1 **Parental feeding preferences rather than sibling competition determine the death**

2 **of smaller nestlings in asynchronous broods**

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## Abstract

Hatching asynchrony is a reproductive tactic that, through the creation of competitive hierarchies among offspring, allows parents for a quick adjustment of brood size via the death of smaller nestlings. This strategy is considered to be adaptive in case of unpredictable and/or poor environments in which it would guarantee that at least larger nestlings will fledge. Brood reduction is the usual outcome in asynchronously hatched broods since first-hatched nestlings are larger and get a disproportionately larger share of the food delivered by parents, often leading the youngest nestling to starve to death soon after hatching. However, we still do not know the proximate mechanisms of such brood reduction. One possibility is that the smallest nestling is not fed because larger nestlings outcompete it, which implies that nestlings control resource allocation. Alternatively, parents might actively ignore the persistent begging from their smallest nestling, which would involve that parents control food allocation. To determine whether parents or nestlings ultimately induce brood reduction in this situation, we experimentally created asynchronous broods of Eurasian blackbird (*Turdus merula*) nestlings and quantified food allocation by parents in two different situations: when sibling competition was allowed and, alternatively, when competition was prevented by physically separating nestlings within the nests by using wooden barriers. Our results showed that experimentally introduced smaller nestlings received less food than their larger nestmates both when competition among nestlings was allowed and when it was prevented. When adult males and females are considered separately, males fed the smallest nestling less often regardless of whether sibling competition was allowed or not, but adult females showed no differences. We can conclude that the smallest nestling starves mainly because parents actively ignore its begging. The higher competitive ability of the larger nestlings seem to have little effect given that although the smallest nestling is fed at a higher rate when

42  physical interactions are prevented by the wooden barrier than when not, this difference

43  is not significant. These findings suggest that parents rather than nestlings have the main

44  control over food allocation.

45

46  **Key words:** Brood reduction, food allocation, sex differences in food allocation, hatching

47  asynchrony, scramble competition, *Turdus merula*.

**Introduction**

In birds, the apparently most effective way to maximize parental fitness is to ensure that all laid eggs eventually result in fledglings. This is indeed what happens in most species: parents start incubation after clutch completion producing a brood of synchronously hatched nestlings of similar size. This strategy avoids the existence of competitive hierarchies among offspring and favours an equalitarian allocation of food among nestlings. Consequently, parents increase the chances that all nestlings will survive to fledge by preferentially feeding the hungriest nestling according to signal of need models (Davis et al. 1999; Soler 2001; Jeon 2008; Caro et al. 2008). Based on available information, it is often assumed that both hatching synchrony and food allocation favouring nestlings in worse condition (i.e. those begging at higher intensity) provide adaptive benefits in predictable and good environments since, when food is abundant, a high provisioning rate would allow parents to provide more food to the undernourished nestling and all offspring will be able to fledge (Lack 1947, 1954; Magrath 1990; Davis et al. 1999; Jeon 2008; Caro et al. 2016). In contrast, a synchronous brood could compromise nestling survival in unpredictable and/or poor environments since feeding all nestlings when food is scarce could provoke starvation in all or most of them. Thus, when food is scarce, any tactic allowing parents to adjust brood size according to food availability would be adaptive because this would guarantee that at least larger nestlings will fledge (Lack 1954; Jeon 2008; Caro et al. 2016). Hatching asynchrony is considered one of such tactics since, in unpredictable and/or poor environments, a size hierarchy among offspring would allow for a quick adaptive adjustment of brood size through death of smaller nestlings (the brood reduction hypothesis (Lack 1945, 1954)).

Brood reduction is the usual outcome in asynchronously hatched broods, in which first-hatched nestlings are larger and exhibit a higher competitive ability that allow them

73    to outcompete later-hatched (smaller) nestlings by getting a disproportionately larger

74    share of the food delivered by parents (Lack 1954; Soler 2001; Jeon 2008). As a

75    consequence, the youngest nestling often starves soon after hatching. This is supported

76    by the fact that a bigger size increases the ability of a nestling to jostle for the best position

77    in the nest, which is considered crucial to successfully compete for food (McRae et al.

