



Original Article

# Favored parent–offspring trait combinations? On the interplay of parental and offspring traits

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The expression of key traits like parental provisioning and offspring begging is confounded by the parent–offspring conflict in species with parental care, with offspring seeking greater parental investment than parents are willing to provide. Given the reciprocal interplay of these traits, selection has likely favored specific parent–offspring trait combinations, and it has been a longstanding question which party benefits most from this linkage. This will become apparent in a mismatch situation, which we here experimentally created by reciprocally cross-fostering blue tit broods. We hypothesized that offspring fledgling mass and their excreted corticosterone metabolite (CM) levels (reflecting stress) should vary with the rate of (foster) parental care (if provisioning is under full parental control), with offspring begging (if offspring is fully in control), or an interaction of both traits reflecting stable end points along a power continuum. We found a significant interaction effect, that is, highly demanding broods reached lowest fledgling mass when raised by low providing parents (due to partly unrewarded costly begging) but highest fledgling mass when raised by high providers. This pattern, however, was not reflected in offspring CM levels. Parental provisioning of the foster parents affected CM levels again in interaction with the offspring's begging level, but this pattern may rather reflect intensity and frequency of sibling competition. Taken together, our results suggest that an adjustment of the offspring's phenotype to the post-hatching social environment is primarily beneficial for highly demanding offspring and that parents have the upper hand (but probably not full control) over provisioning.

**Key words:** begging, blue tit, costs, corticosterone, mismatch, parent–offspring conflict.

## INTRODUCTION

In species with parental care, a large part of early offspring development takes place within the family. This social environment as created by all family members has, therefore, a crucial influence on individual fitness and trait evolution (Clutton-Brock 1991). Obviously, offspring may develop best when its developmental trajectory matches the conditions of its family environment, in particular the parental provisioning capacity. Offspring and parent behaviors have indeed been shown to covary on the phenotypic level (e.g., Kölliker et al. 2000; Hager and Johnstone 2003; Curley et al. 2004; Lock et al. 2004; Hinde et al. 2009, 2010; Estramil et al. 2013), even though the underlying mechanisms are not fully understood yet.

Another yet unresolved question is whether the observed patterns of parent–offspring trait combinations serve the evolutionary

interests of parents, offspring, or both. This question arises because the dynamics between parent and offspring traits are influenced by an evolutionary conflict of interest due to asymmetries in the rating of costs and benefits of parental investment (parent–offspring conflict, Trivers 1974). In short, offspring will seek greater parental investment (e.g., parental provisioning) than parents are willing to provide (Trivers 1974). Addressing whether current parental provisioning represents the optimum for parents (i.e., parents are in control of provisioning) or offspring (i.e., offspring are in control of parental provisioning via means of begging) is thus highly relevant (e.g., Kölliker et al. 2005; Hinde et al. 2010). Understanding who is in control can be studied best in an experimentally induced mismatch situation because the party that is not in control of provisioning is supposed to pay a cost.

Most previous studies have found that offspring suffer from an exchange of young between broods in terms of impaired growth (Hager and Johnstone 2003; Lock et al. 2004; Hinde et al. 2010; but see Estramil et al. 2014). However, these previous studies were

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done in captivity, where relevant selection pressures (e.g., costs of foraging, predators, and parasites) are not acting on the family, which potentially skewed the results. Thus, experiments under natural conditions are essential to test how selection acts on traits in experimentally manipulated conditions in order to understand how fitness costs shape parent–offspring interactions. In addition, the above-mentioned studies suggest that (foster) parents could not (or were not willing to) satisfy offspring requirements. This nutritional stress in turn likely increases levels of corticosterone (Díaz-Muñoz et al. 2000; Lynn et al. 2003), a glucocorticoid hormone that is released as part of the adrenocortical stress response (Sapolsky et al. 2000), and mismatching may, therefore, also be reflected in stress hormone levels. In offspring, an adequate stress response to food scarcity would be an elevation in begging intensity in an attempt to extract more resources from parents. Corticosterone has therefore been hypothesized to provide the mechanism of how the nutritional status of offspring is communicated to parents by elevating begging intensity (reviewed in Smiseth et al. 2011). Hence, it appears vital to further investigate the relationship between corticosterone levels and begging.

