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Article:

Bebbington, K. and Hatchwell, B.J. (2016) Coordinated parental provisioning is related to feeding rate and reproductive success in a songbird. *Behavioral Ecology*, 27 (2). pp. 652-659. ISSN: 1045-2249

<https://doi.org/10.1093/beheco/arv198>

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1 **Coordination of parental provisioning behavior is associated with enhanced food delivery**
2 **rate and increased reproductive success in a passerine bird**

3 **Short title: Parental coordination of provisioning behavior**

4

5 **Abstract**

6 In species with biparental care, there is sexual conflict over parental investment because each
7 parent benefits when their partner bears more of the reproductive costs. Such conflict can be
8 costly for offspring, but recent theoretical work predicts that parents can resolve sexual conflict
9 through behavioral negotiation, specifically by alternating their trips to provision nestlings.
10 However, this idea has received almost no empirical attention. In this study, we test the
11 hypothesis that parents alternate their delivery of food to offspring in long-tailed tits (*Aegithalos*
12 *caudatus*) and investigate whether this coordination of parental care is associated with greater
13 reproductive success. We show that parents alternate provisioning trips more than would be
14 expected by chance and that parental alternation is repeatable across multiple observation periods
15 at a nest. More alternation is associated with increased visit synchrony and increased food
16 delivery to nestlings. Moreover, we found that nests with more alternation were less likely to be
17 predated, probably resulting from reduced activity around the nest when parents coordinate their
18 provisioning behavior. Our results support the hypothesis that alternation of offspring
19 provisioning is a behavioral adaptation to reduce the costs of sexual conflict.

20

21 **Lay summary**

22 Taking it in turns to provide parental care is beneficial for bird parents and chicks. Long-tailed tit
23 parents that alternate their visits to feed chicks more provision their nestlings at a higher total
24 feeding rate and the chicks are less likely to be depredated. Parents who take turns also tend to

25 arrive at the nest together, which may simultaneously allow them to keep an eye on each other's
26 efforts and reduce predation risk.

27

28 **Keywords**

29 parental care; parental investment; behavioral negotiation; sexual conflict; long-tailed tit

30 **Introduction**

31 In most vertebrates, especially birds and mammals, parents must provide some form of parental
32 care for the successful production of offspring (Clutton-Brock 1991). However, parental care is
33 costly and has been linked to reduced lifespan and future reproductive output (Stearns 1992).
34 Therefore, a parent should invest according to the optimal trade-off between the benefits of caring
35 for current offspring and the costs of that investment for future reproduction (Williams 1966). In
36 species with biparental care, an individual's optimal parental investment also depends on the
37 amount that its partner invests in the joint offspring. The shared benefits of offspring fitness
38 means that each parent should prefer to invest less in the current offspring while its partner
39 invests more. Thus, there is conflict between the parents over investment (Trivers 1972), which
40 may in turn be costly to offspring (Parker 1985; McNamara et al. 2003).

41 Various theoretical models have sought to explain how stable systems of biparental care can
42 evolve despite parental conflict over care. Early evolutionary models like that of Houston and
43 Davies (1985) considered parental investment as a fixed trait that could change over evolutionary
44 time. These models have gradually been succeeded by more biologically realistic 'negotiation'
45 models (McNamara et al. 1999; 2003; Johnstone and Hinde 2006; Johnstone 2011; Lessells and
46 McNamara 2012) that accommodate the possibility of parents behaviorally negotiating their
47 relative investment. Negotiation models predict that partial compensation, where one parent
48 partially increases effort in response to a decrease by its partner, facilitates stable biparental care
49 and prevents exploitation by either parent.

50 The predictions of negotiation models have been empirically tested many times, especially in
51 birds where biparental care is the norm (Cockburn 2006). A meta-analysis of experimental studies
52 shows that, in general, parents do compensate incompletely for changes in care by their partners
53 (reviewed in Harrison et al. 2009), as predicted by negotiation models. However, this effect is not
54 universal across species: some studies find complete compensation for a change in partner effort

55 (Mrowka 1982; Paredes et al. 2005), while others show no response (Slagsvold and Lifjeld
56 1988; Schwagmeyer et al. 2002) or even a matching of effort between parents (Hinde 2006;
57 Meade et al. 2011). Hinde and Kilner (2007) suggested that this variation across species could
58 be a function of the mechanisms through which negotiation operates. If parents are to
59 behaviorally respond to each other's effort, they must somehow integrate information about the
60 investment of their partner. This may be achieved indirectly (for example from nestling
61 condition or begging signals (Lessells and McNamara 2012)) or directly from their partner's
62 behavior (Dall et al. 2004). In the latter case, observation of a partner's nestling provisioning
63 frequency may provide a relatively simple way to monitor the investment of that individual.
64 Despite its potential importance for testing negotiation models, the mechanisms of how
65 negotiation would operate have received surprisingly little empirical attention.