78    1993; Malacarne et al. 1994; Kilner 1995; Ostreiher 2001). Preferential feeding of larger

79    nestlings has usually been interpreted as the outcome of scramble competition among

80    offspring, assuming that nestlings exert full control over resource allocation by parents

81    (scramble competition models (Macnair and Parker 1979; Mock and Parker 1997; Parker

82    et al. 2002)). However, empirical and experimental evidence has shown that larger

83    nestlings obtain more food than smaller nestlings even when showing a lower begging

84    behaviour (Smiseth and Amundsen 2002: Mock et al 2011), which indicates that parents

85    may have at least partial control in food allocation within asynchronous broods (Krebs et

86    al 1999; Smiseth et al 2003). Despite this evidence, to what extend parents and nestlings

87    exert control of brood reduction still remains unclear (McRae et al. 1993; Mock et al.

88    2009). Recent studies suggest that parental control is much more relevant than nestling

89    behaviour. For example, house wrens (*Troglodytes aedon*) are able to switch from

90    synchronous hatching with all nestlings surviving to fledge in favourable conditions, to

91    asynchronous hatching with brood reduction in less favourable conditions, even within

92    the same breeding season (Ellis et al 2001). In Eurasian hoopoes (*Upupa epops*), it has

93    been reported that while males feed larger nestlings placed in the best position (entrance

94    of the nest), females usually enter the nest cavity and feed preferentially the smallest

95    nestlings (Ryser et al. 2016). This seems to be the case in many asynchronously hatching

96    species, in which females (and not males) feed the smallest nestling of the brood showing

97    that females have control over food distribution (Gottlander 1987; Stamps et al. 1987;

98   Lifjeld et al. 1992; Leonard and Horn 1996; Slagsvold 1997a, 1997b; Krebs et al. 1999;

99   Ploger and Madeiros 2004; Dickens and Hartley 2007; Budden and Beissinger 2009;

100  Lahaye et al. 2015; Ryser et al. 2016). The frequently reported fact that females (and not

101  males) feed the smallest nestling in the brood has inspired the "Male manipulation

102  hypothesis", which states that females, by provoking hatching asynchrony and keeping

103  alive the smallest nestling (runt), which begs more and at a higher intensity, force males

104  to work harder, carrying more food to the nest in asynchronously hatched broods (Soler

105  et al. In prep.).

106       The fact that males and females differ in their food allocation rules in

107  asynchronously-hatched broods implies that at least one of the sexes (males that are

108  feeding selectively the best competitors, or females that are feeding selectively smaller

109  nestlings) allocates food ignoring nestling begging behaviour, thus exerting the main

110  control over food allocation. The crucial point in this situation is the undernourished

111  smallest nestling who, after becoming a runt (i.e. a nestling with a retarded growth that

112  does not have any probability of survival), starve to death. There are three possibilities to

113  explain why one or more smaller nestlings in asynchronous broods starve: (a) runts are

114  not fed because of sibling competition (i.e. larger nestlings outcompete them), (b) parents

115  actively ignore the persistent begging from their smaller nestling, or (c) a mix of both. As

116  far as we know, no study has assessed the relative importance of these three possibilities

117  in the context of brood reduction. In this experimental study, we aim to determine to what

118  extend either sibling competition or parental preferences are the responsible of runt's

119  starvation. Since previous studies have shown that males and females can follow different

120  rules when allocating food among offspring (see references above), we considered the

121  role of both sexes separately. To fulfill these objectives, we experimentally created

122  asynchronous nests to explore parental food allocation patterns in two different situations:

123     (i) allowing physical interactions among nestlings and (ii) impeding them by using a

124     wooden barrier that forces each nestling to stay in its portion of the nest.

