



Behavioral Ecology (2018), 29(4), 894–903. doi:10.1093/beheco/ary057

Original Article

Coloration of chicks modulates costly interactions among family members

Judith Morales^{a,•} and Alberto Velando^{b,•}

^aMuseo Nacional de Ciencias Naturales – Consejo Superior de Investigaciones Científicas, Departamento de Ecología Evolutiva. c/ José Gutiérrez Abascal 2, 28006 Madrid, Spain and

^bUniversidade de Vigo, Departamento de Ecología e Bioloxía Animal, Campus As Lagoas – Marcosende, Vigo, Spain

Received 12 December 2017; revised 14 March 2018; editorial decision 19 March 2018; accepted 3 April 2018; Advance Access publication 18 April 2018.

The resolution of family conflicts over parental care involves elaborate behavioral interactions where signals and information exchange play a central role. Usually, the focus is on offspring begging and adult signals and their effect on parental provisioning. Yet, despite offspring of many animal species display structural ornaments during parental dependency, their role in intrafamily conflicts remains practically unexplored. In the blue tit, *Cyanistes caeruleus*, we experimentally manipulated nestling ultraviolet (UV) color and food availability in 60 broods to investigate if family members flexibly adjust their decisions according to color under different conditions. Feeding rates were not affected by experimental treatments, but plumage color did affect parent–offspring interactions in the form of prey-testings (when a parent places a prey item into a nestling's gape but removes it again). In nonsupplemented nests, fathers but not mothers tested more prey on UV-reduced offspring, suggesting that fathers evaluate less ornamented chicks when food is scarce. As predicted by theoretical studies, UV-reduced nestlings increased begging in food-supplemented nests, although only to mothers. Moreover, UV-reduced nestlings increased parent-absent begging in all nests, indicating that plumage color affected sib-sib competitive interactions. Finally, UV-reduced offspring gained less body mass and this was probably due to costly intrafamily interactions. Overall, our results suggest that ornamentation during early life plays an important role on social-mediated costs and reveals sex-specific parental strategies according to offspring ornaments.

Key words: begging, behavioral reaction norms, family interactions, parental care, parent–offspring conflict, prey-testings, sibling conflict.

INTRODUCTION

During social interactions, individuals commonly rely on information exchange to make decisions (Arganda et al. 2012). For example, cooperation in humans usually requires prior information about the interacting parties (Nowak and Sigmund 2005; Jordan et al. 2016). Other vertebrates also use social information and have evolved signaling traits that affect the outcome of their encounters (see examples in primates (Allen and Higham 2015), birds (Suzuki et al. 2016), reptiles (Martín and López 2015; Ligon and McGraw 2016), amphibians (Höbel 2015), and fish (Oliveira et al. 2016)). Similarly, insects use badges of status in social interactions (Tibbetts and Dale 2004) and are able to make sophisticated decisions concerning information use (Dunlap et al. 2016). Hence, there is strong evidence that animals adjust their decision rules according to information exchange and the expression of signals,

and this probably shapes the resolution of social conflicts (Laidre and Johnstone 2013).

Family members constitute an interesting social group, where there are overlapping but not identical genetic interests. Given that each offspring is more closely related to itself than to its parents and siblings, they should try to take a disproportionate share of food. Consequently, the sibling conflict arises (O'Connor 1978). Also, optimal parental investment levels for offspring are greater than for parents and thus the parent–offspring conflict occurs (Trivers 1974). Finally, each parent would profit if the other provided more care, leading to a sexual conflict (Lessells 1999). The resolution of these evolutionary conflicts involves a network of behavioral interactions, where signals and information exchange play a central role (Hinde and Kilner 2007; Grodzinski and Johnstone 2012; Morales and Velando 2013). For instance, offspring have evolved elaborate begging displays that inform parents about need and thus about the benefits of giving extra food (Godfray 1991). Nonetheless, they can also be directed at siblings and modify sib-sib interactions (e.g., Roulin et al. 2000; Jimeno and Gil 2015; Romano et al. 2015).

Address correspondence to J. Morales. E-mail: jmorales@mncn.csic.es.

Apart from vocal and postural begging displays, parents also adjust their investment according to offspring structural signals like colorful plumage, mouth and skin UV color in young birds (Lyon et al. 1994; Jourdie et al. 2004; Griggio, Morosinotto, et al. 2009; Parejo et al. 2010). These traits may convey information about offspring quality (e.g., Jourdie et al. 2004; Peters et al. 2007; Caro et al. 2016) and potentially affect social interactions among family members. However, compared to begging displays, they have received scant attention.

This study aims at testing the hypothesis that an offspring structural trait influences the behavioral interactions with other family members. For this purpose, we experimentally reduced the UV color of breast plumage in half of the nestlings of each brood in the blue tit. Also, we supplemented some nests with extra food on 2 consecutive days to simulate a short-term benign environment that could alter the perceived quality of the reproductive event. In theory, parental favoritism may be mediated by food abundance because parents should favor offspring of high reproductive value when the benefits of raising low-quality chicks in relation to costs are low (Haig 1990; Davis et al. 1999; Parker et al. 2002). Accordingly, empirical studies across and within bird species suggest that highly ornamented offspring are favored only when food is scarce (Bize et al. 2006; Ligon and Hill 2010; Caro et al. 2016) or when hatching late (Lyon et al. 1994). At the other extreme, when food is abundant and there is high probability to raise all their progeny, parents are expected to either treat all offspring equally or to favor low-quality ones (Davis et al. 1999), thus following a compensatory strategy (Gowaty et al. 2007; Ratikainen and Kokko 2010). This is also supported by empirical work (Gottlander 1987; Caro et al. 2016), but, to our knowledge, these predictions have not been tested by experimental manipulation of food abundance.

The blue tit is a socially monogamous species with intense parental care by both sexes after hatching. The modal clutch size in European populations is 10 eggs (Fargallo and Merino 2004). Thus, there is high opportunity for conflict over the level of parental care. Ultraviolet reflectance in blue tit plumage has been largely studied. Both sexes, when adults, display brilliant ultraviolet (UV)/blue crown feathers that reflect individual quality and are sexually selected (e.g., Sheldon et al. 1999; Alonso-Álvarez et al. 2004; Limbourg et al. 2004; Peters et al. 2007; Griggio, Serra, et al. 2009; Mahr et al. 2012). When still in the nest, male and female offspring express UV/yellow colored breast feathers that are changed in the post-juvenile molt. In blue tit fledglings, UV reflectance of yellow breast plumage shows condition-dependent expression (Jacot and Kempenaers 2007) that may inform parents (but also siblings) about individual quality. In the closely related great tit, *Parus major*, an experimental increase of nestling breast color intensity did not affect parental feeding rates (Tschirren et al. 2005). However, an experimental reduction of UV reflectance of breast feathers in the same species did result in lower parental provisioning (Tanner and Richner 2008), suggesting a signaling role in parent-offspring interactions.

We first evaluate the effect of offspring coloration on parental favoritism. We predict that UV-reduced nestlings would be fed less often (Tanner and Richner 2008) and consequently would gain less body mass, especially in nonsupplemented broods where parents should favor high quality chicks (Davis et al. 1999). We also explore parental behavior in the form of “prey-testings,” which occurs when a parent places a prey item into a nestling’s open gape but then remove it before the nestling swallows it (Wiebe and Slagsvold 2012). This behavior may elicit offspring begging and could be

used by parents to take decisions about feeding. Lastly, we evaluate the effect of experimental manipulation on nestling begging both during feeding bouts and in the absence of parents, when begging can only function in the context of sib-sib communication (Roulin et al. 2000). We predict that UV-reduced nestlings would beg more intensely, either because parents feed them less or because they perceive their own relatively low quality through feedback from social interactions (i.e., a likely mechanism of self-perception; see Burley 1981, 1986; Cline et al. 2016). According to theoretical models and empirical data (Godfray 1991, 1995; Caro et al. 2016), UV-reduced chicks should beg with more intensity especially in food-supplemented nests because parents have more resources to rear all their progeny and thus there are higher probabilities of being rewarded.