66 Negotiation models also predict that each parent is forced to reduce its own investment below
67 the level at which offspring fitness would be maximized (McNamara et al. 1999; 2003; Houston
68 et al. 2005; Lessells and McNamara 2012). If so, offspring will suffer a fitness cost from
69 parental conflict; a prediction borne out by empirical studies (Royle et al. 2002; 2010).
70 However, Johnstone et al. (2014) have recently argued that this conflict and its potential cost
71 may be reduced through a process referred to as 'conditional cooperation' (Keser and van
72 Winden 2000; Gächter 2007); a tit-for-tat style alternation of provisioning where individuals
73 withhold provisioning until the partner has provisioned. Johnstone et al.'s (2014) model predicts
74 that alternation of provisioning trips results in greater total parental investment and an optimal
75 provisioning rate that maximizes both parents' fitness. The authors tested their model using data
76 on great tits *Parus major* and found empirical evidence for rates of alternation of provisioning
77 trips in that species that were greater than expected by chance (Johnstone et al. 2014). However,
78 whether alternation actually mitigates sexual conflict and improves reproductive success in wild
79 systems, thus functioning as an evolutionary mechanism for maintaining biparental care, was
80 not tested and remains unclear.

81 | In practice, alternation of parental provisioning may also require that male and female [nest](#) visits
82 | are synchronised so that each parent can directly monitor their partner's investment. This type
83 | of nest visit coordination has received far more attention than alternation, with studies focusing
84 | on three principal functions for synchronised provisioning behaviour. First, if provisioning has a
85 | signalling function (Kokko et al. 2002), then it may pay to synchronise visits with other carers
86 | at the same nest or nearby nests (e.g. Doutrelant & Covas 2007; but see McDonald et al.
87 | 2008a,b). Second, synchronised provisioning may function to reduce predation risk for carers or
88 | for broods by reducing nest conspicuousness (e.g. Martin et al. 2000; Raihani et al. 2010).
89 | Finally, synchronous nest visits may serve a similar function to that proposed for alternation, by
90 | facilitating efficient provisioning of broods (Shen et al. 2010) and thereby enhancing
91 | reproductive success (Mariette & Griffith 2012, 2014).

92 | In this study, we [test for the active](#) alternation of provisioning visits by parents in socially
93 | monogamous long-tailed tit *Aegithalos caudatus* pairs and subsequently test the relationship
94 | between alternation, synchrony and reproductive success. [We first pool provisioning data from](#)
95 | [across breeding pairs to establish whether, across the population as a whole, active alternation of](#)
96 | [provisioning trips occurs. Subsequently we use between-pair variation in observed alternation to](#)
97 | [explore the correlates and predictors of this behaviour.](#) Previous experimental investigation of
98 | parental investment in the long-tailed tit has shown that parents match experimental changes in
99 | their partner's provisioning rate (Meade et al. 2011), suggesting that individuals monitor and
100 | coordinate their partner's efforts with their own. Since long-tailed tit adults may forage 100m or
101 | more from the nest (Gaston 1973; BJH unpublished observations), active alternation of
102 | provisioning trips is only possible if parents are able to observe each other entering the nest –
103 | possibly by ensuring that nest visits occur synchronously, or close together. We test three
104 | hypotheses: (i) parents alternate provisioning trips with those of their partner; (ii) alternation
105 | confers fitness benefits for parents and their offspring and (iii) alternation is achieved through

106 synchronous arrival at the nest, allowing each parent to observe the provisioning behavior of its
107 partner.

108

109 **Methods**

110 *Study system*

111 This study was based on a long-term data set from a population of between 25 and 72 pairs of
112 long-tailed tits in the Rivelin Valley, Sheffield, UK (53° 23' N, 1° 34' W). Each year, at least
113 95% of all adults in the population are individually recognizable from unique color ring
114 combinations. Nestlings are ringed when 11 days old and any unringed adult birds are caught in
115 mist nets and color ringed (under British Trust for Ornithology licence). Breeding pairs are
116 identified in early spring, nests are found during nest-building and are then monitored until
117 fledging or failure. Typical clutch size is 10 eggs, which are incubated for around 15 days;
118 hatching is synchronous and nestlings usually fledge aged 16-17 days old. Nests with nestlings
119 are typically observed for 1 hour (mean \pm SD = 52 \pm 0.25 minutes; range = 30-120 minutes) on
120 alternate days from day two of the nestling period (hatch day = day 0) until failure or fledging;
121 the identity of each provisioning parent and the time of each visit is recorded in minutes (for
122 further details on provisioning observations, see MacColl and Hatchwell (2003a)).

123 In this paper, we use provisioning observations of breeding pairs recorded in 2000-2007 and
124 2010-2011. Although approximately half of breeding pairs with nestlings have helpers at the nest
125 who provision the offspring (Hatchwell et al. 2004), we restrict our analyses to nests without
126 helpers. We also excluded any observation periods where adult provisioning rates were
127 experimentally manipulated for other behavioral studies (e.g. Meade et al. 2011). Brooding of
128 young nestlings by females reduces female nestling provisioning rates (MacColl and Hatchwell
129 2003b), so we only included observations that took place after females had ceased brooding (i.e.

130 after day 5 of the nestling stage). Therefore, whilst nests are typically watched every two days
131 from hatching to fledgling, the number of watches per nest used in our analyses is reduced by
132 these constraints, as well as by nest failure and poor weather conditions. The final dataset after
133 these exclusions included 248 nest watches at 98 nests, with an average of 2.5 watches per nest.

