest box, which did not influence feeding behavior of the birds. For each parent, number of feeding trips and prey item size were recorded. Prey item size was estimated by comparing bill length with prey length. According to similar studies prey item size was then categorized in 3 classes: (1) as long as 1 bill length and smaller, (2) 2 bill lengths and (3) 3 bill lengths or larger (Matessi et al. 2009). Feeding trips are quantified as number of visits to the nest per nestling during one hour of observation (total number of feeding trips / nestling number). Food load was measured as the amount of food one nestling received during one hour of observation ((prey item size × total number of feeding trips) / nestling number).

Nest Defense Behavior

To investigate whether reduction of the female UV-reflectance influences male nest defense behaviour on the last day of experiments (13 - 14 post hatching) a rubber dummy of a common terrestrial predator, the aesculapian snake (*Zamenis longissimus*), was placed in and on the nestbox. This snake is known as important predator of nestlings in our area (Johnsen et al. 2005). From the arrival of the first adult individual, the birds were observed for 15 min. During this time the number of attacks and the time individuals spent around rattling were recorded. Latency time was defined as time span between placing the dummy and arrival of the first pair member. All values concerning time were recorded in seconds.

Statistical Methods

All statistical analyses were performed using Statistica 7.1 (Statsoft Inc., Tulsa). The data was tested for normal distribution. For testing effects of UV-reducing and control treatment on female UV-Chroma, paired t-tests were conducted. Independent t-tests between the control and UV-reduced group were used to test for differences in female wing chord length, body condition and UV-Chroma before manipulation. Further analyses on parental investment were carried out with data, standardized for annual effects (Sokal & Rohlfs 1981). To test for treatment effects on parental feeding investment and nestling condition, we carried out General Linear Models (GLM). We included female original UV-Chroma as covariate into the initial models, because UV-Chroma is considered to indicate female quality and condition (Doutrelant et al. 2008; Griggio et al. 2009b; Szigeti et al. 2007). The initial models contained begin of egg laying and brood size on day 13 (±1), respectively, to control for effects of these variables on feeding performance of the birds (Johnsen et al. 2005). Furthermore the initial models contained interactions between each response variable and treatment. Starting with the interactions, non significant terms were step by step eliminated from the model. Each eliminated term was reentered in the final model to confirm the lack of significance (Engqvist 2005). Models testing effects on feeding investment were conducted with absolute and relative values (feeding trips or food load of one parent / feeding trips or food load of both parents). Relative values present the percentage of male and female parental effort and were calculated to test for a shift of parental feeding investment towards one parent. Data describing nest-defence behaviour were not normally distributed. Furthermore the sample size was very small and we did not find significant differences between control and treatment group (Mann-Whitney U-Test), therefore no GLMs were conducted. *P*-values below 0.05 are considered to be significant and all values for parametric tests are given as Mean ± Standard Error (SE), for non parametric tests values are given as Median.

Results

Assortative Mating

UV-Chroma of the crown plumage of male and female blue tits (19 breeding pairs) was positively correlated (*r* = 0.73, *n* = 19, *p* < 0.01; Fig. 1), suggesting the occurrence of assortative mating in respect to UV-reflectance of the blue crown.

