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1 **Coordination of care by breeders and helpers in**
2 **the cooperatively breeding long-tailed tit,**
3 ***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.

41

42

43 **Coordination of care by breeders and helpers in the** 44 **cooperatively breeding long-tailed tit**

45 In species with biparental and cooperative brood care, multiple carers cooperate by
46 contributing costly investment to raise a shared brood. However, shared benefits and
47 individual costs also give rise to conflict among carers over investment. Coordination of
48 provisioning visits has been hypothesized to facilitate the resolution of this conflict,
49 preventing exploitation, and ensuring collective investment in the shared brood. We
50 used a 26-year study of long-tailed tits, *Aegithalos caudatus*, a facultative cooperative
51 breeder, to investigate whether care by parents and helpers is coordinated, whether
52 there are consistent differences in coordination between individuals and reproductive
53 roles, and whether coordination varies with helper relatedness to breeders.

54 Coordination takes the form of turn-taking (alternation) or feeding within a short time
55 interval of another carer (synchrony), and both behaviors were observed to occur more
56 than expected by chance, i.e. 'active' coordination. First, we found that active
57 alternation decreased with group size while active synchrony occurred at all group
58 sizes. Secondly, we show that alternation was repeatable between observations at the
59 same nest, while synchrony was repeatable between observations of the same
60 individual. Active synchrony varied with reproductive status, with helpers synchronizing
61 visits more than breeders, although active alternation did not vary with reproductive
62 status. Finally, we found no significant effect of relatedness on either alternation or
63 synchrony exhibited by helpers. In conclusion, we demonstrate active coordination of
64 provisioning by carers and conclude that coordination is a socially plastic behavior
65 depending on reproductive status and the number of carers raising the brood.

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

67 **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 ~3km² 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 (\pm 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).

278 **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.

292 **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.

304 **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).

371 **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 *Taeniopygia 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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601

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815 **Figure legends**

816 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.

817 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 (\pm 95% CI) are fitted from GLMMs, see Table 1. Total N = 795 watches on 250 nests for each data type.

818 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 (\pm 95% CI) are fitted from GLMMs, see Table 1. Total N = 795 watches on 250 nests for each data type.

819 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).

820 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.

821 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.

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823 **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

	<p>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.</p>
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 1 st of March each year, modelled as integer values (median: 3 rd May; range: 16 th April – 6 th June).
Time of day	<p>The number of hours since the beginning of the day on which the provisioning watch was performed, modelled as a numerical value.</p> <p>Included because previous studies on the same population found higher provisioning activity immediately following sunrise (MacColl and Hatchwell 2002, Hatchwell et al. 2004).</p>
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).
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Kinship with mother	Factor representing pairwise relatedness of helper to breeding female.
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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 \pm SE	F-value	P-value
Intercept	1	2.546 \pm 0.014		<0.001
Data Type (relative to expected)	1	Obs: 0.099 \pm 0.017	38.11	<0.001
Provisioning Rate	1	0.303 \pm 0.010	3452.27	<0.001
Brood Size	1	0.034 \pm 0.011	22.88	<0.001
Carer Number (relative to 2 carers)	3	3: 0.135 \pm 0.024 4: 0.210 \pm 0.029 5: 0.196 \pm 0.050	152.88	<0.001
Watch Duration	1	0.195 \pm 0.008	1247.49	<0.001
AMax	1	0.131 \pm 0.009	209.17	<0.001
Brood Age	1	0.000 \pm 0.007	0.01	0.973
Hatch Date	1	0.012 \pm 0.008	2.21	0.126
Time of Day	1	-0.016 \pm 0.010	6.76	0.055
Data Type * Provisioning Rate	1	0.017 \pm 0.012	0.43	0.133
Data Type * Brood Size	1	0.004 \pm 0.014	0.02	0.798

Data Type * Carer Number	3	Obs, 3: -0.069 ±	2.68	0.024
		0.031		
		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 \pm SE	F-value	P-value
Intercept	1	1.798 \pm 0.055		<0.001
Data Type (relative to expected)	1	Obs: 0.245 \pm 0.024	100.94	<0.001
Provisioning Rate	1	0.472 \pm 0.013	3240.41	<0.001
Brood Size	1	0.064 \pm 0.016	36.85	<0.001
Carer Number (relative to 2 carers)	3	3: 0.113 \pm 0.034 4: 0.221 \pm 0.062 5: 0.182 \pm 0.089	44.41	<0.001
Watch Duration	1	0.200 \pm 0.012	667.33	<0.001
SMax	1	0.147 \pm 0.013	127.52	<0.001
Brood Age	1	0.014 \pm 0.010	1.74	0.186
Hatch Date	1	0.013 \pm 0.012	1.08	0.231
Time of Day	1	-0.023 \pm 0.014	1.3	0.485
Data Type * Provisioning Rate	1	-0.050 \pm 0.015	19.79	<0.001
Data Type * Brood Size	1	<0.001 \pm 0.019	<0.01	0.969
Data Type * Carer Number	3	Obs, 3: -0.030 \pm 0.041 Obs, 4: -0.061 \pm 0.048 Obs, 5: -0.057 \pm 0.085	0.46	0.574
Data Type * Watch Duration	1	0.017 \pm 0.014	1.19	0.186
Data Type * Time of Day	1	0.024 \pm 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

