

The Early Maternal Environment Shapes the Parental Response to Offspring UV Ornamentation

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Abstract

Parents allocate resources to offspring to increase their survival and to maximize their own fitness, while this investment implies costs to their condition and future reproduction. Parents are hence expected to optimally allocate their resources. They should invest equally in all their offspring under good conditions, but when parental capacity is limited, parents should invest in the offspring with the highest probability of survival. Such parental favouritism is facilitated by the fact that offspring have evolved condition-dependent traits to signal their quality to parents. In this study we explore whether the parental response to an offspring quality signal depends on the intrinsic capacity of the parents, here the female. We first manipulated the intrinsic capacity of blue tit (*Cyanistes caeruleus*) females through lutein-supplementation during egg laying, and we subsequently blocked the UV/yellow reflectance of breast feathers on half of the nestlings in each brood. However, we did not find evidence that the female intrinsic capacity shaped parental favouritism for offspring UV/yellow colouration, as there were no differences in parental feeding or sibling competition. However, we found that males were more responsive than females to nestling UV/yellow when rearing capacity was high, as indicated by the prey-testings (when a parent places a prey item into a nestling's gape but removes it again). Furthermore, when considering a more integrative measure, offspring growth, we did find the expected interaction effect. In control nests, UV-blocked nestlings gained less body mass than their non-UV-blocked siblings, whereas in lutein-supplemented nests UV-blocked nestlings gained more mass than their siblings. Overall, our results emphasize the female's environment at an early reproduction stage shaped the role of offspring UV/yellow during family interactions illustrating plasticity in parental feeding rules.

Introduction

Parents invest in their progeny in order to increase the offspring chances of survival, but resources are limited (1). Hence, resource allocation to current offspring entails costs to parents in terms of reduced own survival and future reproductive prospects (2). How parents optimally allocate their resources may not only vary across breeding events, but also among offspring of the same brood, at least in species raising more than one offspring at a time. When conditions are favourable (e.g., in benign environments and under high resource availability), the optimal strategy that guarantees the survival of all the offspring is that parents are egalitarian and feed all the young equally (3–4) or even favour the offspring with the highest need (5). However, under harsh conditions, individuals possess reduced parental capacities, which might not be enough to raise all the offspring. Then, parents are expected to bias their investment to offspring in better condition that will return greater fitness benefits (6), thus following a brood reduction strategy (7–8). Yet, this requires that parents assess offspring quality, which they could do based on the expression of signalling traits, such as behavioural (e.g., vocal or postural begging displays; 9–10) or structural traits (like the colouration of plumage, scales and skin; 11–12).

Signals of quality have been particularly well studied in the context of sexual selection (13–14). A couple of paradigmatic examples are the tail feathers of male peacocks or male deer antlers, and one main mechanism proposed to ensure the honesty of such signals is that they are costly to produce and

maintain (15–16). Interestingly, however, it is evident that signalling can play a significant role in other non-sexual contexts, including the period of parental care (17). Here, both offspring and parents are potential bearers and receivers of signals of quality expressed by other family members (18–19). For instance, one of the most common offspring signals is begging behaviour (i.e., solicitation of food from parents by means of postures and vocalizations), which dynamically transmits information about offspring state and need to both parents (20) and siblings (21). During these family interactions offspring may also display conspicuous structural traits such as colourful scales, gapes or feathers to trigger a parental response (22–23). Honesty is again achieved because there is a cost to displaying or expressing offspring signalling traits that prevents cheating (honest signalling models; 24).

A well-known example of offspring signalling traits with a significant role in parent-offspring communication is the ultraviolet (UV) colouration of skin and other traits like beaks and feathers. Studies in various bird species showed that nestling UV skin colouration reliably reflects body mass and skeletal size (see 25, in alpine swifts *Tachymarptis melba* and European starlings *Sturnus vulgaris*), as well as immune responsiveness (see 26, in European starlings). Body mass is also correlated with nestling UV gape (see 23 in barn swallows *Hirundo rustica*) and feather colouration (see 27 in blue tits *Cyanistes caeruleus*). However, it has been argued that the parental response to offspring signalling traits may vary according to the current circumstances (28). Indeed, evidence suggests that parents favour nestlings with enhanced UV colour as the breeding season progresses - once the resources become limiting (25). However, it has been little explored experimentally whether parents favour specific offspring within a brood according to both the expression of offspring UV coloured signals and their own parental capacity, which is mainly constrained by resource availability. It has in addition to be considered that the expression of signalling traits may be shaped by multiple receivers (29).

In this study, we investigate whether parental care strategies depend on the expression of an offspring quality signal, and whether parental preferences for signal expression vary with the rearing capacity of the parents. To test our hypothesis, we first experimentally manipulated the availability of a specific micronutrient (i.e., lutein) for blue tit females at egg laying, which is the most energy-demanding stage of the females' life. Indeed, we have previously found that lutein supplementation facilitated egg laying, thus improving the female's intrinsic capacity (30). Additionally, we experimentally manipulated a nestling quality signal, the UV/yellow breast plumage colouration in half of the nestlings within each brood. Blue tit nestlings with experimentally reduced UV reflectance are in lower condition and beg more during parent-offspring and sib-sib competitive interactions (29).