125        Our main hypothesis, considering the increasing evidence that control by parents

126     in food allocation is more relevant than previously thought (see references above), is that

127     parents actively discriminate against runt nestlings regardless of nestling competition and

128     nestling need (Hypothesis 1). This hypothesis predicts that the smallest nestling will

129     receive less food than its nestmates not only when physical interactions are allowed, but

130     also when the presence of a wooden barrier would impede those interactions. The other

131     two non-mutually-exclusive alternative hypotheses are: food allocation by parents is

132     determined by scramble competition among nestlings (Hypothesis 2). This hypothesis

133     predicts that in natural conditions, when physical interactions occurs, the smallest nestling

134     will receive less food than its nestmates, but when the presence of a wooden barrier would

135     impede larger nestlings blocking their smaller nestlings, the neediest nestling, should be

136     fed preferentially, or at least at the same frequency as its larger nestmates. Finally, the

137     intermediate possibility is that both adults and offspring exert some control over food

138     allocation by parents (Hypothesis 3). This hypothesis predicts that the smallest nestling

139     should be fed at a significantly higher rate when physical interactions are prevented by

140     the wooden barrier than when not.

141

142     **Methods**

143     *Study area and species*

144     Fieldwork was carried out in the Valley of Lecrín (Southern Spain; 36° 56′ N, 3° 33′ W;

145     580 m a.s.l.) between mid-March and June in 2013 and 2015. As model species, we used

146     the Eurasian blackbird (*Turdus merula*, hereafter blackbird), a medium sized passerine

147     with a clear sexual dimorphism (adult males being black with a distinctive yellow-orange

148     beak and eye-ring, while adult females are dull dark, with lighter brown streaks on their

149     breast), which makes it easy to recognize the sex involved in each feeding event. In our

150     study area blackbirds' clutch size ranges from 2 to 5 eggs (Pers. Observ.). We have chosen

151     this species because females start incubation before the last egg is laid inducing moderate

152     hatching asynchrony (the last egg hatches latter than the rest and in some cases brood

153     reduction occurs, mainly at the end of the breeding season and in other situations of poor

154     environmental conditions (Cramp 1985)).

155     **General field procedures and experimental design**

156     We actively searched for blackbird nests in the study area throughout the breeding season.

157     Once located, nests were visited every two days and, close to hatching, daily in order to

158     detect newly-hatched chicks. In this species, hatching order can easily be assessed by a

159     daily nest checking; even so, in those cases in which two nestlings hatched within 24

160     hours, we relied on the chick's weight to establish the nestling rank. Recently-hatched

161     nestlings were marked on their tarsus by using coloured permanent markers (Lumocolor)

162     and, on days 6-7 post-hatching, with numbered rings for individual recognition.

163     We experimentally created four-nestlings asynchronous broods by conducting a cross-

164     fostering manipulation in nests with similar hatching dates. On the experimental day 0, a

165     one-day old nestling from a donor nest (experimental nestling; mean weight = 7.4 ± 0.3

166     g, n = 14) was introduced into a recipient nest containing three-days old nestlings (± 1

167     day, siblings' mean weight = 14.5 ± 0.3 g, n = 42). The next day (experimental day 1;

168     9:00 – 13:00 h), parental feeding activity was video recorded in two consecutive and non-

169     overlapping trials, each trial lasting 1.5 hours. In one of these trials, siblings were allowed

170     to physically compete for food while, in the other trial, physical interaction among

171     nestlings was prevented by placing a wooden cross-shaped barrier into the cup nest

172     (attached to the base of the nest by a twine thread) so that siblings remained separated in

173    four same-size compartments. Barriers were placed 30 minutes before the start of the

174    recordings so that parents could get used to their presence in the nest. Nestlings were

175    randomly placed into the nest compartments, being able to raise their heads above barriers

176    during begging. In all cases, parents could easily feed all nestlings from the edge of the

177    nest. The experimental trial in which nestlings remained separated by the wooden barrier

178    was alternated in successive nests (first trial or second trial) to clearly separate the effect

179    of the barrier presence from the potential order effect. We avoided altering the nest

180    structure (i.e. relative position of nestlings in the nest) in successive trials. Although

181    previous studies have suggested that the position of a nestling in the nest relative to its

182    nestmates and the feeding parent may influence food obtained by the nestling (McRae et

183    al. 1993; Malacarne et al. 1994; Kilner 1995; Ostreiher 2001), we assume that positional

184    effects are irrelevant in our study because of two reasons. First, barriers and nestlings

185    were placed randomly with regards to the position of the parent, and second, our barrier

186    separating the nest cup in four parts removes the central position, which may be the most

187    favourable.

