

1 The relationship between maternal ornamentation and feeding rate is explained
2 by intrinsic nestling quality

3

4 Dorottya Kiss*, Gergely Hegyi, János Török, Balázs Rosivall

5

6 Behavioural Ecology Group, Department of Systematic Zoology and Ecology, Eötvös Loránd

7 University, Pázmány Péter sétány 1/C, H-1117 Budapest, Hungary

8 *Corresponding author: dorottyakiss@elte.hu

9 Abstract

10 In altricial birds, parental feeding is essential and its amount may depend on the quality of
11 both parents. A relationship between parental quality and feeding rate is generally attributed
12 to an active adjustment by parents in order to retain good quality mates or ensure high fitness
13 through raising high quality offspring. However, the behaviour and need of young may also
14 change with parental quality, and this may affect parental behaviour. A further problem is that
15 most studies have investigated post-hatching parental investment in relation to the secondary
16 sexual signals of males, but not females. In a cross-fostering experiment, we examined the
17 feeding rates of rearing parents in relation to the size and ornamentation of both original and
18 rearing parents in collared flycatchers (*Ficedula albicollis*). Using this setup, we could
19 examine whether the observed feeding patterns were the results of the decision of the parents
20 based on their own and their partner's traits or the constraints imposed by the behaviour or
21 need of offspring. When correcting for clutch size and year, we found that feeding rate of both
22 foster parents correlated with the wing patch size of the original female. This implies that
23 original maternal quality had an offspring mediated indirect effect on investment of foster
24 parents, that is intrinsic nestling quality may constrain parental feeding decisions. This
25 explanation should not be overlooked in future studies on preferential parental investment and
26 our results also point out that maternal ornaments deserve more attention in such studies.

27

28 Keywords: attractiveness, collared flycatcher, female quality, *Ficedula albicollis*, maternal
29 ornamentation, parental investment; parental quality, plumage traits, provisioning

30

31 Introduction

32 Life history theory suggests that the energy expenditure of animals is shared between
33 self-maintenance and reproductive investment. Because nestlings of altricial birds are
34 incapable of acquiring food for themselves, their survival depends entirely on their parents'
35 feeding. Parental investment requires enormous energy investment, thereby affecting parents'
36 survival (Cichoń et al. 1998) and reproductive success in future breeding attempts
37 (Gustafsson and Sutherland 1988). Therefore, in order to maximize their lifetime reproductive
38 success, parents may alter their investment based on the expected value of current and future
39 breeding attempts. The quality of individuals or their mates could be important factors to
40 predict the value of the current brood.

41 Ornamental traits may indicate the quality or attractiveness of individuals (Andersson
42 1994), and as a consequence, the direct or indirect fitness benefits individuals may obtain by
43 mating with a given partner. Potential indirect benefits include ‘good genes’, which result in
44 high quality and viability of offspring and thereby increases the reproductive success of the
45 parents (Petrie 1994; Sheldon et al. 1997). A mate with elaborate traits may provide direct
46 benefits as well, such as high quality territory with abundant food or good breeding site
47 (Keyser and Hill 2000). Secondary sexual traits may also signal the level of parental care (see
48 below).

49 Recently, many studies have focused on the relationship between plumage signals and
50 parental investment (e.g. Sanz 2001; Limbourg et al. 2004; DeMory et al. 2010). The results
51 are often contradictory, but this is not surprising given the opposing predictions of the
52 prevailing hypotheses. For example, the ‘good parent’ hypothesis suggests that good quality
53 individuals with elaborate traits will invest more in their offspring because they are able to do
54 so (Hoelzer 1989; Linville et al. 1998). On the other hand, highly ornamented males should
55 invest less into their first brood if they have the opportunity to increase their reproductive
56 success via extra-pair copulations or by obtaining more partners (Magrath and Komdeur
57 2003; Mitchell et al. 2007). The situation is further complicated by the fact that the quality of
58 the reproductive partner may also influence the decision of an individual about the investment
59 in its current reproductive event. One may argue that an individual mated to a good quality
60 partner should invest more in its offspring because they inherit the good genes of the partner
61 and therefore have higher expected fitness (Mazuc et al. 2003; Johnsen et al. 2005). On the
62 contrary, the ‘compensation hypothesis’ suggests that individuals mated to a less ornamented
63 partner should compensate for the worse quality of their mates and enhance the viability of
64 their nestlings by providing more care (Gowaty et al. 2007; Ratikainen and Kokko 2010).
65 Finally, Burley’s original differential allocation hypothesis predicts that parents should adjust
66 their investment according to their own attractiveness relative to that of the partners rather
67 than according to their own or their partner’s attractiveness *per se*, that is individuals mated to
68 a more attractive partner should invest more into the offspring to retain their mate (Burley
69 1986).

70 Despite the relatively large number of studies, we lack important information
71 concerning the role of parental quality in parental feeding decisions. As we outlined above,
72 most hypotheses argue that parents adjust their feeding rate to retain good quality mates or
73 because the future reproductive success of the offspring may be related to parental quality.

