

1 **Title**

2 Songbird parents coordinate offspring provisioning at fine spatio-temporal scales.

3

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14 **Abstract**

15 For parents, rearing offspring together is far from a purely cooperative exercise, as a conflict of interest
16 ('sexual conflict') exists over their optimum level of care. Recent theory emphasises that sexual conflict
17 can be evolutionarily resolved, and complete parental cooperation can occur if parents directly respond
18 ('negotiate') to each other and coordinate their level of care. Despite numerous experiments show that
19 parents are responsive to each other, we still lack empirical evidence of the behavioural mechanisms by
20 which this negotiation occurs. In this study, we investigated the spatio-temporal coordination of
21 parental provisioning behaviour as a possible mechanism of negotiation over parental care. We
22 deployed an automated radio-tracking technology to track the provisioning activity of wild great tit (*Parus*
23 *major*) pairs during chick rearing. Our analyses represent the first detailed spatial and temporal description
24 of foraging coordination in songbird parents in a natural context. We demonstrate that the foraging
25 behaviour of the two parents is highly coordinated in space and time, with parents changing their foraging
26 locations in conjunction with their partners' movements. Therefore, foraging coordination could be a
27 mechanism by which parents directly monitor and respond to each other's level of investment.

28

29 **Keywords:** Coordination, negotiation, cooperation, parental care, sexual conflict

30 Introduction

31 Parental care is a source of both cooperation and conflict for parents (Royle, Smiseth & Kölliker
32 2012). While caring for young, parents are expected to cooperate as they both invest in the common
33 goal of successfully raising offspring. On the other hand, since parental care is costly for each carer in
34 terms of reduced reproductive opportunities or survival (Williams 1966), each parent is also inclined to
35 exploit the partner and provide a smaller share of the care (hence a 'sexual conflict' exists over the
36 evolutionary interests of the two parents) (Trivers 1972; Lessells 2006). A central goal in evolutionary
37 biology is to understand how this sexual conflict is resolved and whether parents can reach a
38 cooperative agreement over how much to care for offspring (Houston & Davies 1985; Lessells 2006;
39 Servedio *et al.* 2019).

40 Game theoretical models have shown that the evolutionary outcome of sexual conflict depends
41 on the behavioural ('negotiation') rules that parents adopt to assess and respond to each other's level of
42 care over the offspring rearing period (McNamara, Gasson & Houston 1999; McNamara *et al.* 2003;
43 Lessells & McNamara 2012; Johnstone *et al.* 2014; Johnstone & Savage 2019). For instance, early models
44 (McNamara, Gasson & Houston 1999; McNamara *et al.* 2003; Lessells & McNamara 2012) predict that
45 sexual conflict lowers the amount of parental care and reduces parent and offspring fitness compared to
46 a cooperative situation, *i.e.*, each carer withholds part of its potential investment to avoid being
47 exploited by the partner (Lessells & McNamara 2012). McNamara, Gasson and Houston (1999)'s and
48 McNamara *et al.* (2003)'s models do not formally specify the negotiation mechanism through which
49 parents monitor the partner's contribution, but in Lessells & McNamara model, parents decide how
50 much to invest based on the current state of the offspring (which, in turn, reflects the cumulative
51 amount of past investment by the two parents). Recent models, however, show that if parents directly
52 assess each other's behaviour by coordinating their provisioning activity, such as taking turns of duties,
53 the expected outcome is that parents increase parental care, maximising both parent and offspring

54 fitness (Johnstone *et al.* 2014; Johnstone & Savage 2019) (Fig. 1). Because the evolutionary outcome of
55 sexual conflict strictly depends on how parents acquire information and respond to partner's care levels,
56 there is a renewed interest to understand the negotiation mechanisms that parents adopt when caring
57 for young (Griffith 2019).

58 Negotiation mediated via offspring behaviour has been widely investigated in the field. In birds
59 for instance, parents are highly responsive to offspring begging calls (Kilner & Johnstone 1997) and
60 playback experiments of offspring begging elicit an increase of parental provisioning (Hinde & Kilner
61 2007). However, it is not yet fully understood how negotiation mediated via direct response to the
62 partner's behaviour occurs in nature. Empirical studies in songbirds have indicated that individuals
63 modify their provisioning rate in response to the partner's experimentally manipulated behaviour, e.g.,
64 selective playback, handicapping manipulations (reviewed in Harrison *et al.* (2009)). More recently, it
65 has also been argued that parents alternate their visits at the nest more than expected by chance
66 because they actively monitor and respond to each visit of the partner (Johnstone *et al.* 2014; Savage *et al.*
67 *al.* 2017); (but see Schlicht *et al.* (2016) and Baldan, Hinde and Lessells (2019)). Therefore, parents are
68 behaviourally responsive to each other, but it is not currently known which behavioural mechanisms are
69 underlying these responses. One possible mechanism is that parents forage in proximity to each other,
70 directly monitor the foraging behaviour of their partner and adjust their own contribution. This
71 knowledge gap hinders our ability to understand which negotiation rules are used by parents while
72 caring the young, and in turn, how sexual conflict could be ultimately resolved (Griffith 2019). And it
73 persists due to the difficulties in collecting provisioning data beyond video recordings or provisioning
74 patterns at the nest (Savage & Hinde 2019).