188        About 30 minutes before the first trial, a video camera (Panasonic HDC-SD40)

189    was placed near the nest (3 - 5 m) to determine parental feeding decisions and quantify

190    food delivery rates to the first-hatched nestling (a-nestling), the second-hatched nestling

191    (b-nestling), the third-hatched nestling (c-nestling) and the smallest (experimental)

192    nestling. The video camera was attached to a small tripod and hidden in the vegetation

193    near the nest, often at a higher height than the nest so that the filming was made from

194    above in most cases (angles between 15º - 45º). Food allocation patterns were investigated

195    by assessing the overall food load received by each nestling in one hour. To do that, we

196    quantified the number of food items delivered to each chick by parents. One food item is

197    defined as a prey that represents a volume similar to the size of blackbirds' bill. Thus, the

198  size category of food items was estimated from recordings by comparing the volume of

199  each food item relative to the bill volume of the parent within bins of 50% (e.g., 50%,

200  100%, 150%, etc., of bill volume) (Hauber and Moskát 2008). Additionally, food items

201  smaller than 50% of the bill volume were all quantified as 10% of bill volume as they

202  were mostly small insects of similar size. Finally, the volumes (i.e. size categories) of all

203  items delivered to a single nestling were summed to generate the variable "food load". In

204  order to distinguish different nestlings in recordings, we marked their bill with individual

205  colours by using permanent markers.

206  *Statistical analysis*

207  To assess the effects of our experimental manipulation on parents' food allocation

208  patterns, we fitted linear mixed models (LMM) by using the *nlme* package (Pinheiro et

209  al. 2014), with the number of food items that nestlings received per hour (log-

210  transformed) as a dependent variable. As fixed factors, our models included barrier

211  presence (yes/no), nestling rank (a/b/c/experimental) and the interaction between these

212  two terms, while chick identity nested within nest identity was included as random terms.

213  Only significant interactions were retained in the models (Engqvist 2005). Post hoc

214  contrasts were performed using the *lsmeans* package (Lenth 2016). The proportion of

215  variance explained ($R^2$) for our mixed models was calculated according to Nakagawa and

216  Schielzeth (2013) and Nakagawa et al. (2017). In short, two values of $R^2$ were calculated:

217  the marginal r-squared ($R^2_{LMM(m)}$), describing the proportion of variance explained by

218  fixed factors alone, and the conditional r-squared ($R^2_{LMM(c)}$), describing the proportion of

219  variance explained by both fixed and random terms. Assumptions of normality and

220  homogeneity of variances were verified through the visual inspection of residual graphs.

221  All analyses and graphs were performed using R version 3.6.1 (R Core Team 2019).

222

### Results

*Food allocation: general patterns*

The overall amount of food carried to the nest was similar when nestlings were separated by wooden barriers or when they were free to compete for resources ($F_{1,52} = 0.24$; $p = 0.62$; Fig. 1). Importantly, the food was unevenly distributed among nestlings ($F_{3,52} = 9.58$; $p < 0.0001$; Fig. 1), regardless of whether physical sibling competition was allowed or not, as indicated by the non-significant two-way interaction (LMM: nestling rank x barrier presence: $F_{3,49} = 0.83$; $p = 0.486$). These results are in agreement with the prediction derived from Hypothesis 1, while contradict that derived from Hypothesis 2. Overall, the younger experimental nestling received less food than the a-nestling, the b-nestling and the c-nestling (Table 1a; Fig. 1). Regarding to the prediction from Hypothesis 3, although the smallest experimental nestling received more food items per hour ($1.34 \pm 0.26$; n = 14) when separated by the wooden barrier than in natural conditions ($0.80 \pm 0.18$ food items per hour, n = 14), this difference was not significant (estimate $\pm$ se = $0.228 \pm 0.144$; df = 49; t = 1.59; $p = 0.12$). Our statistical model explained 47.6% of total variance, in which the fixed part (i.e. the additive effects of sibling competition and parental preferences) explained 19.7% (Table 1a); however, whether sibling competition is excluded from models, the fixed part still explains 19.7% of variance, which seems to confirm that, while scramble competition among nestlings slightly (although not significantly) reduced the amount of food received by the smallest chick (Fig. 1), food allocation was mainly determined by parental decisions.

