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Within-family parent–offspring co-adaptation in a wild bird: on static traits, behavioural reaction norms, and sex differences

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Summary

1. Parental care, a central component of reproduction in a wide range of animal species, often involves elaborate behavioural interactions between parents and their offspring. Due to the reciprocal nature of these interactions, it has been hypothesized that parental and offspring behaviours (e.g. parental food provisioning and offspring begging) are not only target but also agent of selection. These traits are therefore expected to co-evolve, ultimately leading to co-adaptation of parent and offspring behaviours within families. However, empirical data on such parent–offspring co-adaptation are limited, particularly for wild populations. Furthermore, mean levels of behaviour (as measured in previous studies) may not adequately describe the dynamic nature of the reciprocal interplay between parents and their offspring, and instead rather the behavioural reaction norms for provisioning and begging may be co-adapted.

2. We applied a large-scale cross-fostering study over 3 consecutive breeding seasons to investigate whether provisioning behaviour of wild blue tit (*Cyanistes caeruleus*) parents covaries with the begging behaviour of their genetic, cross-fostered offspring. We simultaneously analysed parent and offspring behaviours, both as static traits (mean levels) and behavioural reaction norms (offspring begging as a function of food deprivation and parental provisioning as a function of short-term experimental changes in brood size).

3. Neither maternal nor paternal provisioning rates covaried with the begging intensity of their genetic offspring when analysed as mean levels of behaviour. However, the slopes of the reaction norms for provisioning and begging were negatively correlated between male, but not female, parents and their genetic offspring. Thus, fathers that change their provisioning rate strongly with brood size sire offspring whose level of begging only weakly increases with hunger, and vice versa.

4. The observed covariation suggests the existence of sex-specific optima for parent–offspring trait combinations. Thus, our study not only highlights the importance of a behavioural reaction norm approach when investigating parent–offspring interactions, but also stresses the relevance of considering parents as separate units, at least for biparental species.

Key-words: behavioural reaction norm, blue tit, evolution, family conflict, interacting phenotypes, offspring solicitation, parental care, passerine bird, provisioning, responsiveness

Introduction

Parental care is a widespread behaviour in the animal kingdom and is thought to increase parental fitness through improved offspring condition and survival

(Clutton-Brock 1991; Kölliker, Royle & Smiseth 2012). However, parental care is costly, for example energetically, in terms of the time it takes, or because of an increased risk of predation. These costs of parental care reduce the parents' survival probability and their future reproductive capacity. Thus, parents should balance the amount of care they provide with the associated costs, leading to the

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fundamental trade-off between reproduction and life span (Stearns 1989).

The optimal investment into parental care made by an individual depends not only on itself, but also on the contribution to care by its partner, at least in biparental species. This cooperation may not be free of conflict as each individual parent gains fitness benefits from the total level of care provided, yet generally only pays the costs for its own contribution (sexual conflict over parental care, Trivers 1972). However, not only parents, but also the offspring may have control over the amount of parental care provided, for example through begging for food (Royle, Hartley & Parker 2002; Hinde 2006). This parent–offspring relationship creates another evolutionary conflict, since individual offspring will seek greater parental investment than parents are willing to provide, as each of the offspring (on average) shares only half its genes with its siblings, while parents are equally related to all of their offspring (parent–offspring conflict, Trivers 1974). Parent–offspring interactions over the amount of parental care provided are typically interpreted in the light of these family conflicts. Conflict resolution, when evolutionary stable behavioural strategies occur (Dobler & Kölliker 2009), has been investigated in numerous theoretical studies (game-theoretical conflict resolution models, e.g. Godfray 1991; quantitative genetic models, e.g. Kölliker, Brodie & Moore 2005).

Parent–offspring interactions are, however, not only of interest in the context of evolutionary conflicts between individuals. Interactions within the family environment also represent an example of *social selection*. Indeed, trait expression may not only depend on an individual's own genotype (direct genetic effects), but also on the genotypes of individuals it interacts with (indirect genetic effects, Moore, Brodie & Wolf 1997; Wolf, Brodie & Moore 1999). In such a situation, traits can be agents and targets of selection at the same time (Lock, Smiseth & Moore 2004), and both the individual as well as its social environment can evolve (Cheverud 2003; Wolf 2003). Parent–offspring communication regarding the amount of food to be provided within the family environment provides an example of such interacting traits, with offspring begging for food and parents responding to their offspring by providing it. The interaction is thus shaped by reciprocal selection. Feldman & Eshel (1982) suggested that there is a '*possibility of co-adaptation*' in interactions between dependent offspring and providing parents when genotypes, and thus phenotypes, of individuals can evolve. The idea of parent–offspring co-adaptation within families was explicitly considered in later co-adaptation models (e.g. Wolf & Brodie 1998). This, in conjunction with the fact that certain trait combinations yield higher fitness (Royle, Russell & Wilson 2014), led to the prediction of an intrafamilial correlation between parent and offspring traits.