We expected that females with enhanced intrinsic capacity (i.e., lutein-supplemented females) should be more egalitarian and preferentially feed the offspring signalling poor quality (i.e., UV-blocked plumage colouration) to allow them to catch up in growth with their siblings (brood survival strategy). On the contrary, control females with a more limited capacity should favour high-quality offspring (brood reduction strategy), which should be reflected in a significant body mass difference between UV-blocked and non-UV-blocked nestlings. Finally, we also expected that UV-blocking would play a role during sibling competition, in particular in the absence of the parents when begging is directed to and perceived only by

siblings. Here, begging has been interpreted as a nestling strategy to negotiate future access to food when parents arrive at the nest again (31). So we expected UV-blocked nestlings to beg more, as previously found in our study population (29), and especially so in control nests, in which the females' rearing capacity was more limited.

Material And Methods

Ethics statement

All the methods were performed in accordance with the Spanish laws in relation to animal research. The study licenses to perform the experimental protocols were approved by the Spanish Research Council (CSIC, ref. 639/2017) and the Consejería de Medio Ambiente, Administración Local y Ordenación del Territorio, Comunidad de Madrid (ref. 10/056536.9/18; PROEX 237/17).

The study was conducted in compliance with the ARRIVE guidelines.

General methods and study species

This study was carried out in the locality of Miraflores de la Sierra (Madrid, Spain, 40° 48'41.07" N, 3°46'57.66" O) during the spring of 2017. The study area embraces 187 nest-boxes spread out in a deciduous forest mainly dominated by Pyrenean oak (*Quercus pyrenaica*) at 1250 m of elevation. We studied a breeding population of blue tits, a territorial-monogamous passerine that in our study area only raises one clutch per season. Brood size is large (in our study population, on average 9.6 eggs \pm 1.8 SD; n = 464 clutches; range 4–15). Both adults and offspring express colourful feather traits that are known to function as signals of quality. The most studied one is the UV reflectance of blue crown feathers in adults (e.g., 32–33), which is not expressed in the offspring. However, the UV reflectance of yellow breast feathers is expressed both by parents (34) and offspring (29), and has been shown to reflect different aspects of individual quality (27, 34–35).

At the start of the breeding season, we visited nest-boxes every two days to record the beginning of nest construction, laying date and hatching date (day 0). Once nest construction was finished in a given nest, that is, when the moss cup was well defined but not filled with feathers and hair, we started lutein supplementation in that nest (see *Lutein supplementation* section below; for more details, see also 30). We continued supplementing blue tit females during egg laying and finished once incubation started. Lutein is the main carotenoid pigment present in the birds' plasma (36) and eggs (37), and is crucial for offspring development and feather colouration (38–39).

Lutein-supplemented females completed their clutch faster than control females, as the treatment reduced the occurrence of egg-laying interruptions (30). Two days before the expected hatching date, we performed a full-brood cross-fostering by exchanging clutches between nests in a fashion that allowed both lutein-supplemented females (n = 24) and control females (n = 23) to raise a control clutch. That is, the original clutches laid by lutein-supplemented females were raised in other nests not included in the present study. The rationale behind using only control clutches raised by both types of females was to

exclude the influence of early maternal effects (i.e., differential carotenoid allocation into eggs) on offspring development.

In the second week after hatching (days 9–12), we trapped adults in their nest-boxes and marked the first one captured on the back feathers with a white marker (Edding 751; code 049), which allowed us to distinguish parents during video observations. On day 12, we ringed the nestlings, measured their body mass using a Pesola spring balance (to the nearest 0.01 g) and marked them individually on the head with the same white marker used for adults. We also collected 3–5 breast feathers per chick for molecular sexing (see Supplementary material). On day 12, we also substituted the original nest-box by a recording nest-box to familiarize parents with the set-up before the video recordings started. On day 13, we placed a night-vision video camera on the recording nest box (DX, 8 LED and 180° vision, China) and recorded the behaviour of all family members for 1.5 h. Just after video recording, we manipulated offspring UV colour within nests (see *Experimental manipulation of UV reflectance* below). On day 14, we again recorded the behaviour for 1.5 h to assess the behavioural change of family members according to offspring UV colour and lutein-supplementation. At the end of the second video recording, we once more weighed all nestlings. We then calculated body mass change from days 12 to 14.

Lutein supplementation prior and during egg laying

At the end of nest construction, we visited nests every two days and lutein was supplied in experimental nests using a dose of 50 mg of Versele Laga Yel-lux Oropharma (lutein 8,000 mg/kg), which corresponds to 0.4 mg of lutein and which is within the natural limits consumed by blue tit females (for a detailed explanation, see 30). Each dosage was mixed with 5 g of commercial bird fat with nuts (GRANA Oryx), whereas the same amount of bird fat without lutein was provided to nests in the control treatment. We confirmed through direct observations that males rarely visited the nest during nest construction and we can thus assume that the supplement was mainly consumed by females (30).