*Food allocation by males*

On average, male blackbirds visited their nests to feed nestlings $4.01 \pm 0.39$ times per hour (range = 1.94 - 7.03, n = 14). Males did not vary the overall amount of food provided to nestlings when they were separated and unable to compete compared with the control

248    situation ($F_{1,52} = 0.80$; $p = 0.38$). However, males differentially distributed food among

249    siblings ($F_{3,52} = 8.05$; $p = 0.0002$), providing less food to the smallest nestling regardless

250    the competitive context in which nestlings were maintained (LMM: nestling rank x barrier

251    presence: $F_{3,49} = 0.55$; $p = 0.648$; Figure 2A). These results support the prediction derived

252    from Hypothesis 1, while contradicts the prediction associated with Hypothesis 2. More

253    specifically, the smallest (experimental) nestling received significantly less food than the

254    a-nestling and the b-nestling, but there were no significant differences between the

255    smallest and the c-nestling (Table 1b; Figure 2A). With respect to the prediction from

256    Hypothesis 3, although the smallest nestling received more food items per hour when

257    separated by the wooden barrier ($0.86 \pm 0.21$; n = 14) than in natural conditions ($0.58 \pm$

258    $0.12$ feeds per hour; n = 14), this difference was not significant (estimate $\pm$ se = $0.112 \pm$

259    $0.147$; df = 49; t = 1.20; $p = 0.49$). Our statistical model for males explained 39.3% of

260    total variance, in which the fixed part explained 17.1% (Table 1b); however, whether

261    sibling competition is excluded from models, parental preferences still explain 16.8% of

262    variance. Taken together these results indicate that, in the case of males, food allocation

263    was mainly determined by parental decisions.

264    *Food allocation by females*

265    Our results showed that female blackbirds visited their nests to feed nestlings $2.27 \pm 0.29$

266    times per hour (range = $0.66 - 4.23$, n = 14). The overall food load that nestlings received

267    from females were not affected by the absence of physical sibling competition ($F_{1,52} =$

268    $0.81$; $p = 0.37$). Females differentially fed nestlings ($F_{3,52} = 3.40$; $p = 0.02$), although such

269    differences tended to soften when nestlings could not compete for food (LMM: nestling

270    rank x barrier presence: $F_{3,49} = 2.27$; $p = 0.092$; Fig. 2B). Interestingly, post hoc tests

271    revealed that, in the absence of physical competition (i.e. nestlings separated by barriers),

272    the smallest experimental nestling was fed by females at similar rates than the other three

273    nestlings (all cases $p > 0.22$). However, when nestlings were free to compete, the smallest

274    nestling received less food than the b-nestling (estimate $\pm$ se = -0.533$\pm$ 0.137; df = 49; t

275    = -3.884; $p$ = 0.0003) and the c-nestling (estimate $\pm$ se = -0.332$\pm$ 0.137; df = 49; t = -

276    2.420; $p$ = 0.019), and tended to receive less food than the a-nestling (estimate $\pm$ se = -

277    0.240$\pm$ 0.137; df = 49; t = -1.752; $p$ = 0.086). Taken together, these results support the

278    Hypothesis 2 stating that food allocation by females is mainly determined by nestling

279    competition. However, the fact that the experimental smallest nestling did not receive

280    significantly more food when scramble competition by larger nestlings was prevented

281    seems to support the Hypothesis 1 too, advocating for a key role of parental decisions.

