Coordination of care by breeders and helpers in the cooperatively breeding long-tailed tit, *Aegithalos caudatus*

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36   **Data availability**

37   Analyses reported in this article can be reproduced using the data provided by Halliwell

38   et al. (2022).

39   **Conflict of interest**

40   The authors declare no conflict of interest.

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In species with biparental and cooperative brood care, multiple carers cooperate by contributing costly investment to raise a shared brood. However, shared benefits and individual costs also give rise to conflict among carers over investment. Coordination of provisioning visits has been hypothesized to facilitate the resolution of this conflict, preventing exploitation, and ensuring collective investment in the shared brood. We used a 26-year study of long-tailed tits, *Aegithalos caudatus*, a facultative cooperative breeder, to investigate whether care by parents and helpers is coordinated, whether there are consistent differences in coordination between individuals and reproductive roles, and whether coordination varies with helper relatedness to breeders. Coordination takes the form of turn-taking (alternation) or feeding within a short time interval of another carer (synchrony), and both behaviors were observed to occur more than expected by chance, i.e. 'active' coordination. First, we found that active alternation decreased with group size while active synchrony occurred at all group sizes. Secondly, we show that alternation was repeatable between observations at the same nest, while synchrony was repeatable between observations of the same individual. Active synchrony varied with reproductive status, with helpers synchronizing visits more than breeders, although active alternation did not vary with reproductive status. Finally, we found no significant effect of relatedness on either alternation or synchrony exhibited by helpers. In conclusion, we demonstrate active coordination of provisioning by carers and conclude that coordination is a socially plastic behavior depending on reproductive status and the number of carers raising the brood.

Key words: Cooperation, coordination, conflict, parental care, alternation, synchrony

Introduction

68 Parental care is observed in some form in most bird species (Cockburn 2006). In

69 altricial species, much of the burden of care occurs postnatally (Godfray and Johnstone

70 2000) and typically involves a shared caring system, with either biparental or

71 cooperative brood care, in which helpers assist with raising a brood (Cockburn 2006).

72 The benefits of parental care to offspring are well documented (Trivers 1974, Godfray

73 1995, Godfray and Johnstone 2000, Hinde et al. 2010), as are the fitness costs to

74 parents, including accelerated senescence (Gustafsson and Pärt 1990), reduced

75 survival (Dijkstra et al. 1990, Visser and Lessells 2001) and lower future reproductive

76 success (Nilsson and Svensson 1996). Therefore, in both biparental and cooperative

77 breeding systems there exists a fundamental conflict over individuals' relative level of

78 investment in the current brood. Shared benefits of increased offspring survival and

79 condition must be traded-off against individual costs of reduced future fitness (Trivers

80 1974, Hinde et al. 2010). This conflict means that optimal parental care behaviors that

81 maximize lifetime reproductive success are dependent on the actions of others, so

82 carers should use information from their social environment to adjust their own

83 behavior (Houston and Davies 1985, McNamara et al. 1999, Johnstone and Hinde

84 2006). Recent work has hypothesized that coordination of care may have a crucial

85 function as a mechanism for negotiating investment between carers, gathering

86 information about others' effort, building trust and therefore resolving this conflict so

87 that carers more closely match their optimal level of (allo)parental investment

88 (Johnstone and Hinde 2006, Johnstone et al. 2014, Johnstone and Savage 2019).

89 Coordination can take the form of two, non-mutually exclusive behaviors: alternation,

90 which is the act of feeding in turn with another carer(s) such that each carer avoids

91 consecutive visits, and synchrony, which is the act of feeding within a short interval of

92 another carer's feed (Figure 1). Previous studies of parental coordination have

93 investigated biparental (e.g. Bebbington and Hatchwell 2016, Leniowski and Wegrzyn

94   2018, Baldan and Griggio 2019, Baldan et al. 2019, Ihle et al. 2019a, Lejeune et al.

95   2019) and cooperative care (e.g. Raihani et al. 2010, Koenig and Walters 2016,

96   Khwaja et al. 2017, Savage et al. 2017). The results, so far, are mixed, with many

97   demonstrating a higher than expected level of alternation (Johnstone et al. 2014,

98   Savage et al. 2017, Baldan et al. 2019, Ihle et al. 2019a), synchrony (Lee et al. 2010,

99   Raihani et al. 2010, Mariette and Griffith 2015) or both (Bebbington and Hatchwell

100 2016, Koenig and Walters 2016, Leniowski and Wegrzyn 2018, Lejeune et al. 2019),

101 while another reported no apparent coordination (Khwaja et al. 2017).

102 An important message emerging from these studies is that researchers must account

103 for a degree of passive coordination expected by chance due to common factors, such

104 as localized predator risk, weather conditions and resource abundance, that potentially

105 influence all carers' provisioning refractory periods (Schlicht et al. 2016, Ihle et al.

106 2019b, Santema et al. 2019). Refractory periods, which are the minimum times it takes

107 carers to gather food and return to the nest, are hypothesized to inflate levels of

108 alternation and synchrony because they create a short period of time after a feeding

109 visit in which a consecutive visit by the same individual is not possible, but alternated

110 and synchronized visits are (Ihle et al. 2019a). For example, if intervals between feeds

111 were consistent and identical for all carers at a nest, the pattern of visits would

112 resemble perfect alternation even in the absence of coordination behavior. To account

113 for passive coordination, randomization and simulation techniques derived from

114 observed behavioral parameters are required to evaluate the level of observed

115 coordination relative to that expected by chance from passive processes (e.g.

116 Johnstone et al. 2014, Baldan and Griggio 2019, Baldan et al. 2019, Khwaja et al.

117 2019). Ihle et al. (2019b) reviewed the different null models used to evaluate

118 coordination. They showed that randomization at the scale of within-nest, within-

119 individual and inter-visit was the most conservative approach (Figure S1,

120   supplementary material), because these conserve provisioning refractory periods. The

121   difference between observed and expected coordination can then be measured,

122   hereafter termed 'active coordination'.

123   In cooperative breeding systems, additional factors such as the number of carers, carer

124   status and relatedness of carers to the brood must also be considered when

125   determining an individual's optimal behavior (Crick 1992, Hatchwell 1999, Savage et al.

126   2013a,b, Savage et al. 2015, Green et al. 2016). Most previous studies have identified

127   some form of coordination, but few have investigated the role of variable numbers of

128   carers on coordination behavior (Savage et al. 2017). Since alternation is hypothesized

129   to facilitate cooperation between carers (Johnstone et al. 2014), variation in the level of

130   coordination between nests with different numbers of carers may inform our

131   understanding of how and why birds coordinate. For example, a change in active

132   coordination between group sizes may represent: (*i*) a change in the importance of

133   coordination, perhaps due to reduced costs of parental care resulting from load

134   lightening in large groups (Crick 1992); (*ii*) a change in the ability of carers to monitor

135   one another; or (*iii*) a change in the potential for analyses to detect active coordination

136   behavior.

137   The status of individual carers within groups might also influence their coordination. For

138   example, fathers, mothers and helpers may provision broods differently (Harrison et al.

139   2009, Green et al. 2016), and Savage et al. (2017) suggested that alternation was most

140   prominent in breeders and helpers that invested more highly in broods. Synchronous

141   feeding has also been proposed as a means of signaling effort to other carers

142   (Doutrelant and Covas 2007, Koenig and Walters 2016, Trapote et al. 2021), so this

143   hypothesis predicts that if signaling confers direct benefits to helpers, such as in a pay-

144   to-stay system (Gaston 1978, Kokko et al. 2002), more active synchrony should be

145   performed by helpers. Alternatively, synchrony may be a result of collective foraging

146 behavior that causes carers to return to the nest synchronously (Mariette and Griffith

147 2012, 2015). Moreover, if coupled with a leader-follower relationship, for example, if

148 helpers are more likely to follow a breeder back to the nest, this may result in greater

149 synchrony by helpers.