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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 \pm SE	F-value	P-value
Intercept	1	0.905 \pm 0.033		<0.001
Data Type (relative to expected)	1	Obs: 0.301 \pm 0.033	59.70	<0.001
Carer status (relative to breeding male)	2	F: 0.059 \pm 0.033 H: 0.035 \pm 0.042	8.89	0.210
Individual Provisioning Rate	1	0.444 \pm 0.014	2132.76	<0.001
Brood Size	1	0.089 \pm 0.017	72.06	<0.001
Carer Number (relative to 2 carers)	3	3: 0.097 \pm 0.039 4: 0.236 \pm 0.048 5: 0.164 \pm 0.075	37.97	0.019
Watch Duration	1	0.180 \pm 0.012	472.16	<0.001
SMax	1	0.177 \pm 0.015	162.39	<0.001
Brood Age	1	0.071 \pm 0.010	60.29	<0.001
Hatch Date	1	0.011 \pm 0.015	0.36	0.464
Time of Day	1	-0.052 \pm 0.014	9.46	0.005
Data Type * Carer status	3	Obs, F: -0.079 \pm 0.037 Obs, H: 0.042 \pm 0.051	1.56	0.024
Data Type * Individual Provisioning Rate	1	-0.084 \pm 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 ±	7.41	<0.001
		0.044		
		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

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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	2	Obs, 0.25: 0.039 ± 0.196	0.04	0.965
Breeding Female		Obs, 0.5: -0.017 ± 0.102		
Data Type * Sex	1	Obs, M: 0.020 ± 0.080	0.16	0.804
Data Type * Individual	1	0.025 ± 0.028	1.30	0.377
Provisioning Rate				
Data Type * Brood Size	1	0.008 ± 0.035	0.01	0.828
Data Type * Carer Number	3	Obs, 3: -0.065 ± 0.172	0.07	0.972
		Obs, 4: -0.077 ± 0.178		
		Obs, 5: -0.048 ± 0.191		
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 \pm SE	F-value	P-value
Intercept	1	0.808 \pm 0.229		<0.001
Data Type (relative to expected)	1	Obs: 0.648 \pm 0.245	25.37	<0.001
Kinship with Breeding Male (relative to r = 0)	2	0.25: 0.084 \pm 0.128 0.5: 0.029 \pm 0.084	1.60	0.683
Kinship with Breeding Female (relative to r = 0)	2	0.25: 0.208 \pm 0.192 0.5: 0.067 \pm 0.106	1.33	0.731
Sex (relative to female)		M: -0.036 \pm 0.081	3.01	0.562
Individual Provisioning Rate	1	0.432 \pm 0.030	558.01	<0.001
Brood Size	1	0.064 \pm 0.039	4.30	0.034
Carer Number (relative to 2 carers)	3	3: 0.132 \pm 0.211 4: 0.285 \pm 0.221 5: 0.116 \pm 0.237	5.17	0.047
Watch Duration	1	0.187 \pm 0.029	153.70	<0.001
SMax	1	0.130 \pm 0.045	8.20	0.004
Brood Age	1	0.047 \pm 0.022	5.44	0.029
Hatch Date	1	0.033 \pm 0.030	1.26	0.276
Time of Day	1	-0.073 \pm 0.032	7.16	0.026
Data Type * Kinship with Breeding Male	2	Obs, 0.25: -0.016 \pm 0.158	0.01	0.982

		Obs, 0.5: 0.016 ± 0.097		
Data Type * Kinship with	2	Obs, 0.25: -0.180 ±	0.43	0.517
Breeding Female		0.246		
		Obs, 0.5: -0.122 ± 0.132		
Data Type * Sex	1	Obs, M: 0.002 ± 0.100	0.50	0.982
Data Type * Individual	1	-0.050 ± 0.035	0.27	0.158
Provisioning Rate				
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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