MATERIAL AND METHODS

ETHICS

Methods were performed in accordance with the Guidelines for the Treatment of Animals in Behavioral Research and Teaching from the Association for the Study of Animal Behavior/Animal Behavior Society (ASAB/ABS) (2012).

Study population and general procedures

The study was conducted in the spring of 2011 in the locality of Miraflores de la Sierra, Madrid, central Spain (40° 48'N, 03° 47'W). We studied a Blue Tit population breeding in 160 wooden nest boxes in a deciduous forest of Pyrenean oak (*Quercus pyrenaica*), at an elevation of 1250 m. Nest boxes were checked regularly to determine laying date, hatching date and clutch size. Hatching date (day 1) was established as the day when at least half of the clutch had hatched.

Between days 10–13 after hatching, a nest-box trap was placed at the nest-box entrance and the first parent to arrive was ringed and marked with a white Edding 751 (code 049) on the scapular region. This mark allowed us to distinguish the male and the female parent in behavioral observations, except in one nest where we could not differentiate them. On day 13 after hatching, all nestlings were ringed, weighed, their tarsus length was measured and 3 of their breast feathers were taken for molecular sexing (see “Molecular sexing of nestlings” in Supplementary Material). In 60 nests, plumage UV color was reduced in half of the nestlings of each brood (see the following section). Immediately after UV color manipulation, half of the nests were assigned to a supplementary-food treatment (see the section “Manipulation of food abundance” for details). On day 14 after hatching, nests were video recorded and their nestlings were reweighed, except 7 nests that were filmed and their nestlings reweighed on day 15. The latter should not affect results, given that body mass change and behavioral parameters were compared between UV-reduced and non-UV-reduced siblings of the same nest (see Statistical analyses). For each nestling, mass change from day 13 to 14 was calculated. Also, the difference in the time of the day between first and second body mass measurements (mean \pm SE: 0.49 \pm 0.12; range: –5.17–5.42 h) was calculated for each nest to control for its effect on body mass change.

Manipulation of nestling plumage color

On day 13, coinciding with peak plumage development in nestling blue tits (Peters et al. 2007), one half of the nestlings in each brood was assigned to a “UV-reduced” group where the UV color of yellow breast feathers was altered by applying an Edding 4500 (code 005)

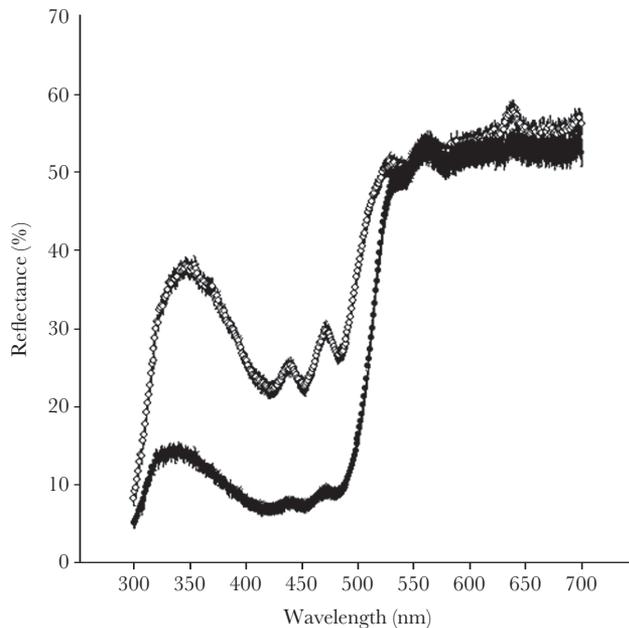


Figure 1

Average \pm SE reflectance spectra from the breast feathers of 30 nestling blue tits measured before and after UV color manipulation (white and black dots, respectively).

T-shirt marker pen (Ahrensburg, Germany). This marker has been shown to reduce reflectance in the UV part of the spectra of blue and great tit feathers (Johnsen et al. 2005; Delhey et al. 2006; Galván et al. 2008). In our experiment, the marker also reduced reflectance in the visible part of feather spectra but to a much lesser extent than in the UV part (see Figure 1). Cavity-nesting passerines are better at detecting changes in UV-reflectance than in visible reflectance (Avilés et al. 2006), and thus it is likely that manipulation of UV-reflectance played a major role.

As we only needed that the color manipulation lasted 1 day, no additional products were added to waterproof feathers (see also Johnsen et al. 2005). The other half of nestlings in each brood was assigned to a “non-UV-reduced” group in which the marker was applied on the interior surface of flight feathers (occupying an area similar to that of yellow breast feathers) to discard differences in behavior due to undesirable side-effects of the marker. The first nestling handled in each brood was randomly assigned to one treatment and its siblings were sequentially assigned to the other one. Siblings in a particular half-brood treatment were marked on the head with the same white marker used for adults, while nestlings in the other treatment were not marked. These marks were alternated between half-brood treatments in successive nests, allowing a blind observation with respect to color manipulation during video recordings. UV color manipulation per se did not alter the total levels of parental provisioning in the 60 experimental nests compared with 10 additional “pure control” nests that were not subjected to any treatment (analysis of variance [Anova] test: coef. [pure controls] = 0.13 ± 0.12 ; $F_{1,64} = 1.11$; $P = 0.30$).

We confirmed with paired *t*-tests that UV chroma and total brightness were reduced after UV manipulation in 30 nestlings (mean \pm SE before and after color manipulation of UV-chroma: 0.19 ± 0.01 and 0.09 ± 0.03 , $t_{30} = 18.82$, $P < 0.001$; total brightness: 40.65 ± 6.34 and 29.63 ± 6.22 , $t_{30} = 9.33$, $P < 0.001$). UV chroma, which represents the purity of UV coloration, was calculated as reflectance in the UV range divided by total reflectance

($R_{300-400}/R_{300-700}$) and total brightness as average reflectance in the 300–700 nm interval (Johnsen et al. 2005). For color measurement, we used a portable Ocean Optics Jaz spectrophotometer with built-in xenon lamp source and connected to a bifurcated optical fibre probe (Ocean Optics Inc. Dunedin, FL). Measurements were taken perpendicularly to the feathers using a probe holder (Ocean Optics RPH-1) and, for each individual, reference measurements were made relative to a diffuse white reflectance standard (Ocean Optics WS-1). Spectral range covered 300–700 nm.

Manipulation of food abundance

On day 13 and immediately after color manipulation, a small green plastic container (semicircular with a radius of 5.4 cm and depth of 3.7 cm) was fixed under the nest-box entrance. Each nest was randomly assigned to either a nonsupplemented group, in which the containers were left empty, or to a food-supplemented one, in which 15 g of live mealworms, *Tenebrio molitor*, was delivered into the containers daily on days 13 and 14 posthatch. Thus, nests were supplemented on 2 consecutive days to simulate a punctual benign environment, coincident to the onset of plumage color manipulation. Food supplementation during the whole nestling period would have affected offspring mass and obscured the effect of UV treatment within broods. The daily amount corresponded to one-half of the estimated food daily requirement of a 9-chick brood of blue tits (Grieco 2002). On day 14, prior to video recording, the amount of mealworms left in the containers of supplemented nests was weighed with a Pesola spring balance to the nearest 0.25 g. Fifteen grams were left again after the visit and mealworms were reweighed after video recording (approximately 2 h later). On average, supplemented nests consumed only 1.93 ± 0.4 g of mealworms during supplementation, which corresponds to approximately 15 mealworms. This could be due to the short time (2 visits) that blue tits had to get used to the new food. This amount might be slightly underestimated because in one third of supplemented nests mealworms were found wet at weighing due to rain. Since all nests were filmed, nonsupplemented broods were also visited without leaving supplementary food. In another experiment performed in our blue tit study population, we corroborated that feeders with supplementary food are only visited by nest-box owners (J.M., García-Campa J, González-Braojos S, and Müller W, unpublished data).

