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1 **Title**

2 Favored parent-offspring trait combinations? On the interplay of parental and offspring traits

3

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14

15 **Short title**

16 Favored parent-offspring trait combinations?

17

18 **Lay summary**

19 Offspring development is thought to be optimized if they are adapted towards the capacities
20 of their parents. Here, we disrupted natural parent-offspring combinations by reciprocally
21 exchanging whole broods of wild blue tits, and investigated whether and how any parent-
22 offspring trait mismatch impinges on nestling development. Foster parents had a particularly
23 strong impact on nestling growth via their provisioning rate. This relationship, however, also
24 depended on the begging behavior of the nestlings.

25

26 **Abstract**

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

47

48

49 **Introduction**

50 In species with parental care a large part of early offspring development takes place within
51 the family. This social environment as created by all family members has, therefore, a crucial
52 influence on individual fitness and trait evolution (Clutton-Brock 1991). Obviously, offspring
53 may develop best when its developmental trajectory matches the conditions of its family
54 environment, in particular the parental provisioning capacity. Offspring and parent behaviors
55 have indeed been shown to co-vary on the phenotypic level (e.g. Kölliker et al. 2000; Hager
56 and Johnstone 2003; Curley et al. 2004; Lock et al. 2004; Hinde et al. 2009; Hinde et al.
57 2010; Estramil et al. 2013), even though the underlying mechanisms are not fully understood
58 yet.

59 Another yet unresolved question is whether the observed patterns of parent-offspring trait
60 combinations serve the evolutionary interests of parents, offspring, or both. This question
61 arises since the dynamics between parent and offspring traits are influenced by an
62 evolutionary conflict of interest due to asymmetries in the rating of costs and benefits of
63 parental investment (parent-offspring conflict, Trivers 1974). In short, offspring will seek
64 greater parental investment (e.g. parental provisioning) than parents are willing to provide
65 (Trivers 1974). Addressing whether current parental provisioning represents the optimum for
66 parents (i.e. parents are in control of provisioning) or offspring (i.e. offspring are in control of
67 parental provisioning via means of begging) is thus highly relevant (e.g. Kölliker et al. 2005;
68 Hinde et al. 2010). Understanding who is in control can be studied best in an experimentally
69 induced mismatch situation, because the party that is not in control of provisioning is
70 supposed to pay a cost.

71 Most previous studies have found that offspring suffer from an exchange of young between
72 broods in terms of impaired growth (Hager and Johnstone 2003; Hinde et al. 2010; Lock et
73 al. 2004; but see Estramil et al. 2014). However, these previous studies were done in
74 captivity, where relevant selection pressures (e.g. costs of foraging, predators and parasites)
75 are not acting on the family, which potentially skewed the results. Thus, experiments under

76 natural conditions are essential to test how selection acts on traits in experimentally
77 manipulated conditions in order to understand how fitness costs shape parent-offspring
78 interactions. In addition, the above mentioned studies suggest that (foster) parents could not
79 (or were not willing to) satisfy offspring requirements. This nutritional stress in turn likely
80 increases levels of corticosterone (Díaz-Muñoz et al. 2000; Lynn et al. 2003), a
81 glucocorticoid hormone that is released as part of the adrenocortical stress-response
82 (Sapolsky et al. 2000), and mismatching may, therefore, also be reflected in stress hormone
83 levels. In offspring, an adequate stress response to food scarcity would be an elevation in
84 begging intensity in an attempt to extract more resources from parents. Corticosterone has
85 therefore been hypothesized to provide the mechanism of how the nutritional status of
86 offspring is communicated to parents by elevating begging intensity (reviewed in Smiseth et
87 al. 2011). Hence it appears vital to further investigate the relationship between corticosterone
88 levels and begging.

