A fixed agreement? Consequences of brood size manipulation on alternation in blue tits

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Recent studies have proposed that conditional cooperation may resolve sexual conflict over the amount of care provided by each parent. Such conditional cooperation may allow parents to equalize their investment by alternating their provisioning visits. This alternated pattern of male and female visits, i.e. alternation, is thought to stimulate each other's investment leading to higher levels of provisioning and potential benefits for offspring development. However, experimental studies testing the role of alternation as an adaptive parental strategy to negotiate the level of investment are still absent. Therefore, we manipulated blue tit (*Cyanistes caeruleus*) parents by temporarily changing their brood sizes to induce changes in demand and thus visit rates. Parents were expected to visit more and alternate at higher levels when confronted with an enlarged brood and thus there will be a greater potential for sexual conflict, assuming that prey sizes were constant. In contrast, in reduced broods visit rates and alternation may become lower due to the smaller investment that is needed for reduced broods. We show that the level of alternation did not differ in response to the manipulated brood sizes, despite a directional change in visit rates for enlarged and reduced broods as expected. Nestlings did not benefit from high levels of alternation as no effects on nestling mass gain were present in either of the different manipulations. These findings indicate that alternation does not serve as a mechanism to motivate each other to feed at higher rates. Parents hence appeared to be inflexible in their level of alternation. We therefore suggest that the level of alternation might reflect a fixed agreement about the relative investment by each of the caring parents.

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40 **ABSTRACT**

41 Recent studies have proposed that conditional cooperation may resolve sexual conflict over the

42 amount of care provided by each parent. Such conditional cooperation may allow parents to

43 equalize their investment by alternating their provisioning visits. This alternated pattern of male

44 and female visits, i.e. alternation, is thought to stimulate each other's investment leading to

45 higher levels of provisioning and potential benefits for offspring development. However,

46 experimental studies testing the role of alternation as an adaptive parental strategy to negotiate

47 the level of investment are still absent. Therefore, we manipulated blue tit (*Cyanistes caeruleus*)

48 parents by temporarily changing their brood sizes to induce changes in demand and thus visit

49 rates. Parents were expected to visit more and alternate at higher levels when confronted with an

50 enlarged brood and thus there will be a greater potential for sexual conflict, assuming that prey

51 sizes were constant. In contrast, in reduced broods visit rates and alternation may become lower

52 due to the smaller investment that is needed for reduced broods. We show that the level of

53 alternation did not differ in response to the manipulated brood sizes, despite a directional change

54 in visit rates for enlarged and reduced broods as expected. Nestlings did not benefit from high

55 levels of alternation as no effects on nestling mass gain were present in either of the different

56 manipulations. These findings indicate that alternation does not serve as a mechanism to

57 motivate each other to feed at higher rates. Parents hence appeared to be inflexible in their level

58 of alternation. We therefore suggest that the level of alternation might reflect a fixed agreement

59 about the relative investment by each of the caring parents.

60

61 **INTRODUCTION**

62 Biparental care is relatively rare among species in the animal kingdom, except among bird

63 species, with more than 81 percent of the species showing this kind of care (Cockburn, 2006). To

64   provide biparental care, two unrelated individuals get together in order to successfully raise their

65   offspring. It secures a joined fitness benefit via improved offspring development and survival,

66   however, both parents have to individually pay for the costs of providing care (Trivers, 1972).

67   Therefore, a conflict is expected between parents about the amount of investment that each

68   should make to their current brood. It is in both parents' interest that their partner provides more

69   care during the breeding attempt so that they themselves can retain energy for self-maintenance

70   and future reproduction (Stearns, 1989). How parents resolve this conflict and how this inflicts

71   their offspring has been given much attention since the formulation of the sexual conflict theory

72   by Trivers (1972). One of the first models hypothesized that each parent could only make a

73   single independent investment so that individual investment could only change on an

74   evolutionary time scale (Houston & Davies, 1985). Whereas more recent models implemented

75   the possibility that parents are able to adjust their investment in response to their partner on a

76   behavioural time scale (Mcnamara, Gasson & Houston, 1999; Johnstone & Hinde, 2006; Lessells

77   & McNamara, 2012), which better captures the natural situation. However, both models predict

78   that parents should invest at suboptimal levels of care, which may reduce offspring fitness but

79   avoids exploitation by the partner (Mcnamara, Gasson & Houston, 1999; McNamara et al., 2003;

80   Johnstone & Hinde, 2006; Lessells & McNamara, 2012; Johnstone et al., 2014). Recently, a

81   more cooperative strategy has been proposed for the resolution of sexual conflict, namely

82   conditional cooperation, which may avoid or reduce such costs of negotiation (Johnstone et al.,

83   2014).