Video recording and behavioral observation

On day 14, nests were filmed for 1 h and 30 min each with a night-vision digital camcorder (wide-angle 8-LED IR DVR camcorder, DX, China). Filming took place between 0800 and 1300 h. One day before filming, the original nest-box was substituted with one that had a ceiling opening with a black plastic cover to allow parents to become used to its presence. On the day of filming, the camera was placed on the opening at an approximate distance of 10 cm from the nest. We discarded the first 30 min of video recording. In most nests, parents started feeding nestlings in the first minutes, but in a few ones it took them 20–25 min to appear without apparent signs of fear. Thus, we ensured that parents fed normally after 30 min.

For each feeding bout, we registered whether the adult was marked or not, the number of marked and unmarked nestlings that begged when the parent was at feeding location, nestling posture (hereafter “begging intensity”) of all nestlings when the parent was at feeding location, whether the fed nestling (typically only one) was marked or not, prey size and the number of marked and unmarked nestlings that were “prey-tested” at least once. A prey-testing occurs

each time a parent places a prey item into a nestling's open gape, but removes it before the nestling swallows the prey (Wiebe and Slagsvold 2012). We counted the number of different chicks that received at least one prey-testing in each feeding bout, regardless of whether they ended up eating the prey or not (note that parents do sometimes feed a chick after prey-testing it). Begging intensity was rated on a 4-point scale, following Kölliker et al. (1998): 0 = calm, 1 = weak gaping, 2 = gaping and neck stretched, 3 = gaping, neck stretched, and standing, 4 = gaping, neck stretched, standing, and wing flapping. Prey size was rated on a 3-point scale: 1 = small (when it was equal or shorter than the adult beak), 2 = medium (larger than the beak but smaller than the adult head), and 3 = large (bigger than the adult head).

Nestling begging was also observed between feeding bouts, when parents were not present. We considered a parent-absent event as the time interval between 10 s after parents leave the nest and a parent return to nest. We also considered that a parent-absent event ceased when nestlings noticed that a parent was in nest surroundings. The latter was clearly perceived as an abrupt change in nestling behavior (i.e., all nestlings started begging or increased begging intensity sharply), often preceded by a characteristic parent's call (J.M., personal observation). In each parent-absent event, the number of marked and unmarked begging nestlings was registered as well as their begging intensity. We discarded those video recordings with parent-absent events in which begging intensity could not be accurately observed (3.4% of the total).

For the whole hour of observation, we calculated the following parameters for each nest, separately for marked and unmarked nestlings: sum of fed and prey-tested nestlings, mean prey size, mean begging intensity per feeding bout, mean begging intensity per parent-absent event and the sum of parent-absent events where nestlings begged. Given that treatment was blind to the observer, the behavior of marked and unmarked nestlings in each nest was ascribed to UV-reduced or non-UV-reduced treatments after data collection from video recording. Similarly, the sex of the parent that entered the nest-box in each feeding bout was blind until the end of behavioral observations, after which the presence/absence of a given mark was ascribed to the male or female parent.

Sample size

We initially included 60 nests in the experiment, but one supplemented and 3 nonsupplemented nests were abandoned before video recording, coinciding with a cold spell. Apart from these total nest failures, only 3 chicks (2 UV-reduced and 1 non-UV-reduced) died before fledging in 2 nonsupplemented nests. One food-supplemented nest had unusually high feeding rates (i.e., almost 4 standard deviations from the mean of the rest of nests: 69 feedings vs. 30.8 ± 9.7 in the rest of nests), and we included it only in the analyses that did not require a normal distribution (see Statistical analyses). Excluding it from these analyses did not qualitatively change the results. Therefore, we could use data from 56 experimental nests with 432 chicks in total. Sample size varies in some analyses due to that inaccurate recordings were discarded. For example, in one nest, it was impossible to distinguish the chicks that were begging in most parent-absent events. In another nest, it was not possible to distinguish the male and the female parent. There were 20 nests in which only one parent fed the chicks during video recording (the mother in 12 nests, the father in 8 nest). Excluding these nests from the analyses does not qualitatively change the results (available upon request), except for prey-testings where a significant effect of parental sex was revealed (see Results section).

Statistical analyses

We used SAS 9.4 (SAS Inst., Cary, NC) for all statistical analyses. Degrees of freedom were estimated by Satterthwaite method. In the tables, we show full models with interactions when significant. In [Supplementary Material](#), we also show initial full models with all nonsignificant interactions. All mixed models were fitted with a random intercept (nest) and a random slope (nest \times UV treatment) to compare UV- and non-UV-reduced siblings within nests. Behavioral variables in the presence of parents also included parent identity as a random intercept.

Prior-to-treatment biases

We first checked whether chicks differed in body mass, tarsus length or sex according to plumage color and food supplementation prior to manipulation. We thus run linear mixed models for body mass and tarsus length (MIXED procedure in SAS with normal error) and a generalized mixed model for sex (GLIMMIX procedure with binomial error), using individual nestling data. We also checked whether the number of UV- and non-UV-reduced chicks within nests differed according to plumage color treatment by a generalized mixed model with Poisson error. Additionally, we explored whether nests differed in hatching date or brood size according to food supplementation prior to treatment. Thus, we run a generalized model for brood size (GENMOD procedure with Poisson error) and an Anova for hatching date.

Behavioral variables

We estimated the experimental effects on behavioral variables separately for UV- and non-UV-reduced nestlings in each nest and for the father and the mother during feeding bouts. This way we could explore whether parents followed sex-specific strategies. Since we did not mark nestlings individually, there are thus 4 mean values per nests during feeding bouts (corresponding to the behavior of UV- and non-UV-reduced nestlings and to the father and mother during feeding bouts) and 2 mean values per nest during parent-absent events (behavior of UV- and non-UV-reduced nestlings). We fitted linear mixed models for variables that approximated a normal distribution (i.e., begging intensity during feeding bouts, parent-absent begging and sum of parent-absent events where nestlings begged) and generalized mixed models with Poisson error for the rest (feeding rates, prey size, and prey-testings). These models included as fixed factors UV color treatment, supplementary food treatment, their interaction, adult sex and its interaction with both treatments, and the triple interaction adult sex \times UV treatment \times supplementary food. Brood size at day 14 was included as a covariate, as well as the number of parent-absent events for the model of sum of parent-absent events where nestlings begged.

Nestling body mass change

The effect of experimental manipulations on individual nestling body mass change were tested by a linear mixed model, including as fixed factors UV color treatment, supplementary food treatment and their interaction. This model also included brood size, tarsus length and the timing difference between body mass measurements. Nestling sex was initially included but then removed because it reduced sample size (see "Molecular sexing of nestlings" in [Supplementary Material](#)) and did not significantly improve the model. Results do not change qualitatively when chick sex was included (see [Supplementary Table S1](#) in [Supplementary Material](#)).

Finally, we explored in a similar linear mixed model whether mean body mass change (2 values per nest for UV-reduced and non-UV-reduced chicks) was affected by the behaviors that we

observed (i.e., total feeding rates (the sum by both parents), mean prey size (the mean provided by both parents), total number of prey-tested chicks, number of parent-absent events where nestlings begged and mean begging intensity during feeding bouts).