We performed a reciprocal full-brood cross-fostering study in blue tits (*Cyanistes caeruleus*), investigating the effects of mismatched parent–offspring interactions in the wild. Full-brood cross-fostering generates variation in the family environment for both offspring and parents (Kölliker et al. 2012). This enabled us to study offspring begging as well as parental provisioning in separation and to detect how they—eventually in interplay—determine offspring growth as measured via their fledgling mass (and thus fitness: e.g., Richner 1992; Krause et al. 2009; Tilgar et al. 2010). Broods that beg most intensely should reach the highest mass at fledging if the rate of parental provisioning is under offspring control by means of begging and vice versa. If, however, the level of food provisioning is mainly determined by the parents, we would expect that offspring mass at fledging is mainly driven by the rate of parental provisioning. The extent of growth reduction should additionally increase with an increasing discrepancy between foster chick begging and parental provisioning, given that begging is costly (e.g., Kilner 2001; Noguera et al. 2010; Moreno-Rueda and Redondo 2011) and that begging remains progressively unrewarded. Previous studies on birds found a positive covariation between offspring begging and parental provisioning (Kölliker et al. 2000; Hinde et al. 2009; Estramil et al. 2013), which has been interpreted as such that parents control provisioning and selection is acting predominantly on offspring begging (Kölliker et al. 2005). Therefore, we focused on costs for offspring, even though all parties involved may suffer fitness consequences from a mismatch. Furthermore, we expect to find either of the above described scenarios to be reflected on an even finer scale, namely in the amount of excreted corticosterone metabolites (CMs), which may also form a mechanism of how offspring need is communicated via begging.

## MATERIALS AND METHODS

### Study area and general methods

We conducted our experiments in a nest-box population of blue tits breeding in Peerdsbos, a mature oak-beech forest near Antwerp (51°16'N, 4°29'E, Belgium) in the spring of 2012 (March–May). Clutch size and onset of incubation (to estimate hatch date of chicks) were assessed via daily checking of nest-boxes. Blue tits show moderate asynchrony between hatching of the first and the last chick, with typically the last 1–2 chicks having 1 or 2 days delay (Stenning 2008). We

disrupted the potentially coadjusted offspring solicitation and parental provisioning behaviors by means of cross-fostering of whole clutches. Eggs of 2 nests (=dyad) that were matched for hatch date (maximum difference 2 days) and clutch size (maximum difference 2 eggs) were reciprocally exchanged 3 days before expected hatching. In total, clutches of 54 nests were cross-fostered. Day of hatching was defined as day 1. On day 15, all chicks were provided with a metal ring with a unique number and individually weighed (=fledgling mass) to the nearest 0.01 g. This day is at the end of the developmental period of chicks and is a standard measure of blue and great tit offspring, predicting post-fledgling survival and recruitment (e.g., Both et al. 1999; Naef-Daenzer et al. 2001; Monrós et al. 2002; Nicolaus et al. 2008). Parents were caught on day 9 when feeding their (foster) chicks using nest-box traps. They were weighed, metal banded, and obtained a unique color ring combination facilitating further identification. All experiments were conducted under licenses from the Ethical Committee for animals (ECD) of the University of Antwerp (license number 2011-10).

### Begging behavior

On day 7, we took the second and fourth chick in a descending weight rank and transferred them to a warmed artificial nest-box to perform a begging test. We chose to perform the begging test on day 7 as the chicks' thermoregulation before day 7 is poorly developed. Thus, we intended to test as late as possible to avoid hypothermia (potentially caused, e.g., by transportation to the begging test), ultimately impinging on the begging performance. However, soon after day 7 (day 8–9), chicks open their eyes and show a fear response, which makes it virtually impossible to elicit a begging response outside their natural environment. The second and fourth chick were chosen to standardize the procedure between nests and to avoid potential effects of the hatching order on begging intensity. We took only 2 chicks per nest as parents may desert due to “predation” (i.e., when chicks were temporarily collected for the begging test), which may be especially problematic in small broods.