150 In this study, we investigated how levels of coordination varied with the number and

151 status of carers in the long-tailed tit, *Aegithalos caudatus*. Long-tailed tits are short-

152 lived passerine birds, with a facultative cooperative breeding system in which failed

153 breeders redirect their care to help raise the offspring of other breeders, to which they

154 are typically related (Hatchwell et al. 2014, Hatchwell 2016). About half of all broods in

155 our study population are raised by their parents alone, the remainder being fed by their

156 parents assisted by helpers. Helping is a kin-selected adaptation that allows failed

157 breeders to gain indirect fitness benefits by caring for their relatives' offspring, thereby

158 increasing relatives' breeding success (Hatchwell et al. 2004, 2014). Previous studies

159 have shown that the care provided by helpers varies with relatedness. First, helpers

160 show an active preference for helping kin rather than non-kin (Russell and Hatchwell

161 2001, Leedale et al. 2018). Second, helpers provision at a higher rate when they are

162 more closely related to a brood (Nam et al. 2010, Leedale et al. 2020).

163 Given that a helper's relatedness influences their investment decisions we might also

164 expect that it would influence coordination behavior. For example, if carer coordination

165 benefits the brood, less related helpers may coordinate less due to their lower genetic

166 investment in the brood (Savage et al. 2017). Alternatively, the shared interest of

167 parents and helpers in the brood may be lower for more distantly related helpers,

168 resulting in greater conflict and hence a greater need for coordination. This cooperative

169 breeding system with variable numbers of carers and variable relatedness between

170 carers and the shared brood is well suited for testing whether carers coordinate their

171 care and the factors influencing the level of coordination.

172 Bebbington and Hatchwell (2016) reported that long-tailed tit parents provisioning at

173 biparental nests coordinate their care so that observed alternation and synchrony were

174 higher than expected by chance. That study, however, utilized a null model that did not

175 fully account for expected alternation and synchrony caused by refractory periods (Ihle

176 et al. 2019a). In this study, we build on the findings of Bebbington and Hatchwell (2016)

177 by investigating the impact of the number of carers, carer status and relatedness of

178 helpers on coordination of care, using a more conservative approach to analyze a

179 larger sample of biparental nests, as well as cooperative nests with up to three helpers.

180 Our first objective was to investigate whether carers working in different group sizes

181 coordinated their provisioning by comparing observed alternation and synchrony to that

182 expected by passive processes (Ihle et al. 2019a). Secondly, we investigated individual

183 variation in coordination, examining the extent of within-individual and within-nest

184 repeatability in the level of active coordination, and whether levels of active alternation

185 and synchrony varied in relation to the status of the carer (male breeder, female

186 breeder or helper). Finally, we examined variation in the degree of coordination by

187 helpers to determine whether either alternation or synchrony was influenced by their

188 relatedness to the brood.

189 ## Methods

190 ### Study system and data collection

191 We used data from a long-term study of a population of long-tailed tits in the Rivelin

192 Valley, Sheffield, UK (53°23′N, 1°34′W) from 1994 to 2019. The field site is ~3km^2 with

193 a population of 25-72 breeding pairs (Hatchwell 2016). Each year ~95% of adult birds

194 were marked (under British Trust for Ornithology license) with a unique combination of

195 two color rings on one leg and a BTO metal ring on the other. The adult annual

196 mortality rate is ~50% (Meade and Hatchwell 2010), and ~20% of new recruits into the

197 adult population were ringed as nestlings in the study site, while the remaining ~80% of

198   new recruits were unringed adult immigrants that dispersed into the population.

199   Unringed birds were captured in mist-nests during the nest-building period and DNA

200   samples collected (under Home Office license) for genotyping and social pedigree

201   reconstruction. Nests were found by following adults and once located, were monitored

202   every 2-3 days, with daily visits around the expected hatch date. Median clutch size is

203   10 eggs (range: 4-12), which are incubated for ~15 days (Hatchwell 2016). Hatching is

204   extremely synchronous within clutches, with all chicks typically hatching within 24 hours

205   of the first. Initial hatch date was recorded as day 0, and chicks were ringed and

206   counted on day 11. Protocols for provisioning watches (hereafter 'watches') were

207   broadly consistent throughout the study. In most cases, watches of duration ~60

208   minutes were carried out every other day, starting on day 2, either by direct field

209   observation or by video camera, for later review (69% of watches were between 45 and

210   65 minutes). Watches were carried out between 04:00 and 18:00, with 89% starting

211   between 06:00 and 14:00. Watches were performed until a nest was predated,

212   abandoned or chicks fledged, typically on day 16-18.

213   For ~5 days post-hatching nestlings are brooded regularly by their mothers, who

214   provision offspring only occasionally, while fathers either feed the offspring directly or

215   give food to the mother, who then feeds the chicks. We restricted our analysis,

216   therefore, to watches at day 6 and older, when both parents provision offspring directly.

217   Long-tailed tits exhibit facultative cooperative breeding (Lack and Lack 1958, Hatchwell

218   2016), meaning nests may be uniparental (1 carer, in the rare event of a parent dying),

219   biparental (2 carers) or cooperative (>2 carers). For this study we restricted analysis to

220   watches of biparental and cooperative nests with up to 5 carers (i.e. social parents and

221   up to 3 helpers). Our dataset contained 65% (516) of watches from biparental nests

222   and 21% (171), 11% (88) and 3% (20) from nests with 3, 4 and 5 carers, respectively.

223   Before starting a watch, ~10 minutes was usually allowed for birds to recover from

224 observer disturbance and we restricted analysis to watches of total duration ≥ 30.0

225 minutes and ≤ 180.0 minutes, with duration defined as the time between first and last

226 observed feeds. Mean watch duration (± SD) was 54.8 ± 14.4 minutes (range 30-118

227 minutes, N = 795 watches). We omitted watches where the identity of any provisioning

228 visit was unknown, and from nests that were manipulated for other behavioral studies

229 (e.g. Meade et al. 2011). Watches were used from 24 years between 1994 and 2019,

230 with 2007 and 2009 excluded because experiments conducted in those years meant

231 that they contained no watches matching our criteria. In total, our dataset included 795

232 watches performed at 250 unique nests, involving 192 different breeding males, 203

233 breeding females and 144 helpers.

234 **Calculating coordination**

235 We analyzed alternation and synchrony as the absolute number of alternated and

236 synchronized feeding visits in a provisioning watch, respectively. We defined an

237 alternated visit as any non-consecutive provisioning visit (i.e. a visit occurring after the

238 provisioning visit of any carer other than itself) and a synchronized visit as an

239 alternated visit occurring within 2-minutes of the previous feed (Figure 1). We chose an

240 interval of 2-minutes in accordance with previous studies (Mariette and Griffith 2015,

241 Bebbington and Hatchwell 2016, Ihle et al. 2019a), and further analyses revealed that

242 number of synchronized visits was highly correlated for 1, 2 and 3-minute intervals

243 (Pearson correlations: 1 v. 2 min, r = 0.97, df = 793, P < 0.001; 2 v. 3 min, r = 0.97, df =

244 793, P < 0.001; 1 v. 3 min, r = 0.94, df = 793, P < 0.001), and analyses of synchrony

245 with different intervals produced qualitatively the same results.