Experimental manipulation of offspring UV feather reflectance in all nests

Prior to UV colour manipulation, we measured the original UV reflectance of nestling yellow breast feathers with a portable spectrophotometer (Jazz, OceanOptics®). UV Chroma was calculated as the reflectance in the UV wave-band region of the spectrum divided by the total reflectance of the spectrum in the avian visual range ($R_{300-400}/R_{300-700}$), following Johnsen et al. (27). Original nestling UV/yellow chroma did not differ between control and lutein-supplemented nests ($F_{1,42.8} = 0.00$; $P = 0.95$) nor between UV-blocked and non-UV-blocked siblings within nests ($F_{1,300} = 1.29$; $P = 0.26$).

On day 13 and just after recording behaviour for the first time, we experimentally reduced the UV reflectance of yellow breast feathers in half of the nestlings in each nest using a yellow marker (Edding 4500; code 005). We randomly assigned the non-UV-blocked and UV-blocked treatment to the first nestling to be handled and then we alternated treatments for the rest of the brood. This manipulation has been successfully applied previously to both blue tit nestlings (29; see 40, in great tits, *Parus major*) and

adults (34). By reducing the UV/yellow reflectance, half of the nestlings in each nest resembled individuals in poor body condition. We applied the same marker to non-UV-blocked siblings but in the lower part of the wing feathers. This was done to control for potential undesired side-effects of the marker but in a similar-sized region that cannot be seen by other family members. Nonetheless, in previous studies, we have not detected side-effects of the markers on blue tit health or behaviour (29–30).

Behavioural variables

We registered the behaviour of all family members individually during 30 minutes (excluding the first half an hour and the last 10 minutes of the video to avoid possible interferences due to placing or removing the camera). We registered parental decisions in the form of feeding rates and prey-testings. The latter occur when parents introduce a prey item in a nestling gape and then remove it again (41–42), and it has been proposed as a strategy used by parents to assess individual offspring hunger levels, since it triggers begging (29). Prey testings are thus like a “hunger test” that might be especially important under conditions of low food availability. Moreover, in the study population, prey-testings have been found to impose a cost to nestlings in terms of growth (29).

We also registered sibling competition, which we measured as parent-absent begging, when begging can only be perceived by siblings (see for instance, 21). Each time the parents had left the nest, we waited 30 seconds and then recorded parent-absent begging during another 30 seconds. For scoring begging behaviour, we followed a 4-point scale adapted from Kölliker et al. (43): 0 = calm, 1 = weak gapping, 2 = gapping and neck stretched, 3 = gapping, neck stretched and standing, 4 = gapping, neck stretched, standing and wing flapping (see also 29). We obtained the behavioural data of individual nestlings (i.e., number of prey items and prey-testings received, as well as the begging levels during parent-absent events). Then, for each behavioural variable we calculated the change between final (post-UV treatment) and initial values (pre-UV treatment). Observers always was unaware of female treatment and nestling UV treatment. Moreover, the sex of the parents was unknown for the observers, who only distinguished between presence/absence of an adult’s back mark.

We were able to register both pre- and post-UV treatment behaviour in 32 nests. Sample sizes differ when the behaviour of fathers and mothers was analysed separately, since the father appeared in both videos in 24 nests and the mother in 29 nests. Finally, we lacked visibility to score prey testings and nestling begging intensity in certain nests when focal nestlings were not visible.

Statistical Analyses

We used SAS 9.4. (SAS Inst., Cary, NC, USA) for all statistical analyses. Since we were interested in the interaction term between both treatments to address the main study question (how parental care strategies depend on UV/yellow of nestlings and how these vary with the availability of lutein for blue tit laying females), models were not simplified and we thus present full models including the interaction. Models were checked for residual normality using a Shapiro Wilk tests. Furthermore, all tests were conducted using a Type III sum of squares. All mixed models included a random intercept (nest ID) and a

random slope (nest ID x nestling UV treatment) in order to account for the fact that half of the nestlings in each nest were UV-blocked and the other half were not.

We analysed the number of prey-testings and the number of prey items received by each nestling using generalized mixed models (GLIMMIX procedure in SAS with Poisson error structure). In these models we included female treatment, nestling UV treatment, nestling sex, brood size, hatching date and the interaction between both treatments as fixed effects. We ran linear mixed models (MIXED procedure in SAS) to analyse parent-absent begging. In these models, we included the same variables as above.

Finally, we examined whether body mass change (\log_{10} transformed) was affected by the treatments with a linear mixed model that included the same variables as above.

Results

Feeding rates of males and females were not affected by the interaction between both treatments (Table 1; Figure 1). However, we found that the number of prey-testings performed by males, but not by females, were indeed affected by the interaction between lutein and UV treatment (Table 2). In lutein-supplemented nests, males prey-tested UV-blocked chicks less often than their non-UV-blocked siblings, while in control nests, males did not prey-test chicks differently according to UV treatment (Figure 2).