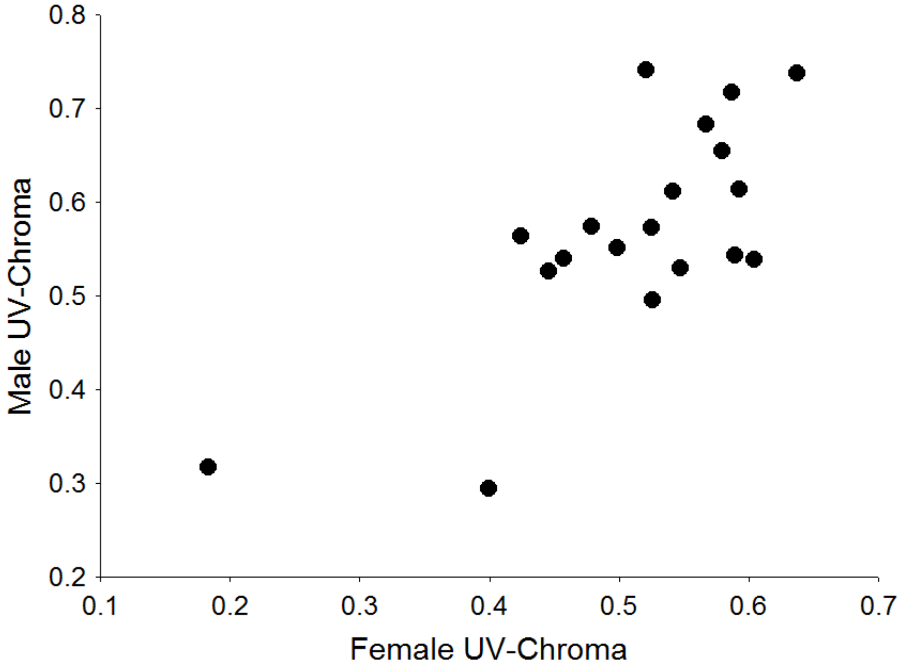

Fig. 2: Relationship between male and female UV-Chroma).

Treatment

Before manipulation females did not vary between control (n = 11) and UV-reduced group (n = 19) in UV-Chroma (Means±SE: control = 0.50±0.03, UV-reduced = 0.46±0.03; t-test: *t* = 0.92, *p* = 0.36), in body condition (control = 25.64±0.85, UV-reduced = 24.10±0.72; t-test: *t* = 1.36, *p* = 0.19) and wing-chord length (control = 6.64±0.05; UV-reduced = 6.59±0.07; t-test: *t* = 0.42, *p*=0.68).

The spectral profile of the crown was strongly affected by the treatment in the UV-reduced group (before = 0.46±0.03, after = 0.40±0.03; paired t- test: *t* = 9.60, *p*< 0.01), but not in the control group (before = 0.50±0.03, after = 0.51±0.03; paired t-test: *t* = -1.59, *p* = 0.14). This corresponds to an enhancement of mean UV-Chroma reflectance of 1.76% in the control group, and an average reduction of 13.36% in the treatment group.

Treatment Effects on Parental Effort

Univariate tests indicate that males provided significantly less feeding trips per nestling when facing a UV-reduced partner (Means±SE: control = 0.56±0.31, *n* = 11; UV-reduced = -0.32±0.19, *n* = 19; t-test: *t* = 2.58, *p* = 0.02; Fig. 2). Furthermore the final model revealed a significant treatment effect on the absolute number of feeding trips per nestling (Tab. 1.) but not on the relative number of feeding trips per nestling (effect size: 0.63; 95% CI: 0.24-1.02; $F_{1,28}$ = 2.76, *B±SE* = 0.29±0.18, *p* = 0.11).

Females did not differ in their feeding trips between UV-reduced and control group (Means±SE: control = -0.05±0.28, n = 11; UV-reduced = 0.26±0.24, *n* = 19; t-test: *t* = -0.19, *p* = 0.85) (Fig. 2). Neither the absolute (effect size: 0.08; CI: -0.30-0.46; $F_{1,28}$ = 0.04, *B±SE* = -0.06±0.19, *p* = 0.85), nor the relative number of female feeding trips per nestling were affected by treatment (effect size: 0.31; 95% CI: -0.07-0.69; $F_{1,26}$ = 0.65, *B±SE* = -0.15±0.18, *p* = 0.43).