134 *Calculating alternation of provisioning visits*

135 For each nest watch, we calculated observed alternation, A , as $A = F / (t-1)$, where F is the
136 number of times a bird fed after the other and t is the total number of feeds in the observation.
137 Repeatability of alternation at a nest was determined by regressing two alternation values from
138 nests where two or more watches were conducted ($n = 54$ nests, mean number of watches = 4).
139 Where three or more watches were conducted, we randomly selected which alternation values
140 were regressed using a random number generator.

141 A certain amount of alternation will occur by chance as a function of the similarity between
142 parents' provisioning rates and also the interval ([henceforth "inter-feed interval"](#)) between
143 successive feeds by each parent. For example, in the case of provisioning rates, only parents
144 feeding at the same rate can have 100% alternation, and this metric must decrease as the
145 difference between provisioning rates increases. Furthermore, the inter-feed interval must
146 inevitably decline as provisioning rate increases. To determine whether individuals alternate
147 feeding more than expected by chance, we calculated expected alternation using a bootstrapping
148 procedure based on these two factors.

149 We first extracted all observed inter-feed intervals of individuals provisioning at rates between 7
150 and 19 feeds per hour. In our observed data, provisioning rates below and above these values were
151 rare (2-7 feeds/hour: $n = 12$, 4.4% of all watches; 19-31 feeds/hour: $n = 10$, 3.7% of all watches)
152 and were excluded due to low sample size. Considering all provisioning rates together, inter-feed
153 intervals varied considerably (range 1 - 55 mins; mean = 6 mins). For provisioning rate x , the
154 inter-feed intervals of birds who provisioned at rate x were randomized so that they were no

155 longer associated with particular nest watches or individuals, which meant that our simulated data
156 would not be derived directly from the observed data. This randomization was repeated for each
157 of the 13 possible provisioning rates (7-19) and separately for males and females. We used these
158 pools of randomized inter-feed intervals to create simulated nest watches for the 169 different
159 possible combinations of male and female feeding rate (13 male provisioning rates x 13 female
160 provisioning rates). To generate expected alternation values where the female provisions at rate x
161 and the male provisions at rate y , we randomly selected $x - 1$ inter-feed intervals from the female
162 pool of intervals associated with rate x and $y - 1$ inter-feeding intervals from the male pool
163 associated with rate y . We made separate cumulative totals of the inter-feed intervals from x and
164 y and then combined the cumulative totals from x and y , in ascending order, into one time series
165 over which all the feeds and inter-feed intervals occur (Table 1). According to the sex associated
166 with each inter-feed interval, we could then calculate alternation as for the observed nest watches
167 described above (see Supplementary Figure A for a schematic of the described method). We
168 repeated this process until all the inter-feed intervals from the female provisioning rate x and male
169 provisioning rate y pools were used up, then moved onto the next combination of provisioning
170 rates. In each combination of provisioning rates, we ran 10000 bootstrap simulations of the
171 resulting alternation values to produce our simulated dataset of expected alternation.

172 The difference between female and male feeding rates has an inevitable influence on the degree of
173 expected alternation, as explained above. Rather than investigate separately the observed and
174 expected alternation for each of our 169 provisioning rate combinations (each with a small
175 number of observed cases), we grouped the bootstrapped alternations of the 169 provisioning rate
176 combinations according to the difference between the feeding rates of the two parents. This
177 process yielded 13 categories of provisioning rate difference (i.e. 0 when parents fed at the same
178 rate, up to 12 when parents fed at 7 and 19 feeds per hour). The observed alternation values
179 calculated from provisioning watches were grouped in the same way. To determine whether
180 observed alternation differed significantly from expected, we tested whether mean observed

181 | alternation [for](#) each provisioning rate difference was greater than the bootstrapped expected
182 | alternation (\pm 95% confidence intervals).

183 *Predictors and fitness correlates of alternation*

184 | To investigate potential predictors of alternation at a nest, we used a mixed model including mean
185 | breeder age (in years), hatch date (to nearest day), duration of the pair bond (in years), brood size
186 | (number of chicks on day 11 of the nestling period) and nestling age (days since hatching) as
187 | fixed effects. We also included the difference between the respective provisioning rates of the
188 | male and female because the difference between their provisioning rates should have a strong
189 | negative effect on alternation (see above). The start time of the nest watch (to nearest minute) was
190 | included to control for potential differences in provisioning behavior across the day and we used
191 | nest identity as a random variable to account for repeated measures across nests.