84

85   In humans, conditional cooperation implies that individuals are more likely to contribute to a

86   public good when others are also willing to do so, which may lead to more efficient, higher

87   overall levels of investment (Gächter, 2007; Johnstone et al., 2014). In the context of biparental

88   care, conditional cooperation could be defined as the tendency of a parent to invest more when

89   the partner invests as well. In other words, parents may become more motivated to feed after

90   their partner has fed and therefore will speed up their visit rate. This may result in the pattern of

91   alternated feeding visits, as well as greater and more equal levels of investment (Johnstone et al.,

92   2014). Some recent studies indeed provided empirical support showing that parents alternated

93   their visits more than predicted by chance (great tits *Parus major:* Johnstone et al. 2014; long-

94   tailed tits *Aegithalos caudatus:* Bebbington & Hatchwell, 2016; canaries *Serinus canaria:* Iserbyt

95   et al., 2017; chestnut-crowned babblers *Pomatostomus ruficeps:* Savage et al., 2017) and that

96   higher total visit rates relate to higher levels of alternation (Bebbington & Hatchwell, 2016).

97   Consequently, this raises the question whether higher levels of alternation also benefit offspring

98   development. Evidence is still limited and confined to unmanipulated conditions, while further

99   experimental studies are needed to answer the questions whether alternation forms a parental

100   strategy to negotiate about investment and how this affects the offspring (e.g. Iserbyt et al.,

101   2019).

102

103   The aim of the study was therefore to test whether the pattern of alternated male and female

104   provisioning visits is maintained when the nest conditions change, and whether higher levels of

105   alternation benefit the offspring. To this end, we performed a temporary brood size manipulation

106   experiment in blue tit (*Cyanistes caeruleus*) parents in which brood size was either increased or

107   decreased (Parejo & Danchin, 2006; García-Navas & Sanz, 2010). Previous studies have shown

108   that brood size manipulations affect parental visit rates (see review in Gow and Wiebe 2014).

109   When brood size is increased, parents are expected to increase their provisioning rate to meet the

110 elevated brood demand, resulting in higher investment costs to both parents. Such elevated

111 demand may therefore intensify the sexual conflict, which may be ameliorated via conditional

112 cooperation through increasing individual costs of parents. When alternation improves between

113 pair members, the likelihood of exploitation may be reduced because parents motivate each other

114 to visit at higher rates. Thus alternation and visit rates are expected to rise in the situation that

115 brood size is increased, assuming that prey size remains constant. When brood size is decreased,

116 parents will likely reduce their alternation level and visit rate because of the lower sexual conflict

117 over parental care. Finally, when alternation represents a form of conditional cooperation, in

118 which parents enhance each other's willingness to invest and increase their visit rates

119 accordingly, then it should benefit the offspring. However, the offspring can only benefit from a

120 high alternation when the profitability of the delivered prey items remain unaltered. If parents

121 cheat in delivered prey sizes, then parents cannot rely on their partners' visit rate as an honest

122 signal of parental investment.

123

MATERIALS & METHODS
124

125 *Study species and measurements*

126 The experiment was conducted in a nest-box population of blue tits near Antwerp, Belgium

127 (Peerdsbos 51^0 16' N, 4^0 29'E) from April-May 2016. Nest boxes (n = 131) were checked twice

128 per week for nest building, egg laying and incubation. Nests were monitored daily for hatching

129 from the expected hatch date onwards. The first day of hatching was defined as day 0. Parents

130 were caught on day 6 for individual measurements and were given a plastic leg band with an

131 integrated PIT tag (which is a standard procedure in our field site and aids the individual

132 recognition by placing the PIT tag on different sides for the individuals of a pair) (Iserbyt et al.,

133 2018). Nestlings were given a unique metal ring on day 6 to allow individual recognition.

134

135   *Brood size manipulation*

136   Each nest was subjected to a control (original brood size), reduced (minus three nestlings) and

137   enlarged (plus three nestlings) treatment each on a separate day, i.e. post hatching day 8, 9, 10

138   (Parejo & Danchin, 2006; García-Navas & Sanz, 2010). This design was chosen to control for

139   potential confounding effects of brood age and date. The specific observation period was

140   selected to make sure that females do not brood the young anymore (females brood nestlings 6-7

141   days when hatched (Perrins, 1979)), given confounding effects of task specialization on

142   alternation (Iserbyt et al., 2017). The three nests that were chosen for the triad structure were

143   matched for hatching date (no difference allowed), mean nestling mass (maximum difference of

144   1.5 gram) and brood size (maximum difference of 2 nestlings) on day 7. When only two nests

145   were available on the same hatch date, dyads were made considering the same selection criteria

146   for brood size and mean nestling mass. Nests with less than 7 nestlings were not used for this

147   experiment.

