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1   Title: Social structure of Coal Tits *Periparus ater* in temperate deciduous forest

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Abstract

Analysis of the impacts of social structure on the behaviour and life history of birds is a rapidly developing area of ornithology. Such studies commonly focus on the Paridae (tits and chickadees) as a model group, but detailed assessment of the basic social structure is lacking for many parids, particularly in the non-breeding season. Such baseline information is essential for understanding the organisation of bird populations, including associations between individuals within social and spatial networks. We assessed the non-breeding (autumn-winter) and spring (i.e. breeding season) social structure of Coal Tits *Periparus ater* in broadleaved forest in southern Britain. Coal Tits were found to be resident and sedentary in this habitat, with birds remaining close to their spring territories during the non-breeding season and associating in small groups averaging 3-4 individuals. Associations were variable, however, with no evidence of stable flock membership, group territoriality or strong pair bonds during autumn-winter. The non-breeding social structure did not change between years of high and low population density, being most similar to a 'basic flock' organisation. This differed from that predicted of a food-hoarding parid, highlighting the potential variation in social behaviour between different populations of bird species. Such variation can inform the understanding of the evolution of avian social structures and associated behavioural traits, such as food hoarding, and aid the interpretation of intra- and inter-specific differences in behaviour.

46   Introduction

47   Social structure is defined as the pattern of associations between individuals and their

48   spatial organisation within a society (reviewed in Whitehead 2008), and can influence the

49   behaviour of birds through the propensity for pair bonding, territoriality and flocking (Emery

50   et al. 2007; Farine et al. 2012; Eguchi 2014). Analysis of avian social structure is a rapidly

51   expanding area of ornithology (Farine et al. 2015a; Croft et al. 2016), which can be important

52   for understanding settlement decisions (Firth and Sheldon 2016), foraging behaviour

53   (Brotons and Herrando 2003; Aplin et al. 2012; Farine and Lang 2013; Farine et al. 2015b)

54   and habitat requirements for species conservation (Broughton et al. 2014, 2015).

55   The Paridae (tits and chickadees) are considered a model group in ornithology (Dhondt

56   2007) and are a frequent topic of social behaviour research (Aplin et al. 2012; Farine et al.

57   2012; Broughton et al. 2015; Firth and Sheldon 2016). However, for many parids over much

58   of their range, there is limited information on social structure, including territoriality, pair

59   bonds or flock associations throughout the year (Ekman 1989; Matthysen 1990; Dhondt

60   2007).

61   Parid species have been classified as conforming to a 'basic flock', 'discrete flock' or 'pair

62   territorial' system in the non-breeding season (reviewed in: Ekman 1989; Matthysen 1990;

63   Dhondt 2007). Basic flocks are characterised by a loose and variable membership of

64   individuals inhabiting overlapping home-ranges, typified by species that do not hoard food,

65   such as the Great Tit *Parus major*. Discrete flocking species exhibit exclusive winter

66   territoriality by small groups with a stable membership, typified by food-hoarding species

67   such as the Willow Tit *Poecile montana*. Pair territorial species, such as the food-hoarding

68   Oak Titmouse *Baeolophus inornatus*, defend an exclusive territory throughout the year.

69   Winter territoriality in discrete-flocking parids has been linked to food hoarding as co-derived

70   traits that assist in defending food resources (Matthysen 1990; Dhondt 2007). However,

71   variation appears to exist in the non-breeding social structure within some food-hoarding

72 species (Matthysen 1990, Dhondt 2007), such as the Marsh Tit *Poecile palustris*, which

73 adopts discrete flocks in Scandinavia (Nilsson and Smith 1988) but basic flocks in Britain

74 (Broughton et al. 2015). Black-capped Chickadees *P. atricapillus* can also display discrete,

75 basic and intermediate flock structures across their North American range, perhaps related

76 to differences in population density or food availability (Smith and Van Buskirk 1988;

77 Desrochers and Hannon 1989).

78 The social structure of the food-hoarding Coal Tit *Periparus ater* may also vary, confusing a

79 simple classification. A small (8-10 g) parid of Eurasian forests, a detailed study from Spain

80 (Brotons 2000) found that the Coal Tit adopted a basic flock system in that region, while

81 assessment of a small sample (two groups totalling six birds) in Sweden (Ekman 1989)

82 indicated a discrete flock structure. This variation suggests that social structure may be a

83 plastic behaviour that varies between populations, as with the Marsh Tit (Broughton et al.

84 2015) and Black-capped Chickadee (Smith and Van Buskirk 1988), but this undermines the

85 theoretical link between food hoarding and group territoriality in parids.