246 We calculated observed alternation and synchrony directly from visit sequences and

247 times recorded through field observation, generating coordination measures per watch

248 and for each individual carer present in each watch (Figure 1). We generated expected

249 data by null model randomization of observed data, with the binary factor 'Data type'

250   specifying whether data were observed or expected. In accordance with the most

251   conservative method of calculating expected alternation and synchrony recommended

252   by Ihle et al. (2019b), our null models used a within-watch, within-individual

253   randomization procedure in which the order of provisioning visits within a watch was

254   randomized in a manner that preserved the length and identity of each period between

255   feeding visits (inter-visit intervals) (Figure S1; supplementary material). We calculated

256   expected numbers of alternated and synchronized visits, both for group total and for

257   individual carers, from the median of 1000 iterations of the null model applied to each

258   provisioning watch. We used median values to preserve integer values for subsequent

259   analysis in Poisson-distributed linear models; mean and median values were highly

260   positively correlated (Pearson correlations: alternated visits, $r = 0.99$, $df = 793$, $P <$

261   0.001; synchronized visits, $r = 0.99$, $df = 793$, $P < 0.001$).

262   **Calculating kinship**

263   To calculate pairwise values of pedigree relatedness of helpers to parents we

264   constructed an additive relationship matrix using the R package NADIV (Wolak 2012),

265   partially reconstructed using molecular genetic data from up to 17 microsatellite loci to

266   perform offspring-parent reconstruction on CERVUS v. 3.0.7 (Kalinowski et al. 2007)

267   and sibling-sibling reconstruction on KINGROUP v.2 (Konovalov et al. 2004). Building

268   on the social pedigree and protocol used in Leedale et al. (2018, 2020) we expanded

269   the pedigree to include 2018 and 2019 data. Our study population is open, so even

270   after reconstruction the social pedigree remained incomplete; therefore, where

271   necessary we omitted data with incomplete pairwise relatedness metrics to either

272   social parent.

273   **Statistical analysis**

274   All statistical analysis was performed in R version 4.0.2 (R core development team,

275   2020). All models were built and analyzed using the lme4 package (Bates et al. 2015)

276   and lmerTest (Kuznetsova et al. 2017), except for our repeatability models which were

277   built and analyzed using the rptR package (Stoffel et al. 2017).

Collective coordination models (Alt-C and Sync-C)

279   To investigate collective alternation and synchrony performed by all carers at a nest we

280   defined two Poisson-distributed generalized linear mixed effects models (GLMM)

281   named 'Alt-C' and 'Sync-C', respectively. The response variables to these models were

282   the number of alternated visits (collective) and synchronized visits (collective) by all

283   carers at each watch, respectively. To control for observation and population structure,

284   these models were built with the following random effects: 'Year', 'Nest ID', 'Watch ID',

285   'Male ID', 'Female ID', 'Helper1 ID', 'Helper2 ID', 'Helper3 ID' and 'Row reference' (see

286   Table 1 for explanation). The fixed effects tested were as follows: 'Data type' (observed

287   vs. expected values of alternation and synchrony), 'Provisioning rate (collective)',

288   'Carer number', 'Watch duration', 'Brood size', 'Time of day', 'Brood age', 'Hatch date'

289   and 'AMax (or SMax)' (Table 1). We focused our analysis on 'Data type' and 2-way

290   interactions with other fixed effect terms, as a disparity between observed and

291   expected data represents the level of active coordination performed.

Individual coordination models (Alt-I and Sync-I)

293   To investigate the effect of carer status on alternation and synchrony performed by a

294   given carer, we built two Poisson-distributed GLMMs named 'Alt-I' and 'Sync-I',

295   respectively. The response variables to these models were the number of alternated

296   visits (individual) and synchronized visits (individual), respectively. These models were

297   built with the following random effects: 'Year', 'Nest ID', 'Watch ID', 'Carer ID' and 'Row

298   reference' (Table 1).The fixed effects tested were as follows: 'Data type', 'Carer status',

299 'Provisioning rate (individual)', 'Carer number', 'Watch duration', 'Brood size', 'Time of

300 day', 'Brood age', 'Hatch date' and 'Amax' or 'SMax' (Table 1). In this analysis, the

301 focus was on the interaction of 'Data type' with 'Carer status' because this term

302 represents the disparity in active coordination between carers of different breeding

303 status.

Repeatability models (Alt-R and Sync-R)

305 To investigate the repeatability of active alternation and synchrony within nests and

306 within individuals we constructed two Gaussian-distributed GLMMs named 'Alt-R' and

307 'Sync-R', respectively. In these models, response variables were the number of actively

308 alternated (individual) and actively synchronized (individual) visits by an individual

309 during a watch, respectively (active alternation range: -3 to 6; active synchrony range: -

310 7 to 9). We used these metrics because repeatability analyses required active

311 coordination to be the response variable, rather than using interaction terms with 'Data

312 type' as in our other models. To control for the effect of confounding factors on active

313 coordination we included all fixed effects previously found to significantly influence

314 either individual alternation or synchrony (Alt-I, Sync-I) and, using the rptR function, ran

315 models with 1000 bootstrapped simulations and 1000 permutations. We investigated

316 both within-nest repeatability ('Nest ID') and within-individual repeatability ('Carer ID') in

317 the same models. Additionally, we included 'Year' as a random effect to account for

318 between-year variation. As active coordination was the response variable and a

319 Gaussian error distribution was used, 'Watch ID' and the 'Row reference' random

320 effects were not required for these models. We present our repeatability results as

321 values of R and extracted 2.5% and 97.5% confidence intervals (CIs) in addition to P-

322 values.

323 In our dataset many individuals were observed provisioning at only one nest, potentially

324 confounding repeatability of an individual's behavior with the potential effect of common

325   nest factors. Therefore, we ran the repeatability analysis on a subset of data, restricted

326   to carers observed provisioning at two or more nests (Table S2, supplementary

327   material). Results from these models were qualitatively the same as those for the full

328   dataset for both within-nest and within-individual repeatability for both alternation and

329   synchrony models.

330   **Kinship models (Alt-K and Sync-K)**

331   To investigate the effect of kinship to the breeding pair on alternation and synchrony

332   performed by helpers we constructed two Poisson-distributed GLMMs named 'Alt-K'

333   and 'Sync-K', respectively. Just as with 'Alt-I' and 'Sync-I', the response variables to

334   these models were the number of alternated visits (individual) and synchronized visits

335   (individual) performed by an individual during a watch, respectively, however analysis

336   was restricted to helpers whose pedigree kinship with breeders was known. These

337   models were built with the same random and fixed effects as 'Alt-I' and 'Sync-I' but with

338   the addition of three fixed effects: 'Sex', 'Kinship with father' and 'Kinship with mother'

339   (Table 1). We focused our analysis on the interactions of 'Data type' with our kinship

340   terms as these represent the relationship between the level of active coordination and

341   relatedness.

342

343   # Results

344   **Carer number**

345   To test the hypothesis that carers exhibited behaviors resulting in alternated visits,

346   model 'Alt-C' compared observed alternation with that expected by chance from null

347   model randomization. We found that observed alternation was indeed significantly

348   higher than expected by chance, as indicated by the significance of the data type

349   term ($P < 0.001$, Table 2). To investigate the effect of other terms on active

350 alternation, we measured their effect on the difference between observed and

351 expected data, i.e. their interaction with data type. Carer number had a positive effect

352 on both expected and observed alternation (Table 2), but the interaction term with

353 data type was significant (P = 0.024, Table 2, Figure 2a), indicating that the difference

354 between them, i.e. active alternation, declined as carer number increased. The

355 degree of active alternation was not significantly related to time of day, watch

356 duration, brood size or provisioning rate (Table 2, Figure 2b).