Indeed, a number of recent studies across a range of different species provided empirical support for within-family co-adaptation between offspring and parental traits. These studies have typically demonstrated that certain (interacting)

traits, such as parental provisioning and offspring begging, covary on a phenotypic level between two consecutive generations (burrower bugs (*Sehirus cinctus*), Agrawal, Brodie & Brown 2001; mice (*Mus musculus*), Curley *et al.* 2004; Hager & Johnstone 2003; burying beetles (*Nicrophorus vespilloides*), Lock, Smiseth & Moore 2004; rhesus macaques (*Macaca mulatta*), Maestriperi 2004; canaries (*Serinus canaria*), Estramil, Eens & Müller 2013; Hinde, Buchanan & Kilner 2009; great tits (*Parus major*) Kölliker *et al.* 2000).

However, one aspect that has thus far hardly been taken into account is that parental care involves a continuous reciprocal interplay between parents and offspring. Parents feed according to changes in offspring begging, and offspring change their begging according to supply and the consequent changes in their hunger level. It has therefore been suggested that the behavioural reaction norms for begging and provisioning rather than mean levels of behaviour should co-adapt (Smiseth, Wright & Kölliker 2008; Dobler & Kölliker 2009). Such behavioural reaction norms provide information on how individuals change their behaviour (here: food provisioning / begging) over an environmental gradient (here: brood demand / food deprivation) (Dingemanse *et al.* 2010). The responsiveness to environmental conditions is thus analogous to the phenotypic plasticity of an individual, which is an important aspect of the individual behavioural phenotype, as recently highlighted (Dingemanse *et al.* 2010). This is obviously also vital in the context of parental care. As a case in point, individual house sparrows vary in how they change their provisioning in response to changes in, amongst other factors, nestling age (Westneat *et al.* 2011). However, phenotypic plasticity has never been considered for parental provisioning and offspring begging simultaneously (see Kölliker *et al.* 2000 for a unilateral approach). Nevertheless, as outlined above, this approach is necessary when studying co-adaptation of parent and offspring behaviours (Royle, Russell & Wilson 2014), because of the highly dynamic nature of the interactions between parents and offspring (Kölliker, Royle & Smiseth 2012).

Here, we performed a large-scale cross-fostering study in a wild population of blue tits (*Cyanistes caeruleus*, former *Parus caeruleus*, L., 1758), a passerine bird with biparental care, to test for parent–offspring co-adaptation within families. We focused on the two central traits shaping the behavioural interactions between parents and offspring in blue tits: the rate of parental provisioning (Kölliker *et al.* 2000) and the intensity of offspring begging, which was measured individually in an established begging test (see Goodship & Buchanan 2006; Hinde, Buchanan & Kilner 2009). We studied co-adaptation of static traits, using mean levels of behaviour as well as – for the first time – co-adaptation of behavioural reaction norms simultaneously for both parties. For the offspring, we measured the change in begging behaviour in relation to changes in their hunger level, which was manipulated via food deprivation. In the case of the parents, we carried out

short-term brood size manipulations to measure the individual responses in provisioning to changes in brood size (and thus begging). Making use of reciprocal cross-fostering of whole clutches, we disrupted potential co-adjustment between offspring solicitation and parental provisioning behaviour. Furthermore, this technique allows us to investigate whether a mechanism potentially causing parent–offspring co-adaptation acts pre- or post-hatching (as the former has been found in other species, e.g. Hinde, Buchanan & Kilner 2009; Estramil, Eens & Müller 2013).

We suggest that potential co-adaptation between parental and offspring behaviours is better reflected by the behavioural reaction norms than by mean levels of behaviour. Furthermore, sex differences may arise if one sex is more responsive to, or better informed about, (foster) offspring need (e.g. Stamps *et al.* 1985; Christe, Richner & Oppliger 1996; Slagsvold 1997; MacGregor & Cockburn 2002). Finally, if co-adaptation is mainly achieved via maternal effects (Hinde, Johnstone & Kilner 2010), females may have more of an opportunity to match offspring begging to their own quality or to that of their partner (Kölliker *et al.* 2000; Müller *et al.* 2007; Hinde, Johnstone & Kilner 2010).