282    Specifically, although the smallest experimental nestling received more food items per

283    hour when separated by the wooden barrier ($0.48 \pm 0.13$; n = 14) than in natural conditions

284    ($0.22 \pm 0.06$ food items per hour; n = 14), this difference was again not significant

285    (estimate $\pm$ se = $0.154 \pm 0.128$; df = 49; t = 1.20; $p$ = 0.24). Our statistical model explained

286    30.1% of total variance, in which the fixed part explained 8.5% (Table 1c). Nevertheless,

287    when sibling competition is excluded from models, the fixed part (i.e. parental decisions)

288    still explains 8.5% of variance.

289    *Survival of nestlings in asynchronous broods*

290    By day 6 post-hatching, a large proportion of experimental nestlings had starved in

291    experimentally asynchronous broods (42.9%; N = 14). Furthermore, 50% of experimental

292    nests were predated before fledgling, so eventually only one experimental nestling

293    successfully fledged (7.1%).

294    **Discussion**

295    In species with asynchronously hatched broods, the smallest nestling obtains less food

296    than their larger nestmates and frequently dies by starvation soon after hatching (Lack

297    1945, 1954; Jeon 2008; Caro et al. 2016). Our results match these previous findings

298    indicating parental favoritism towards larger nestlings. In blackbirds, experimentally

299    introduced smaller nestling received less food than their three larger nestmates (Fig. 1),

300    which usually resulted in the death of the former by starvation. Regarding the main aim

301    of our experimental study, we can state that larger nestlings are not preferentially fed by

302    their parents because of their higher competitive abilities, given that differences in food

303    allocation were maintained in the absence of sibling competition (Fig. 1). The

304    experimental smallest nestling did not receive significantly more food from their parents

305    in the absence of scramble competition than when physical interactions among nestlings

306    were allowed (Fig. 1). Even though a small increase in the food received per hour by the

307    smallest nestling occurs when nestlings are separated by the barrier (Fig. 1), it still

308    receives less food from their parents compared to their lager nestmates. Taken together,

309    our results do not support Hypotheses 2 and 3. However, we have found strong support

310    for Hypothesis 1, which states that food allocation is mainly determined by parental

311    decisions rather than sibling competition. These results imply that, at least in this

312    passerine species with moderate brood reduction, parents have the main control over

313    resources allocation. This could be also the case in other groups such as ardeids, in which

314    brood reduction is much more frequent and larger nestlings even attack smaller ones

315    without parental interference (Mock and Parker 1997). Ploger and Madeiros (2004), in an

316    experiment performed using plastic barriers in the great egret (*Ardea alba*), found that

317    while in natural conditions the largest nestling obtain more food than the other two

318    nestlings in the brood, when nestlings were separated preventing physical interactions,

319    the second nestling in the size hierarchy received more food than the first and the third

320    nestlings. This means that also, in this species, parents may have some control. In our

321    experimental design we have not controlled for nestling position in the nest cup with

322    respect to the feeding parent. However, we are confident that positional effects are

323    irrelevant in our study because barriers and nestlings were placed randomly. Furthermore,

324    several experimental studies in which the relative nestling position was controlled for

325    have found that parents feed their nestlings regardless of their position in the nest (e.g.

326    Kilner 1995, Tanner et al. 2008, Smith et al. 2017).

327        Interestingly, we found differences between sexes in food allocation. In our study,

328    blackbird males provided significantly less food to the smallest nestling regardless the

329    competitive context in which they were maintained (Fig 2a), which means that males do

330    not simply feed the dominant nestling. When physical competition is prevented, males

331    also preferentially feed larger nestlings. Importantly, this implies that nestlings have little

332    or no control over food allocation regarding males' feeding events. On the other hand,

333    females did not provide significantly less food to the smallest nestling in the barrier

334    situation, but instead they evenly distributed the food among nestlings (Fig 2b). These

335    results are similar to those found in the great egret. In their study, Ploger and Madeiros

336    (2004) showed that when nestlings were prevented from aggressive interactions, females,

337    but not males, did not feed preferentially the largest nestling, but the second in the size

338    hierarchy. These results support the broadly confirmed fact that females feed smaller

339    nestlings more than expected according to their size-hierarchy in the brood (see references

340    above), thus exerting the main control over food allocation. These findings have also been

341    found in other species. For instance, in the hoopoe, females, not only can feed

342    preferentially the smallest nestling, usually placed in the worst position (Ryser et al.