148

149   Each treatment was set up in the morning and terminated in the late afternoon (8AM-6PM). At

150   the start of the experiment, an infrared nest-box camera (420TVL; Pakatak PAK-MIR5, Essex,

151   UK) was placed facing downwards to the nest to record parental nest visits and prey sizes

152   (Lucass et al., 2015). Furthermore, all nestlings were weighed individually in the morning at the

153   start of the brood size manipulations. The three nestlings that were used for swapping between

154   nests belonged to the intermediate positions within the weight hierarchy and did not differ more

155   than 1 gram relative to the other selected nestlings from the other nests in the triad. Those three

156   nestlings were taken from the nest that got the reduced treatment and were transported to the

157   enlarged treatment nest in a cloth bag. In the late afternoon when the brood size manipulation

158   was terminated, all nestlings were weighed again and nestlings were returned to their original

159   nest.

160

161   *Statistical analyses*

162   Parental nest visits and prey sizes were scored from the recordings during the afternoon (starting

163   at 4PM), to allow the parents to adjust to their new brood size that was manipulated in the

164   morning. We performed a pilot analysis, in order to determine the minimum number of visits that

165   are required to provide a reliable visit rate estimate. This analysis was based on 8 control videos

166   and showed that the average visit rate remained fairly consistent beyond 10 visits. More

167   specifically, doubling the number of visits from 10 to 20 visits provided very similar visit rates

168   (Pearson correlation: r = 0.84; P < 0.001). Therefore, the videos were analysed until each sex had

169   at least 10 visits or the analysis was terminated after two hours when still one of the parents had

170   not visited for 10 times. The mean time window for an analysed video recording until a parent

171   had a minimum of 10 visits, was 51.5 ± 3.5 minutes (mean ± SE, n = 55), which is likely to

172   provide accurate estimates for individual visit rates (Pagani-Núñez & Senar, 2013; Lendvai et al.,

173   2015). The size of the bird beak was used as a reference to estimate prey size: 1 = small (< 1

174   beak length), 2 = medium (1 - 3 beak lengths), 3 = large (> 3 beak lengths) (*sensu* Kolliker et al.,

175   1998; Lucass et al., 2015). All videos were analysed by M. Griffioen using the ObserverXT

176   program (version 10.5.572, 2011, Noldus Information Technology, The Netherlands). Males and

177   females were distinguished by their PIT tag (different sides or colour) or by their head pattern

178   (males have dark stripes on their head which are visible on the infra-red images due to the grey

179   scale of the videos). Only nests at which both parents visited were used in the analyses because

180   we are interested in the cooperation of the parents (n = 21 out of 23). Due to failures of video

181   recordings we obtained 18 observations of control situations, 17 of reduced and 20 of enlarged.

182   Field work was carried out under the license from the Ethical Committee for animals (ECD) of

183   the University of Antwerp (license number: 2015-85).

184

185   Visit rate was calculated as visits per hour for each parent separately from the video recordings.

186   The alternation was calculated as a pair score via F / (t − 1) with F being the number of visits

187   that were alternated and t the total number of visits (as in Bebbington & Hatchwell, 2016). The

188   proportions of prey sizes (small, medium and large) were calculated separately per treatment for

189   each parent. Mixed effect models were used to analyse how the different parental provisioning

190   estimates varied with our brood size manipulation. The first model (linear mixed model with

191   Gaussian distribution) investigated whether variation in parental visit rate (log transformed)

192   could be explained by experimental treatment (control / reduced / enlarged), sex and the

193   interaction between treatment and sex. Brood age was included as a covariate. Parent ID nested

194   in nest ID was included as random effect to avoid pseudo-replication. The second model

195   (generalized mixed model with binomial distribution) analysed the effect of treatment on

196   parental alternation. Treatment was included as fixed factor and brood age as a covariate. Only

197   nest ID was included as a random factor because alternation is measured here as a couple

198   parameter. To further explore the effects of alternation we investigated whether visit rate

199   increased with a higher level of alternation (see Johnstone et al. 2014; Bebbington and Hatchwell

200   2016, but see Iserbyt et al. 2017). A linear mixed model (Gaussian distribution) was used in

201   which variation in the sum of male and female visit rates (total provisioning, log transformed)

202   was explained by alternation score, treatment and their interaction. Nest ID was added to the

203   model as random effect. The fourth and fifth model (generalized mixed models with binomial

204   distribution) investigated the effect of the brood size manipulation on prey sizes. The fraction of

205   small and medium prey sizes were used as dependent variables in these models. Treatment, sex

206   and the interaction between treatment and sex were used as fixed factors and brood age as

207   covariate. The random factor was parent ID nested in nest ID. The large-sized prey were not

208   analysed because the proportions were too low and zero-inflated. To investigate whether and

209   how alternation affects offspring growth, a linear mixed model (Gaussian distribution) was fitted

210   with the change in nestling mass as response variable. Nestling mass was taken each day at the

211   start and the end of the brood size manipulation, resulting in a mean weight gain for each nest

212   (only resident nestlings). These weight gains were corrected for the variation in time period

213   between both measurements so we acquired an average nestling mass gain per hour for each nest.