74 However, the behaviour, growth rate and therefore energetic requirement of the offspring may
75 also depend on parental quality (Silva et al. 2007), either due to genetic reasons or due to
76 early maternal effects. Begging behaviour of the offspring is suggested to be a reliable signal
77 of need (Cotton et al. 1996; Rodriguez-Girones et al. 2001), and parents of many species are
78 known to respond to this signal in terms of both feeding rate (Ottoesson et al. 1997; Moreno-
79 Rueda et al. 2009) and food allocation to individual offspring (Kölliker et al. 1998; Leonard
80 and Horn 2001; Rosivall et al. 2005). Therefore it is quite plausible to assume that a
81 correlation between a parental trait and feeding rate is the result of a correlation between this
82 parental trait and nestling behaviour/need, rather than an active decision of parents based on
83 their own or their partner's traits. In other words, it is possible that parents do not adjust their
84 investment directly to parental traits (along the lines of the aforementioned hypotheses),
85 rather their investment is constrained by nestling behaviour/need (hereafter 'offspring
86 constraint hypothesis') and the relationship between parental investment and the given
87 parental traits is indirect. To our knowledge this hypothesis has not yet been tested

88 A further problem with the literature on post-hatching parental investment is that
89 despite biparental care in many bird species, most studies focused on parental investment in
90 relation to male quality or attractiveness (e.g. Mazuc et al. 2003; Johnsen et al. 2005; Osorno
91 et al. 2006), while only few have investigated the relationship between parental investment
92 and ornamental traits of females. In addition, the outcome of these studies is quite mixed.
93 Some studies have not found any correlation between paternal feeding rate and female
94 ornaments (Pilastro et al. 2003; Matessi et al. 2009; Maguire and Safran 2010), while others
95 have found positive association between female ornament and male brood defence (Griggio et
96 al. 2003; Matessi et al. 2009) or male feeding rate (Mahr et al. 2012).

97 We studied parental investment in a Hungarian population of the collared flycatcher.
98 Collared flycatchers have two sexually selected plumage traits. In our population, both male
99 and female quality is related to the condition-dependent wing patch size, a heritable plumage
100 signal (Török et al. 2003; Hegyi et al. 2008b). This trait has been reported to play a role in the
101 territorial aggression of males (Garamszegi et al. 2006), and the competitive interactions of
102 females (Hegyi et al. 2008a). Males also have a conspicuous forehead patch. Its size is not
103 condition dependent, but heritable (Hegyi et al. 2002; Hegyi et al. 2006) and might signal the
104 quality of males. Males with larger forehead patches bred earlier in the season (Hegyi et al.
105 2006) and after an immune challenge their song rate decreased less than that of small patched
106 males (Garamszegi et al. 2004a). Furthermore, there was a positive association between the

107 forehead patch size of rearing males and the growth of nestling wing feathers (Szöllősi et al.
108 2009), and between the forehead patch size of both original and foster fathers and nestling
109 mass growth rate (Hegyi et al. 2011b).

110 As we outlined above, male and female ornaments may correlate with feeding rate
111 because (1) parents adjust their investment directly to their own or their partner's traits (e.g.
112 'good parent', 'compensation' and 'differential allocation' hypotheses) or (2) parental quality
113 dependent nestling behaviour/need constrains parental investment ('offspring constraint
114 hypothesis'). The primary aim of this study was to investigate the relationship between
115 parental investment and plumage signals of both males and females in a way that allows us to
116 distinguish between these two main mechanisms. Therefore, we conducted a full-brood cross-
117 fostering experiment. As rearing parents had no information on the traits of original parents,
118 any correlation between the feeding rate of rearing parents and the traits of original parents
119 had to be mediated by intrinsic nestling quality and would support the second mechanism.
120 Correlations between feeding rate and the traits of rearing parents, however, indicate parental
121 decisions based on their own or their partner's traits and would therefore support the first
122 mechanism.

123 Our secondary goal was to deepen our knowledge concerning the role of female
124 ornaments in parental investment decisions after hatching, because only very few papers have
125 been published on this issue.

126 Finally, we aimed to find an explanation for the previously found positive associations
127 between growth of nestlings and forehead patch size of males in our population (Szöllősi et al.
128 2009; Hegyi et al. 2011b). We predicted a positive association between forehead patch size of
129 males and feeding rate of either or both of the parents.

130

131 Methods

132 Study species and field methods

133 Our study was conducted in a Hungarian population of collared flycatchers. Our
134 nestbox plots are located in an oak-dominated woodland in the Pilis Mountains (47°43'N,
135 19°01'E), a protected area of Duna-Ipoly National Park. The collared flycatcher is a small,
136 hole-breeding, insectivorous species with wintering sites in Sub-Saharan Africa (Cramp and
137 Perrins 1993). Males return to the breeding grounds and occupy nestboxes in the middle of
138 April. Females arrive a few weeks later and, after mate choice, they build the nest, lay and

139 incubate the eggs (6-7 on average) alone. After hatching, both parents feed the nestlings, but
140 the brooding of ectothermic (0-6 days old) young is the exclusive task of the female.