75 Fortunately, recent advances in remote monitoring have allowed the study of complex
76 interaction networks between individuals at small spatial and temporal resolution (Krause *et al.* 2013;
77 Smith & Pinter-Wollman 2020). Among these, automated tracking technologies enable researchers to

78 map animal movements and social interplays in detail, especially for species, such as songbirds, that are
79 notoriously difficult to observe in their natural settings due to small size or elevated habitat complexity
80 (Krause, Wilson & Croft 2011; Mennill *et al.* 2012; Snijders, Oers & Naguib 2017). In this study, we
81 deployed an automated radio-tracking technology, Encounternet, to track spatial movements of wild
82 great tit (*Parus major*) pairs during chick rearing with an unprecedented spatio-temporal resolution. We
83 used a metric of similarity in space use between the two parents and analytically shifted (lagged) the
84 movements of one parent relative to the other over time to test the hypothesis that parental
85 provisioning behaviour is coordinated in space and time. If parents forage at different locations over
86 time and are coordinated in space and time, we expect to find the highest parental coordination when
87 time is not lagged and lower levels of coordination when making lagged comparisons (lag zero is the
88 comparison of the location of the two parents at the same whereas lag 1 indicates that spatial locations
89 of one parent is compared with the locations of the other shifted by one time unit, Fig. 1A). If one
90 parent consistently leads the foraging movements over the other, we expect a shift to the side of the
91 leading parent (Fig. 1B). Other non-random scenarios are possible. For instance, if parents are
92 coordinating in space and time but also periodically use their foraging territory, we would expect a
93 cyclical pattern of coordination over time lag (Fig. 1C). Lastly, if parents are foraging independent from
94 each other, we expect coordination not to vary with time lag (Fig. 1D). Using this proposed method of
95 lagging temporal activity and a fine scale monitoring of space use in a free-living songbird, we can have
96 detailed information on the specific behavioural mechanisms underlying parental negotiation.

97

98 **Methods**

99 *Study species*

100 The great tit (*Parus major*) is a common passerine species belonging to the *Paridae* family, that
101 easily breeds in nest-boxes throughout Europe, North Africa and Central Asia. It is a model species for
102 studying parental care, negotiation strategies and foraging ecology (Royama 1966; Naef-Daenzer &
103 Keller 1999; Naef-Daenzer, Naef-Daenzer & Nager 2000; Hinde & Kilner 2007). During the chick
104 provisioning period, both parents feed their offspring mostly on Lepidoptera caterpillars, spiders and
105 other insects (*e.g.* adult dipterous insects) with average chick-provisioning visit frequencies up to once
106 every 2-3min per parent (Royama 1966; Naef-Daenzer, Naef-Daenzer & Nager 2000; Baldan *et al.* 2019).
107 Manual radio-tracking studies on chick-provisioning individuals have shown that great tit parents forage
108 by sampling trees nearby the nest site (90% of the foraging locations samples occurred within 45m from
109 the nest in Naef-Daenzer (2000)), searching for available prey (Naef-Daenzer & Keller 1999; Naef-
110 Daenzer 2000). Nevertheless, simultaneous tracking and analysing the movements of both parents has
111 never been conducted.

112 *Study population and data collection*

113 We conducted this study in 2016 in a great tit population in Roekel, a mixed woodland area in
114 Ede, the Netherlands (52°04'30.7"N, 5°42'48.9"E). This area contains around 250 nest-boxes that we
115 checked weekly from the beginning of April to determine the onset of egg laying and incubation. During
116 early egg laying, we pre-selected active great tit nests to radio-track based on their geographical
117 position. Specifically, we selected nests in which the radio-tracking array would contain relatively
118 homogenous tree coverage in all directions up to *circa* 100 m from the nest site, *i.e.*, avoiding nests close
119 to human paths and open fields. In our field site, nest-boxes were positioned every 50 meters and for
120 this study we used nests that were spaced out between 62 and 1125 m from each other.

121 We caught 16 birds (8 pairs) and fitted these with radio tags during incubation or chick rearing.
122 During the incubation period we caught five males with mist nets nearby the nest, and three females

123 with 'box nets' (te Marvelde *et al.* 2011) placed around the nest box. All the remaining individuals were
124 caught and tagged at the nest during chick provisioning. There was no effect of trapping method or
125 timing on brood characteristics such as hatching date, brood size or parental behaviour such as
126 provisioning rate during data collection (Mann-Whitney tests, all $P > 0.3$).

127 We collected radio tracking data with the automatic tracking system Encounternet
128 (Encounternet LLC, Portland, OR, U.S.A.). Encounternet consists of small radio transmitters of 0.9 g (5%
129 of the body mass of our studied individuals), fitted to the bird with a leg-looped backpack harness
130 (Rappole & Tipton 1991). These tags broadcast a radio signal every 5s, which is recorded by small
131 wireless receivers logging the ID number, time and received signal strength indication (RSSI) of every tag
132 pulse they receive (Mennill *et al.* 2012). To track spatial movements of the eight tagged pairs during
133 chick provisioning, for each pair we deployed 37 receivers around the nest site in a 75m array. We
134 placed these receivers in a triangular array consisting of three 'rings' at 25, 50 and 75 meters from the
135 nest (Fig. 2). We positioned the receivers in trees or plastic poles at *ca.* 3.5m height at a regular distance
136 of approximately 25m distance from one another. We located and surveyed the coordinates of the
137 receivers in the field with a survey-grade GPS (Ashtech ProMark 800, Santa Clara, CA, U.S.A.). At the nest
138 site, we placed one more receiver on the front side of the tree *ca.* 50 cm above the nest-box. On
139 average, parents spent 73% of their time within the array detection area (mean \pm SE: 0.73 ± 0.05) and
140 the proportion of time inside of the array negatively correlated with the number of chicks (GLMM,
141 estimate \pm SE: -1.12 ± 0.25 , $\chi^2 = 9.86$, d.f. = 1, $P = 0.002$, $N = 128$). In addition to the Encounternet array,
142 a small video camera was mounted in the roof of the nest-box and connected to an external video
143 recorder at the foot of the tree. Video recordings (720 x 576 pixels of resolution) started before 0730h
144 and ended on the recording days and were synchronized (to the nearest second) to the Encounternet
145 array to simultaneously monitor spatial movements and visits at the nest of the provisioning parents.
146 We positioned the Encounternet array and the video set-up the day prior to data collection to habituate

147 parents to their presence. We tagged all the parents at least two days before data collection to reduce
148 possible effects of tagging on provisioning activity of the parents.