86 However, the paucity of Coal Tit studies from most of its large geographical range limits

87 assessment of the nature and variability of the species' social structure. All information to

88 date comes from conifer-dominated habitats, although Coal Tits occupy deciduous forest

89 habitats throughout Eurasia (Cramp and Perrins 1993). Whether Coal Tit social structure

90 varies with habitat, in addition to latitude or climate, is unknown. We aimed to contribute

91 further information to this knowledge gap by assessing of the social structure of Coal Tits in

92 native broadleaved forest in southern Britain, i.e. in a contrasting habitat and intermediate

93 latitude relative to the previously published studies in coniferous habitat in northern

94 (Sweden, Ekman 1989) and southern populations (Spain, Brotons 2000).

95 We tested the hypothesis that, as food hoarders in Britain (Perrins 1979), Coal Tits should

96 adopt a discrete flock structure in the non-breeding season (autumn-winter), consisting of

97 small groups of individuals with a regular and exclusive membership, or a pair territorial

98 system of male-female units in an exclusive home-range (Ekman 1989; Matthysen 1990).

99 Groups in a discrete flock system are typically based around sedentary adult pairs

100 accompanied by unrelated juveniles (Ekman 1989; Matthysen 1990), and so autumn-winter

101 ranging of any such groups, or territorial pairs, was expected to be based around the spring

102 territories of adults.

103 The results provide baseline information for the Coal Tit's social structure from a previously

104 unexamined area and habitat, which can inform wider questions regarding the plasticity of

105 avian social behaviour and the theoretical link between food-hoarding and social structure.

106

107 Methods

108 Study system

109 The study was conducted between autumn 2015 and spring 2017 at the 160 ha Monks

110 Wood National Nature Reserve, in England (52°24'N, 0°14'W). Monks Wood is dominated

111 by mature Common Ash *Fraxinus excelsior*, Pedunculate Oak *Quercus robur* and Field

112 Maple *Acer campestre* in the tree canopy, with hawthorns *Crataegus* spp., Common Hazel

113 *Corylus avellana* and Blackthorn *Prunus spinosa* in the understorey. Situated 40 m above

114 sea level, the temperate climate produces little or no snow, with mean daily minimum air

115 temperatures of 0.1-7.1 °C for each October to February month during the study. Nest boxes

116 for parids existed at low density (one per 3 ha), but none were occupied by Coal Tits. Food

117 hoarding by Coal Tits was commonly observed in Monks Wood during the autumn and

118 winter periods (pers.obs.).

119 In the non-breeding seasons of 2015-2016 and 2016-2017, Coal Tits were marked with

120 individual combinations of colour-rings and numbered alloy rings during intensive trapping

121 between August and early October. Birds were caught using portable cage-traps baited with

122 sunflower seeds at 25 locations throughout the forest (Fig. 1). Traps were pre-baited for

123   approximately one week, followed by two 1 h trapping sessions over two days until all

124   visiting birds had been marked, resulting in similar effort across sites and years.

125   Marked birds were assigned to first-year (juveniles less than one year old) or adult age

126   classes, and sexed where possible, based on plumage (King and Griffiths 1994), with further

127   sexing based on spring behaviour (persistent territorial singing and aggression by males,

128   little or no singing from females and/or accompanying or soliciting food from males). Eighty-

129   nine marked birds were present in the first non-breeding period and 44 in the second

130   (including 21 surviving from the previous year) which were treated as years of high and low

131   density respectively.

132

133   Describing the non-breeding social structure

134   A subset of adjacent trap sites in the central 80 ha of Monks Wood (Fig. 1) was baited for

135   intensive observations of associations between individuals visiting feeders (inactive traps)

136   during the two non-breeding seasons. In the first non-breeding season the observations took

137   place at 11 sites during mid-October (five days) and January (four days), and in the second

138   season at eight sites in December (four days) and January (three days). These sampling

139   periods all fell within the local autumn-winter seasons, when ringing recoveries indicate that

140   British Coal Tits are largely sedentary (Wernham et al. 2002), and so were timed to reflect

141   the non-breeding social structure of settled individuals. Unringed individuals that were

142   detected at 2-7 feeding sites each winter were targeted during brief (~20 min.) ad hoc

143   trapping sessions, which were typically captured and marked within an hour of detection.

144   The trapping effort during autumn and winter resulted in no unmarked birds being recorded

145   at the subset of sites by the end of winter observations.

146   Observation sites were 140 m to 1020 m apart each year and were selected according to the

147   available survey effort, while still incorporating the same core area of the forest each year.

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148   This core area maximised the likely number of individuals encountered, including birds

149   inhabiting forest interior and forest edge habitat.