Prior to the test, each chick was fed with defrosted blue bottle maggots until satiation. We videotaped begging behavior (Sony, DCR-SX 30) after 60, 90, and 120 min of food deprivation by opening the nest-box at each of the sampling points until the chick ceased begging. Additionally, we played a parental feeding call back to offspring, each time the box was opened. The feeding call was recorded in 2011 from an individual that was unrelated to all test chicks. Begging was tested in a food deprivation gradient as part of a different study on parent–offspring covariation of behavioral reaction norms (see Lucass et al. 2015). However, for the purpose of this study, we were not interested in the temporal dynamics of how begging changes with hunger but rather in the average begging phenotype parents are confronted with.

After testing, we immediately fed chicks and returned them to their (foster) nest. From the videos we scored chick begging posture every second using an established rating scale (modified from Kilner 2002), ranging from 0 (chick is not begging) to 5 (chick's beak is open, the head is leaned back in a 90° angle, and the back is in vertical position; see also Lucass et al. 2015). Brood begging intensity was calculated as the mean of all begging bouts (60, 90, and 120 min) of the 2 chicks. Thus, begging intensity reflects a combined measure of posture and duration.

### Dropping sampling and CM measurements

When weighing chicks prior to the begging test on day 7, we collected droppings of the second and fourth heaviest chicks (which

also entered the begging test) and 2 additional randomly chosen chicks to calculate a nest estimate of CM. Droppings were collected at day 7 to investigate a potential relationship between CM and begging (which was measured on that day). We measured levels of corticosterone via its CM, as it has a number of advantages. First, collection of droppings is noninvasive, thus there are no effects of disturbance on the levels of CM within the time of sampling in contrast to blood sampling (see Gil et al. 2008). Second, it allows sampling at a very young age (here: blue tit chicks of 7 days of age, ~5.2 g) when taking a blood sample—of an amount that is required for a hormone analysis—can potentially be life-threatening. Finally, it provides a cumulative measure of CM over time in contrast to “snap-shot” concentrations, as obtained from blood samples.

The collected droppings were immediately transferred into a 1.5-mL Eppendorf tube and stored on ice until return to the University of Antwerp where samples were transferred to a  $-80^{\circ}\text{C}$  freezer until processing. After the breeding season, droppings were defrosted. Wet droppings (0.05 g; avoiding the urine part) were vortexed in 0.3 mL methanol (99.9%) and 0.2 mL distilled water for 15 min (Palme et al. 2013), centrifuged, and 0.1 mL of the supernatant was evaporated. The dried supernatants were sent to the University of Veterinary Medicine, Vienna, for further analysis. Samples were then resolved in 0.1 mL of methanol (60%). We included a hydrolysis step before analyzing the samples with the enzyme immunoassay (EIA), which is especially useful when analyzing nestling droppings with the EIA we used (Stöwe et al. 2013). The sample extracts (0.05 mL) were evaporated, afterwards dissolved in 0.1 mL Na-acetate buffer and 0.2  $\mu\text{L}$   $\beta$ -glucuronidase/-aryl sulfatase (Merck 1.04114.0002), and hydrolyzed at  $38^{\circ}\text{C}$  for 18 h. We determined the amounts of immunoreactive metabolites using a cortisone EIA, which has been validated previously for blue tits (Lobato et al. 2008; see also Stöwe et al. 2013). It measures glucocorticoid metabolites with a 3,11-dione structure (detailed description in Rettenbacher et al. 2004). Samples were assayed in duplicate, inter-assay variation was 2% for the high level and 7% for the low level pool.

## Provisioning behavior

In the morning of day 10, we placed an infrared camera inside at the top of the nest-box, facing downward into the nest and provisioning was recorded for 2.5 h in all cross-fostered nests. We discarded the first 30 min of the videos in order to avoid feeding bias due to our disturbance (Kölliker et al. 1998). Provisioning behavior was scored during the remaining 2 h using “The Observer XT” (version 10.0.526, 2010, Noldus Information Technology, The Netherlands).