357 To test the hypothesis that carers actively synchronized provisioning visits, we used

358 model 'Sync-C' to compare observed and expected synchrony. Just as for alternation,

359 observed synchrony was greater than expected by chance, the data type term being

360 significant (P < 0.001, Table 3). However, in contrast to our results for alternation,

361 there was no significant interaction between data type and carer number (Table 3,

362 Figure 3a), indicating that the level of active synchrony was similar at all group sizes.

363 Investigation of the interaction between data type and other predictors of synchrony

364 showed that provisioning rate was the only factor to influence the degree of active

365 synchrony (P < 0.001, Table 3, Figure 3b), the difference between observed and

366 expected synchrony declining with increasing provisioning rate. This result was

367 expected because as provisioning rates increase, the probability that two birds feed

368 within a 2-minute period, even by passive process, inevitably increases. Neither

369 brood size, time of day, nor watch duration was a significant predictor of the level of

370 active synchrony (Table 3).

Carer status

372 To investigate variation in alternation behavior by birds of different status (breeding

373 male, breeding female, helper) we used model 'Alt-I'. Breeding females had higher

374 overall levels of alternation than other categories of carer (P = 0.037, Table 4), but

375   carer status did not influence the extent of active alternation because the interaction

376   term with data type was non-significant (P = 0.975, Table 4, Figure 5a).

377   In contrast, in model 'Sync-I' the extent of active synchrony was influenced

378   significantly by carer status, as indicated by the interaction term with data type (P =

379   0.024, Table 5, Figure 5a), with helpers performing the most active synchrony

380   followed by breeding males then breeding females.

381   The extent of individual active synchrony was also influenced significantly by carer

382   number (P < 0.001, Table 5), a relationship which was not observed in the collective

383   synchrony model 'Sync-C' (P = 0.574, Table 2). We suspected that this trend may be

384   due to covariances between carer number, individual and total provisioning rate,

385   coupled with load-lightening and the provisioning rate dependence of the null model

386   (P < 0.001, Table 2, Figure 3b). Refitting the model with total provisioning rate and

387   appropriate interaction terms revealed that the effect of carer number on active

388   synchrony was contained within multiple significant 3-way interaction terms which are

389   probably a consequence of load-lightening behavior and the rate dependence of the

390   synchrony null model (Table 2, Figure 3b). Importantly, however, the results for the

391   effect of carer status on active synchrony remained qualitatively the same

392   (Supplementary Material, Figure S2).

393   **Repeatability of coordination**

394   Using model 'Alt-R' we assessed whether active alternation was consistent within

395   individuals and/or within groups of carers working together at a nest. Active

396   alternation of carers was significantly repeatable within nests (R = 0.145, CI (2.5-

397   97.5%) = 0.010 – 0.186, P < 0.001), but not within individuals (R = 0.000, CI (2.5-

398   97.5%) = 0.000 – 0.031, P = 0.500, Figure 4a), indicating that the degree of

399   alternation was a property of social or nest-specific factors. In contrast, model 'Sync-

400   R' showed that active synchrony of carers was significantly repeatable within

401   individuals (R = 0.183, CI (2.5-97.5%) = 0.130 – 0.228, P < 0.001), but not within

402   nests (R = 0.000, CI (2.5-97.5%) = 0.000 – 0.009, P = 1.00, Figure 4b), indicating that

403   the level of synchrony was a property of individual identity rather than the nest or

404   social environment.

405   **Helper kinship**

406   We found no significant effects of helper kinship to the helped breeders on any

407   measures of coordination. Model 'Alt-K' investigated variation in alternation behavior

408   between helpers of varying kinship, but neither the overall level of alternation by

409   helpers nor their degree of active alternation was influenced significantly by their

410   kinship with either the breeding male (Table 5, Figure 5b) or breeding female (Table

411   5, Figure 5c). Similarly, model 'Sync-K' showed that neither the overall level of

412   synchrony exhibited by helpers, nor the extent of active synchrony was influenced by

413   kinship with either the breeding male (Table 6, Figure 6b) or breeding female (Table

414   6, Figure 6c).

415   # Discussion

416   We found strong evidence for active coordination of care, with both alternation and

417   synchrony being observed more than expected by chance. Active synchrony was

418   detected across the full range of two to five carers (Figure 3a), whereas active

419   alternation was detected only in biparental nests and cooperative nests with one helper

420   (Figure 2a). Additionally, while breeding males, females and helpers did not differ in

421   their degree of active alternation (Figure 4a), helpers exhibited more active synchrony

422   than breeders, and male breeders showed more active synchrony than female

423   breeders (Figure 5a). We also found that the level of active alternation was linked to

424   nest identity (Figure 6a), whereas active synchrony was linked to individual carer

425   identity (Figure 6b), suggesting that alternation is a plastic behavior in response to

426 social environment, while synchrony is influenced by both an individual's identity and

427 current carer status. Finally, contrary to our expectations, the degree of helper

428 coordination was unaffected by their kinship with either breeding bird (Figure 4b,c,

429 Figure 5b,c).

430   The null hypothesis of a study seeking to quantify coordination of care is not that

431 there is no apparent coordination, but rather that the observed level of coordination

432 may be wholly explained by passive processes that affect provisioning, such as

433 weather, predation threat and resource distributions (Schlicht et al. 2016, Ihle et al.

434 2019b). We used the most conservative randomization approach (Ihle et al. 2019b),

435 conserving individual refractory periods and hence controlling for much of the

436 coordination that may be explained by passive processes. Our methods of data

437 collection and analysis also accounted for potential observer disturbance effects that

438 could enhance apparent coordination. On the other hand, the randomization process

439 effectively decouples the refractory periods of carers at the same nest, so factors such

440 as weather and predation threat that may impact all carers at the same time remain

441 difficult to control for statistically. However, it can also be argued that highly

442 conservative null models which re-order observed data retain a degree of active

443 coordination that is reflected in refractory periods, thereby underestimating the true

444 level of active coordination. Therefore, we conclude that our results support the case

445 for active coordination of care in long-tailed tits.

446   The hypothesized function of alternation is that it facilitates conflict resolution

447 between carers because conditional cooperation prevents exploitation by ensuring that

448 carers match changes in one another's provisioning rates (Johnstone et al. 2014). This

449 enables carers to increase their investment to more closely match the brood's optimum

450 care level (Trivers 1974) without causing other carers to slacken their effort to increase

451 their individual fitness pay-off. Our finding that active alternation declined as the

452   number of carers increased may indicate a reduced need to monitor the investment of

453   others when care is plentiful, especially as individual carers reduce their own costs by

454   load-lightening when they have helpers (Hatchwell and Russell 1996, Meade et al.

455   2010, Adams et al. 2015). This result contrasts with findings from chestnut-crowned

456   babblers *Pomatostomus ruficeps* (Savage et al. 2017) where active alternation was

457   observed across the full range of carer numbers (2-6), using the same null model

458   approach. This disparity may be due to differences in the ecology or social system of

459   chestnut-crowned babblers and long-tailed tits. Babblers must gather food far from the

460   nest despite not being proficient long-distance fliers, thus incurring substantial

461   provisioning costs (Browning et al. 2012). Therefore, a strict and efficient allocation of

462   effort between carers, with close monitoring, may remain important in this species even

463   in large cooperative groups. In contrast, long-tailed tits are thought to suffer relatively

464   modest costs of parental care (Meade and Hatchwell 2010, Hatchwell et al. 2014), so

465   individual effort may be monitored less closely, resulting in a decline in active

466   alternation with carer number.