89

90 We performed a reciprocal full-brood cross-fostering study in blue tits (*Cyanistes caeruleus*),
91 investigating the effects of mismatched parent-offspring interactions in the wild. Full-brood
92 cross-fostering generates variation in the family environment for both offspring and parents
93 (Kölliker et al. 2012). This enabled us to study offspring begging as well as parental
94 provisioning in separation, and to detect how they – eventually in interplay – determine
95 offspring growth as measured via their fledgling mass (and thus fitness: e.g. Richner 1992;
96 Krause et al. 2009; Tilgar et al. 2010). Broods that beg most intensely should reach the
97 highest mass at fledging, if the rate of parental provisioning is under offspring control by
98 means of begging, and vice versa. If, however, the level of food provisioning is mainly
99 determined by the parents we would expect that offspring mass at fledging is mainly driven
100 by the rate of parental provisioning. The extent of growth reduction should additionally
101 increase with an increasing discrepancy between foster chick begging and parental
102 provisioning, given that begging is costly (e.g. Kilner 2001; Noguera et al. 2010; Moreno-

103 Rueda and Redondo 2011) and that begging remains progressively unrewarded. Previous
104 studies on birds found a positive co-variation between offspring begging and parental
105 provisioning (Kölliker et al. 2000; Hinde et al. 2009; Estramil et al. 2013), which has been
106 interpreted as such that parents control provisioning and selection is acting predominantly on
107 offspring begging (Kölliker et al. 2005). Therefore, we focused on costs for offspring, even
108 though all parties involved may suffer fitness consequences from a mismatch. Furthermore,
109 we expect to find either of the above described scenarios to be reflected on an even finer
110 scale, namely in the amount of excreted corticosterone metabolites (CM), which may also
111 form a mechanism of how offspring need is communicated via begging.

112

113 **Material & Methods**

114 *Study area and general methods*

115 We conducted our experiments in a nest-box population of blue tits breeding in Peerdsbos, a
116 mature oak-beech forest near Antwerp (51°16'N, 4°29'E, Belgium) in the spring of 2012
117 (March – May). Clutch size and onset of incubation (to estimate hatch date of chicks) were
118 assessed via daily checking of nest-boxes. Blue tits show moderate asynchrony between
119 hatching of the first and the last chick, with typically the last 1-2 chicks having one or two
120 days delay (Stenning 2008). We disrupted the potentially co-adjusted offspring solicitation
121 and parental provisioning behaviors by means of cross-fostering of whole clutches. Eggs of
122 two nests (=dyad) that were matched for hatch date (maximum difference 2 days) and clutch
123 size (maximum difference 2 eggs) were reciprocally exchanged three days before expected
124 hatching. In total clutches of 54 nests were cross-fostered. Day of hatching was defined as
125 day 1. On day 15 all chicks were provided with a metal ring with a unique number and
126 individually weighed (=fledgling mass) to the nearest 0.01g. This day represents the end of
127 the developmental period of chicks and is a standard measure of blue and great tit offspring,
128 as it predicts post-fledgling survival and recruitment (e.g. Both et al. 1999; Naef-Daenzer et
129 al. 2001; Monrós et al. 2002; Nicolaus et al. 2008). Parents were caught on day 9 when

130 feeding their (foster) chicks using nest-box-traps. They were weighed, metal banded and
131 obtained an unique color ring combination facilitating further identification. All experiments
132 were conducted under licenses from the Ethical Committee for animals (ECD) of the
133 University of Antwerp (license number 2011-10).

134

135 *Begging behavior*

136 On day 7, we took the 2nd and 4th chick in a descending weight rank and transferred them to
137 a warmed artificial nest-box to perform a begging test. We chose to perform the begging test
138 on day 7 as the chicks' thermoregulation before day 7 is poorly developed. Thus, we
139 intended to test as late as possible to avoid hypothermia (potentially caused by
140 transportation to the begging test), ultimately impinging on the begging performance.
141 However, soon after day 7 (day 8-9) chicks open their eyes and show a fear response to
142 human beings, which makes it virtually impossible to elicit a begging response. The second
143 and fourth chick were chosen to standardize the procedure between nests and to avoid
144 potential effects of the hatching order on begging intensity. We took only two chicks as
145 parents may desert the nest when "predation" (i.e. collecting chicks for the begging test) is
146 too high, which may be especially problematic in small broods.