343    2016), but can also ignore begging calls from small nestlings while forcing to swallow

344    food to a silent larger nestling (Martin-Vivaldi et al. 1999). Another fascinating example

345    of parents having full control over food allocation occurs in magpie (*Pica pica*) nests,

346    especially when parasitized by the great spotted cuckoo (*Clamator glandarius*).

347    Sometimes, both in parasitized and non-parasitized nests, magpie parents, when no

348    nestling is begging, may induce one of them to beg by waking it up by touching it softly

349    with the beak. But surprisingly, in parasitized nests, magpies may ignore cuckoos that

350    beg for food (begging magpies are never ignored) and instead wake up one of their magpie

351    nestlings (coax feedings (Soler et al. 2017)). In the presence of the wooden barriers, the

352    amount of food provided to the smallest experimental nestling by males is lower

353    compared to larger nestlings; in contrast, females fed the smallest nestling not

354    significantly less than the other larger nestlings. This result is in agreement with the "Male

355    manipulation hypothesis", which predicts that females will provide some food to the

356    smallest nestling to keep it alive to benefit of their intense begging forcing males to work

357    harder (Soler et al. In prep).

358         In conclusion, our findings show that runts do not starve in asynchronous broods

359    as a consequence of being outcompeted by their larger nestlings, but because both parents

360    ignore their intense begging and prefer to feed one of the larger nestlings.

361

368    **Conflict of interest:** The authors have no conflict of interest to declare.

369    **Data accessibility.** All data that support the findings of this study will be available from

370    the Digibug Digital Repository.

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## Tables and figures

**Table 1.** Summary of linear mixed models (LMM) fitted to assess the effect of nestling rank and barrier presence on parental food allocation. Non-significant interactions were not retained in the models. Table shows log-transformed estimates.

| a) Food allocation: general patterns | β (se) | t-value | p-value |
|---|---|---|---|
| *Intercept* | 0.662 (0.072) | 6.142 | 0.000 |
| c-nestling | 0.335 (0.120) | 2.801 | **0.007** |
| b-nestling | 0.638 (0.121) | 5.284 | **< 0.0001** |
| a-nestling | 0.417 (0.121) | 3.456 | **0.001** |
| barrier presence (*yes*) | -0.036 (0.072) | -0.494 | 0.620 |
| | | | |
| *Random effects* | Variance | | |
| Nest ID | 0.206 | | |
| Chick ID *within* Nest ID | 0.181 | | |
| Residual | 0.376 | | |
| $R^2_{LMM(m)} = 0.197$ | | | |
| $R^2_{LMM(c)} = 0.476$ | | | |

| b) Food allocation by males | β (se) | t-value | p-value |
|---|---|---|---|
| *Intercept* | 0.511 (0.102) | 5.030 | 0.000 |
| c-nestling | 0.171 (0.115) | 1.481 | 0.144 |
| b-nestling | 0.520 (0.115) | 4.520 | **< 0.0001** |
| a-nestling | 0.391 (0.115) | 3.392 | **0.001** |
| barrier presence (*yes*) | -0.067 (0.073) | -0.920 | 0.362 |
| | | | |
| *Random effects* | Variance | | |
| Nest ID | 0.182 | | |
| Chick ID *within* Nest ID | 0.144 | | |
| Residual | 0.384 | | |
| $R^2_{LMM(m)} = 0.171$ | | | |
| $R^2_{LMM(c)} = 0.393$ | | | |