467   Alternatively, the decline in active alternation with carer number may be a

468   consequence of the null model failing to detect active alternation in large groups. In our

469   study, expected alternation approached 90% in 4-5 carer nests, which contrasts with

470   expected synchrony of just 50% or so in larger groups; thus, the scope for detection of

471   active synchrony is greater than it is for active alternation. However, it is unlikely that

472   detectability alone caused our result because Savage et al.'s (2017) study of chestnut-

473   crowned babblers used the same null model approach across a greater range of group

474   sizes (2-6), with expected alternation of >80% at large group sizes, and yet they did not

475   observe the same trend.

476   We observed no significant difference in active alternation by carers of different

477   status and subsequent analysis revealed that the level of active alternation was highly

478   repeatable within nests rather than within individual carers. These results suggest that

479   that if alternation is adaptive, it is performed by all carers at the nest to their collective

480   benefit, rather than by certain individuals. However, we cannot disentangle whether this

481   is a function of common nest factors or common social environment (Ihle et al. 2019b).

482   For example, some nests may experience regular disturbance by predators that

483   temporarily prevents feeding, causing the feeding cycles of carers to align, thus

484   increasing alternation. Our finding that active alternation was unaffected by carer status

485   could be explained by the interests of breeders and helpers being closely aligned.

486   Long-tailed tit helpers gain only kin-selected benefits from their helping behavior

487   (Meade and Hatchwell 2010, Hatchwell et al. 2014), and rates of extra-pair paternity

488   and intraspecific brood parasitism are low (Hatchwell et al. 2002) so all carers have a

489   shared interest in raising a related brood. In species where the dynamics of conflict are

490   different the extent of alternation may vary between carers of different status whilst still

491   ultimately providing the adaptive function of conflict resolution (Johnstone et al. 2014,

492   Johnstone and Savage 2019). This may explain why breeders alternate more to ensure

493   the contribution of helpers in chestnut-crowned babblers (Savage et al. 2017) and our

494   contrary finding does not necessarily invalidate conflict resolution as a function of

495   alternation in long-tailed tits.

496   One proposed function of synchrony is that it facilitates accurate alternation via

497   monitoring of other carers (Mariette and Griffith 2012, 2015, Bebbington and Hatchwell

498   2016), but there are other adaptive hypotheses for synchrony that do not require

499   alternation *per se*. Synchrony may decrease parental activity at the nest, thereby

500   reducing its conspicuousness and exposure to predators (Raihani et al. 2010, Mariette

501   and Griffith 2012, 2015, Leniowski and Wegrzyn 2018, Khwaja et al. 2019). However,

502   our finding that active synchrony was broadly consistent across group sizes does not

503   support this hypothesis, because in larger groups, where the risk of exposing the nest

504   to a predator is greater, active synchrony should increase. Alternatively, synchrony

505   may ensure an even distribution of food between chicks by preventing monopolization

506   (Shen et al. 2010, Mariette and Griffith 2012, 2015). However, contrary to our results,

507   this hypothesis predicts that synchrony would decrease with group size as the

508   increased rate of food delivery reduced the risk of monopolization. A detailed

509   investigation of the consequences of synchrony for parental activity at the nest, the

510   probability of predation, nestling growth and survival is beyond the scope of the current

511   paper.

512   Helpers synchronized their nest visits with other carers more than breeders did.

513   One explanation for this result is that helpers synchronize visits to signal their effort to

514   other carers to increase their 'prestige' (Zahavi 1977a,b). Most studies have refuted

515   this hypothesis (e.g. McDonald et al. 2008a,b, Nomano et al. 2015, Raihani et al.

516   2010), but there is some limited empirical support (Doutrelant and Covas 2007, Trapote

517   et al. 2021). For example, in carrion crows *Corvus corone*, subordinate female helpers

518   overlapped their feeding visits with breeders more than either male helpers or breeders

519   did. This was interpreted as a 'pay-to-stay' system where female helpers, which are

520   typically unrelated to breeders (unlike male helpers), signal their effort to remain within

521   the group until they achieve breeding status in their own group (Trapote et al. 2021).

522   Our results appear to support this hypothesis, but we think it is an unlikely explanation

523   for the relatively high synchrony exhibited by long-tailed tit helpers. Helpers are

524   expected to gain direct fitness via signaling when helping is payment of rent for living

525   on the breeders' territory (Gaston 1978, Kokko et al. 2002, Trapote et al. 2021), or if it

526   increases an individual's social status or perceived quality among other carers (Zahavi

527   1977a,b, Lotem et al. 1999). However, studies have yet to detect any direct fitness

528   benefits for helpers from their altruistic care in long-tailed tits (Hatchwell 2016).

529   Therefore, unlike carrion crows, group membership, breeding opportunities and future

530   direct fitness are not determined by helping behavior (Napper and Hatchwell 2016,

531   Meade and Hatchwell 2010), so there seems to be no advantage for helpers from

532   signaling their quality to other carers.

533   We suggest instead that variation in synchrony between carers of different status

534   may be a consequence of group foraging. Collective foraging behavior may explain

535   synchrony in zebra finches *Taenioptgia guttata* (Mariette and Griffith 2012, 2015),

536   where it is thought to reduce predation risk for carers. This hypothesis would not

537   necessarily predict that carers of different status should differ consistently in their

538   degree of synchrony, nor that synchrony would be highly repeatable within individuals,

539   unless also coupled with a defined feeding order. If helpers tend to follow breeders in

540   their visits to the nest, the way in which we measured synchrony means that they

541   would also tend to have a relatively high synchrony score. Apparent following behavior

542   could result from helpers shadowing breeders or from breeders delaying feeds until

543   helpers are present. In the redirected helping system of long-tailed tits, helpers are

544   likely to be less familiar with the brood and local area than breeders are, so the idea

545   that helpers shadow foraging breeders is plausible. Furthermore, the suggestion that

546   individuals may adopt specific roles, i.e. as leader or follower, when foraging or when

547   visiting nests may also explain why synchrony is individually repeatable. However,

548   more detailed observations of the behavior of individuals as they approach the nest

549   and the sequence in which they do so are needed to investigate these possibilities.

550   Active coordination by helpers was not influenced significantly by their kinship with

551   the breeders they assisted. This result was unexpected because helper decisions in

552   long-tailed tits, both in who to help and how much to help, are a function of their

553   relatedness to the breeding pair (Russell and Hatchwell 2001, Nam et al. 2010,

554   Leedale et al. 2018, 2020). Additionally, if alternation functions to resolve conflict

555   between carers, we might expect greater conflict in less related groups, so we

556 anticipated some effect of kinship on coordination. Comparisons with the repeatability

557 results are potentially instructive. The kinship of a helper to breeders is a function of the

558 group, i.e. it is the dyadic relatedness between a helper and a specific male or female

559 breeder, rather than a property of the helper *per se*. We suggested above that the

560 repeatability of alternation within groups could be a function of the social environment

561 (e.g. group composition), which could include kinship. However, the absence of a

562 kinship effect, suggests either that some ecological rather than social factor specific to

563 a nest or group drives the repeatability of alternation, or that a social factor other than

564 kinship (e.g. group familiarity) influences alternation. In contrast, repeatability in

565 synchrony was at the level of individuals rather than groups. Therefore, it is perhaps

566 unsurprising that synchrony of helpers was not predicted by their kinship with breeders,

567 given that this is a property of two or more individuals rather than an individual helper.

568 To our knowledge, this is the first study to explicitly test whether kinship influences

569 coordination, and it would be interesting to explore this question more widely, and

570 especially in species where the interests of helpers and breeders are not so closely

571 aligned.