149 For each Encounternet nest, we collected radio tracking data of both parents for four
150 consecutive days as part of a brood-size experiment. Here, we used 64 hours of data (eight hours from
151 0800h to 1600h for all nests) collected on the first day of the four-day period under natural and
152 unmanipulated conditions. From the video recordings, we detected a total of 1783 provisioning trips for
153 which we scored the parental sex (determined from the blackness of the crown feathers) and the times
154 that the bird entered and left the nest-box (to the nearest second). We used a triangulation algorithm
155 implemented in MATLAB (The MathWorks, Natick, MA, U.S.A.) to locate the position inside the array of
156 each tagged parents every five seconds from the radio signals logged by the receivers. This triangulation
157 algorithm provides estimated locations with an accuracy of 13.62 ± 0.54 m (mean \pm SE) (for further
158 details on the triangulation algorithm and validation test see supplementary material S1). We estimated
159 a total of 6753 unique locations within the 64 hours used in this study. At the end of the four-day study
160 period, we removed the radio-tags from the parents by catching them at the nest. Our birds were
161 equipped with tags for an average of 10.5 days (range 6-26 days).

162 *Calculation of similarity in spatial utilization distribution between parents*

163 To investigate spatial coordination between provisioning parents, we grouped the location-data
164 per hour and applied the dynamic Brownian bridge movement model (Kranstauber *et al.* 2012) to
165 estimate the utilization distributions (UDs) of each parent per hour (Fig. 2). This method uses the time
166 series of sequential locations for each individual and summarizes its movement into a 2-dimensional
167 spatial representation referred to as utilization distribution (Worton 1989). A comparison between UD
168 of different individuals, via indices of spatio-temporal overlap (Fieberg & Kochanny 2005), have been
169 used to explicitly quantify interactions between individuals (Robert, Garant & Pelletier 2012; Schauber

170 *et al.* 2015; Lewis *et al.* 2017). In this study, we compared male and female UD_s by using the earth
171 mover's distance (EMD), a measure that quantifies the similarity between two UD_s (Kranstauber, Smolla
172 & Safi 2017). Note that EMD increases with increasing dissimilarity between two UD_s, whereas it
173 assumes a value of 0 when two identical UD_s are compared (Kranstauber, Smolla & Safi 2017). We used
174 EMD as measure of spatial coordination (similarity) of male and female parents, with a high EMD value
175 representing low spatial coordination. Calculations of the parental UD_s via dynamic Brownian bridge
176 movement models and EMD were performed in the R package '*move*' (Kranstauber, Smolla & Scharf
177 2017).

178 *Statistical analysis*

179 To investigate whether parents coordinate foraging in space and time we carried out analyses at
180 different temporal scales: a broad scale (among hours) and a fine scale (among 10 minute intervals)
181 analysis. In the broad scale analysis, we used male and female hourly utilization distributions (UD_s). For
182 each nest and each day, we calculated the earth mover's distance (EMD) between the male and female
183 UD_s of the same one-hour period (e.g. male UD from 0800h to 0900h with female UD from 0800h to
184 0900h). These EMD values were defined as "lag 0" EMD as they represent the observed similarity in the
185 parental space use over the same time period. To explore whether parents are coordinated in space and
186 time, within each nest and day, we calculated the EMD between all combinations of male and female
187 hourly UD_s, by progressively lagging the UD_s of one parent relative to the other. For instance, by lagging
188 the female UD_s by one hour, we compared the EMD between male UD_s from 0900h to 1000h with
189 female UD from 0800h to 0900h and so on. These EMD values are defined as "lagged" EMDs, as they
190 represent the similarity in the parental space use when one individual provisioning activity is lagged
191 relative to the other. In this way, we expected that if parents are coordinated in space but also in time,
192 the EMDs at lag 0 would be smaller (higher similarity between the UD_s) compared to the lagged values
193 in absence of any periodicity in foraging territory use (Fig. 1A). On the other hand, if parents are foraging

194 independently from each other at different locations over the course of the day, we would expect the
195 EMD at lag 0 not to differ from the lagged values. We would also expect this pattern (the EMD at lag 0
196 not to differ from the lagged values) if both parents would constantly forage at the same location over
197 the day, regardless of the underlying mechanism (coordination or independent movement). To test for
198 spatio-temporal coordination between parents, we investigated whether the EMD value of a parental
199 UD (focal UD) was smaller when matched with its own partner's UD at the same time (lag 0) or with its
200 own partner's UD at different time (lagged EMD). This approach created a pseudo-replication issue since
201 the same UD was present multiple times in the dataset. To resolve this problem, this analysis was
202 performed using linear mixed models with EMD as response variables, "lag" as fixed effect, and "male
203 UD ID" and "female UD ID" nested into "Nest ID" as random factors. The variable "lag" was used as
204 factor in the analysis. We also ran post-hoc tests to investigate the differences in EMD between the
205 different lag classes. We carried out this broad scale analyses based on 1-hr intervals to broadly
206 investigate whether great tit parents forage together over multiple locations over the course of a day
207 and to rule out the possibility that the observed level of coordination is solely a by-product of parents
208 using the same foraging patch simultaneously but independently from the partner.

209 Subsequently, we investigated spatio-temporal coordination between parents at a finer scale by
210 decomposing parental hourly UDs into six UDs, each covering a ten-minute interval. In this fine scale
211 analysis, we applied the same methodology and statistical models of the broad scale analysis (in the fine
212 scale analysis the lag between UDs occurred in steps of 10 min periods instead of one-hour periods) to
213 explore whether pair coordination in space also occurred at a smaller temporal scale. We chose the 10-
214 minute interval as unit of analysis because great tit foraging trips usually have a duration of few minutes
215 (one visit every 3.76 minutes in this dataset). Our 10-minute blocks enable us to have a more precise
216 indication of the temporal scale to which parents are responsive to changes of partner's movement
217 while having a sufficient number of locations (120 locations) to reliably generate parental UDs.