Materials and methods

STUDY AREA AND GENERAL METHODS

We conducted our experiments from March – May 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 3 consecutive years (2011 – 2013). Daily checking of nest boxes allowed us to determine clutch size and the onset of incubation, in order to estimate the hatching date of the chicks (Table 1).

Table 1. Breeding parameters for each study year for those nests where both parents provisioned the offspring (2011: $N = 29$, 2012: $N = 28$, 2013: $N = 50$).

Parameter	Year		
	2011	2012	2013
Average laying date of 1st egg	10th April	5th April	24th April
Start date of incubation	19th April	21st April	4th May
Average brood size (un-manipulated)	10	10	11
Average hatch date	1st May	1st May	16th May
Individual chick mass on day 15 [g]	11.14	10.72	10.92
Hatched chicks that fledged [%]	98.1	98.5	97.3
Average begging score	7.58	9.67	6.97
Average provisioning rate females [visits / min]	0.25	0.51	0.39
Average provisioning rate males [visits / min]	0.25	0.50	0.48

Three days before the expected hatching, we cross-fostered eggs reciprocally between two nests (=dyad) that were matched for clutch size (maximum difference: two eggs) and anticipated hatching date (maximum difference: 2 days) (2011: 20 dyads = 40 nests; 2012: 27 dyads = 54 nests; 2013: 32 dyads = 64 nests).

We defined the day of hatching of the first chick of a nest as day 1. Chicks were provided with a metal ring with a unique number and individually weighed on day 15. Parents were caught on day 9 using nest box traps, whilst feeding their foster chicks. If caught for the first time, they were weighed, banded and given a unique colour ring combination for identification. For birds that had been caught previously, we only measured body mass (to the nearest 0.01 g).

BEGGING BEHAVIOUR

On day 7, two chicks per nest (in 2011: randomly chosen; in 2012 and 2013: the 2nd and 4th chick in a descending weight ranking) were individually placed in a warmed artificial nest box to record their begging behaviour as a function of duration of food deprivation. In 2011, chicks were fed till satiation with Orlux hand-rearing food (Orlux Handmix, Versele-Laga, Belgium, protein content: 21%, vitamin content / kg: A: 300 µg, D3: 37.5 µg, E: 80 mg; 9 parts warm water + 1 part Orlux powder), administered through a 1-ml plastic syringe. In 2012 and 2013, chicks were fed with defrosted blue bottle maggots. After 60, 90 and 120 min, we opened the artificial nest box and videotaped the begging behaviour of the chick inside until it ceased begging using a video camera (Sony, DCR-SX 30). In addition to the visual stimulus of a change from darkness to natural daylight, we presented an acoustic stimulus. In 2011, we tapped three times with a ball pen against the box (Kölliker *et al.* 2000; as in Estramil, Eens & Müller 2013). In 2012 and 2013, we used a playback of two parental feeding calls, recorded in 2011. We consider it unlikely that the change in protocol influenced the outcome of the within-family relationships that we intended to study, as within each year, only one method was applied (see Fig. S1 in Supporting Information for a graph showing the change in begging with the duration of food deprivation for different years). After testing, we immediately fed the chicks and returned them to the nest.

Following the breeding season, we analysed the chick's begging behaviour from the videotapes, according to a rating scale, modified from Kilner (2002): 0 = chick is not begging, 1 = chick's beak is open and its head is in a horizontal position, 2 = chick's beak is open and its head is leaned back in an angle of ~45°, 3 = chick's beak is open and the head is leaned back in an angle of 90°, 4 = as 3 plus the neck is stretched, and 5 = as 4 plus the back of the chick is in a vertical position. For each begging test, scores were applied every second and then summed. Average values for the begging scores of the two chicks were used for statistical analysis (i.e. the mean of the scores for the two chicks for each of the three measurements taken at 60, 90 and 120 min).

We estimated the responsiveness in begging (i.e. the behavioural reaction norm for offspring begging) as the change in begging across increasing levels of food deprivation by subtracting begging scores of 60 min from that of 120 min.

PROVISIONING BEHAVIOUR

In the morning of day 10, we placed an infrared camera (420TVL) inside underneath the lid of the nest boxes, facing downwards to the nest. We discarded the first 30 min of the video recordings to account for the potential influence of this disturbance on our measurements (Kölliker *et al.* 1998). The following 2 h of the recordings were used for later analysis. Here, provisioning behaviour (towards the cross-fostered but otherwise un-manipulated brood,

henceforth called 'un-manipulated brood') was scored as the number of individual feeding visits per minute (=provisioning rate) using 'The Observer XT' software (version 10.0.526, 2010, Noldus Information Technology, The Netherlands). In addition, we measured prey item size in three categories (1 = small; 2 = intermediate; 3 = large, sensu Kölliker *et al.* 1998).