572   Several explanations for active alternation and synchrony have linked the two

573 phenomena, with synchrony proposed as an adaptation for ensuring accurate

574 monitoring of other carers, thus enabling alternation (Mariette and Griffith 2012, 2015,

575 Bebbington and Hatchwell 2016). Whilst studies have often found a correlation

576 between alternation and synchrony, several of our findings suggest that alternation and

577 synchrony may, in fact, fulfil separate functions. Firstly, active alternation declined with

578 increasing carer number, whilst active synchrony did not. Secondly, active synchrony

579 varied between carers of different status, whilst active alternation did not. Finally, active

580 alternation was repeatable between watches at the same nest, whilst active synchrony

581 was repeatable between watches of the same individual. The independence of

582 alternation and synchrony is also supported by a study of blue tits *Cyanistes caeruleus*

583 which demonstrated that synchrony, but not alternation varied between different

584 habitats (Lejeune et al. 2019). This is compatible with Johnstone et al. (2014)'s theory

585 of conflict resolution for alternation and our suggestions of shadowing for synchrony.

586 Studies of coordination in parental care are still in their infancy, and much work

587 remains to be done to fully understand its occurrence, function, and the causes of

588 interspecific variation. Careful analysis of provisioning visits is essential to generate

589 appropriate null models against which observed schedules of visits can be compared.

590 In this study, adopting a conservative approach, we have shown that coordination is, to

591 some extent, a function of group size in the cooperative breeding system of long-tailed

592 tits. We have also shown that some measures of coordination vary with social role

593 within groups, but not with the kinship of helpers. In addition, we highlight the need for

594 investigation of the proximate mechanisms by which individuals coordinate care, such

595 as delaying feeding or shadowing others, as well as a need for experimental studies

596 that can isolate and test social and environmental influences that are hard to take

597 account of in observational studies. Finally, despite coordination of care being quite

598 widely demonstrated in nature, the function of these behaviors remains poorly

599 understood.

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Figure legends

Figure 1. Illustration of sequence of feeding visits at a hypothetical provisioning watch. Breeding male visits in blue, breeding female visits in red and helper 1 visits in yellow. Alternated and synchronized visits denoted by asterisk (*) and triangle (▼), respectively.

Figure 2. Plots of observed (orange) and expected (purple) percent of maximum alternation achieved by carers *versus*: (a) the number of carers observed provisioning each nest during a watch; and (b) the total provisioning rate by all carers at a nest during a given watch. Predicted relationships (± 95% CI) are fitted from GLMMs, see Table 1. Total N = 795 watches on 250 nests for each data type.

Figure 3. Plots of observed (orange) and expected (purple) percent of maximum synchrony achieved by carers *versus*: (a) the number of carers observed provisioning each nest during a watch; and (b) the total provisioning rate by all carers at a nest during a given watch. Predicted relationships (± 95% CI) are fitted from GLMMs, see Table 1. Total N = 795 watches on 250 nests for each data type.

Figure 4. Estimates (R) of the within nest repeatability (Nest ID) and within individual repeatability (Carer ID) for the absolute number of actively (a) alternated and (b) synchronized visits. Estimates calculated from linear mixed effects models (2.5-97.5% CI).

Figure 5. Boxplots of observed (orange) and expected (purple) percentage of visits alternated by a given individual during a watch *versus*: (a) the status of a carer; (b) the kinship between a helper and the breeding male; and (c) the kinship between a helper and the breeding female. Total N = 408 samples from 130 unique helpers from 273 watches at 95 nests for each data type.

Figure 6. Boxplots of observed (orange) and expected (purple) percentage of visits synchronized by a given individual during a watch *versus*: (a) the status of a carer; (b) the kinship between a helper and the breeding male; and (c) the kinship between a helper and the breeding female. Total N = 408 samples from 130 unique helpers from 273 watches at 95 nests for each data type.

Tables and table legends

Table 1. Details of response variables, fixed effects, random effects used in models and non-model terms.

Response variables	Description
Alternated or synchronized visits (collective)	The absolute number of alternated or synchronized provisioning visits performed by all carers in a group during a watch.
Alternated or synchronized visit (individual)	The absolute number of alternated or synchronized provisioning visits performed by a given carer during a watch.
Active alternated or active synchronized visits (individual)	The absolute number of actively alternated or synchronized visits performed by a given carer during a given watch, calculated by subtracting a carer's expected values from their observed values for each watch.
Random effects	**Description**
Year	The unique identifier for which field season year the provisioning watch was performed in. Included to account for variation caused by site wide environmental factors which may vary between years.
Nest ID	The unique identifier for each nest. Because multiple watches were performed at the same nest, this was included to account for variation caused by factors specific to the local environment e.g. invertebrate abundance and microclimate.
Watch ID	The unique identifier for each nest watch. Included to account for similarity between observed and expected data from the same watch.

Row reference	Observation level random effect, included as per recommendation from Ihle et al. (2019a) to account for overdispersion in Poisson-distributed models.
Individual Carer IDs	The unique identity of each individual carer present during a watch ('Male ID', 'Female ID', 'Helper1 ID', 'Helper2 ID' and 'Helper3 ID'). Included as random effects to account for between individual variation in provisioning behavior because some individuals were observed provisioning over multiple watches and nests (MacColl and Hatchwell 2003, Adams et al. 2015). However, 37/795 watches (4.7%) featured visits by a single unringed carer, these individuals could therefore not be distinguished with a unique Carer ID. Repeating analyses with these watches omitted produced qualitatively the same results in all cases.
Collective Carer ID	The unique identifier for a particular combination of carers seen provisioning during a given watch. Few pairs persist across years due to high annual mortality (Meade et al. 2010) and divorce rate (Hatchwell et al. 2000) and carer combinations may change daily as helpers join and leave, so 'Collective Carer ID' was included to account for between group variation in provisioning coordination.
Fixed effects	**Description**
Data type	Factor designating whether data were observed (from field data) or expected (generated by null model). As we used expected values as our baseline level of coordination 'Data type' was therefore a proxy for the level of active coordination performed. Our assessment of whether other terms significantly impact active coordination was investigated by looking at their interaction with 'Data type'.

Provisioning rate (collective)	The total number of provisioning visits performed by all carers during a given watch per hour, modelled as continuous numerical values (mean: 24.1; range: 5.8-69.2).
Provisioning rate (individual)	The total number of provisioning visits performed by a given carer during a provisioning watch per hour, modelled as continuous numerical values (mean: 9.6; range: 0.5-34.3).
Brood size	The number of live chicks recorded at the nest on day 11, modelled as integer values (median: 8; range 1-12). Included because prior studies have shown that brood size influences provisioning behavior by mediating brood demand (Meade et al 2010). We used a single recorded measure of brood size, rather than recording brood size after each watch to minimise nest disturbance and because brood reductions are rare in long-tailed tits, having only a 0.2% daily chick mortality rate via starvation (Hatchwell et al. 2004).
Carer number	The number of adult birds that provisioned chicks during a given provisioning watch, modelled as an ordinal factor: 5>4>3>2.
Watch duration	The length of time in minutes between the first and last feeding visit during a provisioning watch, included as an interaction term with 'Data type' to account for potential artificial coordination caused by setup disturbance, which would disproportionately affect shorter watches. Watch duration was modelled as a continuous numerical value.
AMax (or SMax)	To account for the upper limit of the number of alternated or synchronized visits we used the variables 'AMax' and 'SMax' which are the theoretical maximum percentage of provisioning visits that can be alternated/synchronized during a given watch, modelled as a continuous numerical value (mean: 87.5; range: 19.4-98.6). If one carer performed