Table 1

Mixed models showing the effects of nestling UV treatment (non-UV-blocked/UV-blocked feather colouration) and female treatment at laying (control/lutein-supplemented) on the number of preys provided by both parents, by males and by females. Coefficients are shown for control nests, non-UV-blocked nestlings and females.

	<i>Parental feeding</i>	<i>Female feeding</i>	<i>Male feeding</i>
<i>Intercept</i>	<i>coef</i> = -0.61 ± 1.68	<i>coef</i> = 1.70 ± 2.28	<i>coef</i> = -2.92 ± 2.87
<i>Female treatment</i> (Control)	<i>coef</i> = -0.24 ± 0.28 $F_{1,66} = 1.83$ $P = 0.18$	<i>coef</i> = -0.23 ± 0.41 $F_{1,67} = 0.69$ $P = 0.41$	<i>coef</i> = -0.05 ± 0.37 $F_{1,55} = 0.26$ $P = 0.61$
<i>Nestling UV treatment</i> (Non-UV-Blocked)	<i>coef</i> = -0.06 ± 0.25 $F_{1,25} = 0.36$ $P = 0.55$	<i>coef</i> = 0.12 ± 0.36 $F_{1,24} = 0.13$ $P = 0.72$	<i>coef</i> = 0.05 ± 0.31 $F_{1,20} = 0.07$ $P = 0.80$
<i>Nestling sex</i> (Females)	<i>coef</i> = 0.02 ± 0.18 $F_{1,66} = 0.01$ $P = 0.92$	<i>coef</i> = 0.21 ± 0.23 $F_{1,67} = 0.79$ $P = 0.38$	<i>coef</i> = -0.02 ± 0.22 $F_{1,55} = 0.01$ $P = 0.92$
<i>Hatching date</i>	<i>coef</i> = -0.003 ± 0.04 $F_{1,66} = 0.01$ $P = 0.94$	<i>coef</i> = -0.06 ± 0.05 $F_{1,67} = 1.03$ $P = 0.31$	<i>coef</i> = 0.03 ± 0.06 $F_{1,55} = 0.26$ $P = 0.61$
<i>Brood size</i>	<i>coef</i> = 0.11 ± 0.08 $F_{1,66} = 1.71$ $P = 0.20$	<i>coef</i> = -0.03 ± 0.11 $F_{1,67} = 0.09$ $P = 0.77$	<i>coef</i> = -0.23 ± 0.15 $F_{1,55} = 2.29$ $P = 0.14$
<i>Female treat. * Nestling UV treat.</i>	<i>coef</i> = -0.11 ± 0.36	<i>coef</i> = -0.07 ± 0.46	<i>coef</i> = -0.22 ± 0.43

$$F_{1,66} = 0.09$$

$$P = 0.77$$

$$F_{1,67} = 0.02$$

$$P = 0.88$$

$$F_{1,55} = 0.26$$

$$P = 0.61$$

We did not find differences in parent-absent begging, thus in sibling negotiation/competition, according to the interaction between both treatments (Table 2).

Table 2

Mixed models showing the effects of nestling UV treatment (non-UV-blocked/UV-blocked feather colouration) and female treatment at laying (control/lutein-supplemented) on the number of prey-testings performed by parents, the parent-absent begging intensity and the (log) body mass change. Coefficients are shown for control nests, non-UV-blocked nestlings and females. Significant differences are marked in bold.

	<i>Prey-testings performed by females</i>	<i>Prey-testings performed by males</i>	<i>Parent-absent begging</i>	<i>Body mass change</i>
Intercept	<i>coef</i> = -6.57 ± 6.50	<i>coef</i> = 0.08 ± 7.09	<i>coef</i> = 0.62 ± 1.05	<i>coef</i> = 0.35 ± 0.21
Female treatment (Control)	<i>coef</i> = 0.12 ± 0.94 <i>F</i> _{1,70} = 0.00 <i>P</i> = 0.99	<i>coef</i> = 1.03 ± 0.78 <i>F</i> _{1,57} = 0.15 <i>P</i> = 0.70	<i>coef</i> = 0.003 ± 0.12 <i>F</i> _{1,17.9} = 0.08 <i>P</i> = 0.77	<i>coef</i> = -0.02 ± 0.03 <i>F</i> _{1,42.6} = 0.32 <i>P</i> = 0.57
Nestling UV treatment (Non-UV-Blocked)	<i>coef</i> = 0.61 ± 0.68 <i>F</i> _{1,18} = 1.15 <i>P</i> = 0.30	<i>coef</i> = 0.83 ± 0.49 <i>F</i> _{1,14} = 0.06 <i>P</i> = 0.81	<i>coef</i> = -0.004 ± 0.099 <i>F</i> _{1,127} = 0.11 <i>P</i> = 0.74	<i>coef</i> = -0.05 ± 0.02 <i>F</i> _{1,293} = 1.51 <i>P</i> = 0.22
Nestling sex (Females)	<i>coef</i> = -0.54 ± 0.27 <i>F</i> _{1,70} = 4.04 <i>P</i> = 0.05	<i>coef</i> = -0.25 ± 0.27 <i>F</i> _{1,57} = 0.86 <i>P</i> = 0.36	<i>coef</i> = -0.10 ± 0.07 <i>F</i> _{1,138} = 2.31 <i>P</i> = 0.13	<i>coef</i> = 0.01 ± 0.01 <i>F</i> _{1,305} = 0.19 <i>P</i> = 0.66
Hatching date	<i>coef</i> = 0.19 ± 0.16 <i>F</i> _{1,70} = 1.30 <i>P</i> = 0.26	<i>coef</i> = 0.01 ± 0.16 <i>F</i> _{1,57} = 0.01 <i>P</i> = 0.94	<i>coef</i> = 0.003 ± 0.025 <i>F</i> _{1,19.6} = 0.02 <i>P</i> = 0.90	<i>coef</i> = -0.003 ± 0.005 <i>F</i> _{1,42.7} = 0.23 <i>P</i> = 0.64