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

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

164

165 *Dropping sampling and CM measurements*

166 When weighing chicks prior to the begging test on day 7, we collected droppings of the 2nd
167 and 4th heaviest chicks (which also entered the begging test) and two additional randomly
168 chosen chicks to calculate a nest estimate of CM. Droppings were collected at day 7 to
169 investigate a potential relationship between CM and begging (which was measured on that
170 day). We measured levels of corticosterone via its CM, as it has a number of advantages.
171 First, collection of droppings is non-invasive, thus there are no effects of disturbance on the
172 levels of CM within the time of sampling in contrast to blood sampling (see Gil et al. 2008).
173 Second, it allows sampling at a very young age (here: blue tit chicks of 7 days of age, ~5.2g)
174 when taking a blood sample – of an amount that is required for a hormone analysis – can
175 potentially be life-threatening. Finally, it provides a cumulative measure of CM over time in
176 contrast to “snap-shot” concentrations, as obtained from blood samples.

177 The collected droppings were immediately transferred into a 1.5 mL Eppendorf tube and
178 stored on ice until return to the University of Antwerp where samples were transferred to a -
179 80°C freezer until processing. After the breeding season droppings were defrosted. 0.05 g of
180 wet droppings (avoiding the urine part) were vortexed in 0.3 mL methanol (99.9%) and 0.2
181 mL distilled water for 15 min (Palme et al. 2013), centrifuged and 0.1 mL of the supernatant
182 was evaporated. The dried supernatants were sent to the University of Veterinary Medicine,
183 Vienna for further analysis. Samples were then re-solved in 0.1 mL of methanol (60%). We

184 included a hydrolysis step before analyzing the samples with the enzyme immunoassay
185 (EIA), which is especially useful when analyzing nestling droppings with the EIA we used
186 (Stöwe et al. 2013). 0.05 mL of the sample extracts were evaporated, afterwards dissolved in
187 0.1 mL Na-acetate buffer and 0.2 μ L β -glucuronidase/-aryl sulfatase (Merck 1.04114.0002)
188 and hydrolyzed at 38 °C for 18 h. We determined the amounts of immuno-reactive
189 metabolites using a cortisone EIA, which has been validated previously for blue tits (Lobato
190 et al. 2008; see also Stöwe et al. 2013). It measures glucocorticoid metabolites with a 3,11-
191 dione structure (detailed description in Rettenbacher et al. 2004). Samples were assayed in
192 duplicate, inter-assay variation was 2 % for the high level and 7 % for the low level pool.

193

194 *Provisioning behavior*

195 In the morning of day 10, we placed an infra-red camera inside at the top of the nest-box,
196 facing downwards into the nest and provisioning was recorded for 2.5h in all cross-fostered
197 nests. We discarded the first 30 minutes of the videos in order to avoid feeding bias due to
198 our disturbance (Kölliker et al. 1998). Provisioning behavior was scored during the remaining
199 2h using “The Observer XT” (version 10.0.526, 2010, Noldus Information Technology, The
200 Netherlands).

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

210

211 *Statistical analyses*

212 To test whether offspring begging or parental provisioning influenced fledgling mass, we
213 performed a multiple regression (MR) on the latter (model A). Explanatory variables were
214 'hatch date' (as Julian date), 'brood size', the 'mean begging score of chicks' and the
215 'weighted provisioning rate of their foster parents'. As we also included the interaction of the
216 latter two (=measure of the behavioral mismatch between begging of chicks and provisioning
217 of their foster parents), we mean-centered both variables prior the analysis to facilitate
218 interpretation of the main effects (Schielzeth 2010). Further, we included the 'mid-parent
219 body mass' of the genetic parents to control for potentially confounding genetic effects on
220 fledgling mass of cross-fostered offspring.

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

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

234 As it has been found in some studies that corticosterone affects begging (e.g. Kitaysky et al.
235 2001; Kitaysky et al. 2003), we investigated whether this relationship also exists in blue tits,
236 using a third MR (model D). 'Begging intensity' was the response variable and 'mean fecal
237 CM levels', 'hatch date' (as Julian date), and 'brood size' were used as predictor variables.