	more than half the total visits then some visits exist which cannot be alternated or synchronized due to insufficient visits to alternate or synchronize with, this applies to all values of carer number. This term is used as a proxy for feed rate asymmetry, i.e. the difference between provisioning rates of male and females, used by Bebbington and Hatchwell (2016), but is also applicable for cooperative nests. AMax and SMax must always be the same value for a given watch because synchrony was defined as an alternated feed occurring within 2 minutes of the previous feed. This time restriction can always theoretically be met, so the only remaining restriction on synchrony is whether a feed can be alternated.
Brood age	The number of days since recorded hatching (day 0) of chicks at a nest, modelled as integer values (range: 6-16).
Hatch date	The number of days after 1st of March each year, modelled as integer values (median: 3rd May; range: 16th April – 6th June).
Time of day	The number of hours since the beginning of the day on which the provisioning watch was performed, modelled as a numerical value. Included because previous studies on the same population found higher provisioning activity immediately following sunrise (MacColl and Hatchwell 2002, Hatchwell et al. 2004).
Sex	Binary factor representing either male or female helpers.
Carer status	Factor designating the relationship each carer had to the brood with three categories: breeding female, breeding male and helper. For our final analysis we did not sub-divide helpers by sex because our investigation on helper coordination (Alt-K, Sync-K, see results) found no effect of sex on helpers' alternation or synchrony (tables 5,6).

Kinship with father	Factor representing the pairwise relatedness of helpers to breeding male. Modelled as factors with three levels representing first order kin (r = 0.50), second order kin (r = 0.25) and unrelated individuals (r = 0.00). These levels were selected in accordance with results from previous studies demonstrating kinship of helpers with breeders (Leedale et al. 2018, 2020).
Kinship with mother	Factor representing pairwise relatedness of helper to breeding female.
Non-model terms	**Description**
Percent of AMax (or Percent of SMax)	The overall percentage of visits which could be alternated/synchronized which were alternated or synchronized. These terms was used as the dependent variables in Figures 2a,b and 3a,b, being the best single metrics for visualising active coordination as they factor in both total feed rate and what proportion of visits could be alternated or synchronized.

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Table 2. Estimates and p-values for fixed effect terms on number of alternated visits per provisioning watch from generalized linear mixed effect model; N = 1,590 from 795 watches at 250 nests, significant values in bold. 'Obs' is shorthand for data observed directly from field, as opposed to expected data generated from null model.

Parameter	df	Estimate ± SE	F-value	P-value
Intercept	**1**	**2.546 ± 0.014**		**<0.001**
Data Type (relative to expected)	**1**	**Obs: 0.099 ± 0.017**	**38.11**	**<0.001**
Provisioning Rate	**1**	**0.303 ± 0.010**	**3452.27**	**<0.001**
Brood Size	**1**	**0.034 ± 0.011**	**22.88**	**<0.001**
Carer Number (relative to 2 carers)	**3**	**3: 0.135 ± 0.024**	**152.88**	**<0.001**
		4: 0.210 ± 0.029		
		5: 0.196 ± 0.050		
Watch Duration	**1**	**0.195 ± 0.008**	**1247.49**	**<0.001**
AMax	**1**	**0.131 ± 0.009**	**209.17**	**<0.001**
Brood Age	1	0.000 ± 0.007	0.01	0.973
Hatch Date	1	0.012 ± 0.008	2.21	0.126
Time of Day	1	-0.016 ± 0.010	6.76	0.055
Data Type * Provisioning Rate	1	0.017 ± 0.012	0.43	0.133
Data Type * Brood Size	1	0.004 ± 0.014	0.02	0.798

Data Type * Carer Number	**3**	**Obs, 3: -0.069 ± 0.031**	**2.68**	**0.024**
		Obs, 4: -0.094 ± 0.037		
		Obs, 5: -0.096 ± 0.067		
Data Type * Watch Duration	1	0.015 ± 0.010	2.11	0.134
Data Type * Time of Day	1	0.005 ± 0.013	0.17	0.683

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Table 3. Output values for fixed effect terms on number of synchronized visits per provisioning watch from generalized linear mixed effect model, N = 1,590 from 795 watches at 250 nests, significant values in bold.

Parameter	df	Estimate ± SE	F-value	P-value
Intercept	**1**	**1.798 ± 0.055**		**<0.001**
Data Type (relative to expected)	**1**	**Obs: 0.245 ± 0.024**	**100.94**	**<0.001**
Provisioning Rate	**1**	**0.472 ± 0.013**	**3240.41**	**<0.001**
Brood Size	**1**	**0.064 ± 0.016**	**36.85**	**<0.001**
Carer Number (relative to 2 carers)	**3**	**3: 0.113 ± 0.034** **4: 0.221 ± 0.062** **5: 0.182 ± 0.089**	**44.41**	**<0.001**
Watch Duration	**1**	**0.200 ± 0.012**	**667.33**	**<0.001**
SMax	**1**	**0.147 ± 0.013**	**127.52**	**<0.001**
Brood Age	1	0.014 ± 0.010	1.74	0.186
Hatch Date	1	0.013 ± 0.012	1.08	0.231
Time of Day	1	-0.023 ± 0.014	1.3	0.485
Data Type * Provisioning Rate	**1**	**-0.050 ± 0.015**	**19.79**	**<0.001**
Data Type * Brood Size	1	<0.001 ± 0.019	<0.01	0.969
Data Type * Carer Number	3	Obs, 3: -0.030 ± 0.041 Obs, 4: -0.061 ± 0.048 Obs, 5: -0.057 ± 0.085	0.46	0.574
Data Type * Watch Duration	1	0.017 ± 0.014	1.19	0.186
Data Type * Time of Day	1	0.024 ± 0.018	2.11	0.146

Table 4. Estimates and p-values for fixed effect terms on number of alternated visits per individual carer during a watch from generalized linear mixed effect model; N = 1,997 samples from 487 unique carers from 795 watches at 250 nests, significant values in bold.

Parameter	df	Estimate ± SE	F-value	P-value
Intercept	**1**	**1.722 ± 0.019**		**<0.001**
Data Type (relative to expected)	**1**	**Obs: 0.056 ± 0.024**	**18.07**	**<0.001**
Carer status (relative to breeding male)	**2**	**F: 0.030 ± 0.020** **H: -0.012 ± 0.028**	**49.90**	**0.037**
Individual Provisioning Rate	**1**	**0.303 ± 0.010**	**2576.93**	**<0.001**
Brood Size	**1**	**0.045 ± 0.011**	**55.89**	**<0.001**
Carer Number (relative to 2 carers)	**3**	**3: 0.008 ± 0.026** **4: 0.027 ± 0.032** **5: -0.093 ± 0.053**	**31.05**	**0.018**
Watch Duration	**1**	**0.181 ± 0.008**	**1089.08**	**<0.001**
AMax	**1**	**0.152 ± 0.009**	**280.17**	**<0.001**
Brood Age	**1**	**0.024 ± 0.007**	**19.37**	**<0.001**
Hatch Date	1	0.015 ± 0.008	3.44	0.079
Time of Day	**1**	**-0.023 ± 0.010**	**15.61**	**0.003**
Data Type * Carer status	3	Obs, F: 0.002 ± 0.028 Obs, H: 0.009 ± 0.039	0.92	0.975
Data Type * Individual Provisioning Rate	1	0.018 ± 0.012	4.38	0.137
Data Type * Brood Size	1	0.007 ± 0.014	0.01	0.609

Data Type * Carer Number	3	Obs, 3: -0.056 ± 0.033	1.28	0.207
		Obs, 4: -0.078 ± 0.041		
		Obs, 5: -0.060 ± 0.070		
Data Type * Watch Duration	**1**	**0.021 ± 0.010**	**3.93**	**0.044**
Data Type * Time of Day	1	0.005 ± 0.013	0.12	0.726

852

Table 5. Estimates and p-values for fixed effect terms on number of synchronized visits per provisioning individual carer during a watch from generalized linear mixed effect model; N = 1,997 samples from 487 unique carers from 795 watches at 250 nests, significant values in bold.