Brood size	<i>coef</i> = -0.15 ± 0.24 <i>F</i> _{1,70} = 0.40 <i>P</i> = 0.53	<i>coef</i> = -0.21 ± 0.26 <i>F</i> _{1,57} = 0.64 <i>P</i> = 0.43	<i>coef</i> = -0.09 ± 0.04 <i>F</i> _{1,24.1} = 6.58 <i>P</i> = 0.017	<i>coef</i> = 0.003 ± 0.010 <i>F</i> _{1,46.4} = 0.09 <i>P</i> = 0.76
Female treat. * Nestling UV treat.	<i>coef</i> = -0.20 ± 0.94 <i>F</i> _{1,70} = 0.05 <i>P</i> = 0.83	<i>coef</i> = -1.51 ± 0.68 <i>F</i> _{1,57} = 4.97 <i>P</i> = 0.029	<i>coef</i> = -0.05 ± 0.13 <i>F</i> _{1,127} = 0.15 <i>P</i> = 0.70	<i>coef</i> = -0.07 ± 0.03 <i>F</i> _{1,293} = 6.81 <i>P</i> = 0.0095

However, as expected, there was a significant effect of the interaction between both treatments on nestling body mass change (Table 2). In lutein-supplemented nests, UV-blocked nestlings gained more body mass than their non-UV-blocked siblings (Figure 3). In control nests, the offspring did not differ in body mass change according to UV treatment.

Discussion

Our results suggest that the UV/yellow colouration of nestlings does not affect parental feeding rates or sibling competition (i.e., parent-absent begging) according to the availability of lutein during egg laying. However, males of lutein-supplemented nests prey-tested UV-blocked nestlings less often than their non-UV-blocked siblings, which was mirrored in the body mass change, since UV-blocked nestlings gained more body mass than their siblings but only in lutein-supplemented nests. Therefore, nestling UV/yellow colour modulated certain intra-family interactions according to the quality of the prenatal environment (and thus to the females' rearing capacity; 30), which ultimately affected offspring growth.

There were no significant differences in parental feeding behaviour between UV-blocked and non-UV-blocked nestlings, independently of lutein availability in the prenatal environment. Thus, neither males nor females favoured high quality offspring (i.e., non-UV-blocked nestlings), while we expected such parental favouritism to arise when rearing capacity was insufficient to raise all the offspring (4) (here, in control broods in which females did not receive the lutein supplementation prior to laying). Although positive effects of lutein supplementation had been observed during egg laying (30), it is possible that the environmental conditions at later stages were too favourable to detect differences. Perhaps a handicapping manipulation such as feather clipping or a more drastic food deprivation experiment (e.g., by temporarily closing the nest-box entrance) (44–45) would have resulted in significant differences. Besides, we only observed thirty minutes of behaviour, which is a snapshot of intra-family interactions during the two days elapsed since UV manipulation took place.

Yet, half an hour of observation was enough to detect significant differences in the prey-testings performed by male parents. In lutein-supplemented nests males tested UV-blocked nestlings (signalling poor condition) less often than their non-UV-blocked siblings, whereas there were no significant differences in control nests. Recently, prey-testings in blue tits have been interpreted as a parental strategy to evaluate nestling hunger levels (29). Similar costly “hunger tests” have been found in other avian, mammal and insect species (46–49) raising more than one offspring at a time and as result of parent-offspring conflict over parental care. Such tests are costly for the offspring since they commonly trigger offspring begging, usually through the expression of signals of parental quality (i.e., the bill red spot in some gull species; 49–50) or active behaviours (i.e., feeding races in penguins; 47, 51). Hence, parents can evaluate the offspring true motivation of being fed and be more efficient in optimizing their investment (e.g., by shifting their care to the neediest sibling when rearing capacity is high). Forced energy expenditure could also explain why more prey-testings impose a growth cost to blue tit nestlings (29). A non-exclusive possibility is that prey-testings occur when nestlings have gapes not large enough to swallow big preys (41). However, this interpretation cannot explain our results, since the occurrence of prey-testings and prey size were not correlated, neither prior to UV-blocking ($r_{32} = -0.21$; $P = 0.25$) nor after it ($r_{20} = 0.16$; $P = 0.53$). Our results rather suggest that, under conditions of high resource availability, at least fathers were more inclined to favour UV-blocked nestlings without testing them, suggesting parental preference based on quality signals. Interestingly, previous results in the same study population suggested that only males but not females modified prey-testings according to both nestling UV colour and food availability at the end of the nestling period (29). Our results together with previous evidence points to the possibility that males are more responsive to nestling UV colouration than females.