RESULTS

Prior-to-treatment biases

Prior to manipulation, chicks did not differ in body mass, tarsus length, or sex according to either plumage color manipulation or food supplementation (Supplementary Table S2). Additionally, nests did not differ in the number of UV- and non-UV-reduced chicks, or in hatching date and brood size prior to food supplementation (Supplementary Table S2).

Parental feeding rates, prey size, and prey-testings

Parents performed on average (\pm SE) 31.5 ± 1.5 feeding trips per nest (range: 10–69). During the hour of video recording, neither UV color treatment nor food supplementation affected feeding rates (Table 1). None of the interactions significantly affected feeding rates either (Supplementary Table S3). Similarly, the size of prey was not significantly affected by any of the treatments (Table 1) or their interaction (Supplementary Table S3). Fathers provided larger prey than mothers (Table 1).

Prey-testings occurred in all 56 nests (mean \pm SE number of feeding bouts with at least one prey-testing during the hour of observation: 13.9 ± 1.5 ; range: 1–47; mean total number of prey-testings performed during the hour of observation: 25.5 ± 3.6 ; range: 1–111). Although the triple interaction between parental sex and experimental treatments was not significant (Supplementary Table S3), the model estimates suggested that males and females may differ in prey-testings according to chick UV color and food availability. Thus, we also explored parental prey-testings in separate models for fathers and mothers to better understand this pattern.

We found that prey-testings performed by mothers were not affected by any of the treatments (Table 1) or their interaction (coef. = -0.35 ± 1.01 , $F_{1,31.6} = 0.12$, $P = 0.73$). On the contrary, paternal prey-testings were strongly and significantly affected by the interaction between both treatments (Table 1), even when controlling for prey size (UV treatment \times supplementary food: coef. = -2.32 ± 0.71 , $F_{1,79} = 10.67$, $P = 0.002$; prey-size: coef. = -0.43 ± 0.56 , $F_{1,79} = 0.60$, $P = 0.44$). In nonsupplemented nests, fathers tended to test prey more often on UV-reduced than on non-UV-reduced chicks (Figure 2; post-hoc LS-means comparison: $t_{81} = -3.18$, $P = 0.002$), while in supplemented nests the pattern was apparently reversed but nonsignificant (Figure 2; post-hoc LS-means comparison: $t_{81} = 1.73$, $P = 0.088$). When we excluded the nests where only one parent appeared during behavioral observations, the main effect of parental sex on prey-testings was significant in the full model of Table 1, fathers performing more prey-testings than mothers (coef. = -1.95 ± 1.77 , $F_{1,33.5} = 6.21$, $P = 0.018$). This suggests that prey-testings could be a sex-specific strategy.

Nestling begging

During feeding bouts, the triple interaction between parental sex and experimental treatments was significant (coef = 0.40 ± 0.18 , $F_{1,36.6} = 4.84$, $P = 0.034$). We thus explored in separate models whether chick begging directed to either fathers or mothers was affected by the interaction between both treatments. Indeed, the interaction

Table 1
Mixed models with the effects of nestling UV color treatment and food supplementation on parental and chick behavior

	Feeding rates	Prey size	Maternal prey-testings	Paternal prey-testings	Begging intensity to mothers	Begging intensity to fathers	Parent-absent begging intensity	Parent-absent events with begging
<i>Intercept</i>	coef = 2.18 ± 0.06	coef = 1.82 ± 0.02	coef = 1.12 ± 0.16	coef = 1.32 ± 0.18	coef = 0.26 ± 0.22	coef = 0.16 ± 0.17	coef = 0.23 ± 0.18	coef = -1.71 ± 0.31
<i>UV treatment</i>	coef = -0.44 ± 0.33	coef = -0.37 ± 0.21	coef = 0.22 ± 0.58	coef = 0.97 ± 0.56	coef = -0.32 ± 0.15	coef = -0.11 ± 0.11	coef = -0.26 ± 0.13	coef = -0.18 ± 0.09
	$F_{1,175} = 1.81$	$F_{1,37.7} = 3.11$	$F_{1,39.0} = 0.15$	$F_{1,81} = 0.92$	$F_{1,44} = 0.27$	$F_{1,41} = 0.97$	$F_{1,33} = 4.29$	$F_{1,53} = 4.69$
	$P = 0.18$	$P = 0.083$	$P = 0.70$	$P = 0.34$	$P = 0.61$	$P = 0.33$	$P = 0.043$	$P = 0.035$
<i>Suppl. Food</i>	coef = -1.49 ± 0.83	coef = 0.04 ± 0.30	coef = -0.29 ± 1.55	coef = 2.19 ± 1.72	coef = -0.29 ± 0.32	coef = -0.39 ± 0.21	coef = -0.16 ± 0.24	coef = -0.13 ± 0.19
	$F_{1,30.3} = 3.24$	$F_{1,54.1} = 0.01$	$F_{1,44.8} = 0.04$	$F_{1,35.8} = 0.26$	$F_{1,43} = 0.01$	$F_{1,39} = 3.66$	$F_{1,51} = 0.45$	$F_{1,50} = 0.48$
	$P = 0.082$	$P = 0.91$	$P = 0.85$	$P = 0.61$	$P = 0.94$	$P = 0.063$	$P = 0.51$	$P = 0.49$
<i>Brood size</i>	coef = 1.11 ± 0.84	coef = 0.57 ± 0.29	coef = 2.66 ± 1.58	coef = 5.16 ± 1.72	coef = 0.37 ± 0.14	coef = 0.34 ± 0.10	coef = 0.16 ± 0.12	coef = -0.01 ± 0.10
	$F_{1,27.7} = 1.72$	$F_{1,51.3} = 3.71$	$F_{1,47.4} = 2.85$	$F_{1,37.8} = 9.04$	$F_{1,43} = 6.45$	$F_{1,39} = 13.07$	$F_{1,51} = 1.86$	$F_{1,50} = 0.01$
	$P = 0.20$	$P = 0.060$	$P = 0.10$	$P = 0.005$	$P = 0.015$	$P < 0.001$	$P = 0.18$	$P = 0.93$
<i>Parental sex</i>	coef = -0.88 ± 0.71	coef = -0.90 ± 0.29						
	$F_{1,42.8} = 1.54$	$F_{1,60.0} = 9.71$						
	$P = 0.22$	$P = 0.003$						
<i>UV treat. \times suppl. Food</i>				coef = -2.41 ± 0.70	coef = 0.53 ± 0.22			
				$F_{1,81} = 11.92$	$F_{1,44} = 5.93$			
				$P < 0.001$	$P = 0.019$			

Nonsignificant interactions were excluded. Two values per nest are used for parent-absent events, which correspond to UV- and non-UV-reduced chicks. For variables during feeding bouts, 4 values per nest are used, which correspond to maternal and paternal behavior toward UV-reduced and non-UV-reduced siblings, and to begging intensity of UV- and non-UV-reduced chicks toward the mother and the father. Coefficients are shown for nonsupplemented nests, non-UV-reduced chicks and for mothers. Significant differences are marked in bold.

between experimental treatments had an effect on begging intensity directed to mothers (Table 1), but not to fathers (coef = 0.14 ± 0.22 , $F_{1,40} = 0.42$, $P = 0.52$). In supplemented nests, UV-reduced chicks begged more to their mothers than non-UV-reduced ones (Figure 3; post-hoc LS-means comparison: $t_{44} = -2.09$, $P = 0.043$), while in nonsupplemented nests begging intensity did not differ according to UV treatment (Figure 3; post-hoc LS-means comparison: $t_{44} = 1.36$, $P = 0.18$). This suggests that chick rules dynamically changed according to parental sex and environmental conditions.