214   The total provisiong, alternation scores, treatment and the interaction between treatment and

215   alternation were included in the model as a fixed effects and brood age as covariate. One outlier

216   in mass gain was removed from the analyses to get the model residuals normally distributed.

217   All mixed models were run using the package lme4 (Bates et al., 2015) and lmerTest

218   (Kuznetsova, Brockhoff & Christensen, 2017) in R studio (version 1.1.423 and R version 3.4.3,

219   R core team, 2017). To investigate the significance of the fixed factors we performed backward

220   stepwise elimination with a critical α level of 0.05. In two models the response variables 'visit

221   rate' and 'total provisioning' were log transformed to meet the normality of assumption of the

222   model residuals, tested with a Shapiro normality test and visual inspection of the residuals.

223

224   **RESULTS**

225   *Parental feeding rates*

226 There was no significant interaction effect between treatment and sex on parental visit rates ($F_{2,}$

227 $_{69.5} = 0.30$, P = 0.739; figure 1). Parents changed their visit rate according to experimentally

228 manipulated brood sizes ($F_{2,70.3} = 18.7$, P <0.0001). Specifically, parents decreased their visit rate

229 from control (unmanipulated) to reduced brood sizes (differences of LSmeans: t = 2.73, df =

230 68.9, P = 0.008), and increased from control to enlarged brood sizes (differences of LSmeans: t =

231 -3.22, df = 67.5, P = 0.002). Furthermore, females had an overall lower visit rate than males

232 ($F_{1,20.4} = 9.75$, P = 0.005; figure 1). Brood age also had a significant effect ($F_{2,70.2} = 5.72$, P =

233 0.005). The visit rate was higher when nestlings were 8 days old when compared to 9 days old

234 nestlings (differences of LSmeans: t = 3.34, df = 69.5, P = 0.0014) but not with 10 day old

235 nestlings (differences of LSmeans: t = 1.60, df = 69.0, P = 0.113).

236

237 *Parental alternation*

238 The alternation of feeding visits did not change as a function of our brood size manipulation (χ^2

239 = 1.15, df = 2, P = 0.564; see figure 2). Brood age also did not significantly affect alternation (χ^2

240 = 4.68, df = 2, P = 0.096). The analyses of the model with total parental visit rates revealed no

241 interaction effect of treatment with alternation ($F_{2,38.7} = 0.192$, P = 0.826; see figure 3) and as

242 well no overall relationship with alternation scores ($F_{1,48.7} = 0.027$, P = 0.870) or brood age

243 ($F_{2,34.1} = 3.07$, P = 0.059).

244

245 *Prey sizes*

246 The effect of the brood size manipulation on the proportion of the small prey size did not differ

247 between the sexes ($\chi^2 = 3.65$, df = 2, P = 0.161; see figure 4). However, the brood size

248 manipulation had a significant effect (treatment $\chi^2 = 8.54$, df = 2, P = 0.014) with birds bringing

249 a higher proportion of small prey items in the control treatment when compared to the enlarged

250 treatment (post hoc Tukey: enlarged - control Z = -2.91, P = 0.010), whilst there was no

251 difference in proportion of small prey items when control was compared to the reduced treatment

252 (post hoc Tukey: reduced – control Z = -1.47, P = 0.304). Overall males brought more small prey

253 items than females (post hoc Tukey: Z = 2.73, P = 0.006). Brood age did not affect the

254 proportion of small prey brought to the nest (χ^2 = 4.39, df = 2, P = 0.116).

255

256 The analyses of the proportion of medium prey sizes revealed similar effects. There was no

257 significant interaction effect of treatment and sex (χ^2 = 0.78, df = 2, P = 0.677). Brood size

258 manipulation hada significant effect on the proportion of medium prey (treatment: χ^2 = 7.43, df =

259 2, P = 0.024), with the proportion of medium prey sizes being higher in the enlarged than in the

260 control brood sizes and no change between the control and reduced (post hoc Tukey: enlarged –

261 control Z = 2.64, P = 0.023; reduced – control Z = 0.74, P = 0.737). There was a significant sex

262 effect, females brought more medium prey items compared to males (sex: χ^2 = 3.97, df = 2, P =

263 0.046; see figure 4). Brood age did not affect the proportion of medium prey items (χ^2 = 1.72, df

264 = 2, P = 0.422).