Blue tit parents perform a few hundred feeding visits per day and nestlings fledge on average after 20 days (Schlicht *et al.* 2012). To assess the responsiveness (i.e. the behavioural reaction norm) of the parents to changes in brood demand, we reciprocally manipulated the brood size on day 11 within two nests of a cross-fostering dyad in a short-term experiment in the years 2011 and 2012. We reduced broods by taking 2 chicks from one nest (henceforth called 'reduced' treatment) and placing them in the partner nest, thereby also creating an enlarged brood (henceforth called 'enlarged' treatment). After 2.5 h, we swapped the treatment for another 2.5 h. The reduced and enlarged broods were filmed during the treatment. Again, we discarded the first 30 min of the recordings and scored the provisioning rates (and prey item size) for the subsequent 2 h (see above). The responsiveness of the parents to offspring demand (i.e. the behavioural reaction norm for parental provisioning) was calculated as the difference between the parental provisioning rates during the enlarged and reduced treatment.

STATISTICAL ANALYSES

Co-adaptation between the mean levels of parent and offspring behaviours was investigated using linear mixed effect models (LMEs) with restricted maximum likelihood (REML), where the dependent variable was the parental provisioning rate (square root transformed, model 1). We only included nests where both parents contributed to provisioning, as we are interested in sex differences (2011: 29 out of 40; 2012: 28 out of 54; 2013: 50 out of 64). Each year, some nests are raised by the female alone. This is due to, among other reasons, polygyny and male desertion under harsh conditions. Nest ID nested in Dyad ID was included as a random effect; year, parent sex, mean begging score of genetic chicks (raised in a foster nest) and mean begging score of foster chicks (raised in the focal nest) were included as fixed factors. Furthermore, we included the interaction effects 'parent sex \times begging scores of foster chicks' and 'parent sex \times begging scores of genetic chicks' to test whether the slopes of the relationship between parental provisioning rate and (foster) offspring begging score differed between the sexes. We additionally included the interaction 'year \times begging score of genetic chicks' as chicks were selected differently for the tests in 2011 vs. those in 2012 and 2013.

We then repeated the analysis described above, but this time replaced mean levels of behaviour with the behavioural responsiveness of parents and offspring (reaction norms, model 2). Random effects were the same as in model 1. However, the sample size is smaller given that brood size manipulations were only performed in two out of the three years. We again only included nests where both parents contributed to provisioning in both the 'reduced' and 'enlarged' treatment (2011: $N = 22$; 2012: $N = 29$). As we found that the interaction of the sex of the providing parent and the begging responsiveness of genetic chicks had a significant effect on parental provisioning responsiveness, we ran the model for each sex separately, to further investigate this result. Data are available from the Dryad Digital Repository (doi: 10.5061/dryad.hn390; Lucass *et al.* 2015).

For implementing LMEs, we used the package 'lme4' (Bates *et al.* 2013) in R (version 3.0.2, R Core Team, 2013, <http://www.R-project.org>). To obtain a minimal model, we performed a stepwise backwards elimination by sequentially deleting terms with a P -value higher than 0.05, starting with the least significant interaction. Since this procedure is associated with increased type 1

errors (see Forstmeier & Schielzeth 2011), we provide the outcomes for both full and reduced models. P -values of fixed factors that were dropped from the reduced models were obtained via a comparison between the model with the fixed effect in question included and removed, using an F-test with Kenward–Roger modification from the package 'pbkrtest' (Højsgaard & Halekoh 2014). We confirmed the validity of all final models by visual inspection of residuals for normality, heteroscedasticity and non-linear patterns. Alpha was set at 0.05.

Incomplete dyads may occur, for example in cases where parents deserted the nest after day 7 but before day 10 (i.e. after quantifying begging intensity of foster chicks but before parental provisioning), leading to a potentially uneven sample size within years. The applied technique, however, is appropriate for dealing with unbalanced data (Bates 2010).

Data from a small proportion of females (9 out of 101) and males (2 out of 74) were used in two consecutive years. Although probably not completely independent, we did not account for this in our models as all birds had new partners and experienced a new ecological environment.