141 Nestboxes were continuously monitored after the arrival of birds. Full broods with
142 similar brood size were cross-fostered two days after hatching. Four days after hatching,
143 approximately 1.5 hours (82.9 ± 16.8 min) long video recordings were taken inside the
144 nestboxes to estimate parental feeding effort. One day before the video recording, we
145 exchanged the nestboxes for special ones, which had the same inner sizes, but had a special
146 back chamber (hidden from the parents) for the videocamera. This method had previously
147 been successfully applied in this population (Rosivall et al. 2005). The video records were
148 taken between 8:30 and 20:00, but we tried to avoid the midday time (12:00 to 15:30) when
149 feeding activity may be reduced. There was no difference in the feeding rates between the
150 morning and afternoon hours (female: $t=0.78$; $df=23$; $p=0.45$; male: $t=-1.27$; $df=23$; $p=0.22$),
151 and feeding activity did not change within these periods either (morning/ female: $df=1,8$
152 $F=1.01$; $p=0.34$; male: $df=1,8$; $F=0.38$; $p=0.55$; afternoon/ female: $df=1,17$; $F=0.62$; $p=0.44$;
153 male: $df=1,17$; $F=0.0$; $p=0.98$).

154 When the chicks became 10 days old, we caught the parents with spring traps and
155 measured their morphological traits. The binary age of males (yearling or older) was
156 determined based on the colour of remiges (Svensson 1992). The size of the forehead patch
157 was estimated as the product of maximum width and maximum height (Hegyí et al. 2002).
158 We estimated the wing patch size of both parents by the sum of the lengths of non-covered
159 white bars on the 4th-8th primaries (Török et al. 2003). Body size was estimated by tarsus
160 length. All of these traits were measured with caliper to the nearest 0.1 mm.

161

162 Statistical analysis

163 We used altogether 36 broods (16 in 2002 and 20 broods in 2003) in our experiment,
164 but excluded 2 secondary broods of polygynous males, and 3 broods with five chicks, because
165 of low sample size in this brood size category. One brood was removed to avoid
166 pseudoreplication as the female was included in the experiment in both years. In 3 cases,
167 brood-predation occurred before the chicks were 10 days old, therefore the parents were not
168 caught. The sample size may differ between analyses, because some measurements were
169 occasionally missing (in the final models it was 25).

170 We used general linear models to investigate the effect of rearing and original parental
171 traits on the feeding rate of rearing parents. The proportion of time females spent with

172 brooding during the videorecording varied considerably. Because our recording times were
173 relatively short (82.9 ± 16.8 min), differences in the incubation times were more likely to be
174 the result of mere chance than biologically meaningful differences between the females.
175 Therefore, the feeding rates of females were calculated for the period when they were not
176 incubating. Feeding rates of the males were calculated for the whole period. In both cases,
177 feeding rate was calculated as the number of feedings per hour. Year-standardized laying date,
178 tarsus length, forehead patch size of males and female wing patch size were used in our
179 analyses as covariates (in case of laying date, used the deviation from the yearly median, for
180 all other variables, we used the deviation from the yearly mean divided by SD). Wing patch
181 size of males was year- and also age-standardized because it strongly differs between adults
182 and yearlings (Török et al. 2003). Year, brood size and age of males were used as fixed
183 factors.

184 To avoid overparameterization, we performed two analyses with backward stepwise
185 model selection. First, we analysed the effect of laying date, brood size and the traits of
186 original parents on the feeding rate of rearing parents. Second, we added the traits of rearing
187 parents to the final model (i.e. which included only significant variables) of the first analysis.
188 Values indicated for the non-significant terms are derived from analyses, in which the given
189 terms were reentered to the final model one by one (Hegyi and Garamszegi 2011). We also
190 performed our analyses using an Information Theoretic approach, by calculating the AICc
191 parameter weights of our independent variables (not shown). The parameter weight is
192 analogous to the probability that the given variable is a component of the AICc best model
193 (see details in Burnham and Anderson 2002; Symonds and Moussalli 2011). All variables
194 included in the final models of the stepwise regressions received high parameter weights
195 (ranging from 0.622 to 0.885), thereby confirming the results presented below.

196 Given that the feeding strategy of a parent may depend on the feeding effort of its
197 mate (Linville et al. 1998; Mitchell et al. 2007; Maguire and Safran 2010), we also
198 investigated the relationship between the feeding rate of male and female parents. For this
199 analysis, we used a general linear model. In each above mentioned analyses, model residuals
200 were normally distributed. We used Statistica 6.1 (StatSoft, Inc. 2003. Tulsa, Oklahoma,
201 U.S.A.), and SAS 9.1 (SAS Institute Inc., Cary, North Carolina, U.S.A.) for the statistical
202 analyses.

203

204 Results

205 The provisioning rate of rearing males increased with the wing patch size of original females
206 (Table 1, Fig. 1). None of the remaining variables (traits of original males and rearing parents,
207 brood parameters) correlated with the feeding activity of males (Table 1). The feeding rate of
208 females was significantly higher when rearing more chicks (7 compared to 6; Table 1). It also
209 differed between years (Table 1), and similarly to males, it was significantly positively
210 correlated with the wing patch size of original females (Table 1, Fig. 1). However, just like in
211 males, laying date, the traits of the original males, and that of the rearing parents did not
212 correlate with the feeding activity (Table 1). There was no correlation between the feeding
213 rates of males and females ($F_{1,28} = 0.09$; $P = 0.927$).