Blue tits are single-prey loaders, that is, per visit a parent brings only 1 prey item and feeds it to only 1 chick. Prey consists of invertebrates like spiders, caterpillars, and small insects. In order to obtain a measure of the food quantity brought to the nest we scored for every feeding visit the prey size, classified as small (1), intermediate (2), or large (3) (sensu Kölliker et al. 1998). The *weighted provisioning rate* (calculated as the provisioning rate multiplied with the average prey item size, sensu Kölliker et al. 1998) integrates the prey item size in parental provisioning, which, although the exact scaling of the nutritional value of prey items is largely unknown, may provide a better estimate of provided food quantity than provisioning rate only.

## Statistical analyses

To test whether offspring begging or parental provisioning influenced fledgling mass, we performed a multiple regression (MR) on

the latter (model A). Explanatory variables were “hatch date” (as Julian date), “brood size,” the “mean begging score of chicks,” and the “weighted provisioning rate of their foster parents.” As we also included the interaction of the latter 2 (=measure of the behavioral mismatch between begging of chicks and provisioning of their foster parents), we mean-centered both variables prior the analysis to facilitate interpretation of the main effects (Schielzeth 2010). Further, we included the “midparent body mass” of the genetic parents to control for potentially confounding genetic effects on fledgling mass of cross-fostered offspring.

In a mismatch situation, chicks might suffer nutritional stress, which could not only be reflected in fledgling mass but also on a finer scale, that is on the level of stress hormones. Thus, in a second MR, we aimed to test whether levels of CM (square root transformed to increase model fit) were predicted by a measure of mismatch (model B). We used the same explanatory variables as in model A but instead of “midparent body mass,” we used the “time of the day” (henceforth called “time of collection”) at which the dropping was collected, as it has been shown that levels of CM follow a circadian rhythm (e.g., Carere et al. 2003), and the “mean chick weight” on day 7.

If mismatched traits of parent–offspring combinations are associated with the existence of costs, we would expect to find coadaptation. Thus, we tested for a relationship between parental provisioning and offspring begging. We performed a third MR (model C) on the “begging intensity,” using “hatch date,” “brood size,” and the “weighted provisioning rate” of both foster and genetic parents as explanatory variables.

As it has been found in some studies that corticosterone affects begging (e.g., Kitaysky et al. 2001; Kitaysky et al. 2003), we investigated whether this relationship also exists in blue tits, using a third MR (model D). “Begging intensity” was the response variable and “mean fecal CM levels,” “hatch date” (as Julian date), and “brood size” were used as predictor variables.

We checked the models by inspection of residuals for normality, heteroscedasticity and nonlinear patterns. All statistical tests were performed in R, version 3.0.2 (R Core Team 2013, <http://www.R-project.org>). Beta values of variables of MRs were extracted using the package “QuantPsyc” (Fletcher 2012). Alpha value was 0.05. Sample size may differ as we were not able to collect all data at all times.

## RESULTS

### Factors influencing fledgling mass

Fledgling mass was negatively linked to begging intensity ( $t_{44} = -2.040$ ;  $P = 0.047$ ), increased with higher weighted provisioning rates of foster parents ( $t_{44} = 2.739$ ;  $P = 0.009$ ) and also affected by the interaction of the latter 2 ( $t_{44} = 2.183$ ;  $P = 0.034$ ) (Table 1A, Figure 1). Further, brood size ( $t_{44} = -2.228$ ;  $P = 0.031$ ) but neither hatch date ( $t_{44} = 0.787$ ;  $P = 0.436$ ) nor midparent body mass of the genetic parents ( $t_{44} = 1.046$ ;  $P = 0.301$ ) had a significant effect on fledgling mass.