150   Observations consisted of recording all marked individuals at a site within the visual range of

151   approximately 15 m of a stationary observer during a 0.5 h period. This protocol was

152   considered to detect all visiting individuals by their colour-ring combinations, including those

153   birds that did not approach the feeder but were in close vocal and visual contact with birds

154   that did. Individuals recorded at the same site within the same 0.5 h period were considered

155   to be associated, in the manner of a 'gambit of the group' approach (Whitehead 2008,

156   Franks et al. 2010). This sampling period was considered suitable, as Psorakis et al. (2015)

157   showed that social network metrics derived for groups of Great Tits visiting feeders would be

158   similar over time windows of between 30 s and 1 h, and it was of shorter temporal duration

159   (i.e. higher resolution) than the 1 h sampling period used by Ficken et al. (1981) to record

160   Black-capped Chickadee associations at feeders.

161   Up to two sites were observed simultaneously by two observers, and individual sites were

162   revisited after a minimum of 1 h from the end of the previous observation, with a maximum of

163   three visits per day. Observation sessions per site ranged from 5-11 (mean 8, total 85) in the

164   first non-breeding season and 7-12 (mean 9, total 68) in the second. Bait was allowed to run

165   out at alternate sites on alternate days in order to disrupt coincidental aggregations at

166   feeding sites and detect social units moving between locations. This helped to counter any

167   limitations of visually logging birds at feeder sites, such as recording spurious aggregations

168   of birds attracted to a rich food source, as individuals and any associates could be 'tracked'

169   between separate locations, revealing any coherent pairs or flocks that associated together

170   over space and time.

171   Analyses of the non-breeding social structure were conducted using SOCPROG version 2.8

172   (Whitehead 2009). SOCPROG is a series of programs designed for analysing the social and

173   population structure of marked animals (for further detailed description of functionality and

174   theory, see also Whitehead 2008). A separate social network was constructed for each non-

175   breeding season to compare the high and low population density between years. The

176   chosen sampling period was a half-day unit, which was defined as falling either before or

177   after 12:00 GMT, giving approximately 4 h of recording time in each period, with each

178   sampling period containing groups of birds recorded during 0.5 h observations that fell within

179   it. This sampling resolution was previously used to assess Marsh Tit social structure

180   (Broughton et al. 2015) and maximised the number of periods with multiple groups for

181   analysis.

182   Sampling periods were treated as independent, as Coal Tits were considered capable of

183   flocking and disassociating between sites and observations at the spatial and temporal

184   scales concerned. As recommended by Whitehead (2008), to enhance the robustness of

185   results only those birds with five or more observations were included in SOCPROG

186   analyses, comprising 33 of 60 individuals detected during feeder observations in the first

187   non-breeding season, and 22 of 27 birds detected in the second, including 14 birds present

188   in both years. This gave a mean of 14 birds per half-day sampling period in each season,

189   with respective ranges of 7-20 and 9-21 birds, representing an 'intermediate' sized study

190   population for social analyses using Whitehead's (2008) definition.

191   An association matrix was constructed for each non-breeding season using the 'simple ratio

192   index' (Whitehead 2008), defined as:

193    $$S_{AB} = \frac{x}{x + y_{AB} + y_A + y_B}$$

194   where S_{AB} is the association between birds A and B, x is the number of half-day sampling

195   periods where A and B were observed together, y_{AB} is the number of sampling periods

196   where A and B were observed separately, and y_A and y_B are the respective number of

197   sampling periods where only bird A or bird B were observed. An association index of zero

198   indicates birds that were never recorded together, and an index of 1.0 indicates birds that

199   were always seen together.

200 To summarise the general population structure, an eigenvector method (Newman 2006) was

201 implemented within SOCPROG to generate a modularity statistic (Q) to identify the degree

202 of clustering resulting from close associations between birds. Modularity is defined as the

203 difference between the proportion of the total number of associations between individuals

204 that fall within clusters versus the expected proportion from random association between

205 birds (Newman 2004; Whitehead 2008). Randomisation tests generated expected

206 proportions using 10000 permutations of the association matrix data with 1000 sequential

207 flips of two records per trial (Manly 1995, Bejder et al. 1998), controlling for individual

208 gregariousness (Whitehead 2008). A resulting modularity statistic of $Q = 0$ would indicate

209 random association between birds, $Q > 0.3$ would indicate meaningful groupings within the

210 population, and $Q = 1$ would indicate groups of individuals that associated only within

211 specific units (Newman 2004). A discrete flock structure would, therefore, have a relatively

212 high modularity statistic.