214

215 Discussion

216 In our whole-brood fostering experiment, we investigated whether the feeding activity
217 of parents was related to ornamental traits of the original and rearing parents, while
218 controlling for clutch size, laying date and study years. The experimental design allowed us to
219 examine whether foster parents adjusted their feeding activity to their own or their partners'
220 traits or rather to nestling quality/behaviour which is dependent on the quality of the original
221 parents. We found that the wing patch size of original females positively correlated with the
222 feeding rate of both rearing parents. This result suggests a nestling-mediated indirect
223 association between the ornamentation of the original female and feeding rate of the foster
224 parents and thereby supports the 'offspring constraint hypothesis'. Though in this study, we
225 did not investigate the need or behaviour of nestlings, the offspring of more ornamented
226 females might differ in behaviour from the chicks of small-patched mothers. Thus, one
227 possible explanation would be that, as a result of inherited maternal genes, nestlings of high
228 quality females were larger and begged more. However, the body mass of nestlings on the day
229 of videorecording was not related to the wing patch size of the original female (our
230 unpublished data). Nonetheless, this result does not preclude the possibility that inherited
231 genes influence the begging intensity of nestlings *per se* or via their growth rate. Though there
232 is so far no clear experimental evidence for genetic effects of female ornaments on offspring
233 growth, a study of male ornaments suggests that such effects may exist (Parker 2003).
234 Alternatively, females may allocate different amounts of nutrients or hormones into their eggs
235 depending on their quality (Navara et al. 2006), which in turn may affect the begging intensity
236 of nestlings and the feeding activity of rearing parents. For example, it is known of several
237 yolk steroid hormones such as corticosterone (Loiseau et al. 2008), androgens (Eising and

238 Groothuis 2003) or specifically testosterone (Quillfeldt et al. 2006), that they affect the
239 begging activity of nestlings. An earlier study in our collared flycatcher population found no
240 correlation between female wing patch size and the concentration of testosterone in the eggs
241 (Hegyi et al. 2011a). However, yolk androstenedione level significantly increased with laying
242 order in small patched females, while it did not change in females with large wing patch
243 (Hegyi et al. 2011a). When the interaction between laying order and wing patch size was
244 removed from the model, the overall effect of wing patch size became significant: there was
245 on average more androstenedione in eggs of females with smaller wing patches (Hegyi et al,
246 unpublished results). The same study found that nestlings from eggs with less
247 androstenedione hatched with smaller mass and grew faster (Hegyi et al. 2011a). If, in line
248 with these results, nestlings of large patched females hatched with smaller mass and grew
249 faster in our study, they may have required more food during early development, and this
250 could explain our results. Unfortunately, we could not test this, because we had no
251 information on hatching mass in this study.

252 Though, as we have shown, female ornamentation may correlate with post-hatching
253 parental investment, so far only very few studies have investigated this possibility. Even these
254 are hard to compare because some of them focused on brood defence, while others on feeding
255 rate. Two studies (Pilastro et al. 2003; Maguire and Safran 2010) found no correlation
256 between female colouration and the feeding rate of males, while there was a non-significant
257 tendency for female feeding rate to correlate positively with female attractiveness in the study
258 of Pilastro et al. (2003). Griggio et al. (2003) found a positive relationship between male
259 brood defence and female ornamentation. Interestingly, the two studies which estimated
260 parental investment in both ways came to mixed results. Male rock sparrows (*Petronia*
261 *petronia*) defended, but did not feed their chicks more when paired with reduced breast
262 patched females (Matessi et al. 2009). On the contrary, a blue tit (*Cyanistes caeruleus*) study
263 showed that males invested less in feeding, but did not defend the brood less, when paired to
264 UV-reduced females (Mahr et al. 2012). Thus it seems (based on the above results) that the
265 investment of males is either unrelated to or positively correlated with female ornaments and
266 the authors suggested that the latter result supported the differential allocation hypothesis.
267 However, as our results show, this is not necessarily the case. Positive correlation may also
268 occur if males do not directly adjust their investment to female ornaments (as suggested e.g.
269 by the ‘differential allocation hypothesis’), but rather respond to the need/behaviour of the
270 nestlings (as suggested by the ‘offspring constraint hypothesis’).

271 Many more studies focused on the relationship between male ornamentation and
272 parental feeding behaviour, though none of them considered the possibility that such a
273 relationship may be constrained by nestling quality. The results are again quite mixed. Some
274 studies showed a positive correlation between male attractiveness and male feeding rate
275 (Buchanan and Catchpole 2000), others found a negative (Sanz 2001) or no relationship
276 (Maguire and Safran 2010). In addition, in species with multiple colour signals, the two
277 feather ornaments may show contrasting relationship with male feeding rate (Johnsen et al.
278 2005). The association between male ornaments and female feeding rate also varies (positive:
279 Maguire and Safran 2010; none: Mazuc et al. 2003; Sanz 2001; negative: Limbourg et al.
280 2004)