218 In addition to the previous analysis, we explored whether pair coordination varied over time
219 (such as time of day, period during breeding season) or was related to brood size and age. For this we
220 used linear mixed models with EMD as the response variable and 'hour of the day', 'day in April',
221 'number of chicks' and 'chick age' as fixed effects. The correlation coefficients among these variables
222 were small ($R^2 < 0.3$), so that they could be included in the same model without problems.

223 To better explore the extent to which foraging movements are coordinated between the
224 parents we also carried out an analysis of the foraging angles and an analysis of proximity between the
225 parents. For the analysis of the foraging angles, we calculated the angles of each parental location
226 relative to the nest site and correlated males' and females' angles at each time point. Here we used a
227 Circular correlation test (function *cor.circular*) implemented in the R package *circular* (Agostinelli & Lund
228 2017). Because angles of consecutive locations are highly correlated (Pearson correlation of 0.72 for a
229 lag of 5s =; and 0.53 for a lag of 60s), we carried out the same correlation test on a resampled subset of
230 the data by using one location every minute to not inflate the statistical results. For the analyses of
231 proximity, we defined the two parents to occur in proximity with each other when they were located
232 within 10m at the same time point (as in Snijders *et al.* (2014)). As the Encounternet accuracy in this
233 study is 13.6m, we consider our 10m cut-off to be a conservative value to estimate parents' encounters.
234 In this way, we explored the locations in which parents were found in proximity and grouped them by
235 binning distances every 10m from the nest site until the edge of the array. In this way, we investigated
236 in which areas parents are more frequently in contact with each other. We did this by fitting a linear
237 mixed model with 'cumulative time spent in proximity' as the response variable, 'distance from the nest'
238 (treated as categorical variable) as fixed effect and 'Nest ID' as random factor. Lastly, we explored
239 whether parental coordination of the provisioning was related to period of higher provisioning activity.
240 Here we correlated the hourly values of EMD as measure of foraging coordination with the hourly
241 provisioning rate at the nest.

242 All the statistical analyses were performed in R environment (version 3.2.3). All mixed models
243 were performed with the *lme4* package (Bates *et al.* 2015). We used a backward selection procedure,
244 starting with the full models containing all the main effects, then dropped the predictor with the highest
245 P-value in each step until only significant effects remained in the final model if any. The significance of
246 the main effects was calculated with the Kenward-Roger approximation implemented in the *pbkrtest*
247 package (Halekoh & Hojsgaard 2014). In all models, the proportion of available locations for each period
248 used to generate the UD_s was included to weight the cases.

249

250 Results

251 In the broad scale analysis, earth mover's distance (EMD) between male and female UD_s
252 differed between lags ($F_{14,231} = 2.71$, $P = 0.001$; Fig. 3A). Post hoc comparisons showed that EMD was
253 significantly smaller at lag 0, indicating that parental provisioning activity was coordinated in space and
254 time (Fig. 3A). This pattern was not influenced by the presence of un-estimated locations produced by
255 parents foraging outside the detection zone of the Encounternet array (see supplementary material S2).
256 The same pattern was found in the fine scale analysis ($F_{10,1765} = 21.87$, $P < 0.001$, Fig. 3B) showing that
257 parental coordination occurred at a short temporal scale (ten minutes). Hour of day, day in April,
258 number of chicks and chick age did not influence parental coordination (Table 1).

259 The angle of the foraging locations significantly correlated between the two parents ($r = 0.38$; $t =$
260 40.07 , $P < 0.001$ for the full dataset; $r = 0.37$, $t = 13.58$, $P < 0.001$ for the restricted dataset) revealing
261 that great tit parents foraged together and visited together multiple locations in their territories (Fig.
262 4A). In their foraging activity, parents were on average at a distance of 34.7m from each other (range:
263 0.29-123.29m; Fig. 4B). Great tit parents occurred in proximity with each other both at the nest site
264 (within 10m from the nest location) and at the foraging areas (Fig. 4C). In particular, the frequency of

265 proximity significantly differed between areas ($F_{6,42} = 4.87$, $P < 0.001$). Lastly, we found a significant
266 correlation between EMD and provisioning rate ($F_{1,30} = 4.98$, $P = 0.03$; Fig. 4D); hourly periods of higher
267 provisioning at the nest were associated with greater spatial coordination between the two parents
268 (indicated by lower EMD values).

269 **Discussion**

270 We deployed an automated radio-tracking system to investigate whether great tit parents
271 coordinate their provisioning movements in space and time, as measured by similarity in parental space-
272 use. By using a methodological approach in which we analytically alter the temporal activity of one
273 parent over the other, we showed that spatial coordination is higher when the activity of one parent
274 was not lagged over time, demonstrating that the movements of foraging great tit pairs are highly
275 coordinated in space and time. In addition, parental encounters (periods in which parents occurred in
276 close proximity with each other) occurred both at the nest site and at the foraging locations, and
277 parents' level of coordination positively correlated with the rate of chick provisioning. These results
278 provide concrete evidence of spatio-temporal coordination of parental provisioning in wild songbirds.

279 To our knowledge, this is the first time that fine scale spatial data has been collected on pair
280 coordination in songbird parents in a natural setting. In zebra finches (*Taeniopygia guttata*), Mariette
281 and Griffith (2015) found that pairs coordinated their foraging by synchronizing their visits to feeders
282 deployed in their territory. Our study reinforces their findings, showing that pair coordination also
283 occurs in natural situations where individuals were free to search for food in their environment.
284 Moreover, by analytically lagging the provisioning activity of one parent over the other by blocks of ten
285 minutes, we show that this spatio-temporal coordination takes place on the order of a few minutes in
286 natural conditions. Because foraging trips also occur at a similar time scale (in this dataset parents visits
287 on average every two minutes), these findings indicate that parents can continuously monitor and

288 promptly respond to the spatial movements of the partner. Our study provides one possible negotiation
289 mechanism for decades of studies that have shown parental behavioural adjustments due to
290 experimental manipulation (see Harrison *et al.* (2009) for a meta-analysis on the topic). In conjunction
291 with spatial coordination of foraging, another non-mutually exclusive mechanism of negotiation is vocal
292 communication within the pair (Mariette 2019). In birds, parents often vocally communicate with each
293 other to coordinate activities, such as incubation breaks (Boucaud *et al.* 2017), so coordinated spatial
294 movements between parents could also be regulated by contact calls or calls conveying information on
295 newly discovered food sources. Future studies should combine spatial and acoustic data to reach a
296 comprehensive understanding of the negotiation mechanisms in use during parental care.