Tab. 1: Determinants of male feeding trips per nestling (n = 30) (variables entering the final model are in bold).

	df	*F*	*B*±SE	*p*
Treatment	**1, 28**	**5.43**	**0.39±0.17**	**0.03**
Brood Size		0.01	-0.03±0.19	0.89
Female UV- Chroma		0.34	-0.10±0.18	0.56
Egg-Laying Date		0.11	-0.06±0.19	0.74
Treatment*Egg Laying Date		4.25	-0.38±0.18	0.05
Treatment*Brood Size		0.96	-0.19±0.19	0.33
Experiment*Female UV-Chroma		0.11	-0.06±0.18	0.74

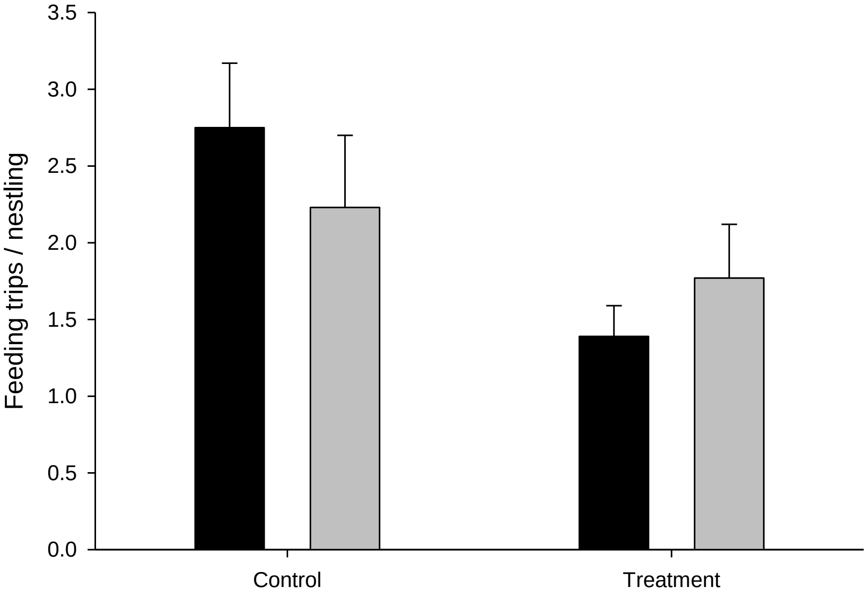

Fig. 3: Males (black bars) differ significantly in their feeding behaviour facing either control or treatment females, whereas females (grey bars) differed not in their feeding effort between the experimental groups (whiskers show SE).

Furthermore, the absolute food load provided per nestling by males paired to UV-reduced females was lower than in males paired to control females (Means±SE: control = 0.70±0.31, n = 10; UV-reduced = -0.37±0.18, *n* = 19; t-test: *t* = 3.23, *p* < 0.01; Fig. 4). Absolute food load per nestling and relative food load per nestling, respectively, were incorporated in the model, demonstrating effects of treatment on absolute (Tab. 2) but not on relative food load (effect size: 0.54; 95% CI: 0.15-0.91; $F_{1, 26}$ = 1.94, *B±SE* = 0.26±0.19, *p* = 0.17). Female absolute food load did not show variation between control and UV-reduced females (Means±SE: control = 0.10±0.34, n = 10; UV-reduced = -0.05±0.22, *n* = 19; t-test: *t* = 0.39, *p* = 0.69). Treatment did not retain in the final model indicating that there was no significant effect on female absolute (effect size: 0.16; 95% CI: -0.23-0.55; $F_{1,27}$ = 0.16, *B±SE* = 0.07±0.19, *p* = 0.69) or relative (effect size: 0.35; 95% CI: -0.04-0.74; $F_{1,26}$ = 0.79, *B±SE* = -0.17±0.19, *p* = 0.38) food load provided per nestling. We excluded one male and one female from the analyses of the effect of treatment on food load provided per nestling, because prey item size was not clearly visible during observation.

Tab. 2: Determinants of male food load per nestling (n = 29) (variables entering the final model are in bold).