265

266 *Offspring mass gain*

267 There was no significant overall effect of alternation ($F_{1,45.3}$ = 0.135, P = 0.715), treatment ($F_{2,35.2}$

268 = 2.53, P = 0.094), total provisioning ($F_{1,46.1}$ = 0.05, P = 0.823) and brood age ($F_{1,33.9}$ = 0.0003, P

269 = 0.989) on nestling mass gain. Neither did the effect of alternation on the mass gain of nestlings

270 differ between treatments ($F_{2,43.2}$ = 1.66, P = 0.202; see figure 5).

271

272   **DISCUSSION**

273   Our study shows that blue tit parents adjust their visit rates in response to experimentally

274   manipulated brood sizes. Couples nevertheless maintained similar levels of cooperation as their

275   alternation of feeding visits did not change in function of the brood size manipulations. We

276   discuss the implications of our results for the resolution of parental conflict and conditional

277   cooperation theory, as well as the functional consequences for offspring development.

278

279   *Effects of brood size manipulation*

280   We hypothesized that parents when faced with extra nestlings have to increase their visit rates to

281   meet the enhanced offspring demand, which likely reinforces sexual conflict over parental care.

282   Parents may negotiate and resolve this conflict by increasing the level of alternated visits,

283   because conditional cooperation and therewith alternation should enhance each other's

284   willingness to invest (Johnstone et al. 2014). The blue tit parents in our study indeed increased

285   their visit rates when confronted with three extra nestling, which is in line with observations in

286   several other species (house wrens: Bowers et al., 2014; great tits: Hinde & Kilner, 2007; blue

287   tits: Nur, 1984; Parejo & Danchin, 2006; García-Navas & Sanz, 2010). However, we did not

288   observe an increase of the alternation levels. Therefore, the extra investment and thus the

289   probably reinforced conflict seems not to be mediated by alternation. Furthermore, parents

290   additionally increased their investment when confronted with extra nestlings by increasing the

291   number of medium-sized prey while lowering the proportion of small prey items. This contrasts

292   previous studies that bringing smaller prey items could possibly minimize the search time for

293   prey facilitating an increase of visit rates (Nour et al., 1998; Grieco, 2002). However, both sexes

294   show the same pattern in prey size which makes it unlikely that parents cheat in their investment

295   via prey sizes. Yet, females brought overall more medium-sized prey items than males

296   suggesting a sexual difference in investment. However, this difference is likely mitigated by the

297   lower visit rates of females, relative to males.

298

299   For the reduced nests we hypothesized that parents would decrease their alternation due to lower

300   conflict about investment caused by lower brood demand. Indeed, the blue tit parents in our

301   study did lower their visit rates as predicted. However, again their alternation level was not

302   changed. Furthermore, prey sizes were not altered in the reduced manipulations by the parents.

303   When brood demand and consequently visit rate is reduced, more time becomes available as

304   potential search time for big profitable prey (Nour et al., 1998; Grieco, 2002). However, both

305   males and females did not elevate the small or medium prey sizes. The prey size that they

306   brought to the nest might have been optimal in terms of foraging efficiency which is determined

307   by the search time and energetic value of the prey (Naef-Daenzer & Keller, 1999; Naef-Daenzer,

308   Naef-Daenzer & Nager, 2000).

309

310   A meta-analysis revealed that partial compensation is the general parental response in mate

311   handicapping or mate removal studies (Harrison et al., 2009). However, manipulation of one or

312   both parents can also result in no response (e.g. Schwagmeyer, Mock & Parker, 2002; Santema et

313   al., 2017) and even a matching response (Hinde, 2006; Meade et al., 2011). Such variation in

314   parental responses may in part stem from multitude of applied methods and may even be observed

315   within the same study. For example in the same blue tit population which is used here, a sex-

316   specific partial compensation was observed in response to a temporal mate removal experiment,

317   but a clear matched response followed upon the reunion of the pair (Iserbyt et al., 2019).

318   Interestingly, we here found that male and female parents responded in similar, matched ways to

319   the brood size manipulation (García-Navas & Sanz, 2010), which allows limited fluctuations in

320   within-pair alternation levels (see further, Bebbington & Hatchwell, 2016).

321

322

323   *Effects on offspring development*

324   If alternation represents a form of conditional cooperation, in which parents enhance each other's

325   willingness to invest, it should benefit the offspring development. Here, we did not find a

326   relationship between total provisioning and alternation which suggests that there is no positive

327   effect for nestlings (see also Iserbyt et al. 2017, but see Bebbington and Hatchwell 2016).