281 The fact that we found no correlation between the rearing parents' feather ornaments
282 and their feeding rate is still surprising for the following reasons. First, in a Swedish
283 population of collared flycatchers, males with an experimentally enlarged forehead patch
284 reduced their feeding rate because they had to defend their territory more intensively against
285 other males (Qvarnström 1997). Given that in our population the wing patch size but not the
286 forehead patch size has an important role in intrasexual competition (Garamszegi et al. 2006;
287 Hegyi et al. 2008a), we expected a negative correlation between wing patch size and feeding
288 rate, something we did not observe. Second, earlier studies in our population have found
289 positive correlations between nestling growth and the forehead patch size of the original
290 males (Szöllösi et al. 2009), or both original and rearing males (Hegyi et al. 2011b). Therefore
291 we predicted that, contrary to results in the Swedish population, males with larger forehead
292 patch (or their mates) would feed their nestlings more. However, in our study, feeding rate of
293 the rearing parents did not change with the forehead patch size of rearing males. The earlier
294 found growth patterns are therefore the result of either attractive males or their partners
295 feeding the chicks with higher quality prey (Sejberg et al. 2000; Grieco 2002), or the
296 offspring of large patched males being of superior genetic quality (Petrie 1994).

297 The feeding rate of females differed between years. The abundance of caterpillar,
298 which is a major food type for developing chicks (Török 1986), was much higher in the year
299 when females had higher feeding rates (our unpublished data). This suggests that females
300 increased their feeding rate when surplus food was available, while this was not true for
301 males. It is possible that, when chicks are young (feeding rate was recorded 4 days after
302 hatching), males do not invest as much energy into parental care and do not respond as readily
303 to environmental conditions as females do, because the value of the brood is not equal for

304 males and females. Though in our population less than 10% of males were socially
305 polygynous (Garamszegi et al. 2004b), 55.7% of broods contained offspring sired by extra-
306 pair males (Rosivall et al. 2009). This means that males have a chance to mate with a
307 secondary female or to sire extra-pair young when their primary brood is young (Magrath and
308 Elgar 1997; Magrath and Komdeur 2003). For females, in contrast, the number of progeny in
309 a breeding season is limited by the number of eggs laid and chicks reared (there is no
310 evidence for intraspecific brood parasitism in this species).

311 The brood value argument may apply also to the effect of brood size, because females
312 rearing seven nestlings fed more frequently than those rearing six, while there was no
313 relationship between brood size and feeding rate of the rearing males. However, our results
314 are in contrast with an earlier brood-size manipulation experiment in the same population,
315 which found that feeding rate of both parents were influenced by brood size (Török and Tóth
316 1990). Nevertheless, it should be noted that in the previous study brood size was manipulated
317 with two nestlings, and feeding rate was measured at an older nestling age when the value of
318 the brood may be higher for the males (Michl et al. 2000).

319 In summary, the main finding of our study is an association between a condition-
320 dependent plumage ornament of the original mother and the provisioning rate of the rearing
321 parents. This indirect effect is important to understand the factors shaping parental
322 investment. Our results indicate that a relationship between parental traits and feeding rate
323 may be explained not only by direct parental adjustment of feeding effort to these traits, but
324 also by differences in the need or behaviour of the nestlings. Further studies should examine
325 the generality of such offspring quality constraints, and explore their potential mechanisms.
326 Our results also show that the role of female ornaments in parental investment decisions
327 deserves more attention than it has received so far.

328
329 Acknowledgements

330 We thank Rita Hargitai, Márton Herényi, Beáta Szigeti and Eszter Szöllősi for their
331 help in the field, and Orsolya Molnár, Marty Leonard and two anonymous reviewers for
332 helpful comments on the manuscript. The study was supported by Hungarian Scientific
333 Research Fund (OTKA) grants (K75618 to JT, PD75481 and F68295 to BR, and PD72117
334 and K101611 to GH), the Erdők a Közjóért Alapítvány, the Eötvös Loránd University, and
335 the Pilis Park Forestry.

336

337 Ethical standards

338 Work at the study site was done under permits from Duna-Ipoly National Park. All
339 experiments comply with the laws of Hungary.

340

341 References

342

343 Andersson M (1994) Sexual selection. Princeton University Press, Princeton, New Jersey

344 Buchanan KL, Catchpole CK (2000) Song as an indicator of male parental effort in the sedge
345 warbler. Proc R Soc Lond B 267:321-326

346 Burley N (1986) Sexual selection for aesthetic traits in species with biparental care. Am Nat
347 127:415-445

348 Burnham KP, Anderson DR (2002) Model Selection and Multi-Model Inference. Springer,
349 New York

350 Cichoń M, Olejniczak P, Gustafsson L (1998) The effect of body condition on the cost of
351 reproduction in female collared flycatchers *Ficedula albicollis*. Ibis 140:128-130

352 Cotton PA, Kacelnik A, Wright J (1996) Chick begging as a signal: Are nestlings honest?
353 Behav Ecol 7:178-182

354 Cramp S, Perrins CM (1993) The Birds of the Western Palearctic, vol VII. Oxford University
355 Press, Oxford

356 DeMory ML, Thompson CF, Sakaluk SK (2010) Male quality influences male provisioning in
357 house wrens independent of attractiveness. Behav Ecol 21:1156-1164

358 Eising CM, Groothuis TGG (2003) Yolk androgens and begging behaviour in black-headed
359 gull chicks: an experimental field study. Anim Behav 66:1027-1034