297 While movement data on foraging parents are common and available in other bird species, such
298 as sea birds and raptors (Cagnacci *et al.* 2010), studies on parental coordination in those species are
299 recent (Tyson *et al.* 2017; Wojczulanis-Jakubas, Araya-Salas & Jakubas 2018; Grissot *et al.* 2019;
300 Kavelaars *et al.* 2021). For pelagic species in particular, the attention has been primarily directed to the
301 study of dual-foraging strategy, in which alternation of short, chick-provisioning and long, self-
302 provisioning foraging trips by the two parents occurs as a mechanism to steadily deliver food over time
303 to the offspring (Shoji *et al.* 2015; Tyson *et al.* 2017). Nevertheless, these studies have not formally
304 quantified similarity in parental movements and have not proposed a concrete explanation for how
305 parents gain information on the partner's activity in the context of negotiation rules (but see Kavelaars
306 *et al.* (2021)). In this study, we investigate fine scale coordination of the foraging trips and propose that
307 constant spatial proximity with the partner could function as a monitoring mechanism of the mate's
308 investments.

309 Our radio-tracking data and analysis of the foraging angles revealed that great tit parents forage
310 together and sample multiple locations in their territory over the course of the day. These findings
311 confirm previous radio-tracking studies on single great tit individuals showing that provisioning

312 individuals changed foraging locations over time when a food patch become unprofitable (Naef-Daenzer
313 & Keller 1999; Naef-Daenzer 2000). In our study, we did not quantify and measured food availability and
314 distribution as in Naef-Daenzer (2000), and therefore we have no information on parental decisions to
315 change foraging patches. However, by finding that parents switched foraging locations over time and by
316 showing that a change in the foraging locations by one parent is matched by a change in the partner's
317 movements in the same direction within a ten-minute interval, we showed that foraging decisions also
318 depend on the behaviour of the breeding partner. The only other possible explanation for these
319 coordinated movements, although we consider it unlikely given the temporal scale examined in this
320 study, that does not involve any form of interaction/information exchange between the parents, is that
321 both parents, simultaneously and independently from each other, constantly are aware and move to
322 newly emerged food patches during the day. We also found that parents forage closer to the nest
323 (within the array) when there are fewer chicks to provision and parental coordination was higher at high
324 feeding rates. This relationship between home range size and offspring number could be created by
325 resource depletion and low renewal rate of food items in a patchy environment (Ford 1983). In our
326 provisioning great tits, parents feeding larger broods may have already depleted food sources closer to
327 the nest by the time our data were collected (between day nine and 13 of chick age), and therefore had
328 to forage further away from the nest. Furthermore, in periods of more intense foraging activity parents
329 may benefit from foraging together by promoting information exchange about patch availability (Valone
330 1989). Taken together, these findings suggest that foraging decisions of chick-provisioning parents may
331 be regulated both by their need to monitor (and negotiate with) their partner but also to maximize
332 energy delivered to the offspring (Orians & Pearson 1979; Olsson, Brown & Helf 2008). Future studies
333 should integrate radio-tracking of foraging pairs and food distribution data at fine spatial scales, e.g. via
334 frass sampling or branch samples (Zandt 1994; Naef-Daenzer & Keller 1999), to integrate in a
335 comprehensive framework both negotiation and central place foraging rules during the chick

336 provisioning period. Other than being a potential negotiation and foraging mechanism, parental
337 coordination could also act as an antipredator strategy. Social foraging has been shown to decrease
338 predation risk via diluted pre-capita risk of being predated or more efficient vigilance (Caraco 1981;
339 Wrona 1991; Sorato *et al.* 2012). Therefore, it is possible that coordinated movements between parents
340 could have multiple functions for the breeding pairs during the chick provisioning period.

341 The finding that parents coordinate their provisioning activities in space and time has important
342 evolutionary implications in the resolution of sexual conflict. The two most recent theoretical models
343 have emphasized that if parents negotiate by directly monitoring and responding to each other, they
344 can maximize their investment in care, leading to complete cooperation and higher parental and
345 offspring fitness (Johnstone *et al.* 2014; Johnstone & Savage 2019). Our study provides evidence of a
346 mechanism, spatio-temporal coordination of the provisioning, by which parents negotiate and respond
347 to partners' activity. This is a first step in our understanding of how the specific rules that parents use
348 during care affect their investment decisions and ultimately how sexual conflict is resolved within pairs
349 (Lessells & McNamara 2012; Johnstone *et al.* 2014; Griffith 2019; Servedio *et al.* 2019). Because the
350 great tit pairs used in this study were also part of a later brood size manipulation experiment and do not
351 belong to a long-term monitored study site (Baldan *et al.* 2019), we could not reliably investigate fitness
352 consequences of coordinated provisioning nor its relationship with pair bonding behaviour (Griffith
353 2019; Culina, Firth & Hinde 2020). However, experimental manipulations of parental coordination, *i.e.*,
354 via selective feeders that allow only specific individuals to gain access to prey items (Aplin *et al.* 2015;
355 Sonnenberg *et al.* 2019), will be needed to further test the causal link that coordination ameliorates
356 sexual conflict and increases offspring fitness.