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

243

244 **Results**

245 *Factors influencing fledgling mass*

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

252

253 *Factors influencing CM levels in chick droppings*

254 Time of collection had a negative effect on (square root transformed) chick CM levels ($t_{43}=-$
255 3.665 ; $P<0.001$). Also, the interaction term begging intensity \times weighted provisioning rate of
256 the foster parents ($t_{43}=2.033$; $P=0.048$; Table 1B, Fig. 2) had a significant effect on (square
257 root transformed) chick CM levels. However, there was no significant effect of begging
258 intensity ($t_{43}=0.353$; $P=0.725$), weighted provisioning rate of the foster parents ($t_{43}=-1.176$;
259 $P=0.246$), hatch date ($t_{43}=-0.667$; $P=0.508$), mean chick weight ($t_{43}=-1.792$; $P=0.080$) or
260 brood size ($t_{43}=1.643$; $P=0.108$) on CM levels (Table 1B).

261

262 *Parent-offspring co-adaptation?*

263 Begging intensity was negatively influenced by hatch date ($t_{48}=-2.343$; $P=0.023$), but neither
264 brood size ($t_{48}=0.360$; $P=0.720$), nor weighted provisioning rates of foster ($t_{48}=-0.274$;

265 P=0.785) or genetic parents ($t_{48}=-0.080$; $P=0.937$) had a significant effect on begging (model
266 C: $R^2=0.14$; $F_{4,48}=1.927$; $P=0.121$, $N=53$).

267

268 *The relationship between begging and CM*

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

273

274 **Discussion**

275 Parental care benefits all family members, although it involves costs for the caregiver but
276 also for those that have to elicit care via vigorous begging displays. Selection may minimize
277 these costs by favoring particular parent-offspring combinations, which may be skewed
278 towards one party's optimum. We found that matched parent-offspring combinations
279 benefited offspring particularly in terms of body mass as parents have control over the level
280 of provided care in terms of provisioning. Yet, this pattern also depended on the behavioral
281 phenotype of the offspring.

282

283 *Consequences of mismatched parent-offspring combinations for offspring growth*

284 Offspring growth, in terms of fledgling mass, largely depended on parental provisioning, but
285 also on their own begging behavior as well as on the interplay between parent and offspring
286 traits. More to the point, highly demanding broods reached the highest fledgling mass when
287 raised by parents that provided food at a high rate, but lowest fledgling mass when raised by
288 low provisioning parents. The observed strong growth reduction among high begging
289 offspring raised by parents that provide little, is likely to be due to the costs of begging, which
290 remains partly unrewarded (e.g. Kilner 2001; Noguera et al. 2010; Moreno-Rueda and
291 Redondo 2011). These nestlings are unable to obtain resources beyond a (predetermined)

292 generosity of their (foster) parents. Thus, a pre-hatching adjustment to the post-hatching
293 social environment is – in the first place – beneficial for highly demanding offspring
294 (obviously parents benefit indirectly through offspring fitness). This is also supported by the
295 fact that fledgling mass of less demanding broods was intermediate, both, when raised by
296 high or low providing parents (Fig. 1).

297 Low begging may represent another, more conservative, strategy which is largely
298 independent from the level of parental care. Even when mismatched to their advantage (i.e.
299 a low begging brood raised by high providing parents), offspring do not acquire a higher
300 fledgling mass than low begging broods raised by low providing parents (see Fig. 1). To
301 crystallize, foster parents provided food at a high rate irrespective of the low levels of
302 begging by their foster chicks, but these resources were apparently not converted in body
303 mass gain. We currently lack an explanation for this and can only speculate that chicks
304 potentially re-allocate nutrients received from high-providing parents to other physiological
305 processes, that are not measured here, such as immunity (Hasselquist and Nilsson 2012).
306 Indeed, low begging offspring raised by high providing foster parents differed physiologically
307 as indicated by low levels of stress hormones (see below for a detailed discussion).