	Df	*F*	*B*±SE	*p*
Treatment	**1, 27**	**7.51**	**0.49±0.18**	**0.01**
Brood Size		0.09	-0.06±0.22	0.77
Female UV- Chroma		0.14	-0.07±0.19	0.71
Egg-Laying Date		0.28	0.09±0.18	0.60
Treatment*Egg Laying Date		1.29	-0.19±0.18	0.27
Treatment*Brood Size		1.56	-0.26±0.21	0.23
Treatment*Female UV-Chroma		0.01	0.02±0.19	0.91

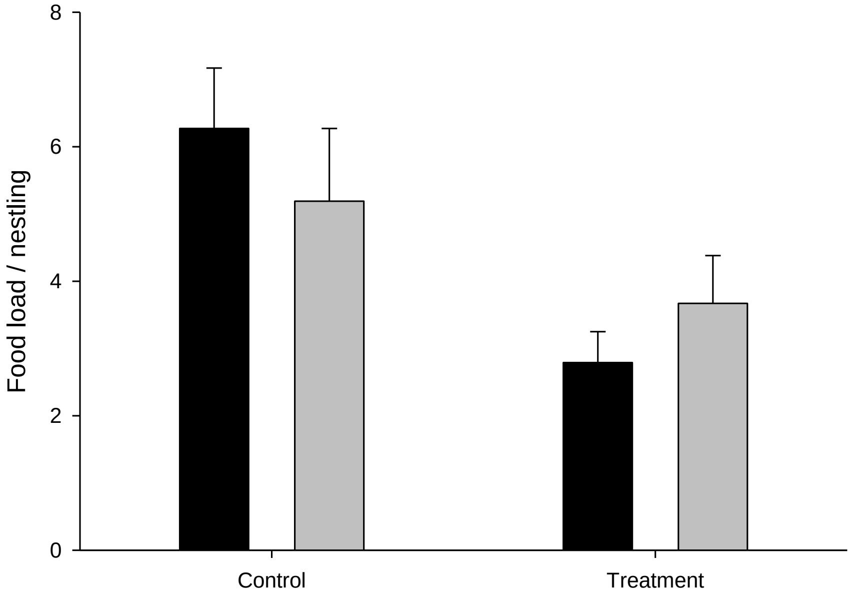

Fig. 4: Males (black bars) provide a significant lower food load per nestling when paired to UV-reduced females than to control females. Females (grey bars) did not feed at significantly different levels between control and UV-reduced group (whiskers show SE).

We did not find statistically significant differences between average body mass of nestlings from nests of control or UV- reduced females (Means±SE: control

= 0.05±1.06, *n* = 10; UV-reduced = -0.03±0.93, *n* = 18; t-test: *t* = 0.23, *p* = 0.53). Brood size and begin of egg-laying respectively, entered the final model and therefore seem to explain certain variation of average nestling body mass between nests. Female UV-Chroma also retained in the model, suggesting a weak negative effect of female UV-reflectance of the crown on nestling body mass (Tab. 3), but further analyzes do not show correlation between female UV-Chroma and nestlings body mass (*r* = -0.18, *n* = 28, *p* = 0.36).

Tab. 3: Determinants of nestling body mass (*n* = 28) (variables entering the final model are in bold).

	df	*F*	*B*±SE	*p*
Treatment		0.03	0.02±0.15	0.87
Brood Size	**1, 20**	**9.10**	**-0.59±0.18**	**<0.01**
Female UV-Chroma	**1, 20**	**1.80**	**-0.41±0.17**	**0.03**
Egg-Laying Date	**1, 20**	**11.95**	**0.64±0.18**	**<0.01**
Treatment*Egg Laying Date		0.28	0.09±0.18	0.61
Treatment*Brood Size		0.46	-0.12±0.18	0.50
Treatment*Female UV-Chroma		0.91	-0.17±0.18	0.35

Treatment Effect on Nest Defence Behaviour

Univariate models did not reveal significant statistical differences in the three variables (Latency, Rattling, Attacks) describing nest defence behaviour between males paired to control and UV-reduced females, respectively (Tab. 4). Furthermore, no behavioural differences related to nest defence behaviour between females from either control or UV-reduced group were found (Tab. 5).