328   Consequently, there was no evidence that higher levels of alternation resulted in increased

329   nestling mass gain. However, the duration of the manipulation might have been too short to

330   detect any differences in mass gain. Unfortunately, studies investigating the effects of

331   conditional cooperation on offspring development are still limited and thus far have shown

332   contradicting results (benefit: increased brood success, Bebbington and Hatchwell 2016; no

333   effect: offspring development and physiological state; Bebbington and Hatchwell 2016; Iserbyt

334   et al. 2017). That renders it difficult to draw definite conclusions about the adaptive significance

335   and fitness consequences of alternation. We suggest that future research should not only

336   incorporate measures of offspring development, but also estimates of parental fitness. In

337   particular since conditional cooperation should be costly for the caring parents, or at least for the

338   parent with the lowest physiological condition.

339
340   **CONCLUSIONS**

341   Alternation of parental nest visits is thought to be the outcome of a behavioural mechanism in

342   which both parents co-adjust their visit rates, thereby avoiding exploitation by their partner

343   (Johnstone et al. 2014). However, in our study we did not find such evidence that alternation and

344   visit rates (total visit rates) were related (Iserbyt et al. 2017, but see Bebbington and Hatchwell

345   2016). Furthermore, alternation remained rather constant regardless of experimentally induced

346   changes in parental visit rates. Consequently, parents might have had a fixed agreement about the

347   level of alternation (Iserbyt et al. 2019). They might use this to control for any free riding of their

348   partner and it might have already been established during earlier phases of the reproductive

349   cycle. Thus independent of the environmental conditions and brood demand, the proportion of

350   alternated visits should be kept relatively constant within pairs. This, however, does not

351   necessarily require that all visits should be alternated, especially when it might be costly to

352   monitor each other. A specific fraction of monitoring the partner's feeding behaviour might

353   provide a sufficient estimate of its investment and could serve as a signal to avoid substantial

354   exploitation. This might imply that the level of alternation should thus mainly vary among but

355   not within couples. The variation in alternation among couples could relate to quality differences

356   between parents or the compatibility of pairs (see e.g. Ihle, Kempenaers & Forstmeier, 2015).

357   However, this remains as yet speculative as we do not know if and when such an agreement is

358   established. In this context, further research needs to specifically consider how differences in

359   quality of parents within a pair affect the alternation levels, as they have the potential to lower

360   the levels of care towards the parent of lower quality. Furthermore, environmental factors that

361   can shape the distribution of provisioning visits via prey abundance and patchy distributions in

362   the pairs' environment should be investigated to understand the role of environmental effects on

363   alternation.