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

319 see Estramil et al. 2014), which we unfortunately could not measure here as parents
320 frequently disperse out of the study population.

321

322 *Physiological consequences of trait mismatching*

323 The interplay of both begging and foster parental provisioning influenced CM levels in chick
324 droppings too, but the pattern, as shown in Fig. 2, does not reflect the results from the growth
325 analysis (Fig. 1). More to the point, CM levels were particularly low when offspring that
326 begged very little were raised by parents that provided food at a high rate. This is interesting,
327 because the growth pattern of these nestlings was below what one would expect (see
328 above). Although these chicks did not convert given resources into body mass gain, they,
329 nevertheless, benefited from high levels of provisioning via lower stress hormone levels.

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

342 Following this argumentation one may expect CM levels of high begging offspring raised by
343 low providing foster parents to be highest, as they experience the most intense sibling
344 competition (from high begging siblings) in infrequently occurring feeding events. However,
345 an elevation above the (threshold of the) concentrations observed among high begging

346 chicks could be particularly costly. High levels of corticosterone have been associated with
347 impaired cognitive abilities (Kitaysky et al. 2003), a weaker immune response (Loiseau et al.
348 2008), depressed growth rates (Spencer and Verhulst 2007), and inhibition of feather growth
349 (Romero et al. 2005).

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

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

370

371 *Corticosterone and begging: signaling nutritional need?*

372 We did not find that levels of corticosterone significantly affected nestling begging intensity.
373 However, in the context of our analyses it needs to be noted that metabolites of hormones
374 are excreted after they have acted on the individual, while we collected the samples prior to
375 the begging test. Collecting samples after the begging test, however, would not be ideal,
376 since corticosterone is central to the adrenocortical stress-response and stressors (e.g.
377 transportation to the begging test) could influence corticosterone measures, an argument
378 that may apply to previous correlative studies as well (e.g. Quillfeldt et al. 2006; Gil et al.
379 2008).
380 Finally, corticosterone may provide a physiological mechanism for some but not all begging
381 traits (reviewed in Smiseth et al. 2011). Our measure of begging intensity was a combination
382 of posture and duration, and both traits have been shown to be unaffected by the
383 experimental administration of corticosterone in earlier studies in passerine birds (Loiseau et
384 al. 2008; Wada and Breuner 2008), although reflecting hunger (Dickens et al. 2008).
385 Most convincing evidence that endogenous corticosterone regulates begging comes from
386 experimental studies on black-legged kittiwakes (Kitaysky et al. 2001; Kitaysky et al. 2003).
387 Thus, it remains unclear whether and how the applied study design (observational vs
388 experimental, see also Quillfeldt et al. 2006), the developmental mode of chicks (altricial
389 passerines vs semi-precocial seabirds) or species-specific differences contribute to the
390 different study outcomes.

391

392 *Conclusions*

393 Using a full-brood cross-fostering approach to create a mismatch between (foster) parental
394 provisioning and begging in a wild blue tit population, we show that offspring fitness, here
395 measured in terms of their mass at fledging, is determined by the joint influences of (foster)
396 parental provisioning and own begging. Parental provisioning had a particularly strong effect
397 on fledgling mass and intensely begging offspring could extract sufficient resources only from
398 high but not low providing foster parents. This indicates that parents have the upper hand in

399 an ongoing battle about control of provisioning. Further, the consequences of a mismatch for
400 offspring were apparent on an even finer scale than fledgling mass, namely their
401 corticosterone levels. This measure was influenced by the interaction of foster parental
402 provisioning and own begging, potentially reflecting effects of stress due to intensity and
403 frequency of sibling competition. Future studies are now needed to investigate potential costs
404 for the parents in order to get a full understanding of the costs and benefits shaping parent-
405 offspring interactions under natural conditions. Lastly, we failed to find that endogenous
406 corticosterone presents a physiological mechanism of begging, which, in combination with a
407 number of previous studies, questions the role of corticosterone for the regulation of begging
408 in passerine bird species.