Moreover, UV-reduced chicks begged in more parent-absent events and did it with more intensity than their non-UV-reduced siblings (Table 2). This effect was consistent across all nests, since the interaction between treatments did not affect parent-absent begging intensity (UV treatment \times supplementary food: coef. = -0.04 ± 0.26 , $F_{1,52} = 0.03$, $P = 0.87$; Figure 4) or the number of parent-absent events where nestlings begged (UV treatment \times supplementary food: coef. = -0.02 ± 0.17 , $F_{1,52} = 0.01$, $P = 0.93$).

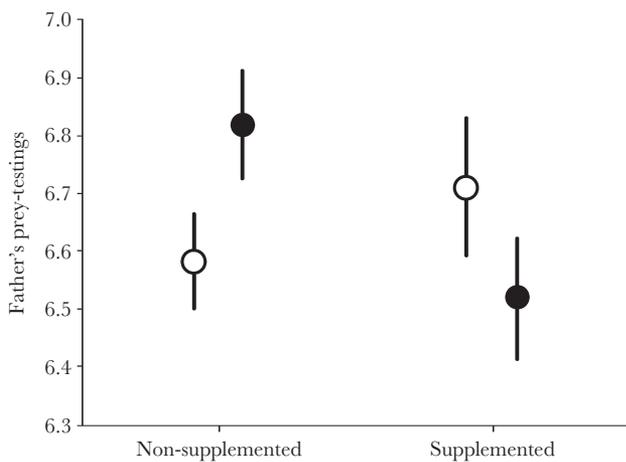


Figure 2
Total number of “prey-tested” nestlings by the father in relation to UV color treatment and supplementary food. Values are the mean of prey-tested chicks by the father plus residuals of a mixed model that controlled for the effect of brood size. White and black dots are, respectively, non-UV- and UV-reduced chicks.

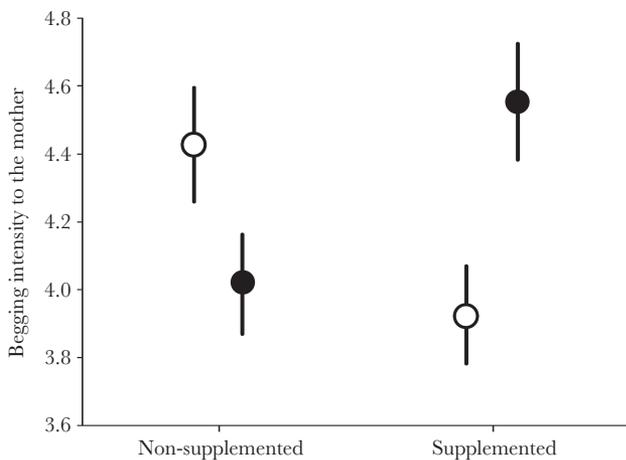


Figure 3
Experimental effects on begging intensity directed to mothers. Values are the mean begging intensity (postural display; see Material and Methods). White and black dots are, respectively, non-UV- and UV-reduced chicks.

Nestling body mass change

At the end of the experiment, nestlings in the non-UV-reduced group gained more body mass (approximately 100 mg) than their siblings in the UV-reduced group (Table 2; Figure 5). This effect was consistent across all nests, since the interaction between UV color treatment and supplementary food was not significant (coef. = -0.03 ± 0.14 , $F_{1,367} = 0.04$, $P = 0.84$; see Figure 5). Supplementary food per se did not affect body mass change (Table 2; Figure 5).

The behavioral variable that best explained body mass change was the number of prey-tested chicks, the higher the number of prey-tested chicks the lower mean body mass gain (Table 3). The relationship between body mass gain with other behavioral variables was not significant (Table 3).

Table 2
Mixed models with the effects of nestling plumage UV color treatment and food supplementation on chick log-body mass change (individual chick values)

	log-body mass change (g)
<i>Intercept</i>	coef = -0.05 ± 0.13
<i>UV treatment (non-UV-reduced)</i>	coef = 0.15 ± 0.07 $F_{1,368} = 4.87$ P = 0.028
<i>Suppl. food (nonsuppl.)</i>	coef = -0.06 ± 0.18 $F_{1,51.4} = 0.09$ $P = 0.76$
<i>Brood size</i>	coef = -0.11 ± 0.09 $F_{1,53.5} = 1.48$ $P = 0.23$
<i>Tarsus length</i>	coef = -0.13 ± 0.05 $F_{1,417} = 7.00$ P = 0.009
<i>Timing difference in body mass measurement</i>	coef = 0.28 ± 0.10 $F_{1,52.6} = 7.87$ P = 0.007

The nonsignificant interaction between treatments was excluded. Coefficients are shown for nonsupplemented nests and for non-UV-reduced chicks. Significant differences are marked in bold.

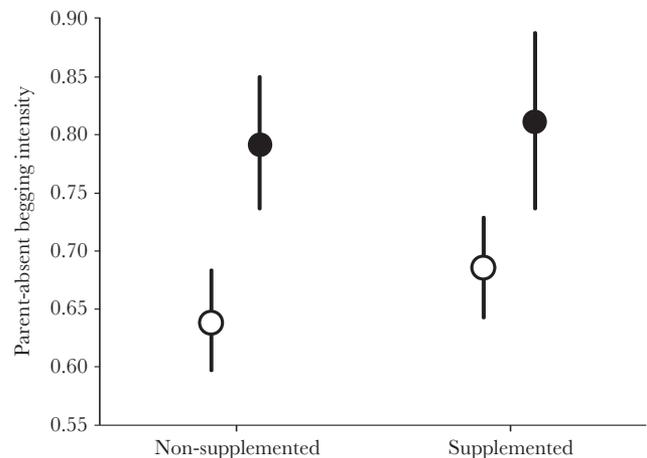


Figure 4
Begging intensity in parent-absent events in relation to UV color treatment and supplementary food. Values are the mean begging intensity (postural display; see Material and Methods) among all nestlings during parent-absent events plus residuals of a mixed only-intercept model without predictors. White and black dots are, respectively, non-UV- and UV-reduced chicks.

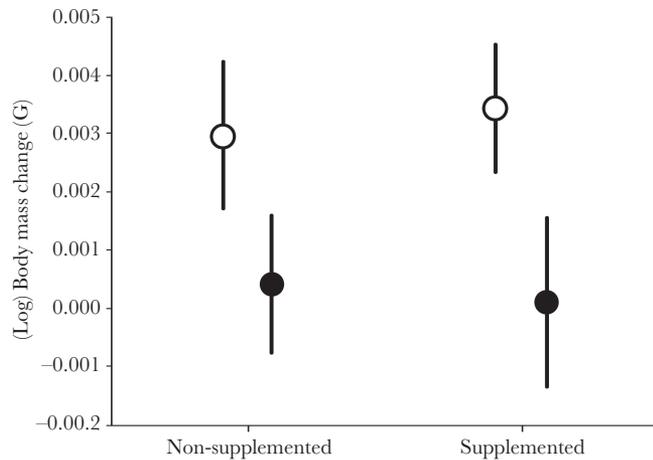


Figure 5

Nestling body mass change (\log_{10} transformed) in relation to plumage color treatment and supplementary food. Individual values are the mean body mass change of all nestlings plus residuals of a mixed model that controlled for the effect of tarsus length and the timing difference between body mass measurements. White and black dots are, respectively, non-UV- and UV-reduced chicks.