We also hypothesized that UV-blocked nestlings - those signalling poor condition - should beg more than their non-UV-blocked siblings when parents are absent, since they should try to discourage their siblings from competing for the next parental feeding (“sibling negotiation hypothesis”; 31). However, we did not detect significant effects on sibling competition, in contrast to a previous study (31). As discussed above, it is possible that environmental conditions were too favourable in the postnatal environment (well after lutein supplementation) so that differences on nestling need among UV treatments diminished.

Interestingly, however, in lutein-supplemented nests, UV-blocked nestlings gained more body mass than their non-UV-blocked siblings, but in control nests, offspring did not differ in body mass change according to UV treatment.

Thus, when rearing capacity was low, UV-blocked offspring were not favoured over high-quality offspring while the opposite was true when rearing capacity was high. Since all the offspring included in the experiment belonged to a clutch laid by a control female, we can be sure that body mass change was not affected by early maternal effects but rather by behavioural interactions among family members. One likely possibility is that the father’s prey-testings mediated body mass change, and thus low-quality chicks gained more body mass because they were prey-tested less often in lutein-supplemented nests (see the contrasting patterns in Figs. 2 and 3). Besides, in control nests, UV-blocked offspring tended (not significantly) to gain less body mass and to receive more prey-testings than their non-UV-blocked

siblings. Thus, by reducing the prey-testings to UV-blocked nestlings in lutein-supplemented nests, fathers would be compensating for their low quality and facilitating a brood survival strategy. Moreover, even small differences in behaviour would become relevant since significant effects were found for nestling body mass, which is a more integrative measure

In conclusion, our results thus suggest that conditions in the prenatal environment determine the importance of offspring UV signals in mediating behavioural intra-family interactions. Finally, males were more responsive than females to nestling UV colouration when rearing capacity was high, thus supporting previous findings on sex-specific care strategies.

Declarations

Acknowledgments:

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Author contribution:

JGC & JM performed fieldwork. JGC performed the statistical analyses. JGC wrote the manuscript, which was reviewed by the rest of co-authors. JGC & EHC analysed behavioural data. JM & WM conceived the research and designed the experiment.

Competing interests:

The authors declare no competing interests.

Data availability:

The datasets generated and analysed during the current study are available in:

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<https://doi.org/10.6084/m9.figshare.14054756.v1>