192 | To explore the fitness correlates of parental alternation, we used a set of linear models to test the
193 | relationship between alternation (mean across watches at a given nest) and four response
194 | variables. (1) Mean total provisioning rate: this was modelled as a Gaussian response, with brood
195 | size included as a covariate to control for potential variation in provisioning rate with the number
196 | of chicks. Because alternation is expected to increase with provisioning rate by chance as the
197 | inter-feed intervals become smaller (see above, and Johnstone et al. 2014) we modelled
198 | alternation as deviation from that expected by chance, to account for the random influence of
199 | provisioning rate. Deviation scores were calculated by subtracting the mean expected alternation
200 | from the mean observed alternation across all watches at each nest. (2) Mean chick mass: this was
201 | modelled as a Gaussian response, including alternation, brood size and mean tarsus length as
202 | covariates, the latter of which controlled for structural body size variation. (3) Parental survival:
203 | expressed as survival of parents to the year following observations of provisioning behavior. We
204 | modelled survival as a binary response in a mixed model including alternation as a predictor and
205 | year as a random effect to account for survival differences between years. Dispersal out of the

206 study area occurs in an individual's first winter and thereafter the probability of re-sighting is
207 almost 100% in our study population (McGowan et al. 2003), so we could reliably measure
208 survival from re-sighting data. We did not account for adult age effects in the survival model,
209 because there is no discernible effect of age on survival in the study population (Meade et al.
210 2010). (4) Nest fate: nests were categorized as either 'depredated' or 'fledged' and nest fate was
211 modelled as a binary response variable. Nestling age is expected to be lower on average in nests
212 that fail before fledging, so here we restricted our analysis to nests watched on day 6 of the
213 nestling period (n = 64). We included alternation, provisioning rate and brood size as fixed effects
214 and year as a random effect.

215 *Analysis of provisioning synchrony*

216 For each nest watch we calculated a synchrony score from the time intervals between alternating
217 parental nest visits. Synchrony, s , was calculated as: $s = F/t$, where F is the number of alternated
218 nest visits where the second visit was within one minute of the first and t is the total number of
219 visits in the observation period. We tested the relationship between alternation and synchrony
220 using a generalized linear mixed model with Poisson error and nest identity as a random effect.
221 The provisioning rate during an observation period inevitably influences synchrony because as
222 the rate increases, a greater proportion of feeds occur within a minute of each other. We therefore
223 also included provisioning rate as an explanatory variable.

224 To investigate potential fitness correlates of coordinated parental nest visits, we examined nest
225 activity by estimating the time that parents spend in the immediate vicinity of nests per
226 provisioning visit. Data for this analysis were obtained from filmed observations in
227 2012 (n = 10 nest watches at 7 nests) where the nest and the surrounding 10m was visible
228 throughout a provisioning watch of 40-50 minutes. From the start of each nest watch, we timed
229 (to the nearest second) how long one or both parent(s) were visible (i.e. within 10m of the nest)
230 until a cumulative total of 5 minutes with one or both parents in the vicinity of the nest was

231 reached. The total number of feeds during this 5 minutes provided a measure of the number of
232 feeds per unit time spent near the nest; pairs that provision more often during this cumulative five
233 minutes logically spend less time near the nest per feed. Mean synchrony scores for each of these
234 nests were also calculated, using provisioning data available from separate observations recorded
235 in the same breeding attempt. We then investigated the relationship between the number of feeds
236 per 5 minutes around the nest and mean synchrony scores across nests.

237 All statistical analyses were carried out in R Studio, version 2.15.3 (R core development team,
238 2014). In each analysis, we sequentially removed non-significant terms in order of lowest
239 significance until only significant terms remained. Mixed models were performed in the “nlme”
240 package (Pinheiro et al. 2015) and general linear models were performed using r base packages.
241 Figures were produced using the “ggplot2” package (Wickham 2009).

242

243 **Results**

244 *Alternation of provisioning visits*

245 Across all provisioning rate difference categories, alternation occurred more often than expected
246 by chance, alternation being significantly higher in all categories than the upper 95% CI for
247 bootstrapped expected alternation (Fig. 1). As expected, the difference in provisioning rate
248 between males and females was a strong predictor of observed alternation: smaller differences in
249 the feeding rates of the two parents corresponded with greater mean alternation (ANOVA: $F_{11,451}$
250 = 457.21, $P < 0.001$; Fig. 1). Mean alternation was significantly different for all 13 categories of
251 provisioning rate difference (Tukey HSD, all $P < 0.05$). Observed alternation for a given pair of
252 birds provisioning the same nest was significantly correlated across watches (Fig. 2).

253

254 *Predictors of parental alternation*

255 Alternation was not predicted by any of the variables we tested: hatch date, time of day, combined
256 breeder age (mean = 3.70 years \pm 0.12 SE), pair-bond duration (mean = 0.19 years \pm 0.03 SE),
257 brood size (mean = 8.31 \pm 0.14), nestling age (mean = 9.57 days \pm 0.20 SE) but was significantly
258 negatively correlated with provisioning rate difference (Table 1) .

259

260 *Parental alternation and reproductive success*

261 Mean provisioning rate was not significantly related to brood size, but was weakly but
262 significantly positively correlated with deviation from expected alternation (Table 1,(Fig. 3a).
263 This increase in provisioning rate with alternation was not reflected in mean chick mass, which
264 was not significantly correlated with alternation (Table 1). Removing tarsus as a covariate
265 improved the relationship between alternation and chick mass but it remained non-significant ($P =$
266 0.07). Alternation was not significantly associated with parental survival to the following year for
267 either sex (Table 1).