357 Understanding how cooperation between parents can evolve and what are the proximate
358 mechanisms are fundamental questions that have recently seen a growing interest (Griffith 2019;
359 Servedio *et al.* 2019). In this study, we demonstrate the existence of fine scale coordination of offspring

360 provisioning activity by parents, which has been proposed to promote cooperation between breeding
361 pairs and ameliorate sexual conflict. Uncovering the physiological and genetic mechanisms underlying
362 variation in coordination (Donaldson & Young 2008; Taborsky & Taborsky 2015; Fischer, Nowicki &
363 O'Connell 2019) and possible environmental constraints on the emergence of coordinated care (Baldan
364 & Ouyang 2020) will also be necessary to reach a comprehensive understanding of the evolution of
365 parental care.

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375 **Author Contributions**

376 D.B and E.E.v.L conceived the study. D.B. collected the data. D.B. and E.E.v.L analysed the data and
377 wrote the paper. All authors revised, edited and approved the manuscript before submission.

378 **Data availability statement**

379 Data available from the Zenodo Repository: <https://doi.org/10.5281/zenodo.4722817>.

380 **Ethics statement**

381 Permission for this study was granted by the Dutch legal entity: KNAW Dier Experimenten Commissie
382 (DEC) no. NIOO-14.17.

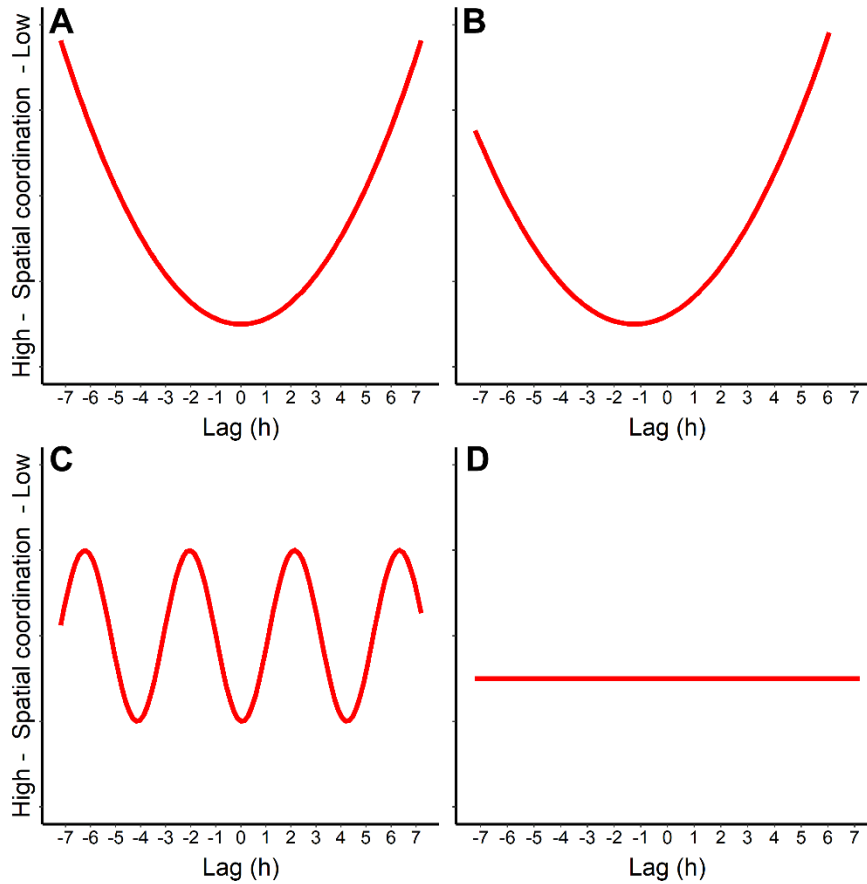
383 **Declaration of Interests**

384 The authors declare no competing interests.

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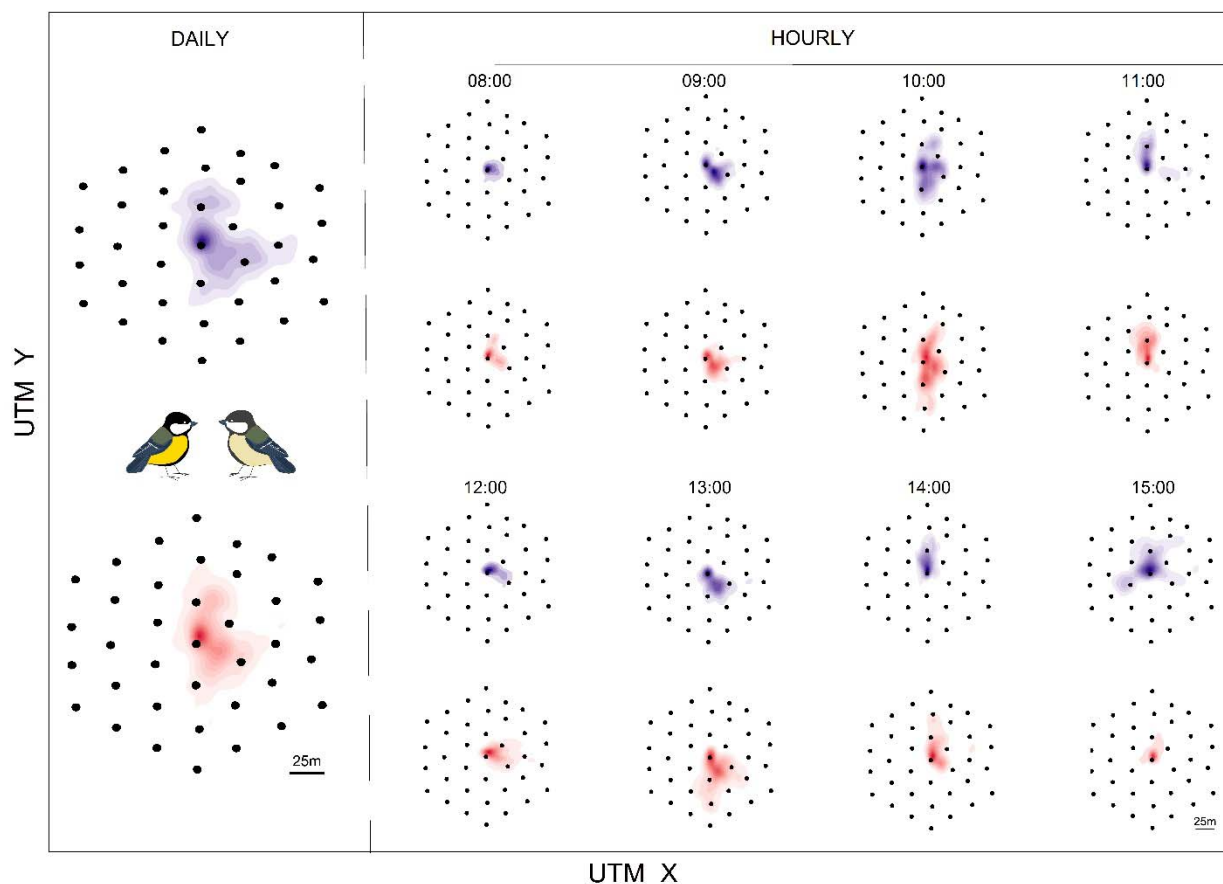
388 **Figures**