360 Garamszegi LZ, Møller AP, Török J, Michl G, Péczely P, Richard M (2004a) Immune
361 challenge mediates vocal communication in a passerine bird: an experiment. Behav
362 Ecol 15:148-157

363 Garamszegi LZ, Rosivall B, Hegyi G, Szöllősi E, Török J, Eens M (2006) Determinants of
364 male territorial behavior in a Hungarian collared flycatcher population: plumage traits
365 of residents and challengers. Behav Ecol Sociobiol 60:663-671

366 Garamszegi LZ, Török J, Michl G, Møller AP (2004b) Female survival, lifetime reproductive
367 success and mating status in a passerine bird. Oecologia 138:48-56

368 Gowaty PA, Anderson WW, Bluhm CK, Drickamer LC, Kim YK, Moore AJ (2007) The
369 hypothesis of reproductive compensation and its assumptions about mate preferences
370 and offspring viability. P Natl Acad Sci USA 104:15023-15027

- 371 Grieco F (2002) Time constraint on food choice in provisioning blue tits, *Parus caeruleus*: the
372 relationship between feeding rate and prey size. *Anim Behav* 64:517-526
- 373 Griggio M, Matessi G, Pilastro A (2003) Male rock sparrow (*Petronia petronia*) nest defence
374 correlates with female ornament size. *Ethology* 109:659-669
- 375 Gustafsson L, Sutherland WJ (1988) The cost of reproduction in the collared flycatcher
376 *Ficedula albicollis*. *Nature* 335:813-815
- 377 Hegyi G, Garamszegi LZ (2011) Using information theory as a substitute for stepwise
378 regression in ecology and behavior. *Behav Ecol Sociobiol* 65:69-76
- 379 Hegyi G, Garamszegi LZ, Eens M, Török J (2008a) Female ornamentation and territorial
380 conflicts in collared flycatchers (*Ficedula albicollis*). *Naturwissenschaften* 95:993-996
- 381 Hegyi G, Herényi M, Szöllösi E, Rosivall B, Török J, Groothuis TGG (2011a) Yolk
382 androstenedione, but not testosterone, predicts offspring fate and reflects parental
383 quality. *Behav Ecol* 22:29-38
- 384 Hegyi G, Rosivall B, Szöllösi E, Eens M, Török J (2011b) Context-dependent effects of
385 nestling growth trajectories on recruitment probability in the collared flycatcher.
386 *Behav Ecol Sociobiol* 65:1647-1658
- 387 Hegyi G, Rosivall B, Szöllösi E, Hargitai R, Eens M, Török J (2008b) Phenotypic plasticity in
388 a conspicuous female plumage trait: information content and mating patterns. *Anim*
389 *Behav* 75:977-989
- 390 Hegyi G, Török J, Tóth L (2002) Qualitative population divergence in proximate
391 determination of a sexually selected trait in the collared flycatcher. *J Evol Biol*
392 15:710-719
- 393 Hegyi G, Török J, Tóth L, Garamszegi LZ, Rosivall B (2006) Rapid temporal change in the
394 expression and age-related information content of a sexually selected trait. *J Evol Biol*
395 19:228-238
- 396 Hoelzer GA (1989) The good parent process of sexual selection. *Anim Behav* 38:1067-1078
- 397 Johnsen A, Delhey K, Schlicht E, Peters A, Kempenaers B (2005) Male sexual attractiveness
398 and parental effort in blue tits: a test of the differential allocation hypothesis. *Anim*
399 *Behav* 70:877-888
- 400 Keyser AJ, Hill GE (2000) Structurally based plumage coloration is an honest signal of
401 quality in male blue grosbeaks. *Behav Ecol* 11:202-209
- 402 Kölliker M, Richner H, Werner I, Heeb P (1998) Begging signals and biparental care: nestling
403 choice between parental feeding locations. *Anim Behav* 55:215-222
- 404 Leonard ML, Horn AG (2001) Begging calls and parental feeding decisions in tree swallows
405 (*Tachycineta bicolor*). *Behav Ecol Sociobiol* 49:170-175

