

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

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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 (Ottoosson 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 ( $82.9 \pm 16.8$  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 ( $82.9 \pm 16.8$  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  
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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.

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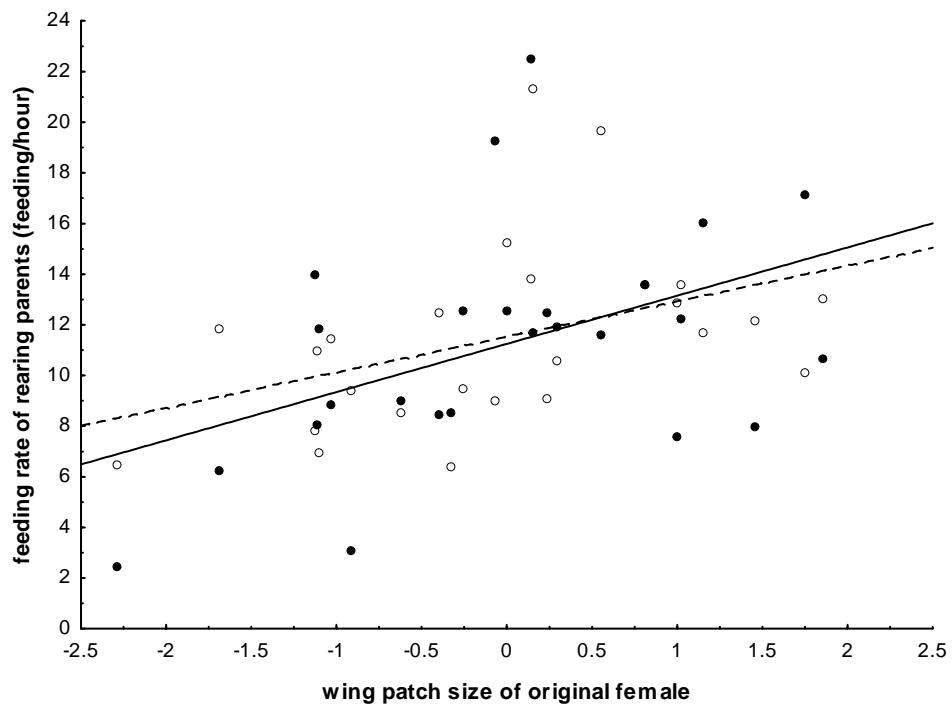
494 Table 1 Relationship between the provisioning rate of rearing parents and brood size, laying  
 495 date and morphology of original and rearing parents. Values indicated for the non-significant  
 496 terms are derived from analyses, in which the given terms were reentered to the final model  
 497 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	<b>1;21</b>	<b>5.08</b>	<b>0.035</b>
brood size	1;22	0.09	0.770	<b>1;21</b>	<b>5.32</b>	<b>0.031</b>
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
<b>WPS</b>	<b>1;23</b>	<b>4.83</b>	<b>0.038</b>	<b>1;21</b>	<b>5.13</b>	<b>0.034</b>
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