Tab. 4: Differences in three variables describing nest defence behaviour tested for males paired either to control (C) or UV-reduced (UV-) females.

	Males		
	UV- (n =13)	C (n = 8)	results of Mann-Whitney U-test
Latency	-0.46	-0.45	U = 47.5, p = 0.74
Rattling	-0.62	0.41	U = 34.5, p = 0.21
Number of Attacks	-0.19	-0.56	U = 37.5, p = 0.29

Tab. 5: Differences in three variables describing nest defence behaviour tested for females assigned either to control (C) or UV-reduced (UV-) group.

	Females		
	UV- (n =1 3)	C (n = 8)	results of Mann-Whitney U-test
Latency	-0.31	-0.32	U = 46.0, p = 0.66
Rattling	-0.12	-0.15	U = 46.0, p = 0.66
Number of Attacks	-0.32	-0.29	U = 50.0, p = 0.88

Discussion

The treatment of the UV-reflectance of the crown plumage of female blue tits significantly affected male investment in feeding of nestlings. Males decreased their feeding trips and provided smaller food load per nestling, when paired to UV-reduced females, as it is predicted by Burley (1986). The original idea of the DAH predicts that individuals face a trade off between current and future reproduction and therefore adjust their parental effort in accordance to their mate´ s aesthetic traits, whenever these traits are linked to the mate´ s quality (Burley 1986). In consequence males should invest more into offspring provisioning when paired to ornamented females, if ornamentation signals female quality and high male parental investment is necessary. In blue tits UV-colouration is known as an indicator for individual quality and sexually selected trait in several bird species (Delhey et al. 2006; Griffith et al. 2003; Griggio et al. 2009b; Sheldon et al. 1999). The UV-reflectance of structural feathers is caused by a combination of pigments and nanometer-scale structures (Prum 2006; Shawkey et al. 2003), which are produced in costly physiological processes and therefore only individuals in good condition can afford them. It is known that fast moult and nutritional stress can affect the colours of structural feathers (Prum 2006; Griggio et al. 2009b). Recent studies revealed that UV-reflectance of the structural feathers is sensible to wear and might easily be affected by accumulation of dirt and parasites (Griggio et al. 2011; Griggio et al. 2010c; Örnborg et al. 2002; Zampiga et al. 2004). Individuals need to invest time in feather maintenance to keep the feathers in good condition. Plumage maintenance is a costly and time-consuming process, which forces individuals into a trade-off between plumage maintenance and time they need for other activities (e.g. foraging) (Cucco & Malacarne 1997; Redpath 1988; Walther & Clayton 2005). Hence, only individuals in good condition can afford this high investment into feather maintenance and therefore a higher percentage of UV-reflectance (Griggio et al. 2010a).

Our results and recent studies suggest a linkage between female blue tit UV-colouration and condition as well as female breeding performance (Doutrelant et al. 2008; Griggio et al. 2009b; Szigeti et al. 2007). Therefore, we consider UV-reflectance as potential indicator for female quality that might be used by males to assess female quality. Even though a decrease in UV-reflectance during breeding season is a normal process (Delhey et al. 2006) the sudden decrease caused by our treatment might indicate a drop in condition and parental quality for the current mate. Considering that food provisioning for the offspring is costly for the feeding parent (Owens & Bennett 1994), our data indicate that males allocate feeding investment to enhance their chances of future reproduction. Females in bad condition might not be able to provide sufficient parental care, which in turn affects nestling condition and growth. Ohlsson (2002) revealed, that adult sexual selected ornamentation can reflect nutritional condition during early phases of growth in young pheasants. Furthermore recent studies on blue tits indicate that UV-colouration of nestlings is affected by condition (Jacot & Kempenaers 2006; Johnsen et al. 2003). Juvenile males with better condition appear to develop more colourful tail feathers (Jacot & Kempenaers 2006), which are not moulted during post juvenile molt (Cramp & Perrins 1993, p.25-248) and therefore might enhance attractiveness in the first breeding year.