268

269 Nest fate (i.e. fledged successfully or depredated) was not significantly related to total parental
270 provisioning rate or brood size. The probability of fledging was significantly higher in broods
271 where parents alternated more (Table 1, Fig. 4).

272 *Provisioning synchrony*

273 The mean synchrony score of provisioning parents was 13.3% \pm 0.51SE of feeds occurring within
274 the same minute (n = 247 nest watches on 97 pairs). Synchrony increased with both alternation
275 (GLMM: $\beta = 0.012 \pm 0.002$, $P < 0.001$; Fig. 3b) and, logically, with total provisioning rate
276 (GLMM: $\beta = 0.041 \pm 0.002$, $P < 0.001$). In the sample of seven nests filmed in 2012, pairs that

277 provisioned more synchronously fed broods more often per five minutes of nest activity by one or
278 both parents (Fig. 5). We interpret this pattern as evidence that when parents are more
279 synchronised in their provisioning visits, the number of feeds per unit time of parental activity
280 near the nest increases. In other words, synchronised visits reduced the amount of parental
281 activity near the nest per feed and hence may reduce nest conspicuousness to predators.

282

283 **Discussion**

284 Our study shows that long-tailed tit parents alternate their provisioning visits significantly more
285 often than expected by chance, and that they do so consistently over the nestling period.
286 Moreover, higher rates of alternation were associated with higher total provisioning and lower
287 depredation risk. The latter is probably the result of the fact that pairs who alternated their
288 provisioning more also provisioned more synchronously and therefore reduced the time they spent
289 near the nest. We discuss these findings and their implications below.

290

291 *Alternation of provisioning trips*

292 Parental alternation of provisioning was recently suggested as a mechanism by which parents can
293 reduce their conflict over care, but actual tests of this idea are largely missing. To our knowledge,
294 the only previous study that investigated parental alternation is that of Johnstone et al. (2014),
295 who show that great tit parents take turns in feeding young more than expected by chance.
296 However, some evidence suggests that parental coordination may occur in other species. First,
297 two experimental studies have shown that parents match the effort of their partner, which
298 suggests some form of tit-for-tat negotiation or bargaining (Hinde 2006; Meade et al. 2011).
299 Second, synchrony of provisioning visits has been reported in several biparental species (e.g.
300 long-tailed finches *Poephila acuticauda* (van Rooij & Griffith 2013) and zebra finches

301 *Taeniopygia guttata* (Mariette and Griffith 2012; 2015)), and cooperative breeders (e.g. bell
302 miners *Manorina melanophrys* (McDonald et al. 2008) and pied babblers *Turdoides bicolor*
303 (Raihani et al. 2010)). Since synchrony in the current study appears to be closely linked with
304 alternation, it seems likely that behavioral coordination of provisioning might be a common way
305 in which parents reduce sexual conflict, as predicted by Johnstone et al. (2014).

306 Our finding of a significant repeatability of alternation between observations of the same pairs
307 provisioning at the same nest suggests that alternation may be associated with either properties of
308 individuals or the nest environment. However, because long-tailed tits are single-brooded and
309 have high mortality (Meade et al. 2010) and divorce rate (Hatchwell et al. 2000), we had only
310 very few observations from more than one nest belonging to the same pair, so we could not make
311 pairwise comparisons of alternation values from the same pairs in different breeding attempts. If
312 such observations were possible, pairs might be expected to alternate more in their first joint
313 breeding attempt in order to establish response rules and parental effort levels (Johnstone 2011;
314 Lessells and McNamara 2012), then relax the degree to which they alternate in subsequent
315 attempts. On the other hand, the coordination of pair activities may improve as the number of
316 pair's breeding attempts increases, thus providing a mechanism for the frequently observed
317 relationship between reproductive success and pair-bond longevity (Black 1996). It would be
318 interesting to test these alternative predictions in species with longer pair-bonds.

319 Repeatable alternation of provisioning visits for individual pairs could also arise simply as a
320 function of repeatable provisioning rate differences. If a pair deviates the same amount from
321 expected alternation in each observation and also maintains a fairly constant feeding rate,
322 alternation would be similar across observations. Provisioning rate difference might be stable if
323 birds are following the negotiation rules of Lessells and McNamara (2012), where the male and
324 female each establish and maintain a negotiated parental effort early in the breeding attempt.
325 Indeed, previous studies indicate that parental effort is repeatable in long-tailed tits (MacColl and
326 Hatchwell 2003b), as is the effect of an individual's care on the effort of others (Adams et al.

2015), supporting the notion of individual consistency in provisioning behavior. Thus it seems most likely that repeatability in alternation can be explained by an early negotiation of effort and consistent subsequent behavior by each pair member, rather than being determined by other (e.g. environmental) factors.