Results

COVARIATION BETWEEN MEAN LEVELS OF PARENTAL PROVISIONING AND OFFSPRING BEGGING

We did not find a significant relationship between parental provisioning rate and either 'begging of genetic chicks', raised in a foster nest or 'begging of foster chicks', raised in the focal nest. Similarly, neither of the interactions of these two terms with parental sex was significant (Table 2, model 1, Fig. 1), indicating no sex differences in the relationship. The 'year \times begging score of genetic chicks' interaction was not significant, indicating that the parent–offspring relationship did not differ between years. Therefore, all of these terms were excluded from the final model. There was a non-significant trend for males to have higher provisioning rates than females (Tables 1 and 2).

Table 2. LME model of parental provisioning rate. Nest ID nested in Dyad ID was included as a random effect. Predictors retained in the reduced model (see text) are in bold. $N = 107$ nests.

Source of variation	Full model		
	<i>F</i>	d.f.	<i>P</i>
Parental provisioning rate (sqrt)			
Year	15.59	4,79.71	<0.001
Parent sex	2.24	3,104.0	0.088
Begging score of genetic chicks	0.86	4,130.91	0.489
Begging score of foster chicks	2.64	2,133.24	0.075
Begging score of genetic chicks \times Parent sex	1.09	1,104.0	0.300
Begging score of foster chicks \times Parent sex	2.36	1,104.0	0.127
Year \times Begging score of genetic chicks	0.97	2,96.81	0.384

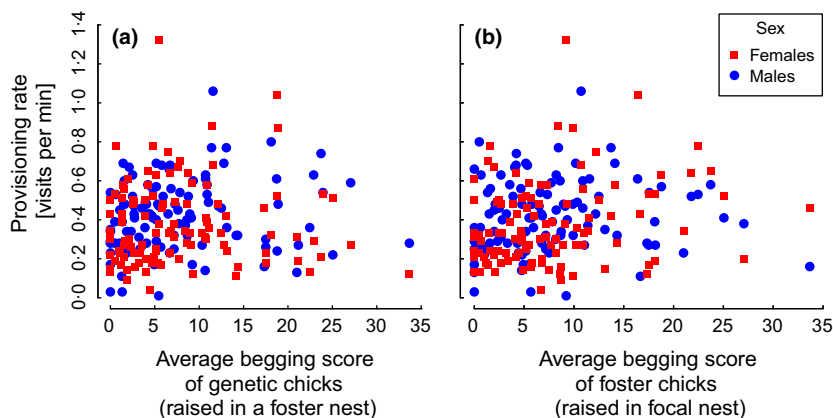


Fig. 1. Provisioning rates [visits / minute] of mothers (red squares) and fathers (blue dots) plotted against the begging scores of (a) genetic chicks raised in the foster nest and (b) foster chicks raised by the focal parents.

Provisioning rates differed between years (reduced model: year: $F_{2,60.0} = 31.48$; $P < 0.001$, Tables 1 and 2, Estimate, mean \pm SE: 2012: 0.196 ± 0.027 , 2013: 0.159 ± 0.024).

COVARIATION BETWEEN THE RESPONSIVENESS FOR PARENTAL PROVISIONING AND OFFSPRING BEGGING

We found a significant interaction effect for ‘begging responsiveness of genetic chicks \times parental sex’ (Table 3), indicating that the sexes differ with regard to the relationship between their provisioning responsiveness and the begging responsiveness of their genetic chicks (raised in a foster nest) (Fig. 2a). None of the other terms included had a significant effect (in all cases, $P > 0.22$, see Table 3).

We further investigated the above-mentioned significant interaction by repeating the analysis for the two sexes separately and found that the begging responsiveness of genetic chicks was negatively correlated with male ($F_{1,46.93} = 4.55$, $P = 0.038$), but not female ($F_{1,46.13} = 0.56$, $P = 0.459$) provisioning responsiveness.

To satisfy brood need, parents could also adjust the prey size per feeding event. This would remain undetected when only the provisioning rate is considered. Consequently, we repeated our analyses (models 1 and 2) using a measure that integrates the prey item size in parental provisioning (termed weighted provisioning rate, calculated as the provisioning rate multiplied by the average prey item size using three size categories, sensu Kölliker *et al.* 1998,

2000), which yielded similar results (see Tables S1 and S2). That being said, the interpretation of such an approach is difficult, as the exact scaling of the nutritional value of the different prey items is unknown.

Discussion

We hypothesized that the reaction norms of parental provisioning and offspring begging should be co-adapted within families, due to their dynamic and reciprocal interplay. We indeed found evidence for such parent–offspring co-adaptation, but only the paternal provisioning responsiveness covaried with the begging responsiveness of the genetic offspring. This relationship, however, was not observed when using a static trait approach. The latter result contrasts with the findings of a number of previous studies. Potential mechanisms explaining the observed sex differences, as well as their consequences, are discussed below.