Table 3

Mixed model with the effects of parental and chick behavior on chick log-body mass change

	<i>log-body mass change (g)</i>
<i>Intercept</i>	<i>coef</i> = -0.06 ± 0.19
<i>UV treatment (non-UV-reduced)</i>	<i>coef</i> = 0.20 ± 0.10 $F_{1,50.4} = 4.10$ <i>P</i> = 0.048
<i>Suppl. Food (nonsuppl.)</i>	<i>coef</i> = -0.05 ± 0.25 $F_{1,49} = 0.03$ <i>P</i> = 0.86
<i>Tarsus length</i>	<i>coef</i> = -0.29 ± 0.10 $F_{1,97.3} = 10.65$ <i>P</i> = 0.002
<i>Total feeding rates</i>	<i>coef</i> = 0.001 ± 0.09 $F_{1,93.4} = 0.00$ <i>P</i> = 0.99
<i>Prey size</i>	<i>coef</i> = 0.08 ± 0.07 $F_{1,74.5} = 1.26$ <i>P</i> = 0.27
<i>Total number of prey-tested chicks</i>	<i>coef</i> = -0.22 ± 0.11 $F_{1,95.5} = 4.35$ <i>P</i> = 0.040
<i>Begging intensity during feeding bouts</i>	<i>coef</i> = -0.09 ± 0.13 $F_{1,98.8} = 0.47$ <i>P</i> = 0.50
<i>Parent-absent events with begging</i>	<i>coef</i> = -0.04 ± 0.13 $F_{1,98.4} = 0.10$ <i>P</i> = 0.75

Two mean values per nest are used, corresponding to UV-reduced and non-UV-reduced chicks. Coefficients are shown for nonsupplemented nests and non-UV-reduced chicks. Significant differences are marked in bold.

DISCUSSION

Our results suggest that the color of blue tit chicks affects condition-dependent sibling competition and certain parental behavioral rules. Although parental feeding rates were not influenced by experimental manipulation, UV-reduced offspring were tested more often by fathers in nonsupplemented nests, suggesting that fathers,

but not mothers, followed dissimilar rules concerning offspring evaluation under different environmental scenarios. Nestlings also changed their rules dynamically according to parental sex, since UV-reduced chicks increased begging to their mothers in supplemented nests. Moreover, UV-reduced chicks generally increased begging in the absence of parents, indicating that plumage color affected sib-sib competition. Finally, UV-reduced chicks gained less body mass. These results highlight the role of social information (feather coloration) on complex family dynamics.

Neither prey size nor feeding rates were significantly affected by nestling color manipulation or by food supplementation. However, plumage color did affect offspring interactions with fathers, but not with mothers, in the form of prey-testings. In the blue tit, it has been suggested that prey-testings occur when nestlings have gapes not large enough to swallow big prey (Wiebe and Slagsvold 2012). Nevertheless, this does not explain the difference in father's prey-testings according to experimental manipulation, since treatment effects were highly significant even after controlling for prey size. In nonsupplemented nests, fathers tested UV-reduced chicks more often than non-UV-reduced ones, while the pattern was apparently reversed but not significant in supplemented nests. The interpretation of prey-testings is open to discussion, but we hypothesized that parents are evaluating chick hunger as occurs in several taxa (Santucci et al. 1994; Smiseth et al. 2010; Velando et al. 2013). Prey-testings seemed to impose a cost to chicks because they were negatively related with body mass gain and, thus, it is possible that they prevent begging exaggeration (see Morales and Velando 2013). Under natural conditions, fathers were more reluctant to feed UV-reduced offspring without testing them, suggesting paternal favoritism for ornamented high-quality offspring (note this trait is condition-dependent; Jacot and Kempenaers 2007). Only when fathers perceived higher food availability in the environment, they tended to favor UV-reduced chicks, suggesting a compensatory strategy as could be predicted (Davis et al. 1999). Unlike begging, plumage color is a structural signal that offspring cannot control and, in this sense, it is a more reliable information source about offspring condition. Male blue tits could thus use dynamic (begging) and static signals in combination when deciding their rules over investment under varying conditions. Importantly, our results suggest sex-specific rules of parental care according to a structural offspring trait.

We found that UV-reduced nestlings begged more to their mothers in food-supplemented nests than their non-UV-reduced siblings. In contrast, begging intensity did not differ between UV- and non-UV-reduced siblings under natural conditions, when food availability is usually scarce or unpredictable. This result supports the prediction that low-quality chicks should increase begging in benign environments because parents favor the neediest offspring when resources are plentiful to raise all their progeny (Godfray 1991, 1995; Moreno-Rueda et al. 2009; Mock et al. 2011; Caro et al. 2016). How chicks learnt that food availability was higher in supplemented nests deserves further attention, since feeding rates were not affected by the extra food. In this direction, as mentioned above, we observed that fathers changed their prey-testing rules according to UV color and supplementary food. Surprisingly, begging was only increased in the presence of mothers, possibly because they are more responsive to begging than fathers, as previously found in great tits (Kölliker et al. 2000).

UV-reduced chicks also begged more than non-UV-reduced ones during parent-absent events regardless of food availability. Begging when parents are absent has been interpreted in the light of the

sibling conflict, where offspring compete and inform each other about their willingness to contest the following prey (Roulin et al. 2000). Studies in the barn owl, *Tyto alba*, reveal that offspring are able to retain the information exchanged during parent-absent events and use it in the following feeding bout in the presence of parents (Dreiss et al. 2015, 2017). In this context, it could be that UV-reduced nestlings were hungrier (perhaps as a consequence of reduced body mass) and thus they were more motivated to compete with the siblings for the following prey (an indirect effect of UV color on parent-absent begging). However, UV-reduced nestlings could not be hungry due to reduced feeding rates, since they received the same amount than their sibs. Another possibility is that UV-reduced chicks were not hungrier when we recorded behavior, but they perceived their own reduced UV color through feedback from social interactions with other family members and, thus, they increased parent-absent begging (a direct effect of UV color). Indeed, previous studies have suggested a self-perception mechanism for signals of quality (see for instance Burley 1981, 1986; Cline et al. 2016). Also, non-UV-reduced chicks could have observed the poorer ornamentation of their siblings and perceived them as low-quality competitors, thus reducing parent-absent begging themselves (another direct effect of UV color). Probably both mechanisms (direct and indirect effects of UV color) were at work in the withdrawal of non-UV-reduced chicks from the competition.

The question remains which is the benefit of increasing parent-absent begging, as well as begging directed to mothers, if UV-reduced chicks did not receive higher feeding rates than their control sibs. Had parents in supplemented nests consumed more extra-food, we may have found clearer effects on feeding rates. Nonetheless, at least, UV-reduced chicks did not receive less food than their siblings, as could be expected according to previous findings in great tits (Tanner and Richner 2008), indicating that they were not disfavored.

We found that UV color manipulation had an effect on a fitness component, since nestlings with reduced UV color lost approximately 100 mg compared with their non-UV-reduced siblings. Body mass gain in blue tit nestlings from day 13 to 14 is about 0.5 g (Mainwaring et al. 2011), implying that our manipulation inflicted a difference of 20% with respect to the average mass gain at this age. Although nearly all nestlings fledged during the study season, body mass gain in this species decisively affects postfledging survival (Nur 1984; Adriaensen et al. 1998). Lower body mass in UV-reduced chicks cannot be explained by parental feeding rates, but by intra-family interactions. Indeed, UV-reduced chicks were tested more often by their fathers in nonsupplemented nests, and prey-testings negatively affected body mass gain. Although the rest of behavioral parameters seemed not to be related with body mass gain, we cannot discard that parent-absent begging came at a cost, since begging signals have been shown to impair growth and condition (e.g., Kilner 2001; Neuenschwander et al. 2003; Moreno-Rueda 2010; Noguera et al. 2010; Soler et al. 2014). Furthermore, UV-reduced chicks begged more to their mothers in supplemented nests. We cannot identify the exact cause of reduced body mass, since it is the result of complex interactions with other family members that are not captured by a single variable during one hour of observation. However, our results tentatively suggest that intrafamily interactions imply fitness costs. Further studies are needed to explore this idea.