Parameter	df	Estimate ± SE	F-value	P-value
Intercept	**1**	**0.905 ± 0.033**		**<0.001**
Data Type (relative to expected)	**1**	**Obs: 0.301 ± 0.033**	**59.70**	**<0.001**
Carer status (relative to breeding male)	2	F: 0.059 ± 0.033 H: 0.035 ± 0.042	8.89	0.210
Individual Provisioning Rate	**1**	**0.444 ± 0.014**	**2132.76**	**<0.001**
Brood Size	**1**	**0.089 ± 0.017**	**72.06**	**<0.001**
Carer Number (relative to 2 carers)	**3**	**3: 0.097 ± 0.039** **4: 0.236 ± 0.048** **5: 0.164 ± 0.075**	**37.97**	**0.019**
Watch Duration	**1**	**0.180 ± 0.012**	**472.16**	**<0.001**
SMax	**1**	**0.177 ± 0.015**	**162.39**	**<0.001**
Brood Age	**1**	**0.071 ± 0.010**	**60.29**	**<0.001**
Hatch Date	1	0.011 ± 0.015	0.36	0.464
Time of Day	**1**	-0.052 ± 0.014	9.46	**0.005**
Data Type * Carer status	**3**	**Obs, F: -0.079 ± 0.037** **Obs, H: 0.042 ± 0.051**	**1.56**	**0.024**
Data Type * Individual Provisioning Rate	**1**	**-0.084 ± 0.016**	**21.42**	**<0.001**

Data Type * Brood Size	1	0.010 ± 0.019	0.11	0.602
Data Type * Carer Number	**3**	**Obs, 3: -0.133 ± 0.044**	**7.41**	**<0.001**
		Obs, 4: -0.234 ± 0.053		
		Obs, 5: -0.252 ± 0.089		
Data Type * Watch Duration	1	0.023 ± 0.014	1.74	0.092
Data Type * Time of Day	**1**	**0.004 ± 0.017**	**5.80**	**0.016**

853

Table 6. Estimates and p-values for fixed effect terms on number of alternated visits per individual helper during a watch from generalized linear mixed effect model; N = 408 samples from 130 unique helpers from 273 watches at 95 nests, significant values in bold.

Parameter	df	Estimate ± SE	F-value	P-value
Intercept	**1**	**1.486 ± 0.159**		**<0.001**
Data Type (relative to expected)	1	Obs: 0.038 ± 0.190	0.97	0.782
Kinship with Breeding Male (relative to r = 0)	2	0.25: 0.059 ± 0.088 0.5: -0.022 ± 0.057	1.47	0.837
Kinship with Breeding Female (relative to r = 0)	2	0.25: -0.079 ± 0.141 0.5: 0.012 ± 0.073	6.88	0.837
Sex (relative to female)		M: -0.024 ± 0.057	0.04	0.728
Individual Provisioning Rate	**1**	**0.352 ± 0.022**	**786.89**	**<0.001**
Brood Size	1	0.024 ± 0.026	0.06	0.139
Carer Number	3	3: 0.166 ± 0.147 4: 0.206 ± 0.155 5: 0.069 ± 0.164	8.63	0.088
Watch Duration	**1**	**0.228 ± 0.020**	**390.19**	**<0.001**
AMax	**1**	**0.070 ± 0.030**	**5.84**	**0.019**
Brood Age	1	0.019 ± 0.016	1.47	0.238
Hatch Date	1	0.033 ± 0.018	3.44	0.078
Time of Day	1	-0.022 ± 0.023	3.76	0.175
Data Type * Kinship with Breeding Male	2	Obs, 0.25: -0.066 ± 0.123	0.22	0.818

		Obs, 0.5: 0.017 ± 0.075		
Data Type * Kinship with Breeding Female	2	Obs, 0.25: 0.039 ± 0.196 Obs, 0.5: -0.017 ± 0.102	0.04	0.965
Data Type * Sex	1	Obs, M: 0.020 ± 0.080	0.16	0.804
Data Type * Individual Provisioning Rate	1	0.025 ± 0.028	1.30	0.377
Data Type * Brood Size	1	0.008 ± 0.035	0.01	0.828
Data Type * Carer Number	3	Obs, 3: -0.065 ± 0.172 Obs, 4: -0.077 ± 0.178 Obs, 5: -0.048 ± 0.191	0.07	0.972
Data Type * Watch Duration	1	0.023 ± 0.025	0.92	0.348
Data Type * Time of Day	1	-0.001 ± 0.032	0.00	0.984

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Table 7. Estimates and p-values for fixed effect terms on number of synchronized visits per individual helper during a watch from generalized linear mixed effect model; N = 408 samples from 130 unique helpers from 273 watches at 95 nests, significant values in bold.

Parameter	df	Estimate ± SE	F-value	P-value
Intercept	**1**	**0.808 ± 0.229**		**<0.001**
Data Type (relative to expected)	1	Obs: 0.648 ± 0.245	25.37	**<0.001**
Kinship with Breeding Male (relative to r = 0)	2	0.25: 0.084 ± 0.128 0.5: 0.029 ± 0.084	1.60	0.683
Kinship with Breeding Female (relative to r = 0)	2	0.25: 0.208 ± 0.192 0.5: 0.067 ± 0.106	1.33	0.731
Sex (relative to female)		M: -0.036 ± 0.081	3.01	0.562
Individual Provisioning Rate	**1**	**0.432 ± 0.030**	**558.01**	**<0.001**
Brood Size	**1**	**0.064 ± 0.039**	**4.30**	**0.034**
Carer Number (relative to 2 carers)	**3**	**3: 0.132 ± 0.211** **4: 0.285 ± 0.221** **5: 0.116 ± 0.237**	**5.17**	**0.047**
Watch Duration	**1**	**0.187 ± 0.029**	**153.70**	**<0.001**
SMax	**1**	**0.130 ± 0.045**	**8.20**	**0.004**
Brood Age	**1**	**0.047 ± 0.022**	**5.44**	**0.029**
Hatch Date	1	0.033 ± 0.030	1.26	0.276
Time of Day	**1**	**-0.073 ± 0.032**	**7.16**	**0.026**
Data Type * Kinship with Breeding Male	2	Obs, 0.25: -0.016 ± 0.158	0.01	0.982

		Obs, 0.5: 0.016 ± 0.097		
Data Type * Kinship with Breeding Female	2	Obs, 0.25: -0.180 ± 0.246	0.43	0.517
		Obs, 0.5: -0.122 ± 0.132		
Data Type * Sex	1	Obs, M: 0.002 ± 0.100	0.50	0.982
Data Type * Individual Provisioning Rate	1	-0.050 ± 0.035	0.27	0.158
Data Type * Brood Size	1	-0.001 ± 0.045	0.79	0.981
Data Type * Carer Number	3	Obs, 3: -0.409 ± 0.222	1.73	0.190
		Obs, 4: -0.487 ± 0.229		
		Obs, 5: -0.470 ± 0.244		
Data Type * Watch Duration	**1**	**0.063 ± 0.031**	**3.52**	**0.043**
Data Type * Time of Day	1	0.039 ± 0.041	0.92	0.337

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