331

Fitness correlates of alternation

We found a positive relationship between parental alternation and total provisioning rate, as predicted by the model of Johnstone et al. (2014), thus supporting the notion that alternation can reduce the costs of sexual conflict for offspring. It should be noted, however, that neither the current study nor previous ones are able to rule out potential confounds of parental quality, which might simultaneously affect provisioning effort and the ability to coordinate care. Contrary to expectations, neither higher total provisioning rate nor alternation directly resulted in improved nestling condition. It is possible that in this study the increase in provisioning rate with alternation (Fig. 3a) was too weak to cause detectable differences in nestling mass. Indeed, previous studies have shown that helpers in this facultative cooperatively breeding species cause a substantial increase in provisioning rate with positive consequences for nestling growth and subsequent recruitment (MacColl & Hatchwell 2002; Hatchwell et al. 2004). On the other hand, evidence from other biparental passerines suggests that increased parental provisioning does not necessarily result in greater chick mass (Titulaer et al. 2012), especially in species with large broods where any increases in provisioning rate are likely to be diluted by the high demand for food by the offspring (Bonneaud et al. 2003). Therefore, subtle links between provisioning rate and alternation, such as long-term survival benefits for offspring, may remain undetected in this study.

Alternation of nest visits could also allow parents to moderate the survival costs of reproduction through negotiation of parental investment, but we found no relationship between alternation and adult survival to the following year. This result is perhaps not surprising considering the high

352 annual mortality (c.44%) in our study population (McGowan et al. 2003; Meade et al. 2010).

353 Furthermore, the fact that total provisioning rate increases with alternation suggests that any

354 benefit of increased efficiency of care through negotiation may be masked by increased

355 provisioning effort by parents.

356 The more marked relationship between alternation on reproductive success reported here is that

357 alternation in successful nests was significantly higher than that in nests that were depredated.

358 Predators are likely to be attracted to nests through the activity of the parents (Lima 2009), so we

359 suggest that this finding may be linked to the positive relationship between alternation and

360 synchrony, because overall, parents spent less time at the nest when provisioning visits were more

361 synchronized. Therefore, alternation and the associated synchrony of provisioning visits appear to

362 confer a direct fitness benefit by improving the chances that offspring survive to fledging.

363 It should also be noted that we investigated the coordination of provisioning visits in long-tailed

364 tit broods fed by parents only, omitting those broods where helpers assisted parents in caring for

365 nestlings. A previous study found that the presence of helpers at the nest did not increase the risk

366 of nest predation (Hatchwell et al. 2004), a result that appeared counter-intuitive given that

367 activity near the nest is likely to increase its conspicuousness, and given that long-tailed tits are

368 too small to defend the nest against their principal nest predators (BJH pers obs). It would be

369 interesting to extend the analysis to examine the provisioning behaviour of carers at helped nests

370 to investigate whether nest visits exhibit similar, or even greater levels, of coordination to avoid

371 an increased risk of attracting nest predators.

372

373 *General conclusions*

374 Long-tailed tit pairs alternated their provisioning visits more than would be expected by chance.

375 This coordination of parental care was associated with an increase in total provisioning rate and a

376 reduction in nest predation. The finding of a positive relationship between reproductive success
377 and alternation, combined with the repeatable nature of alternation, is correlative in nature but
378 strongly supports the contention of Johnstone et al. (2014) that alternation of visits provides a
379 means of mitigating the cost of sexual conflict for offspring. The behavioral mechanisms
380 underlying parental investment strategies are vital to our understanding of the evolution of stable
381 biparental systems and our results contribute substantially to the notion that coordination of nest
382 visits is a behavioral adaptation to mitigate the costs of sexual conflict over care.

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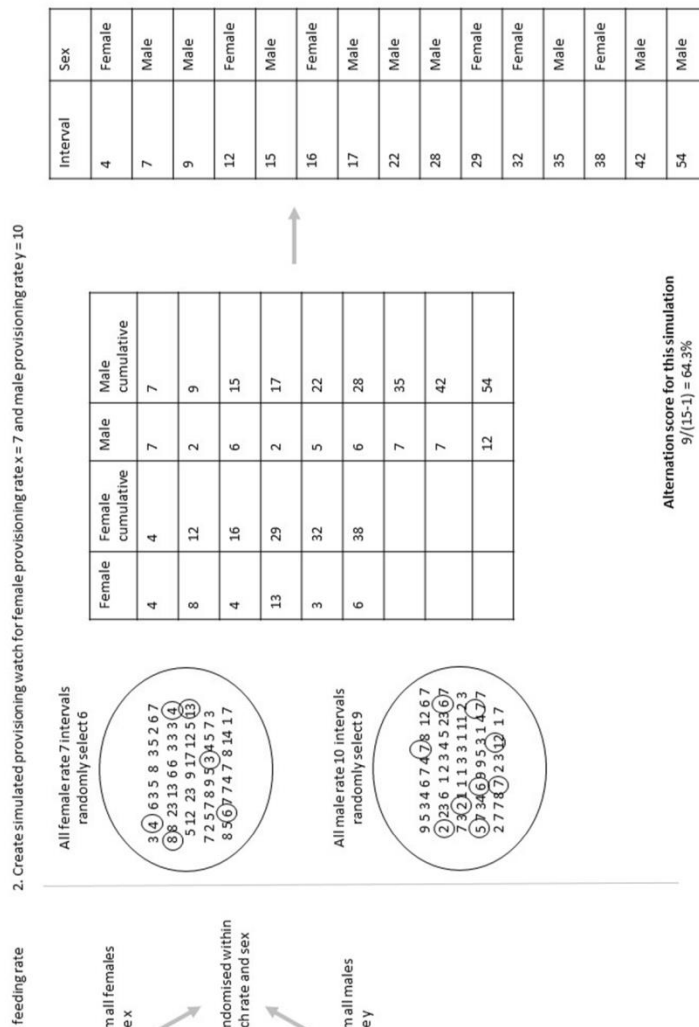
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492