To summarize, we have found that fathers and mothers responded differently to offspring plumage color, revealing sex-specific rules over parental care. Moreover, chicks also followed different begging strategies according to parental sex and food

availability. Thus, a structural signal affects other signals (begging) well known to influence the behavioral reaction norms of parents and offspring (Lucass et al. 2016). Finally, plumage color manipulation reduced fitness (in terms of chick growth), which cannot be explained by feedings rates but suggests costly behavioral interactions among family members. Overall, our results support that offspring structural signals form part of the social environment that family members experience and, together with environmental cues, they contribute to the evolution of flexible parenting (Royle et al. 2014).

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

FUNDING

This study was covered by projects CGL2016-79390-P to J.M. and CGL2013-48193-C3-3-P to Juan Moreno (Ministerio de Economía y Competitividad, MINECO, Spain). J.M. is supported by a Ramón y Cajal contract from MINECO.

We thank Wendt Müller and Juan Moreno for insightful discussions. We also thank Miguel Fernández for invaluable help during fieldwork and Pilar Ochoa-Cao for molecular sexing. The study was conducted with the approval of Dirección del Parque Regional de la Cuenca Alta del Manzanares (number of permit 10/014163.9/11), Consejería de Medio Ambiente, Vivienda y Ordenación del Territorio, Comunidad de Madrid, Spain, and was performed in accordance with the Spanish laws.

Data accessibility: Analyses reported in this article can be reproduced using the data provided by Morales and Velando (2018).

Conflict of Interest: The authors declare no conflict of interest.

Handling editor: Anna Lindholm

REFERENCES

- Adriaensen F, Dhondt AA, Van Dongen S, Lens L, Matthysen E. 1998. Stabilizing selection on blue tit fledgling mass in the presence of sparrowhawks. *Proc R Soc Lond B*. 265:1011–1016.
- Allen WL, Higham JP. 2015. Assessing the potential information content of multicomponent visual signals: a machine learning approach. *Proc R Soc Lond B*. 282:20142284.
- Alonso-Álvarez C, Doutrelant C, Sorci G. 2004. Ultraviolet reflectance affects male-male interactions in the blue tit (*Parus caeruleus ultramarinus*). *Behav Ecol*. 15:805–809.
- Arganda S, Pérez-Escudero A, de Polavieja GG. 2012. A common rule for decision making in animal collectives across species. *Proc Natl Acad Sci USA*. 110:3651–3651.
- Association for the Study of Animal Behavior/Animal Behavior Society (ASAB/ABS). 2012. Guidelines for the treatment of animals in behavioural research and teaching. *Anim Behav*. 83:301–309.
- Avilés JM, Soler JJ, Pérez-Contreras T. 2006. Dark nests and egg colour in birds: a possible functional role of ultraviolet reflectance in egg detectability. *Proc Biol Sci*. 273:2821–2829.
- Bize P, Paillet R, Moureau B, Heeb P. 2006. A UV signal of offspring condition mediates context-dependent parental favouritism. *Proc Biol Sci*. 273:2063–2068.
- Burley N. 1981. Mate choice by multiple criteria in a monogamous species. *Am Nat*. 117:515–528.
- Burley N. 1986. Sexual selection for aesthetic traits in species with biparental care. *Am Nat*. 127:415–445.
- Caro SM, Griffin AS, Hinde CA, West SA. 2016. Unpredictable environments lead to the evolution of parental neglect in birds. *Nat Commun*. 7:10985.
- Cline MH, Hatt JL, Conroy MJ, Cooper RJ. 2016. Experimental evidence for a phenotypic trait as an age-dependent intrasexual social signal between familiar individuals. *Anim Behav*. 111:319–327.