389

390 **Figure 1.** Expected patterns of different forms of spatio-temporal coordination between provisioning
391 parents in the form of correlograms (spatial coordination on the y-axis, and shift in time along the x-
392 axis). **A** occurs when parents coordinate their provisioning in space and time, **B** is the expected pattern if
393 a parent constantly leads the other, **C** represents situations in which parents are coordinated in space
394 and time with a cyclical use of their foraging sites, **D** is the expected pattern when no spatio-temporal
395 coordination occurs, and parents are foraging independently from each other. Note that the direction
396 on the y-axis is flipped for visualization purposes to be consistent with the results.

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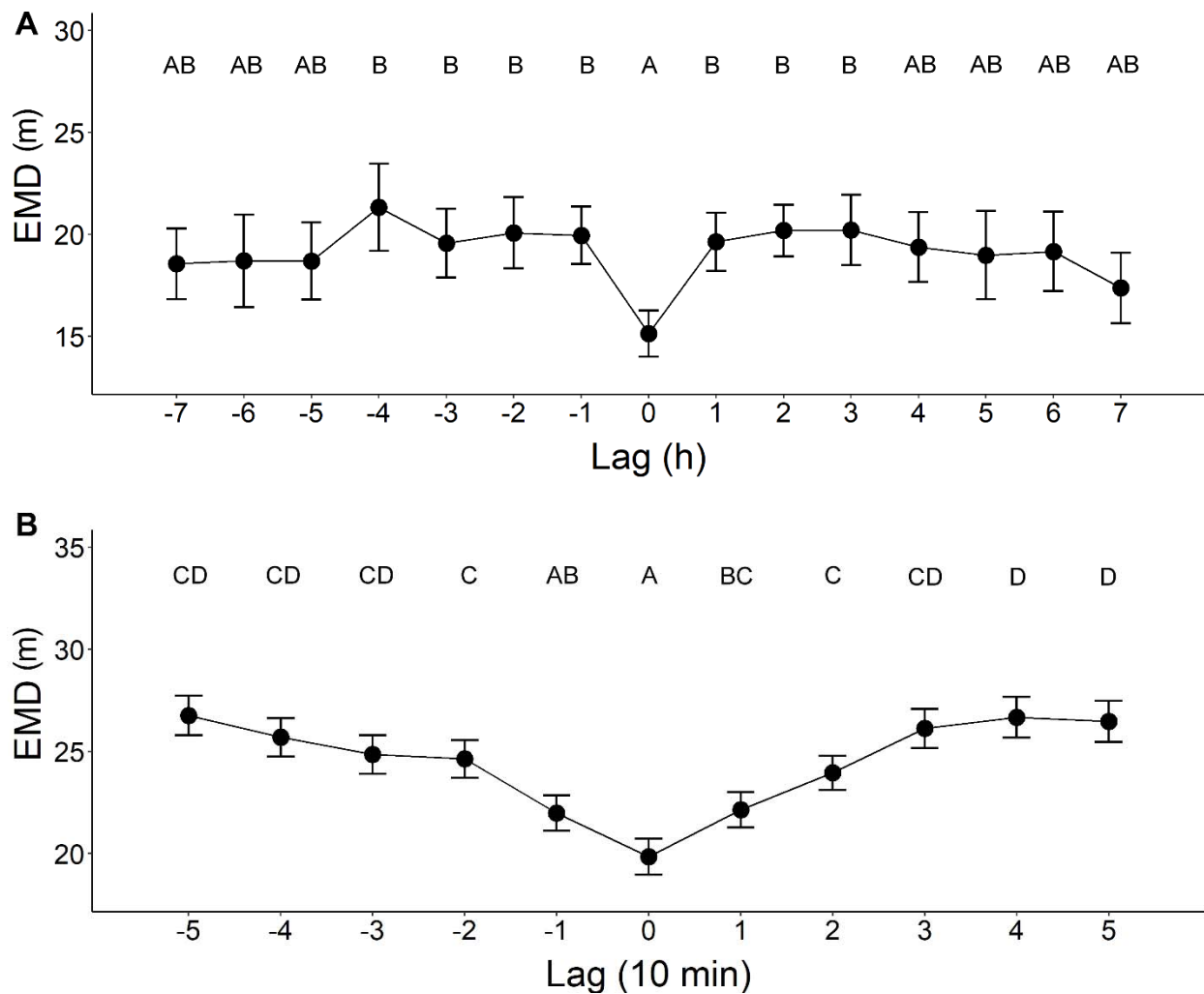
399 **Figure 2.** Example of utilization distributions (UDs; space use) of a single pair (male and female,
400 respectively in blue and red). The two leftmost UD's represent male and female daily space use over the
401 full period of eight hours. The other 16 UD's, represent the hourly UD's for each sex. UTM represents the
402 geographical coordinates of the Encounternet array expressed as Universal Transverse Mercator such that
403 one unit corresponds to one meter. The black dots are the Encounternet receivers used to automatically
404 track pairs in their environment with the centre being the nest site.