364

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370

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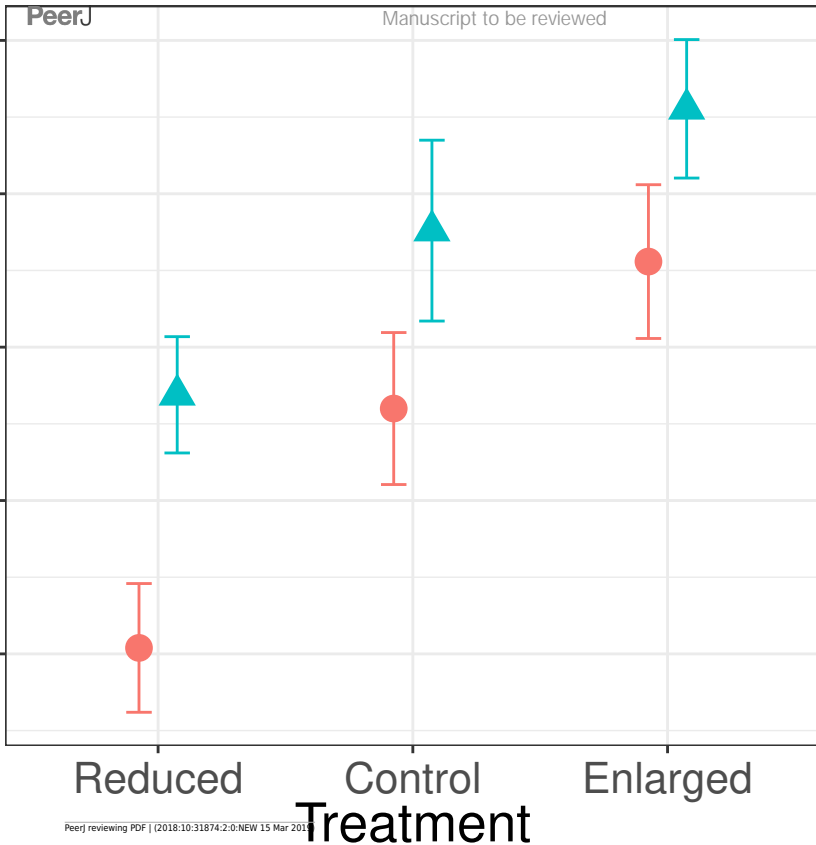
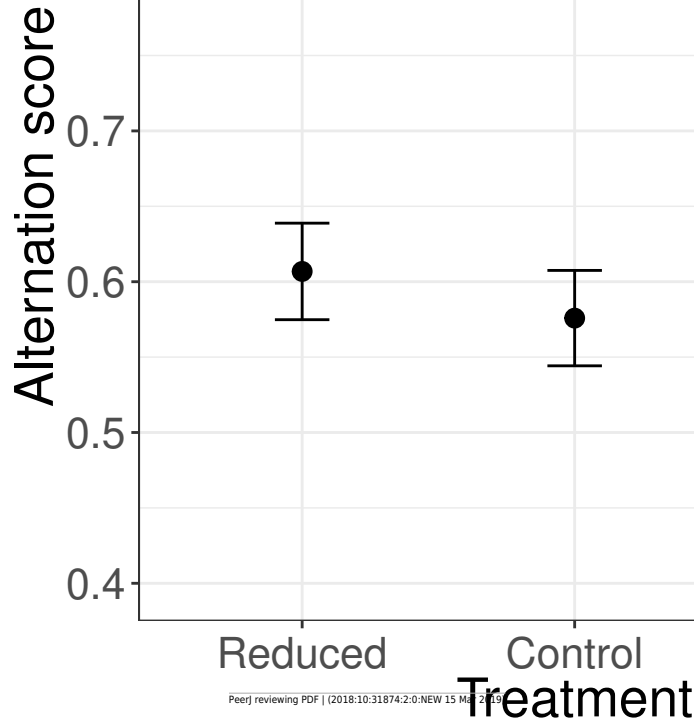
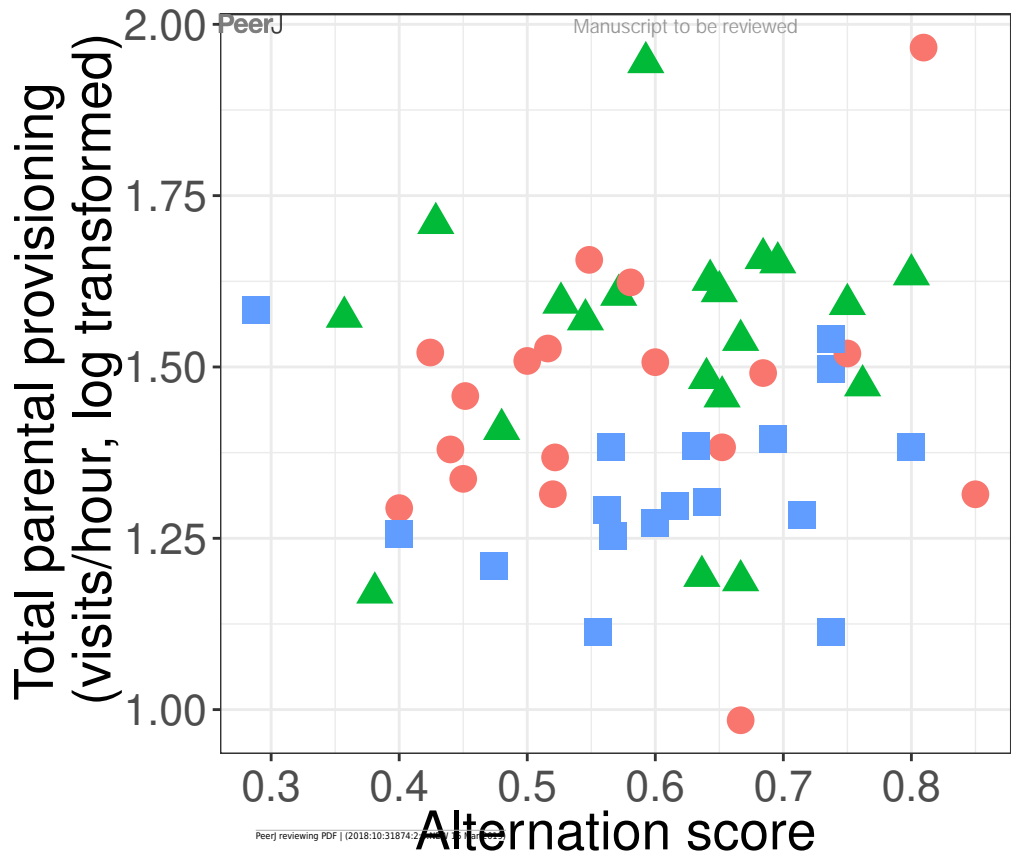
Parental feeding rates (visits / hour, log transformed) for each treatment (reduced (n = 17), control (n = 18), and enlarged (n = 20) brood size) and sex (blue triangles: males, red circles: females).

Symbols represent means ± SE.