### Factors influencing CM levels in chick droppings

Time of collection had a negative effect on (square root transformed) chick CM levels ( $t_{43} = -3.665$ ;  $P < 0.001$ ). Also, the interaction term begging intensity  $\times$  weighted provisioning rate of the foster parents ( $t_{43} = 2.033$ ;  $P = 0.048$ ; Table 1B, Figure 2) had a significant effect on (square root transformed)

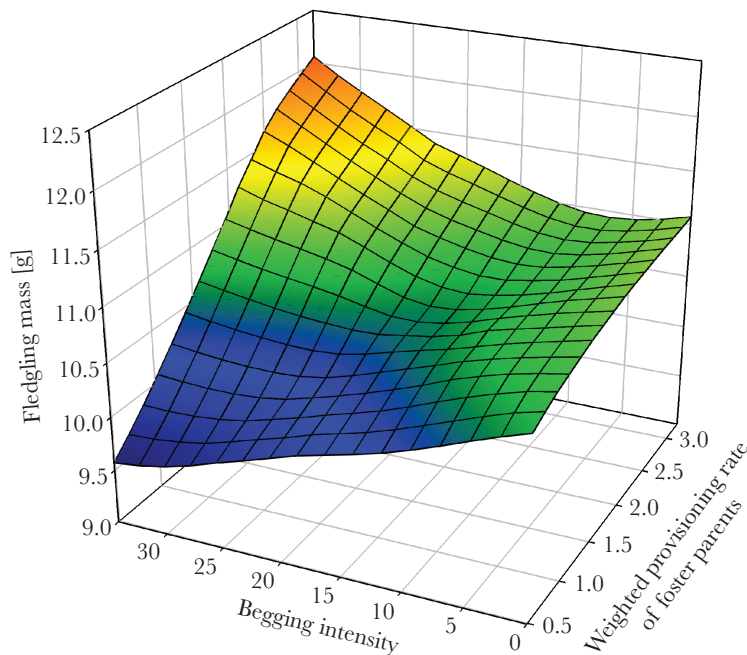
**Table 1**

**MR analysis of factors influencing fledgling mass (A,  $R^2 = 0.37$ ;  $F_{6,44} = 4.372$ ;  $P = 0.002$ ;  $N = 51$ ), CM levels (B,  $R^2 = 0.43$ ;  $F_{7,43} = 4.678$ ;  $P < 0.001$ ,  $N = 51$ ), and begging intensity (D,  $R^2 = 0.19$ ;  $F_{3,47} = 3.736$ ;  $P = 0.017$ ,  $N = 50$ ) of chicks**

Source of variation	A) Fledgling mass		B) Fecal CM levels (sqrt)		D) Begging intensity	
	$\beta$	$P$	$\beta$	$P$	$\beta$	$P$
Begging intensity <sup>a</sup>	-0.268	<b>0.047</b>	0.052	0.725	Not included	
Weighted provisioning rate of foster parents <sup>a</sup>	0.421	<b>0.009</b>	-0.171	0.246	Not included	
Hatch date (Julian date)	0.112	0.436	-0.093	0.508	-0.364	<b>0.009</b>
Brood size	-0.306	<b>0.031</b>	0.213	0.108	-0.045	0.744
Midparent body mass of genetic parents (g)	0.135	0.301	Not included		Not included	
Begging intensity <sup>a</sup> × weighted provisioning rate of foster parents <sup>a</sup>	0.244	<b>0.034</b>	0.258	<b>0.048</b>	Not included	
Time of dropping collection (minutes after midnight)	Not included		-0.437	<b>&lt;0.001</b>	Not included	
Mean chick weight (g)	Not included		-0.253	0.080	Not included	
Fecal CM levels	Not included		Not included		0.233	0.092

Significant  $P$ -values are indicated in bold.

<sup>a</sup>Mean-centered.

**Figure 1**

A 3D scatterplot with a regression plane on how (foster) parental provisioning and own begging impinge on fledgling mass (g). For ease of visibility, the color of the regression plane corresponds to  $y$  axis values ranging from blue (low) to orange (high).

chick CM levels. However, there was no significant effect of begging intensity ( $t_{43} = 0.353$ ;  $P = 0.725$ ), weighted provisioning rate of the foster parents ( $t_{43} = -1.176$ ;  $P = 0.246$ ), hatch date ( $t_{43} = -0.667$ ;  $P = 0.508$ ), mean chick weight ( $t_{43} = -1.792$ ;  $P = 0.080$ ), or brood size ( $t_{43} = 1.643$ ;  $P = 0.108$ ) on CM levels (Table 1B).