- Davis JN, Todd PM, Bullock S. 1999. Environment quality predicts parental provisioning decisions. *Proc R Soc Lond B*. 266:1791–1797.
- Delhey K, Peters A, Johnsen A, Kempenaers B. 2006. Seasonal changes in blue tit crown color: do they signal individual quality? *Behav Ecol*. 17:790–798.
- Dreiss AN, Ruppli CA, Antille S, Roulin A. 2015. Information retention during competitive interactions: siblings need to constantly repeat vocal displays. *Evol Biol*. 42:63–74.
- Dreiss AN, Ruppli CA, Delarbre A, Faller C, Roulin A. 2017. Responsiveness to siblings' need increases with age in vocally negotiating barn owl nestlings. *Behav Ecol Sociobiol*. 71:109.
- Dunlap AS, Nielsen ME, Dornhaus A, Papaj DR. 2016. Foraging bumble bees weigh the reliability of personal and social information. *Curr Biol*. 26:1195–1199.
- Fargallo JA, Merino S. 2004. Clutch size and haemoparasite species richness in adult and nestling blue tits. *Ecoscience*. 11:168–174.
- Galván I, Amo L, Sanz JJ. 2008. Ultraviolet-blue reflectance of some nestling plumage patches mediates parental favouritism in great tits *Parus major*. *J Avian Biol*. 39:277–282.
- Godfray HCJ. 1991. Signalling of need by offspring to their parents. *Nature*. 352:328–330.
- Godfray HC. 1995. Evolutionary theory of parent-offspring conflict. *Nature*. 376:133–138.
- Gottlander K. 1987. Parental feeding behavior and sibling competition in the pied flycatcher, *Ficedula hypoleuca*. *Ornis Scand*. 18:269–276.
- Gowaty PA, Anderson WW, Bluhm CK, Drickamer LC, Kim YK, Moore AJ. 2007. The hypothesis of reproductive compensation and its assumptions about mate preferences and offspring viability. *Proc Natl Acad Sci USA*. 104:15023–15027.
- Grieco F. 2002. Time constraint on food choice in provisioning blue tits, *Parus caeruleus*: the relationship between feeding rate and prey size. *Anim Behav*. 64:517–526.
- Griggio M, Morosinotto C, Pilastro A. 2009. Nestlings' carotenoid feather ornament affects parental allocation strategy and reduces maternal survival. *J Evol Biol*. 22:2077–2085.
- Griggio M, Serra L, Licheri D, Campomori C, Pilastro A. 2009. Moulting speed affects structural feather ornaments in the blue tit. *J Evol Biol*. 22:782–792.
- Grodzinski U, Johnstone RA. 2012. Parents and offspring in an evolutionary game: the effect of supply on demand when costs of care vary. *Proc Biol Sci*. 279:109–115.
- Haig D. 1990. Brood reduction and optimal parental investment when offspring differ in quality. *Am Nat*. 136:550–556.
- Hinde CA, Kilner MR. 2007. Negotiations within the family over the supply of parental care. *Proc R Soc Lond B*. 274:53–60.
- Höbel G. 2015. Socially mediated plasticity of chorusing behavior in the gladiator frog *Hypsiboas rosenbergi*. *Acta Ethol*. 18:145–152.
- Jacot A, Kempenaers B. 2007. Effects of nestling condition on UV plumage traits in blue tits: an experimental approach. *Behav Ecol*. 18:34–40.
- Jimeno B, Gil D. 2015. Parent-absent calls are related to nestling reaction time and parental food allocation in the spotless starling. *Behaviour*. 152:1413–1431.
- Johnsen A, Delhey K, Schlicht E, Peters A, Kempenaers B. 2005. Male sexual attractiveness and parental effort in blue tits: an experimental test of the differential allocation hypothesis. *Anim Behav*. 70:877–888.
- Jordan JJ, Hoffman M, Bloom P, Rand DG. 2016. Third-party punishment as a costly signal of trustworthiness. *Nature*. 530:473–476.
- Jourdie V, Moureau B, Bennett AT, Heeb P. 2004. Ultraviolet reflectance by the skin of nestlings. *Nature*. 431:262–262.
- Kilner RM. 2001. A growth cost of begging in captive canary chicks. *Proc Natl Acad Sci USA*. 98:11394–11398.
- Kölliker M, Richner H, Werner I, Heeb P. 1998. Begging signals and biparental care: nestling choice between parental feeding locations. *Anim Behav*. 55:215–222.
- Kölliker M, Brinkhof MW, Heeb P, Fitze PS, Richner H. 2000. The quantitative genetic basis of offspring solicitation and parental response in a passerine bird with biparental care. *Proc Biol Sci*. 267:2127–2132.
- Laidre ME, Johnstone RA. 2013. Animal signals. *Curr Biol*. 23:R829–R833.
- Lessells CM. 1999. Sexual conflict. In: Keller L, editor. *Levels of selection in evolution*. Princeton (NJ): Princeton University Press. p. 75–99.
- Ligon RA, Hill GE. 2010. Feeding decisions of eastern bluebirds are situationally influenced by fledgling plumage color. *Behav Ecol*. 21:456–464.
- Ligon RA, McGraw KJ. 2016. Social costs enforce honesty of a dynamic signal of motivation. *Proc R Soc Lond B*. 283:20161873.
- Limbouurg T, Mateman AC, Andersson S, Lessells CM. 2004. Female blue tits adjust parental effort to manipulated male UV attractiveness. *Proc Biol Sci*. 271:1903–1908.
- Lucass C, Korsten P, Eens M, Müller W. 2016. Within-family parent-offspring co-adaptation in a wild bird: on static traits, behavioural reaction norms, and sex differences. *Funct Ecol*. 30:274–282.
- Lyon BE, Eadie JM, Hamilton LD. 1994. Parental choice selects for ornamental plumage in American coot chicks. *Nature*. 371:240–243.
- Mahr K, Griggio M, Granatiero M, Hoi H. 2012. Female attractiveness affects paternal investment: experimental evidence for male differential allocation in blue tits. *Front Zool*. 9:14.
- Mainwaring MC, Dickens M, Hartley IR. 2011. Sexual dimorphism and growth trade-offs in blue tit *Cyanistes caeruleus* nestlings. *Ibis*. 153:175–179.
- Martín J, López P. 2015. Condition-dependent chemosignals in reproductive behavior of lizards. *Horm Behav*. 68:14–24.
- Mock DW, Dugas MB, Strickler SA. 2011. Honest begging: expanding from signal of need. *Behav Ecol*. 22:909–917.
- Morales J, Velando A. 2013. Signals in family conflicts. *Anim Behav*. 86:11–16.
- Morales J, Velando A. 2018. Data from: coloration of chicks modulates costly interactions among family members. Dryad Digital Repository. <http://dx.doi.org/10.5061/dryad.6vd5d71>
- Moreno-Rueda G. 2010. An immunological cost of begging in house sparrow nestlings. *Proc Biol Sci*. 277:2083–2088.
- Moreno-Rueda G, Soler M, Martín-Vivaldi M, Palomino JJ. 2009. Brood provisioning rate and food allocation rules according to nestling begging in a clutch adjusting species, the Rufous-tailed Scrub-robin *Cercotrichas galactotes*. *Acta Ornithol*. 44:167–175.
- Neuenschwander S, Brinkhof MWG, Kölliker M, Richner H. 2003. Brood size, sibling competition, and the cost of begging in great tits (*Parus major*). *Behav Ecol*. 14:457–462.
- Noguera JC, Morales J, Pérez C, Velando A. 2010. On the oxidative cost of begging: antioxidants enhance vocalizations in gull chicks. *Behav Ecol*. 21:479–484.
- Nowak MA, Sigmund K. 2005. Evolution of indirect reciprocity. *Nature*. 437:1291–1298.
- Nur N. 1984. The consequences of brood size for breeding blue tits II. Nestling weight, offspring survival and optimal brood size. *J Anim Ecol*. 53:497–517.
- O'Connor RJ. 1978. Brood reduction in birds: selection for fratricide, infanticide and suicide? *Anim Behav*. 26:79–96.
- Oliveira RF, Simões JM, Teles MC, Oliveira CR, Becker JD, Lopes JS. 2016. Assessment of fight outcome is needed to activate socially driven transcriptional changes in the zebrafish brain. *Proc Natl Acad Sci USA*. 113:E654–E661.
- Parejo D, Avilés JM, Rodríguez J. 2010. Visual cues and parental favouritism in a nocturnal bird. *Biol Lett*. 6:171–173.
- Parker GA, Royle NJ, Hartley IR. 2002. Intrafamilial conflict and parental investment: a synthesis. *Phil Trans R Soc B*. 357:295–307.
- Peters A, Delhey K, Johnsen A, Kempenaers B. 2007. The condition-dependent development of carotenoid-based and structural plumage in nestling blue tits: males and females differ. *Am Nat*. 169:S122–S136.
- Ratikainen II, Kokko H. 2010. Differential allocation and compensation: who deserves the silver spoon? *Behav Ecol*. 21:195–200.
- Romano A, Rubolini D, Caprioli M, Musitelli F, Ambrosini R, Saino N. 2015. Parent-absent begging in barn swallow broods: causes of individual variation and effects on sibling interactions and food allocation. *Evol Biol*. 42:432–442.
- Roulin A, Kölliker M, Richner H. 2000. Barn owl (*Tyto alba*) siblings vocally negotiate resources. *Proc Biol Sci*. 267:459–463.
- Royle NJ, Russell AF, Wilson AJ. 2014. The evolution of flexible parenting. *Science*. 345:776–781.
- Santucci D, Masterson D, Elwood RW. 1994. Effects of age, sex, and odours from conspecific adult males on ultrasonic vocalizations of infant CS1 mice. *Behav Processes*. 32:285–295.
- Sheldon BC, Andersson S, Griffith SC, Ornbjör J, Sendecka J. 1999. Ultraviolet color variation influences blue tit sex ratios. *Nature*. 402:874–877.
- Smiseth PT, Andrews C, Brown E, Prentice PM. 2010. Chemical stimuli from parents trigger larval begging in burying beetles. *Behav Ecol*. 21:526–531.

- Soler M, Ruiz-Raya F, Carra LG, Medina-Molina E, Ibáñez-Álamo JD, Martín-Gálvez D. 2014. A long-term experimental study demonstrates the costs of begging that were not found over the short term. *PLoS One*. 9:e111929.
- Suzuki TN, Wheatcroft D, Griesser M. 2016. Experimental evidence for compositional syntax in bird calls. *Nat Commun*. 7:10986.
- Tanner M, Richner H. 2008. Ultraviolet reflectance of plumage for parent-offspring communication in the great tit (*Parus major*). *Behav Ecol*. 19:369–373.
- Tibbetts EA, Dale J. 2004. A socially enforced signal of quality in a paper wasp. *Nature*. 432:218–222.
- Trivers R. 1974. Parent-offspring conflict. *Am Zool*. 14:249–264.
- Tschirren B, Fitze PS, Richner H. 2005. Carotenoid-based nestling colouration and parental favouritism in the great tit. *Oecologia*. 143:477–482.
- Velando A, Kim S-Y, Noguera JC. 2013. Begging response of gull chicks to the red spot on the parental bill. *Anim Behav*. 85:1359–1366.
- Wiebe KL, Slagsvold T. 2012. Brood parasites may use gape size constraints to exploit provisioning rules of smaller hosts: an experimental test of mechanisms of food allocation. *Behav Ecol*. 23:391–396.