WITHIN-FAMILY PARENT–OFFSPRING CO-ADAPTATION

Parental care involves a continuous reciprocal interplay between parental provisioning (in response to changes in begging) and offspring begging (in response to the amount of parental care). Given the dynamics of this relationship, it has been suggested that behavioural reaction norms of individuals rather than mean levels of traits should

Table 3. LME model of parental provisioning responsiveness. Nest ID nested in Dyad ID was included as a random effect. Significant variables in the reduced model are highlighted in bold. $N = 51$ nests.

Source of variation	Full model			Reduced model			Estimate	SE
	<i>F</i>	d.f.	<i>P</i>	<i>F</i>	d.f.	<i>P</i>		
Parental provisioning responsiveness								
Year	1.12	2,38.14	0.335	—	—	—	—	—
Parent sex	2.05	3,48.0	0.119	2.29	2,49.0	0.112	Male: 0.044	0.025
Begging responsiveness of genetic chicks	1.51	3,61.67	0.220	2.23	2,61.16	0.117	0.001	0.001
Begging responsiveness of foster chicks	0.81	2,61.56	0.451	—	—	—	—	—
Begging responsiveness of genetic chicks \times Parent sex	4.01	1,48.0	0.051	4.33	1,49.0	0.043	Male:-0.003	0.002
Begging responsiveness of foster chicks \times Parent sex	1.53	1,48.0	0.222	—	—	—	—	—
Year \times Begging responsiveness of genetic chicks	0.34	1,42.58	0.562	—	—	—	—	—

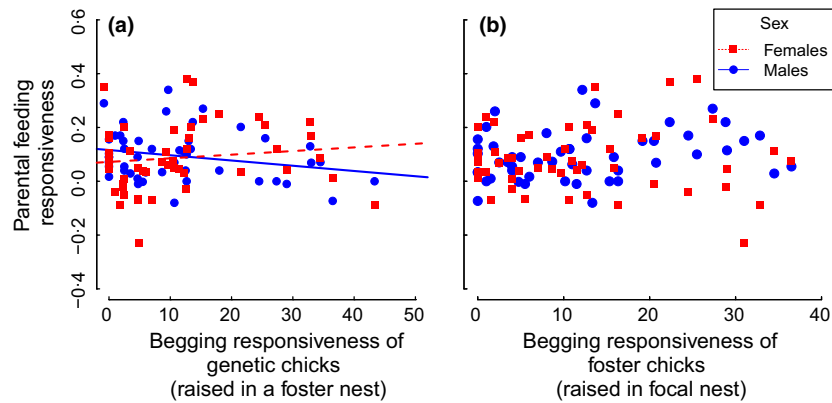


Fig. 2. Provisioning responsiveness [the difference in the number of feeding visits per minute between an enlarged (+2 chicks) and a reduced brood (−2 chicks)] of mothers (red squares, dotted line) and fathers (blue dots, solid line) plotted against begging responsiveness (the difference in the begging scores after 60 and 120 min of food deprivation) for (a) genetic chicks raised in the foster nest and (b) foster chicks raised by the focal parents.

co-adapt (Smiseth, Wright & Kölliker 2008; Dobler & Kölliker 2009), but this has thus far only rarely been considered, either theoretically (Kölliker, Ridenhour & Gaba 2010) or empirically. Following such a behavioural reaction norm approach, we found a negative correlation between the paternal but not maternal responsiveness in provisioning (to changes in brood size) and the offspring's responsiveness in begging (to changes in hunger). Thus, fathers that strongly alter their provisioning rate with experimentally manipulated brood size have offspring that exhibit limited variation in their level of begging with food deprivation, and vice versa.

A quantitative genetic model by Kölliker, Brodie & Moore (2005) suggested that – assuming the observed phenotypic correlation between parent and offspring behaviours reflects an underlying genetic correlation – a negative sign of the correlation may indicate that offspring are in control of parental provisioning and selection is expected to predominantly act on the parental generation (Agrawal, Brodie & Brown 2001; Maestriperieri 2004). In contrast, a positive relationship, as has been found in many previous studies (Kölliker *et al.* 2000; Curley *et al.* 2004; Lock, Smiseth & Moore 2004; Hinde, Buchanan & Kilner 2009; Estramil, Eens & Müller 2013), indicates that selection is acting on the offspring generation. Unfortunately, we are lacking theoretical work on the co-adaptation of behavioural reaction norms between family members, which would enable us to properly interpret the negative relationship found in this study. Thus, we can only speculate. However, being relatively unresponsive to changes in demand as a parent is likely to prevent exploitation by offspring if offspring begging is highly responsive to changes in hunger. Thus, fathers with demanding offspring may largely ignore changes in offspring begging behaviour. But whether selection predominantly acts on offspring responsiveness still needs to be demonstrated.