### Parent–offspring coadaptation?

Begging intensity was negatively influenced by hatch date ( $t_{48} = -2.343$ ;  $P = 0.023$ ), but neither brood size ( $t_{48} = 0.360$ ;  $P = 0.720$ ) nor weighted provisioning rates of foster ( $t_{48} = -0.274$ ;  $P = 0.785$ ) or genetic parents ( $t_{48} = -0.080$ ;  $P = 0.937$ ) had a significant effect on begging (model C:  $R^2 = 0.14$ ;  $F_{4,48} = 1.927$ ;  $P = 0.121$ ,  $N = 53$ ).

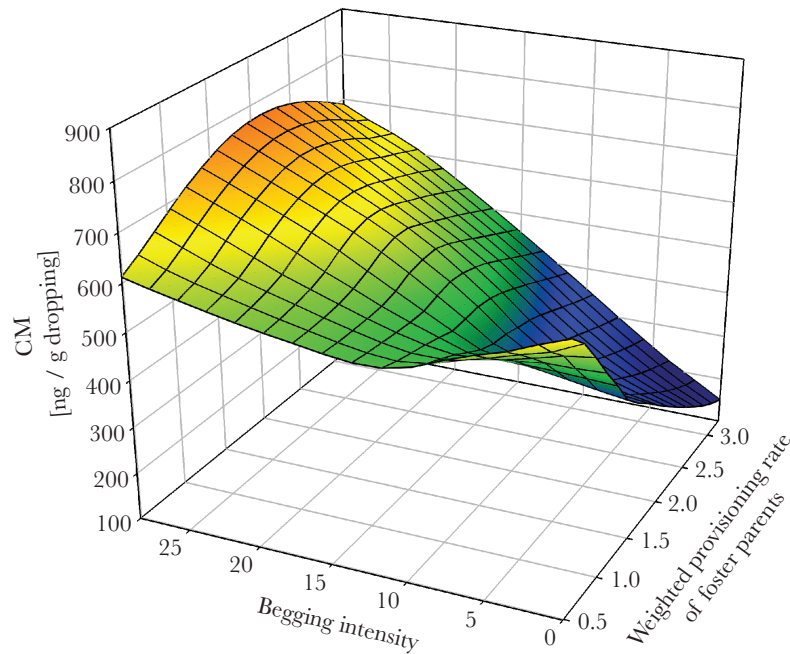
### The relationship between begging and CM

Brood size did not significantly influence begging intensity ( $t_{46} = -0.329$ ;  $P = 0.744$ ), but hatch date ( $t_{46} = -2.737$ ;  $P = 0.009$ ) had a negative effect on the latter. Further, we found a nonsignificant trend ( $t_{46} = 1.720$ ;  $P = 0.092$ ) for a positive effect of mean CM levels on begging intensity (Table 1D).

### DISCUSSION

Parental care benefits all family members, although it involves costs for the caregiver but also for those that have to elicit care via vigorous begging displays. Selection may minimize these costs by favoring particular parent–offspring combinations, which may be skewed toward one party's optimum. We found that matched





**Figure 2**

A 3D scatterplot with a regression plane on how (foster) parental provisioning and own begging impinge on CM levels of chicks (ng/g dropping). For ease of visibility, the color of the regression plane corresponds to  $z$  axis values ranging from blue (low) to orange (high).

parent–offspring combinations benefited offspring particularly in terms of body mass as parents have control over the level of provided care in terms of provisioning. Yet, this pattern also depended on the behavioral phenotype of the offspring.