409

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423

424

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546 **Tables**

547

548 Table 1. Multiple regression analysis of factors influencing fledgling mass (A, $R^2=0.37$;
 549 $F_{6,44}=4.372$; $P=0.002$; $N=51$), CM levels (B, $R^2=0.43$; $F_{7,43}=4.678$; $P<0.001$, $N=51$), and
 550 begging intensity (D, $R^2=0.19$; $F_{3,47}=3.736$; $P=0.017$, $N=50$) of chicks.

551

Source of variation	A) Fledgling mass		B) Fecal CM levels (sqrt)		D) Begging intensity	
	β	P	β	P	β	P
Begging intensity ^a	-0.268	0.047	0.052	0.725	Not included	
Weighted provisioning rate of foster parents ^a	0.421	0.009	-0.171	0.246	Not included	
Hatch date (Julian date)	0.112	0.436	-0.093	0.508	-0.364	0.009
Brood size	-0.306	0.031	0.213	0.108	-0.045	0.744
Mid-parent body mass of genetic parents [g]	0.135	0.301	Not included		Not included	
Begging intensity ^a × weighted provisioning rate of foster parents ^a	0.244	0.034	0.258	0.048	Not included	
Time of dropping collection [minutes after midnight]	Not included		-0.437	<0.001	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

552

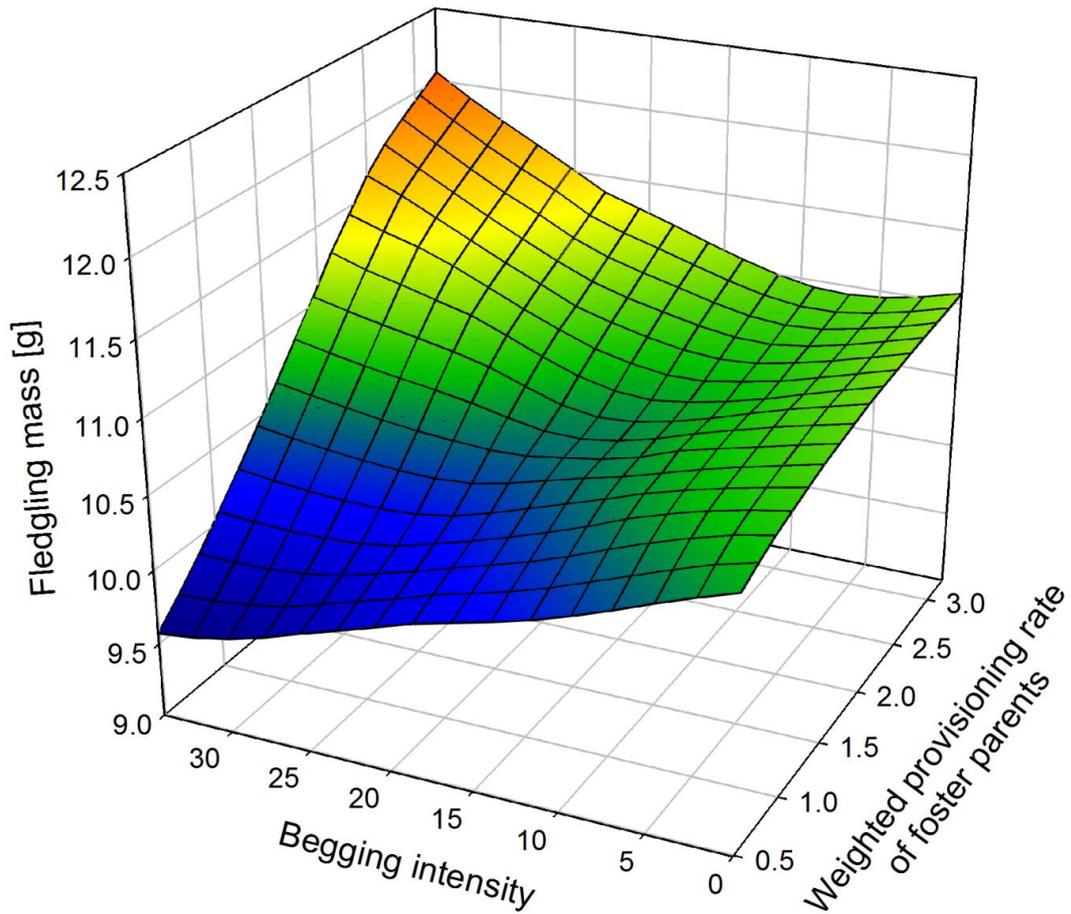
553 Significant p-values are indicated in bold.