- 406 Limbourg T, Mateman AC, Andersson S, Lessells CM (2004) Female blue tits adjust parental
407 effort to manipulated male UV attractiveness. *Proc R Soc Lond B* 271:1903-1908
- 408 Linville SU, Breitwisch R, Schilling AJ (1998) Plumage brightness as an indicator of parental
409 care in northern cardinals. *Anim Behav* 55:119-127
- 410 Loiseau C, Sorci G, Dano S, Chastel O (2008) Effects of experimental increase of
411 corticosterone levels on begging behavior, immunity and parental provisioning rate in
412 house sparrows. *Gen Comp Endocr* 155:101-108
- 413 Magrath MJL, Elgar MA (1997) Paternal care declines with increased opportunity for extra-
414 pair matings in fairy martins. *Proc R Soc Lond B* 264:1731-1736
- 415 Magrath MJL, Komdeur J (2003) Is male care compromised by additional mating
416 opportunity? *Trends Ecol Evol* 18:424-430
- 417 Maguire SE, Safran RJ (2010) Morphological and genetic predictors of parental care in the
418 North American barn swallow *Hirundo rustica erythrogaster*. *J Avian Biol* 41:74-82
- 419 Mahr K, Griggio M, Granatiero M, Hoi H (2012) Female attractiveness affects paternal
420 investment: Experimental evidence for male differential allocation in blue tits. *Front*
421 *Zool* 9
- 422 Matessi G, Carmagnani C, Griggio M, Pilastro A (2009) Male rock sparrows differentially
423 allocate nest defence but not food provisioning to offspring. *Behaviour* 146:209-223
- 424 Mazuc J, Chastel O, Sorci G (2003) No evidence for differential maternal allocation to
425 offspring in the house sparrow (*Passer domesticus*). *Behav Ecol* 14:340-346
- 426 Michl G, Török J, Garamszegi LZ, Tóth L (2000) Sex-dependent risk taking in the collared
427 flycatcher, *Ficedula albicollis*, when exposed to a predator at the nestling stage. *Anim*
428 *Behav* 59:623-628
- 429 Mitchell DP, Dunn PO, Whittingham LA, Freeman-Gallant CR (2007) Attractive males
430 provide less parental care in two populations of the common yellowthroat. *Anim*
431 *Behav* 73:165-170
- 432 Moreno-Rueda G, Soler M, Martín-Vivaldi M, Palomino JJ (2009) Brood provisioning rate
433 and food allocation rules according to nestling begging in a clutch-adjusting species,
434 the Rufous-tailed Scrub-robin *Cercotrichas galactotes*. *Acta Ornithol* 44:167-175
- 435 Navara KJ, Badyaev AV, Mendonça MT, Hill GE (2006) Yolk antioxidants vary with male
436 attractiveness and female condition in the house finch (*Carpodacus mexicanus*). *Phys*
437 *Biochem Zool* 79:1098-1105
- 438 Osorno JL, Morales J, Moreno J, Merino S, Tomás G, Vásquez RA (2006) Evidence for
439 differential maternal allocation to eggs in relation to manipulated male attractiveness
440 in the pied flycatcher (*Ficedula hypoleuca*). *J Ornithol* 147:605-611
- 441 Ottosson U, Backman J, Smith HG (1997) Begging affects parental effort in the pied
442 flycatcher, *Ficedula hypoleuca*. *Behav Ecol Sociobiol* 41:381-384

- 443 Parker TH (2003) Genetic benefits of mate choice separated from differential maternal
444 investment in red junglefowl (*Gallus gallus*). *Evolution* 57:2157-2165
- 445 Petrie M (1994) Improved growth and survival of offspring of peacocks with more elaborate
446 trains. *Nature* 371:598-599
- 447 Pilastro A, Griggio M, Matessi G (2003) Male rock sparrows adjust their breeding strategy
448 according to female ornamentation: parental or mating investment? *Anim Behav*
449 66:265-271
- 450 Quillfeldt P, Masello JF, Strange IJ, Buchanan KL (2006) Begging and provisioning of thin-
451 billed prions, *Pachyptila belcheri*, are related to testosterone and corticosterone. *Anim*
452 *Behav* 71:1359-1369
- 453 Qvarnström A (1997) Experimentally increased badge size increases male competition and
454 reduces male parental care in the collared flycatcher. *Proc R Soc Lond B* 264:1225-
455 1231
- 456 Ratikainen I, Kokko H (2010) Differential allocation and compensation: who deserves the
457 silver spoon? *Behav Ecol* 21:195-200
- 458 Rodriguez-Girones MA, Zuniga JM, Redondo T (2001) Effects of begging on growth rates of
459 nestling chicks. *Behav Ecol* 12:269-274
- 460 Rosivall B, Szöllösi E, Hasselquist D, Török J (2009) Effects of extrapair paternity and sex on
461 nestling growth and condition in the collared flycatcher, *Ficedula albicollis*. *Anim*
462 *Behav* 77:611-617
- 463 Rosivall B, Török J, Szöllösi E (2005) Food allocation in collared flycatcher (*Ficedula*
464 *albicollis*) broods: Do rules change with the age of nestlings? *Auk* 122:1112-1122
- 465 Sanz JJ (2001) Experimentally reduced male attractiveness increases parental care in the pied
466 flycatcher *Ficedula hypoleuca*. *Behav Ecol* 12:171-176
- 467 Sejberg D, Bensch S, Hasselquist D (2000) Nestling provisioning in polygynous great reed
468 warblers (*Acrocephalus arundinaceus*): do males bring larger prey to compensate for
469 fewer nest visits? *Behav Ecol Sociobiol* 47:213-219
- 470 Sheldon BC, Merilä J, Qvarnström A, Gustafsson L, Ellegren H (1997) Paternal genetic
471 contribution to offspring condition predicted by size of male secondary sexual
472 character. *Proc R Soc Lond B* 264:297-302
- 473 Silva MC, Boersma PD, Mackay S, Strange I (2007) Egg size and parental quality in thin-
474 billed prions, *Pachyptila belcheri*: effects on offspring fitness. *Anim Behav* 74:1403-
475 1412
- 476 Svensson L (1992) Identification guide to european passerines. Published by the author,
477 Stockholm