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Figures

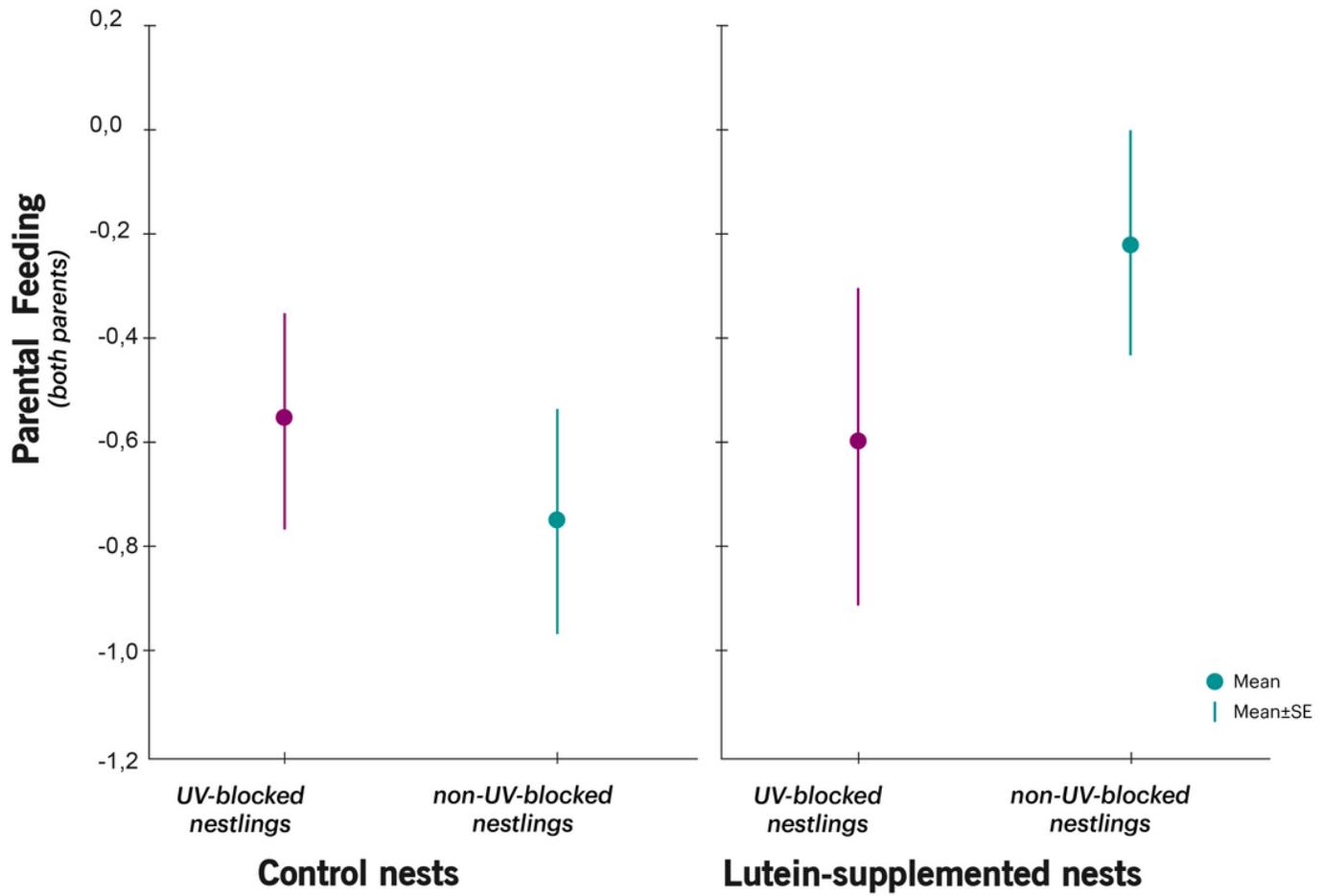


Figure 1

Difference in parental feeding rates (Post UV manipulation – Prior UV manipulation) according to nestling UV colour manipulation and female supplementation treatment. Values are (mean ± SE) residuals plus the average difference in feeding rates. Sample sizes for control females and lutein-supplemented females are shown.