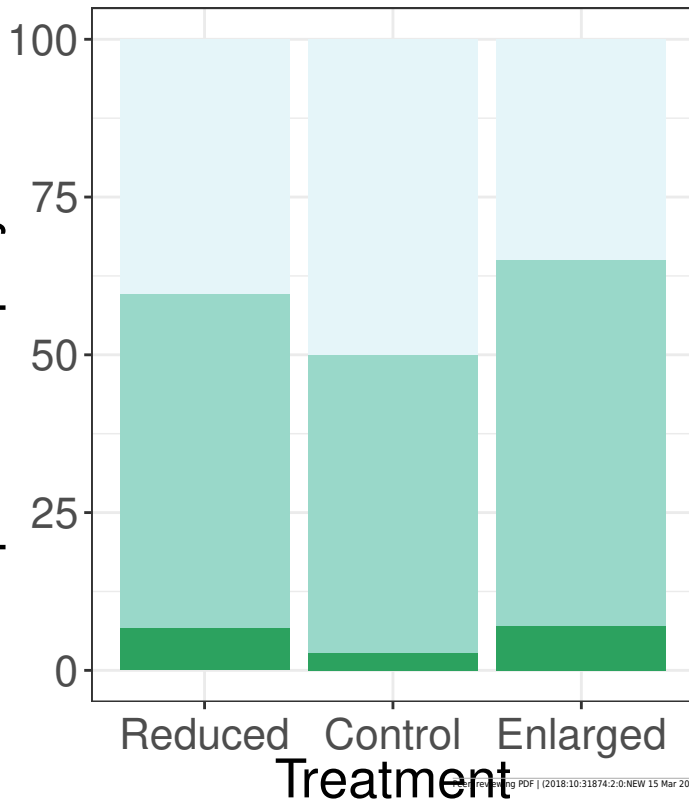
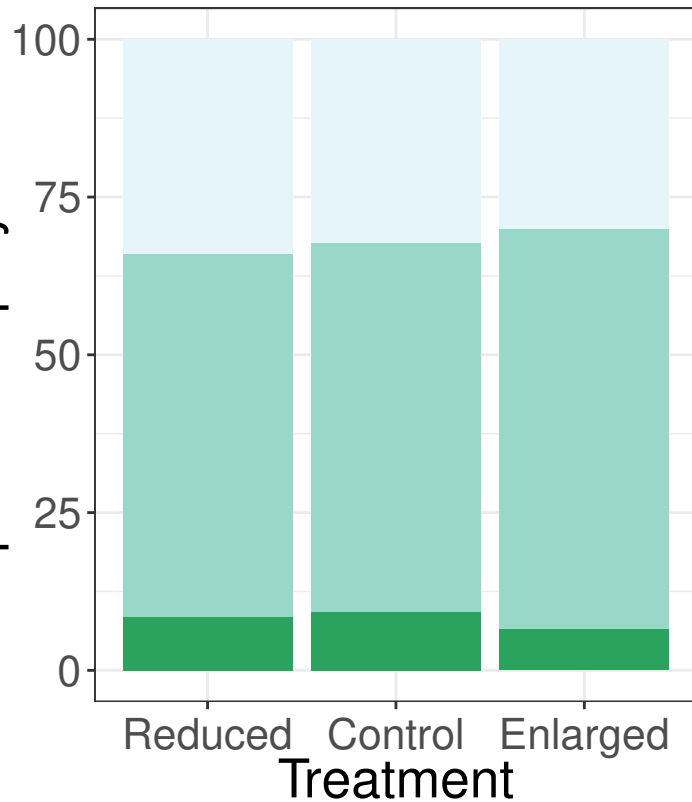
The alternation levels (number of alternated visits / total number of visits - 1) for each of the treatments (reduced n = 17, control n = 18, enlarged n = 20).

Symbols represent means ± SE.

Total parental provisioning rates (visits / hour, log transformed) per nest in relation to alternation score (number of alternated visits / total number of visits - 1).

The symbols indicate the different treatments (red circle: control brood size (n = 18), green triangles: enlarged (n = 20), and blue squares: reduced (n = 17)).

The proportions of prey sizes of (A) males and (B) females for the different treatments (reduced (n = 17), control (n = 18), and enlarged (n = 20) brood size).

The dark green bars (lowest bars) indicate the proportions of large prey items, medium green (middle bars) the proportions of medium-sized prey and the light green (top bars) the proportions of small prey. Symbols represent means ± SE.

A) Males

B) Females

Mass gain of the nestlings (gram per hour) and alternation level of their parents.

Alternation was calculated as number of visits alternated divided by total number of visits minus one. The symbols represent the reduced (blue squares; n = 16 (one outlier removed, see statistical analyses)), control (red circles; n = 18) and enlarged (green triangles; n = 20) treatment.