### Consequences of mismatched parent–offspring combinations for offspring growth

Offspring growth, in terms of fledgling mass, largely depended on parental provisioning but also on their own begging behavior as well as on the interplay between parent and offspring traits. More to the point, highly demanding broods reached the highest fledgling mass when raised by parents that provided food at a high rate, but lowest fledgling mass when raised by low provisioning parents. The observed strong growth reduction among high begging offspring raised by parents that provide little is likely to be due to the costs of begging, which remains partly unrewarded (e.g., Kilner 2001; Noguera et al. 2010; Moreno-Rueda and Redondo 2011). These nestlings are unable to obtain resources beyond a (predetermined) generosity of their (foster) parents. Thus, a pre-hatching adjustment to the post-hatching social environment is—in the first place—beneficial for highly demanding offspring (obviously parents benefit indirectly through offspring fitness). This is also supported by the fact that fledgling mass of less demanding broods was intermediate, both, when raised by high or low providing parents (Figure 1).

Low begging may represent another, more conservative, strategy that is largely independent from the level of parental care. Even when mismatched to their advantage (i.e., a low begging brood raised by high providing parents), offspring do not acquire a higher fledgling mass than low begging broods raised by low providing parents (see Figure 1). To crystallize, foster parents provided food at a high rate irrespective of the low levels of begging by their foster chicks, but these resources were apparently not converted in body mass gain. We currently lack an explanation for this and can only

speculate that chicks potentially reallocate nutrients received from high providing parents to other physiological processes, that are not measured here, such as immunity (Hasselquist and Nilsson 2012). Indeed, low begging offspring raised by high providing foster parents differed physiologically as indicated by low levels of stress hormones (see below for a detailed discussion).

The fact that high begging nestlings can extract sufficient resources only from high but not low providing foster parents (Figure 1), suggests that parents have the upper hand (but probably not full control) in an ongoing battle for control over provisioning. This is supported by most (e.g., Hager and Johnstone 2003; Lock et al. 2004; Hinde et al. 2010) but not all (Estramil et al. 2014) previous studies, providing evidence that offspring raised by foster parents suffered fitness costs compared with offspring raised by own genetic parents. However, differences between, but also within, species may occur due to different ratings of costs and benefits. Thus, it is possible that dynamic changes occur on a power continuum during the phase of parental care (Royle et al. 2002; Royle et al. 2012), ranging from full parental control (Hinde et al. 2010) to full offspring control. In fact, parents may suffer costs in terms of reduced survival or lower future reproductive performance (Hinde et al. 2010; but see Estramil et al. 2014), which we unfortunately could not measure here as parents frequently disperse out of the study population.

### Physiological consequences of trait mismatching

The interplay of both begging and foster parental provisioning influenced CM levels in chick droppings too, but the pattern, as shown in Figure 2, does not reflect the results from the growth analysis (Figure 1). More to the point, CM levels were particularly low when offspring that begged very little were raised by parents that provided food at a high rate. This is interesting because the growth pattern of these nestlings was below what one would expect

(see above). Although these chicks did not convert given resources into body mass gain, they, nevertheless, benefited from high levels of provisioning via lower stress hormone levels.

In contrast, stress hormone levels of high begging broods were comparatively high, largely independent from the provisioning behavior of their foster parents. This may, on the one hand, result from a causal relationship as corticosterone has been argued to affect begging behavior (Kitaysky et al. 2001; Kitaysky et al. 2003, see below for a more detailed discussion). However, given that we study the brood level, an alternative explanation may be that begging intensity reflects the intensity of competition over a given prey item (i.e., sibling competition is less fierce, and thus less stressful, in low than in high begging broods). In addition, the frequency of parental provisioning may correspond to the level of perceived (nutritional) stress, with frequent nest visits being less stressful as it diminishes periods of starvation. Thus, frequency and intensity of competition among siblings may impinge on stress hormone levels, leading to a most advantageous situation for low begging offspring (i.e., low intensity of competition) raised by frequently providing parents.