493 **Supplementary material**

494 **Figure S1 Schematic demonstrating how observed inter-feed intervals from nest watches**
 495 **were converted into simulated provisioning watches to calculate expected alternation (see**
 496 **Methods)**

497



498 **Table S1 Demonstration of how randomly selected female and male inter-feed intervals are**
 499 **combined to produce a time-series from which simulated alternation can be scored.**

Female intervals	Cumulative female intervals	Male intervals	Cumulative male intervals	Cumulative combined intervals	Sex identity of interval
4	4	7	7	4	Female
8	12	2	9	7	Male
4	16	6	15	9	Male
13	29	2	17	12	Female
6	32	5	23	15	Male
	38	7	30	16	Female
		7	37	17	Male
		12	44	23	Male
			56	29	Female
				30	Male
				32	Female
				37	Male
				38	Female
				44	Male
				56	Male

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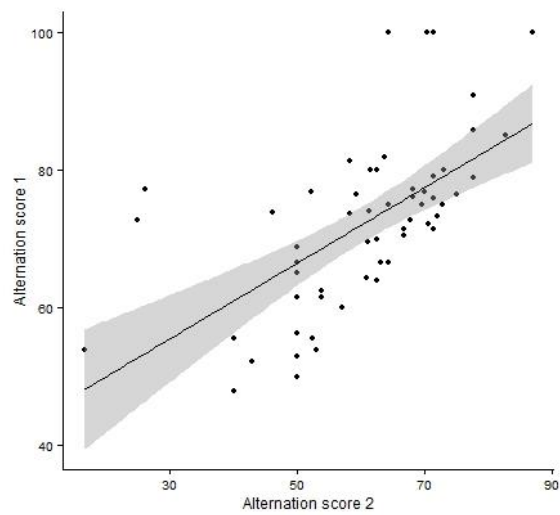
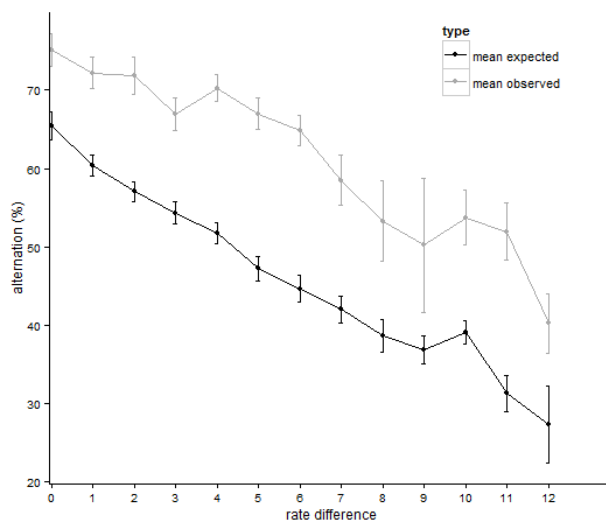
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502 **Table 1 Coefficients for parameters predicting and correlating with measures of parental**
 503 **alternation, with significant terms in bold text.**

		Parameter	Estimate \pm SE	<i>P</i> value
Predictors of alternation		Provisioning rate difference	-2.55 \pm 0.45	<0.01
		Combined breeder age	-0.26 \pm 0.60	0.67
		Hatch day	0.09 \pm 0.16	0.57
		Length of pair bond	0.09 \pm 2.19	0.97
		Brood size	0.80 \pm 0.53	0.14
		Time of day	-0.63 \pm 0.36	0.08
		Nestling age	0.03 \pm 0.31	0.92
Fitness correlates				
	Provisioning rate	Deviation from expected alternation	-0.37 \pm 1.10	0.03
		Brood size	0.49 \pm 0.34	0.15
	Chick mass	Mean alternation	<0.01 \pm <0.01	0.11
		Mean chick tarsus	0.43 \pm 0.06	<0.01
		Brood size	-0.05 \pm 0.002	<0.01
	Male survival	Mean alternation	-0.02 \pm 0.02	0.34
	Female survival	Mean alternation	0.02 \pm 0.02	0.29
	Nest fate	Alternation	-0.04 \pm 0.02	0.04
		Brood size	0.28 \pm 0.66	0.51
		Provisioning rate	0.03 \pm 0.05	0.54