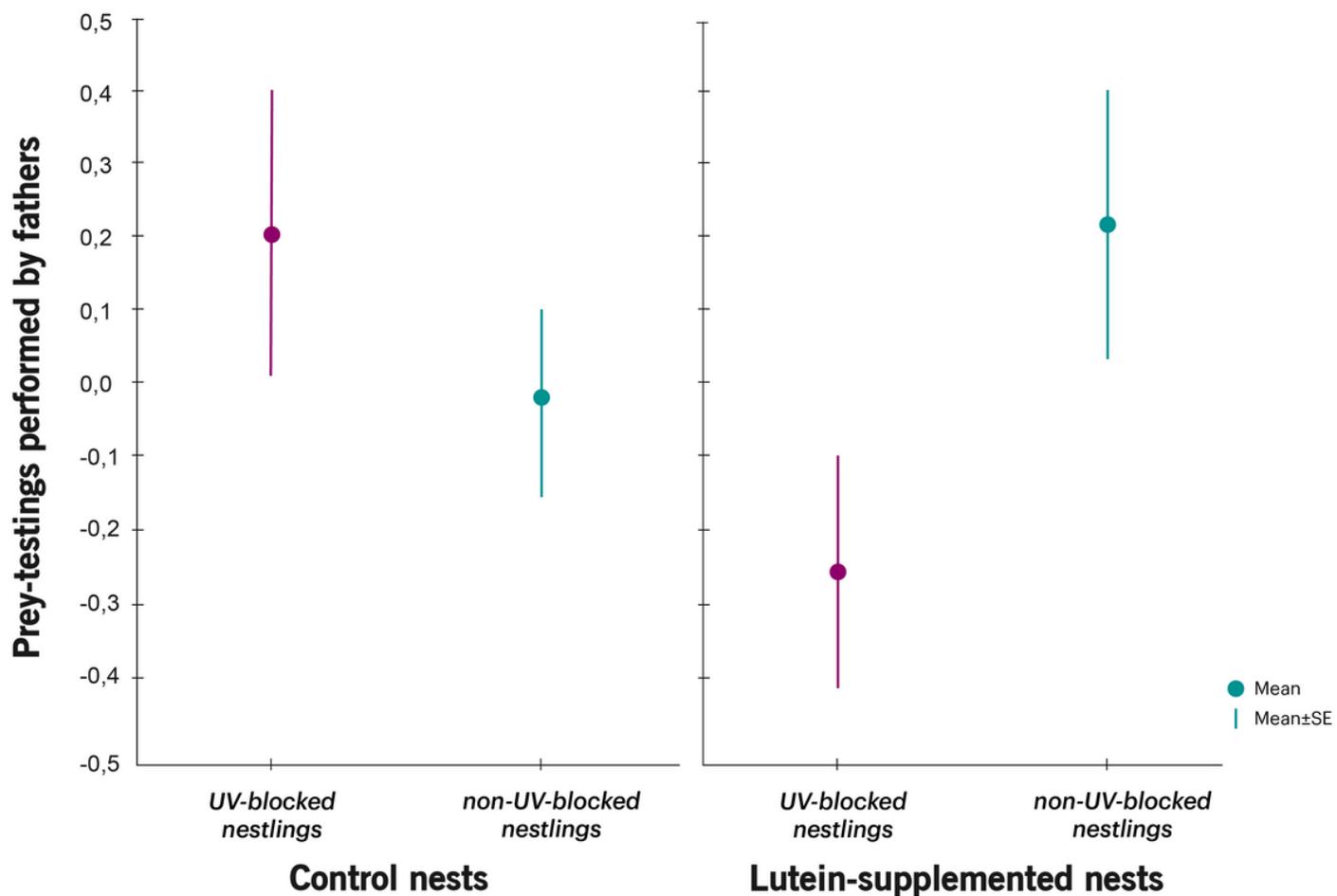


Figure 2

Difference (mean \pm SE) in prey-testings performed by males (Post UV manipulation – Prior UV manipulation) according to nestling UV colour manipulation and female supplementation treatment. Sample sizes for control females and lutein-supplemented females are shown.

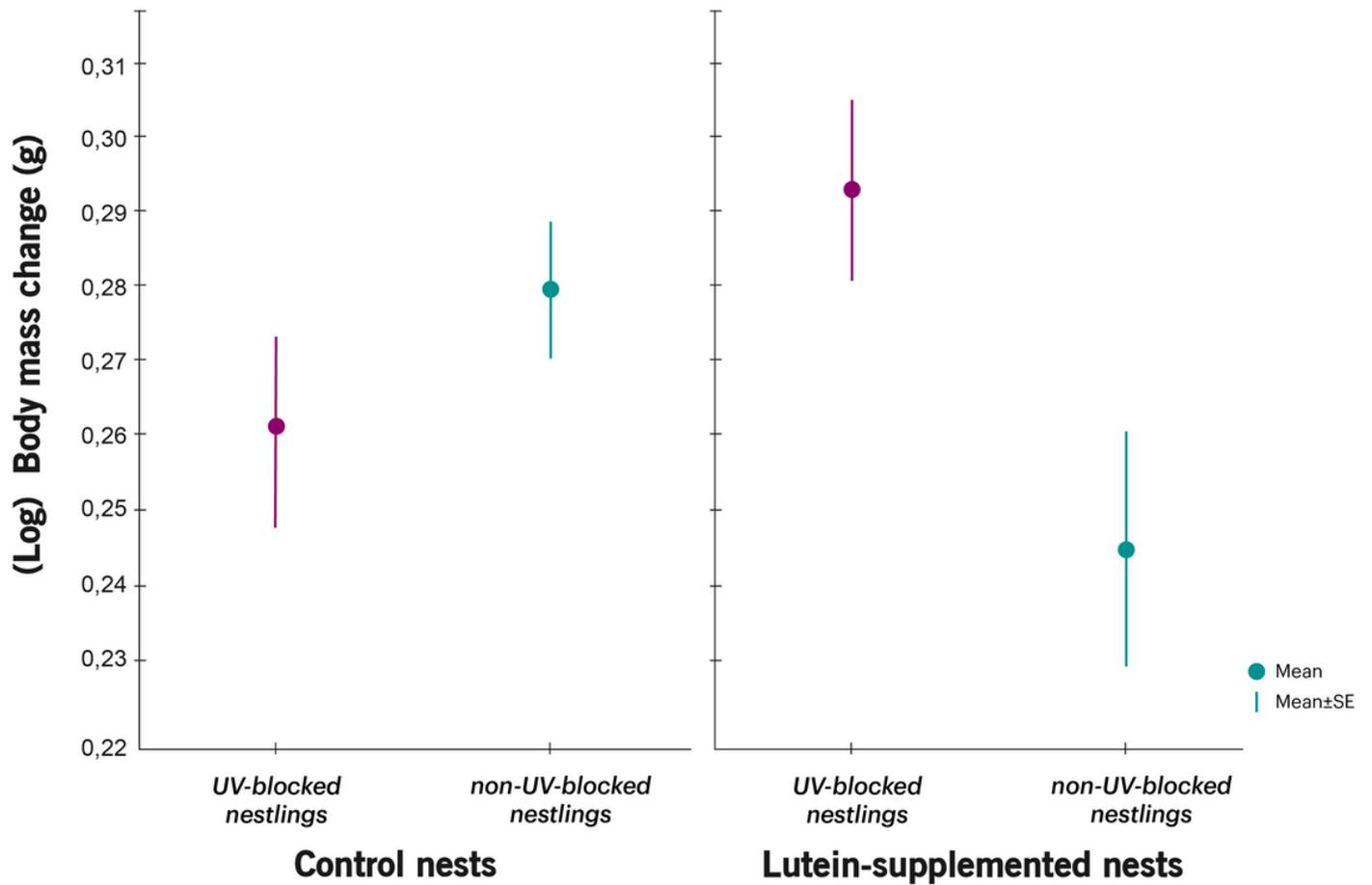


Figure 3

Nestling (log₁₀) body mass change (mean ± SE) according to nestling UV manipulation and female supplementation treatment. Sample sizes for control females and lutein-supplemented females are shown.

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