Most previous co-adaptation studies in birds found positive covariation between (mean values of) parental provisioning and offspring begging, which suggests that selection may act on offspring begging (Hinde, Buchanan & Kilner 2009; Hinde, Johnstone & Kilner 2010; Estramil, Eens & Müller 2013; but see Dor & Lotem 2010). In fact, two of these studies inferred the level of parental provisioning via

the growth rates of foster chicks (Hinde, Buchanan & Kilner 2009; Estramil, Eens & Müller 2013). Growth represents an estimate of mean provisioning, since it reflects the total amount of food received over a given time period. Moreover, growth integrates the provisioning of both parents (Hinde, Buchanan & Kilner 2009; Estramil, Eens & Müller 2013). This assumes both parents respond the same way and prevents the study of sex-specific patterns, which we show to be potentially relevant. At present, we do not have any information on whether patterns similar to those presented here would be found when applying a behavioural reaction norm approach to previous studies that only considered mean levels (Hinde, Buchanan & Kilner 2009; Dor & Lotem 2010; Estramil, Eens & Müller 2013). The reason for this is that it is unclear whether mean levels (in statistical terms: the intercept) of behaviour correlate with the reaction norms (the slope across an environmental gradient, Dingemanse *et al.* 2010).

SEX-SPECIFIC OPPORTUNITIES FOR CO-ADAPTATION?

The pattern of father–offspring covariation as revealed by our behavioural reaction norm approach is novel. Until now, sex-specific co-adaptation has only been reported between traits of the mother and her offspring (Kölliker *et al.* 2000; Agrawal, Brodie & Brown 2001; Curley *et al.* 2004; Lock, Smiseth & Moore 2004; Maestriperieri 2004). Unfortunately, some of these studies investigated care traits that are exclusively expressed in females (i.e. uniparental maternal care only, Agrawal, Brodie & Brown 2001; contact behaviour, Maestriperieri 2004; milk let-down, Curley *et al.* 2004). In burying beetles, maternal – but not paternal – provisioning covaried with offspring begging under uniparental conditions (Lock, Smiseth & Moore 2004; Head *et al.* 2012), and a similar sex difference was found in a study on great tits investigating maternal and paternal care simultaneously (Kölliker *et al.* 2000). In this latter study, covariation of parental behavioural reaction norms (obtained via playbacks of high- and low- energy levels of begging) and offspring begging (static trait) were investigated, showing that the maternal but not paternal provisioning responsiveness covaried with offspring begging (Kölliker *et al.* 2000). This study is most comparable

to ours, not only in terms of the study species but also the concept applied.

Mother–offspring co-adaptation is typically explained by the fact that females have more opportunities to alter offspring behaviour by means of maternal effects. This increases their opportunity to match offspring to their own quality and thus the likelihood of co-adaptation. In fact, it has been suggested that prenatal maternal effects are the main mechanism driving covariation, at least in canaries (Hinde, Buchanan & Kilner 2009; Hinde, Johnstone & Kilner 2010; Estramil, Eens & Müller 2013). However, females may also match (but not necessarily manipulate, see Müller *et al.* 2007) offspring begging to paternal quality, promoting father–offspring co-adaptation, as we found here. Females may obtain information on prospective paternal provisioning via, for example, (sexually selected) male phenotypic traits (e.g. Buchanan & Catchpole 2000; Garcia-Navas, Ferrer & Jose Sanz 2012) or male courtship feeding pre-laying. Maternal effects influencing mean levels of offspring begging have been found to be mediated by maternal yolk hormones in particular (reviewed in Groothuis *et al.* 2005; Smiseth, Scott & Andrews 2011), but we currently lack evidence for such maternal effects on offspring begging responsiveness (but see Buchanan *et al.* 2007 for hormonal regulation of begging responsiveness post-hatching).