Following this argumentation, one may expect CM levels of high begging offspring raised by low providing foster parents to be highest, as they experience the most intense sibling competition (from high begging siblings) in infrequently occurring feeding events. However, an elevation above the (threshold of the) concentrations observed among high begging chicks could be particularly costly. High levels of corticosterone have been associated with impaired cognitive abilities (Kitaysky et al. 2003), a weaker immune response (Loiseau et al. 2008), depressed growth rates (Spencer and Verhulst 2007), and inhibition of feather growth (Romero et al. 2005).

However, we did not find coadaptation between offspring begging and provisioning of their (genetic) parents, which is highly demanding offspring having parents that provide at a high rate and vice versa (see also Lucass et al. 2015 for a more comprehensive analysis). This is despite the fact that we provide evidence for offspring costs if parental and offspring traits are mismatched, which are thought to stabilize coadaptation of offspring begging and parental provisioning (Kilner and Hinde 2012). But the optimal offspring performance is not necessarily reached along the axis where parent–offspring trait combinations are matched. Offspring in a mismatch situation can yield an equal performance than matched offspring, for example, when comparing CM levels of high begging offspring raised by low providing parents with CM levels of matched combinations. This suggests the existence of different optimal parent–offspring trait combinations, which may impinge on the pattern of coadaptation.

Lastly, we have to stress that we collected droppings at day 7, whereas fledgling mass was measured at day 15. Hence, the duration during which both measurements were affected by the mismatch is different, and this temporal variation may possibly contribute to the observed disparity between the pattern of the stress hormones and the one of the growth analysis (see above). Nevertheless, we think that measures of stress, such as corticosterone, in the context of parent–offspring coadaptation may represent a fruitful avenue for future research. It would be particularly interesting to collect droppings more frequently instead of only once during the developmental period.

### Corticosterone and begging: signaling nutritional need?

We did not find that levels of corticosterone significantly affected nestling begging intensity. However, in the context of our analyses,

it needs to be noted that metabolites of hormones are excreted after they have acted on the individual, while we collected the samples prior to the begging test. Collecting samples after the begging test, however, would not be ideal because corticosterone is central to the adrenocortical stress response and stressors (e.g., transportation to the begging test) could influence corticosterone measures, an argument that may apply to previous correlative studies as well (e.g., Quillfeldt et al. 2006; Gil et al. 2008).

Finally, corticosterone may provide a physiological mechanism for some but not all begging traits (reviewed in Smiseth et al. 2011). Our measure of begging intensity was a combination of posture and duration, and both traits have been shown to be unaffected by the experimental administration of corticosterone in earlier studies in passerine birds (Loiseau et al. 2008; Wada and Breuner 2008), although reflecting hunger (Dickens et al. 2008).

Most convincing evidence that endogenous corticosterone regulates begging comes from experimental studies on black-legged kittiwakes (Kitaysky et al. 2001; Kitaysky et al. 2003). Thus, it remains unclear whether and how the applied study design (observational vs. experimental, see also Quillfeldt et al. 2006), the developmental mode of chicks (altricial passerines vs. semi-precocial seabirds), or species-specific differences contribute to the different study outcomes.

## CONCLUSIONS

Using a full-brood cross-fostering approach to create a mismatch between (foster) parental provisioning and begging in a wild blue tit population, we show that offspring fitness, here measured in terms of their mass at fledging, is determined by the joint influences of (foster) parental provisioning and own begging. Parental provisioning had a particularly strong effect on fledgling mass and intensely begging offspring could extract sufficient resources only from high but not low providing foster parents. This indicates that parents have the upper hand in an ongoing battle about control of provisioning. Further, the consequences of a mismatch for offspring were apparent on an even finer scale than fledgling mass, namely their corticosterone levels. This measure was influenced by the interaction of foster parental provisioning and own begging, potentially reflecting effects of stress due to intensity and frequency of sibling competition. Future studies are now needed to investigate potential costs for the parents in order to get a full understanding of the costs and benefits shaping parent–offspring interactions under natural conditions. Lastly, we failed to find that endogenous corticosterone presents a physiological mechanism of begging, which, in combination with a number of previous studies, questions the role of corticosterone for the regulation of begging in passerine bird species.

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