504 **Figures 1-5**

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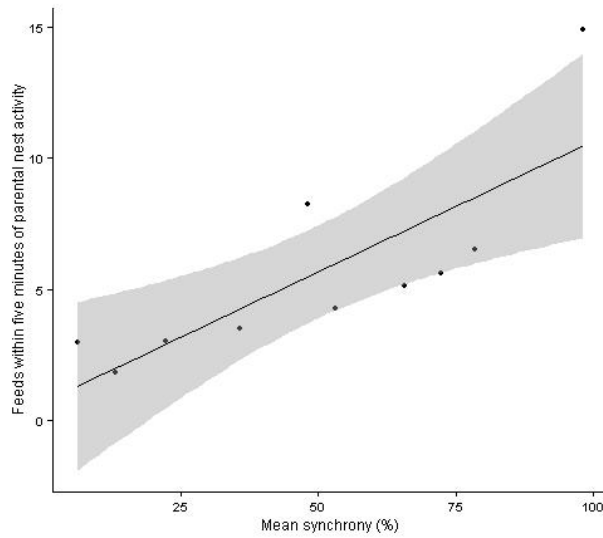
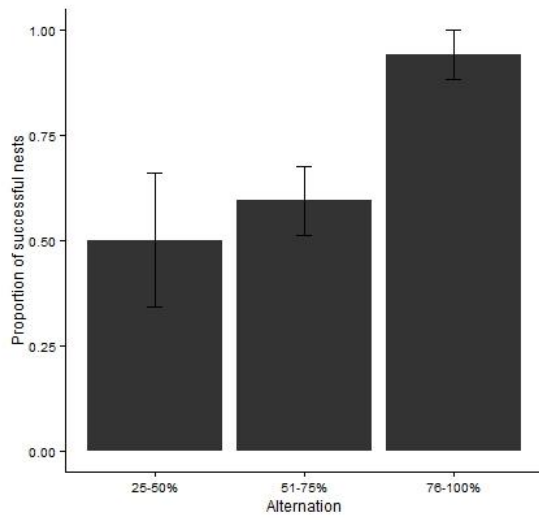
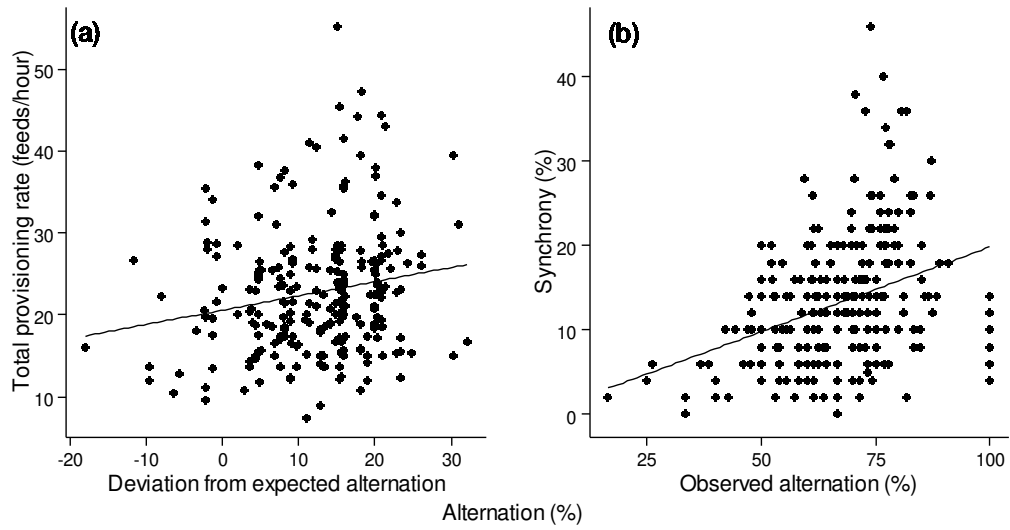
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526 Figure legends 1-5

527

528 Figure 1. Mean observed and expected alternation in relation to the difference in provisioning rate
529 between the parents. Bars for observed values represent standard error and bars for expected
530 values represent 5 and 95% confidence intervals. All observed mean alternation values exceed the
531 upper 95% confidence intervals of expected scores and, as expected, alternation decrease as a
532 function of increasing provisioning rate difference.

533

534 Figure 2. Relationship between two randomly sampled measures of alternation values from
535 repeated observations at the same nest. The line represents fitted values (LM: $F_{1,52} = 33.1$, $P <$
536 0.001 , $R^2 = 0.377$) with its standard error represented by shaded areas.

537

538 Figure 3. Relationships between: (a) total provisioning rate (feeds/hour) and alternation ($F_{1,245} =$
539 7.447 , $P < 0.01$); and (b) synchrony of provisioning visits between parents (number of alternated
540 feeds that occurred within a minute of the previous feed) and alternation ($F_{1,245} = 35.98$, $P <$
541 0.001). Lines show the predicted values.

542

543 Figure 4. Mean +SE proportion of nests that produced fledglings as a function of varying degrees
544 of alternation, which was modelled as a continuous variable but for visualization purposes is
545 grouped according to the level of alternation achieved on day 6 of the nestling period.

546

547 Figure 5. Relationship between the mean nest activity (see methods) and mean synchrony scores
548 for nests in 2012. The regression line is derived from values predicted by a linear model and

549 shows a significant relationship between nest activity and mean synchrony score (LM: $F_{1,5} =$
550 13.78, $P = 0.014$), with standard error represented by shading.

551