According to the basic idea that individuals choose mates on the basis of ornaments reflecting quality, males paired to females in poor condition may face the problem to produce offspring with low chances for reproduction and indirectly decrease their own reproductive output. The difference in male feeding investment as response to the female treatment would therefore meet the prediction that DA is in linked to reproductive life-history and occurs whenever only high-quality offspring will be able to reproduce (Kempenaers et al. 1992; reviewed in Sheldon 2000). Our results about parental care are in line with two studies, which demonstrated female allocation of parental care in blue tits as response to manipulation of male UV-colouration of the crown (Johnsen et al. 2005; Limbourg et al. 2004). Both studies indicate that male UV-coloration is under selection pressure, created by female allocation of parental care. In consideration of our results and other studies (Johnsen et al. 2005; Limbourg et al. 2004), which also show assortative mating in respect to UV-reflectance, we suggest that also males may create selective pressure towards female UV-colouration of the crown plumage.

Whereas the original idea of DAH also suggests, that less attractive partners should increase their parental investment (Burley 1986), we did not find any effects of the treatment on female parental care. Johnsen et al. (2005) demonstrated that males invested more into parental care when their UV-reflectance was reduced. One possible explanation for the female lack of compensation could be that females were already at the maximum of their possible investment (Trivers 1972). The weather during spring 2009 and especially 2010, was cold and rainy. Food resources for the birds were probably limited and female food provisioning was restricted by the availability of resources.

Although males provided significantly less food to nestlings from UV-reduced females than to females from the control group and females did not compensate the drop in paternal feeding investment, we did not find any effects of the treatment on body mass between nestlings of both experimental groups. The experiment was conducted only few days before fledging, a time during which the growth of passerine nestlings often stops and weight decreases, this might have covered effects of treatment on nestlings´ body-mass (see O'Connor 1985, p.73-74). Furthermore we did not collect daily data about nestlings' development after female treatment, which could have been more informative. Nestlings' body mass might not be a sensible indicator for testing the treatment effects on nestling development.

An experimental approach of Burley (1988) revealed a correlation between female attractiveness and male feeding investment in zebra finches, whereas no linkage between attractiveness of the female and nest defence behaviour of their mates was found. In contrast a recent experiment on rock sparrows presents a reduction of male nest defence intensity as response to reduction of female attractiveness, but not in feeding investment (Matessi et al. 2009; Pilastro et al. 2003). We did not find differences in nest defence behaviour of males paired to either control or UV-reduced females. This is not in line with the experiment from Johnsen et al. (2005), which indicated female allocation of nest defence behaviour as response to male UV-reduction in blue tits. Our results could have been caused by a lack of treatment effect during the nest defence experiment. The decrease of the UV-reflectance might have been too small (13.36%) to avoid a “strange-mate” effect, which could have influenced the experiment. The treatment is known to diminish the UV-reflectance for only several days in wild birds (Korsten et al. 2007). Whereas the feeding investment observation was conducted the day after manipulation of the female crown plumage, nest defence behaviour was observed 3-4 days after treatment. During this period the UV-reducing chemical could have been removed by plumage preening.

To test whether males allocate only in certain stages of parental investment and to test in which stages of the breeding cycle male allocation can appear, further research has to be done. Eventually in addition to a UV-reduced and control group also the generation of an UV-enhanced group could be of interest as demonstrated by Johnsen et al. (2005).

In conclusion, our results show that male blue tits make parental care decisions in accordance to their mate´ s quality. To our knowledge this is one out of very few experimental studies demonstrating male differential allocation in relation to female attractiveness.

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Italienisch:	Grundkenntnisse
Französisch:	Grundkenntnisse