554 ^a mean-centered

555

556 **Figure 1:**

557 A 3D scatterplot with a regression plane on how (foster) parental provisioning and own
558 begging impinge on fledgling mass [g]. For ease of visibility the color of the regression plane
559 corresponds to Y-axis values ranging from blue (low) to orange (high).



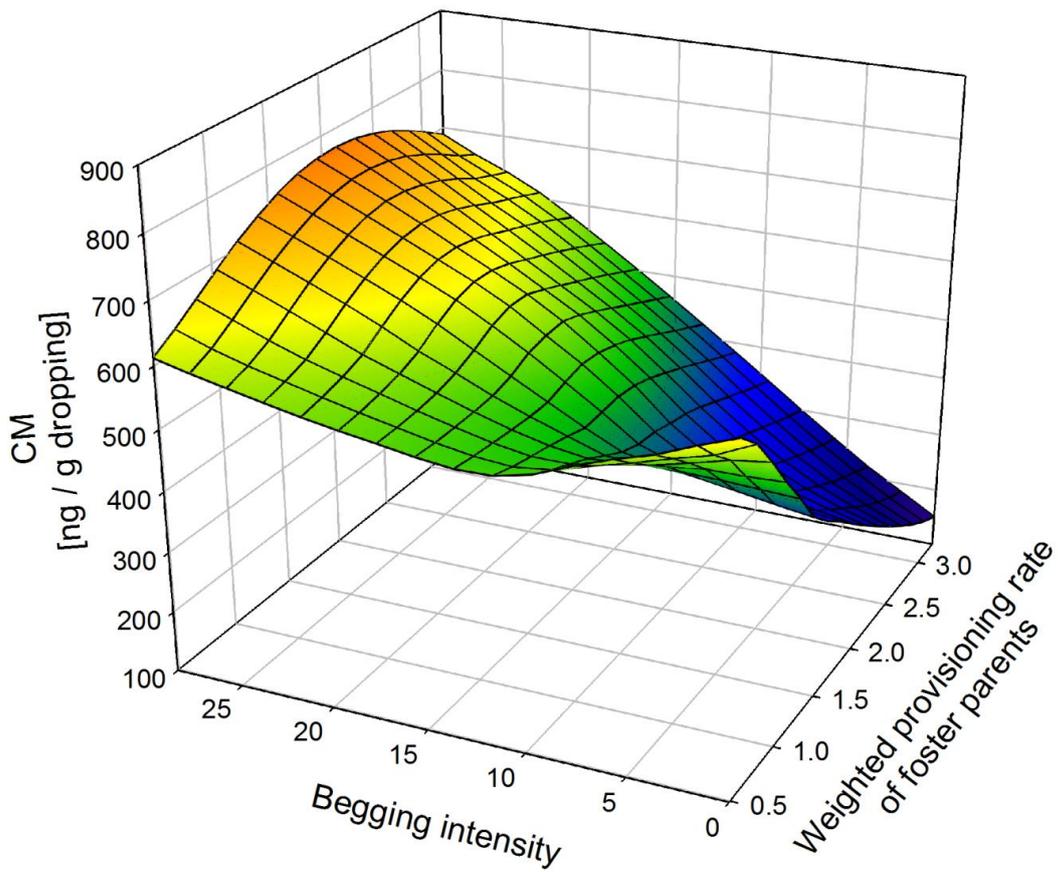
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562 **Figure 2:**

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

566



567