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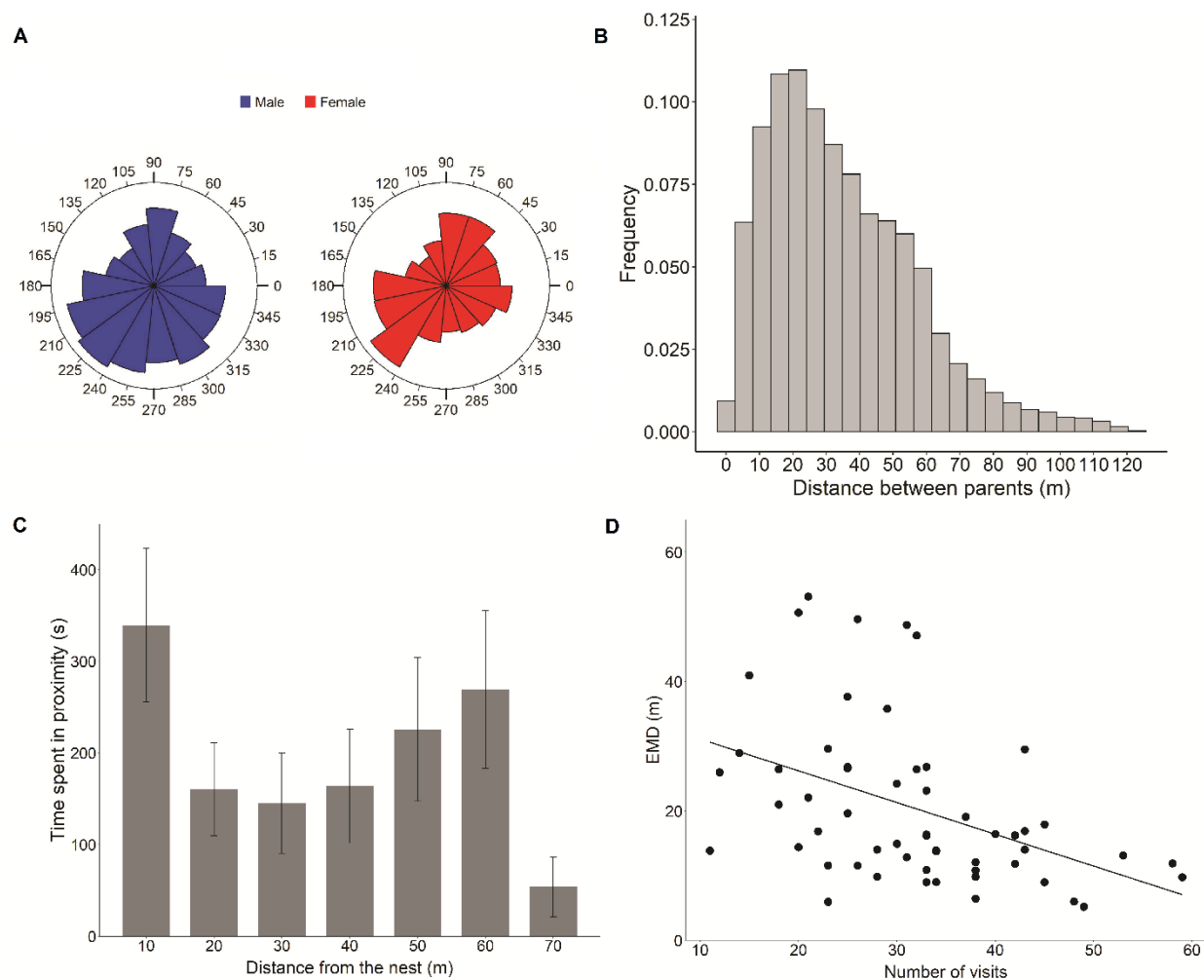


409

410 **Figure 3.** Broad (A) and fine (B) scale analysis of similarity in parental spatial utilization distribution (EMD)
411 in relation to lag. **A** – Effect of lag on EMD in the broad scale analysis. Positive lag values refer to a situation
412 when female UD are compared with male UD at an earlier point in time (e.g. female UD at 1000h with
413 male UD at 0800 has a +2 lag). Negative values of lag refer to the opposite situation when male UD are
414 compared with female UD at an earlier point in time (e.g. male UD at 1000h with female UD at 0800 has a
415 lag value of -2). **B** – Effect of lag on EMD in the fine scale analysis. Also in here, positive values of lag occur
416 when female UD are compared with male UD occurred earlier in time, whereas negative values of lag
417 occur when male UD are compared with female UD occurred earlier in time. Mean \pm SE are shown in the

418 graphs. Different letters on top of the datapoints indicate significant differences among lag classes in the
419 post-hoc tests.

420



421

422 **Figure 4. A** – Histogram of the angles of the foraging locations for male (in blue) and female (in red) great
423 tit parents. **B** – Frequency histogram of the distances (in meters) between male and female parents. **C** –
424 Cumulative time in which male and female parental locations occurred within 10m from each other at
425 different distances from the nest. Mean \pm SE are shown in the graph. **D** – Relationship between similarity
426 in parental space use (EMD) and number of visits at the nest during 1-hour periods.

427 **Table**

428 **Table 1.** Estimated parameters of the linear mixed models investigating the effect of nest characteristics
429 on similarity in parental space use (EMD). 'Nest ID' was included as random effect in the models. For
430 each variable, the statistics expresses whether the model including this variable is explaining more
431 variance than the smaller model, without the respective variable.

Variables	F-test	ndf	ddf	P-value
Hour of day	0.39	1	31.17	0.536
Day in April	4.11	1	5.31	0.095
Number of chicks	0.09	1	3.14	0.774
Chick age	1.68	1	3.60	0.271

432

433

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