| c) Food allocation by females | β (se) | t-value | p-value |
|---|---|---|---|
| *Intercept* | 0.229 (0.090) | 2.552 | 0.014 |
| c-nestling | 0.253 (0.104) | 2.433 | **0.018** |
| b-nestling | 0.638 (0.104) | 2.900 | **0.005** |
| a-nestling | 0.417 (0.104) | 1.200 | 0.235 |
| barrier presence (*yes*) | 0.059 (0.066) | 0.884 | 0.381 |
| | | | |
| *Random effects* | Variance | | |
| Nest ID | 0.148 | | |
| Chick ID *within* Nest ID | 0.126 | | |
| Residual | 0.349 | | |
| $R^2_{LMM(m)} = 0.085$ | | | |
| $R^2_{LMM(c)} = 0.301$ | | | |

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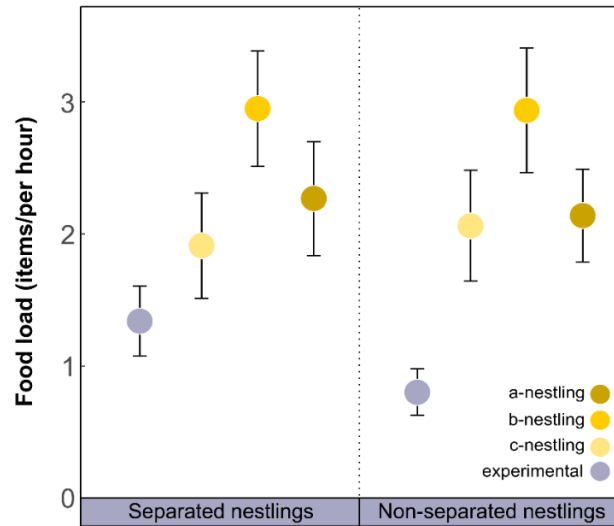


**Figure 1.** Parental food allocation among non-experimental siblings (n = 42; yellow palette) and the smaller experimental nestling (n = 14; grey). Values are presented as means ± se.



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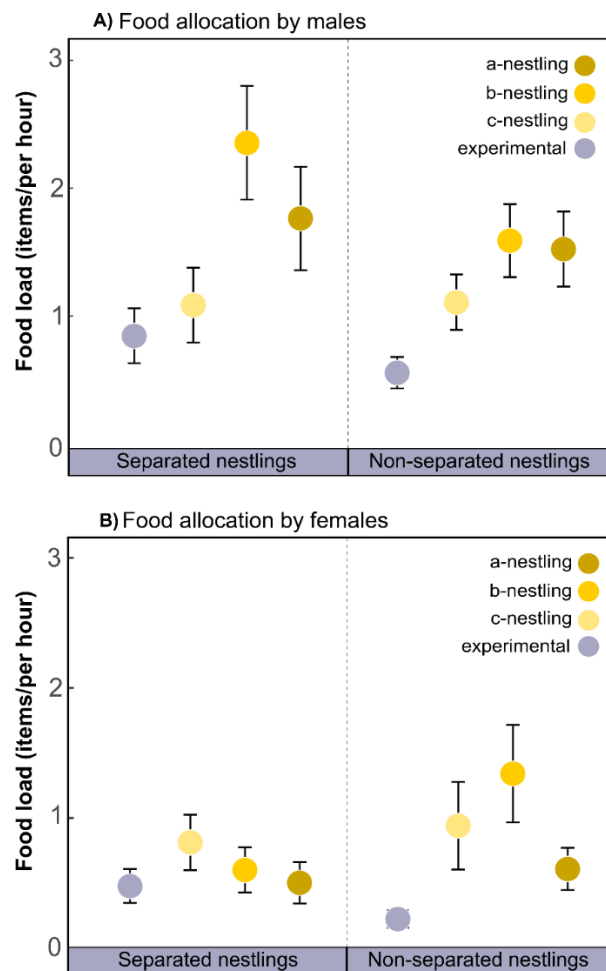
**Figure 2.** Food allocation among non-experimental siblings (n = 42; yellow palette) and the smaller experimental nestling (n = 42; grey) by male (A) and female blackbirds (B). Values are presented as means ± se.