Covariation between the phenotypic expressions of offspring begging and parental provisioning may also reflect an underlying genetic correlation (Wolf & Brodie 1998). A prerequisite for a genetic correlation between behaviours is the behavioural variation to be heritable, which has already been shown for both begging and provisioning (Webster & Hurnik 1987; Freeman-Gallant 1999; MacColl & Hatchwell 2003; Dor & Lotem 2009, 2010; Kim *et al.* 2011; Estramil, Eens & Müller 2014). However, studies on *genetic correlations* between mean levels of behaviour are rare (but see Hager & Johnstone 2003 for an exceptional study on mice) and as yet have not been conducted for behavioural reaction norms. Further work on the heritability and potential genetic correlations between parent and offspring behaviours, particularly of the behavioural reaction norms, is strongly needed (Royle, Russell & Wilson 2014; see also the discussion by Smiseth, Wright & Kölliker 2008). Even though it appears unlikely that the underlying mechanism(s) would be purely genetic (Kilner & Hinde 2012), it seems even more unlikely that such a mechanism should differ between the sexes. However, phenotypic differences may arise – despite a common mechanism – if one sex is, for example, more responsive to, or better informed about, (foster) offspring need. Likewise, Kölliker *et al.* (2000) argued that the lack of a paternal response may be due to sex differences in the cues used for adjusting provisioning, with males using cues other than vocal begging (but see e.g. Hinde 2006). The lack of a paternal response may have hindered an investigation of the relationship between male responsiveness in provisioning and offspring begging. In our study, we manipulated

brood size, thus most likely begging with all its components (vocal and visual displays), and we found that male and female parents equally adjusted their provisioning rates in response to changes in brood size. Furthermore, mothers were not more responsive to actual begging (of foster chicks) than fathers, which may have masked an existing co-adaptation with their genetic offspring. Thus, taken together, we could not identify any variable that may have confounded our estimate of female responsiveness. Obviously, the social environment will play a significant role, and this should be taken into account (Royle, Russell & Wilson 2014) since a parent responds to both (plastic responses in) the parental effort of the mate and (changes in) offspring demand when adjusting its level of investment.

Environmental variation may in general influence outcomes of studies under natural conditions. For example, in 2012, weather conditions were harsh, likely causing the large number of nests with maternal uniparental care, which were excluded from our analyses. Potentially, this could have led to a biased subset of pairs with comparatively high-quality males for which we investigated parental and offspring behaviours in that year. This again highlights the importance of considering more than one year.

LIMITATIONS OF THE BEHAVIOURAL MEASUREMENTS

This is, to our knowledge, the first such study in the context of co-adaptation of parental and offspring reaction norms (but see Kölliker *et al.* 2000; Westneat *et al.* 2011 for a behavioural reaction norm approach focusing on parental provisioning), and so further studies are required to confirm our results. Such studies should take into account whether the respective behavioural measures (mean values and responsiveness) are repeatable (Dor & Lotem 2010), which we unfortunately could not consider in this study. Blue tit breeding is highly synchronized and the nestlings have only a short developmental period. The time window to test begging is thus restricted, while the begging tests itself are very time-consuming, particularly because of the implemented food deprivation. A previous study on provisioning of blue tit parents suggested significant repeatability at least in terms of mean values of this behaviour (Mutzel *et al.* 2013). Our two-hour video recordings of provisioning are, compared with other studies, already substantial (e.g. Kölliker *et al.* 2000). Nevertheless, it represents a snapshot of a much longer period of parental care (Pagani-Núñez & Senar 2013). At present, PIT (passive integrated transponder) tags are a valuable tool to provide more data over longer time periods (Mutzel *et al.* 2013).

Conclusions

We applied a novel behavioural reaction norm approach in the context of within-family parent–offspring covariation, to better capture the dynamic and reciprocal

interplay between parents and their offspring during parental care. In addition, our extensive 3-year cross-fostering study was performed in a wild blue tit population, since environmental conditions should be integrated when studying social selection in an evolutionary ecology framework. We found that the paternal but not maternal responsiveness in provisioning covaried negatively with the begging responsiveness of their offspring. This sex difference in covariation was not detected in previous studies, as parents were not always treated as separate actors. However, this difference has significant implications for conflict resolution and parental investment within the family. We did not identify a mechanism that causes parent-offspring covariation, but any mechanism must have acted pre-hatching as all clutches were cross-fostered prior to hatching.

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Data accessibility

Data deposited in the Dryad repository: <http://dx.doi.org/10.5061/dryad.hn390> (Lucass *et al.* 2015).

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Supporting Information

Additional Supporting information may be found in the online version of this article:

Fig. S1 The change in begging with the duration of food deprivation for different years.

Table S1 LME model of the weighted parental provisioning rate. Nest ID nested in Dyad ID was included as a random effect. $N = 107$ nests.

Table S2 LME model of the weighted parental provisioning responsiveness. Nest ID nested in Dyad ID was included as a random effect. $N = 51$ nests.