- 478 Symonds MRE, Moussalli A (2011) A brief guide to model selection, multimodel inference
479 and model averaging in behavioural ecology using Akaike's information criterion.
480 Behav Ecol Sociobiol 65:13-21
- 481 Szöllősi E, Rosivall B, Hasselquist D, Török J (2009) The effect of parental quality and
482 malaria infection on nestling performance in the Collared Flycatcher (*Ficedula*
483 *albicollis*). J Ornithol 150:519-527
- 484 Török J (1986) Food segregation in three hole-nesting bird species during the breeding
485 season. Ardea 74:129-136
- 486 Török J, Hegyi G, Garamszegi LZ (2003) Depigmented wing patch size is a condition-
487 dependent indicator of viability in male collared flycatchers. Behav Ecol 14:382-388
- 488 Török J, Tóth L (1990) Costs and benefits of reproduction of the collared flycatcher, *Ficedula*
489 *albicollis*. In: Blondel J, Gosler A, Lebreton D-J, McCleery R (eds) Population
490 biology of passerine birds: an integrated approach (NATO ASI series). Springer,
491 Berlin Heidelberg New York, pp 307-319
492
493

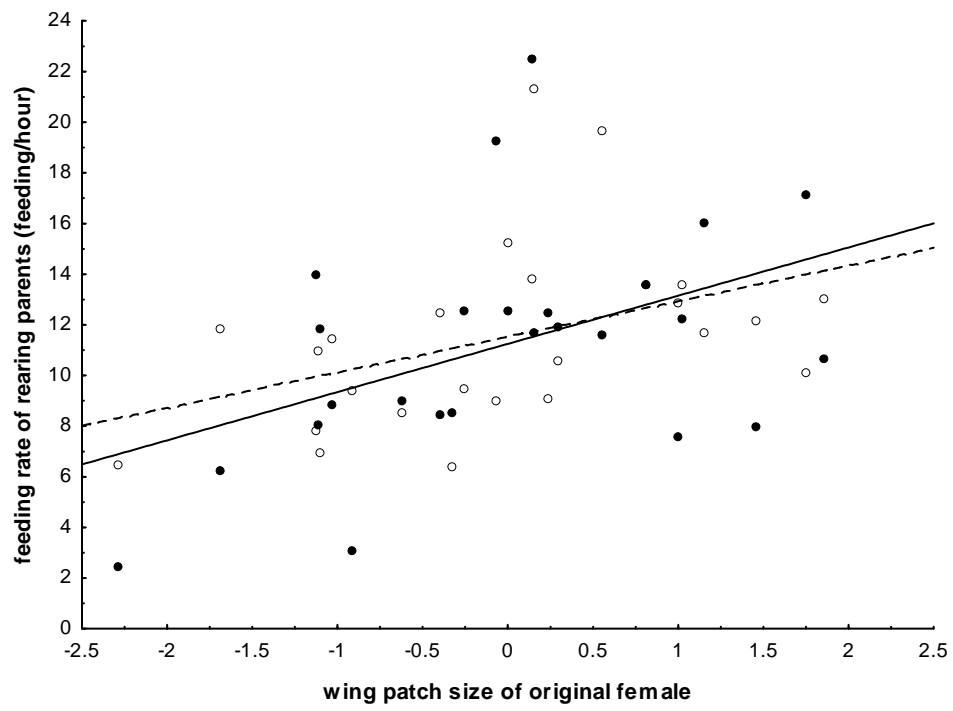
494 Table 1 Relationship between the provisioning rate of rearing parents and brood size, laying
 495 date and morphology of original and rearing parents. Values indicated for the non-significant
 496 terms are derived from analyses, in which the given terms were reentered to the final model
 497 one by one. The variables retained in the final model are indicated in bold. WPS stands for
 498 wing patch size, FPS stands for forehead patch size

variable	feeding rate of rearing male			feeding rate of rearing female		
	df	F	P	df	F	P
year	1;22	0.00	0.960	1;21	5.08	0.035
brood size	1;22	0.09	0.770	1;21	5.32	0.031
laying date	1;22	0.00	0.946	1;20	0.02	0.876
original female's tarsus	1;22	2.44	0.132	1;20	0.37	0.552
WPS	1;23	4.83	0.038	1;21	5.13	0.034
original male's age	1;22	0.15	0.702	1;20	1.23	0.281
tarsus	1;20	0.14	0.715	1;18	2.83	0.110
FPS	1;21	1.26	0.275	1;19	0.63	0.437
WPS	1;21	1.26	0.275	1;19	0.22	0.642
rearing female's tarsus	1;22	0.75	0.397	1;20	0.13	0.722
WPS	1;22	0.33	0.573	1;20	1.98	0.175
rearing male's age	1;22	1.26	0.274	1;20	0.89	0.356
tarsus	1;21	2.25	0.148	1;19	0.22	0.642
FPS	1;22	0.92	0.349	1;20	1.71	0.206
WPS	1;22	0.45	0.507	1;20	0.03	0.874

499

500 **Fig. 1** Provisioning rate of rearing parents in relation to the year-standardized wing patch size
501 of original females (rearing females - open circles, dashed line; rearing males - filled circles,
502 solid line).

503 Fig. 1



504