213 To further assess the broad population structure, frequency distributions of the mean

214 number of associates per individual, in relation to the strength of association, were derived

215 for each non-breeding season by dividing the total number of dyads in bins of association

216 index by the population size minus 1 (Whitehead 2008). This would show the distribution of

217 associations of a typical bird in the population. A strongly bimodal distribution, dominated by

218 many dyads with low or high association, would support a discrete flock population structure

219 composed of stable groups that rarely associate with other individuals. Conversely, a more

220 even distribution of non-zero associations would support a basic flock structure of variable

221 associations (Broughton et al. 2015).

222 Mean gregariousness of individuals was defined for both non-breeding seasons as the sum

223 of association indices between an individual and all other birds, and was used as a measure

224 of the mean number of associates of each bird by age class (juvenile and adult), and for

225 combined age classes (Whitehead 2008). Mean group size was calculated from the

226 maximum number of all individuals observed in each sample, including those birds with

227 fewer than five records.

228 Randomisation tests implemented within SOCPROG were used to detect whether preferred

229 associations existed within groupings in the non-breeding populations, i.e. whether some

230 birds associated more strongly than by chance, using 10000 permutations of the association

231 indices and 1000 sequential flips of record pairs per trial (Manly 1995; Bejder et al. 1998;

232 Whitehead 2008). In these tests a significantly high coefficient of variation (CV) in the real

233 data compared to the randomised set would indicate significant associations over time (i.e.

234 between observation periods) within the population (Whitehead 2009). The test also

235 identified those specific dyads with significant associations, which were used to assess

236 whether established male-female pairs detected in spring maintained strong social bonds

237 during the non-breeding season, which would support a pair-based or discrete flock

238 structure.

239

240 Spring territories and site tenacity

241 Following each non-breeding season, and shortly before nesting commenced in mid April,

242 intensive surveying located spring territories and identified the occupants. Mapping took

243 place during March and early April, during the territorial period of Coal Tits pairs, over 12

244 days in 2016 and 11 days in 2017, totalling approximately 100 hours per year. Singing or

245 calling birds were located through observations with the use of playback on at least five visits

246 to all parts of the forest. Detected males, which typically sang intensively to playback, were

247 followed for at least 15 minutes per visit to map movements and behaviour. Playback was

248 used to elicit defence of territory boundaries (counter-singing, aggression) by the observer

249 moving away from the responding bird and mapping where territorial behaviour ceased or

250 counter-singing occurred between neighbouring birds. Particular attention was given to

251 searches for females closely accompanying males on each occasion.

252 Spring observations were digitised into a geographical information system (GIS) and
253 minimum convex polygons (MCP) were delineated around locations of territorial behaviour
254 (singing, aggression) of males responding to playback or the presence of other Coal Tits
255 (Bibby et al. 2000) as an estimate of territory extent. The MCP method was chosen due to
256 the non-systematic sampling, such as the use of playback to elicit territorial responses and
257 movements, which meant that methods such as kernel estimation were inappropriate (Bibby
258 et al. 2000; Barg et al. 2005).

259 Strong site tenacity between seasons and years would indicate sedentary, resident birds,
260 where restricted ranging could limit social interaction across the population (Brotons 2000).
261 Site tenacity between the breeding and non-breeding season was determined from the
262 proportion of trap sites at which individuals were recorded in August to January (trapping
263 and observation records) of the second-non-breeding season that fell within an arbitrary 100
264 m buffer of their territory boundary in the preceding spring. A low proportion of records from
265 more distant sites would indicate that adults remained close to their spring territory in the
266 non-breeding season.

267 For individuals recorded on more than one occasion at any of the 25 sites across the forest
268 during the August-January trapping and observations, the maximum distance between
269 observations was calculated for each bird in each non-breeding season. These distances
270 were summarised as median and range values, to indicate typical and maximum ranging
271 distances of Coal Tits during the non-breeding seasons.

272 Site tenacity of surviving adults between springs was calculated as the proportion of territory
273 centroids (geographical central point) in the second spring season that fell within the territory
274 polygon of the same bird from the previous spring. Strong site tenacity between seasons and
275 years, combined with several very strong associations and many negligible ones in the non-
276 breeding season (with few moderate associations between these extremes), would be strong
277 evidence for a discrete flock structure.

278

279   Results

280   Non-breeding social structure

281   The SOCPROG metrics describing the general non-breeding social structure of the Coal Tit

282   population were similar for both non-breeding seasons (Table 1), with the modularity

283   statistics indicating moderate clustering within the population. Adults and juveniles were

284   slightly more gregarious in the first non-breeding season compared to when the population

285   was lower in the second year, and juveniles were slightly more gregarious than adults

286   overall, but differences were not substantial and standard deviations were relatively large

287   (Table 1).

288   The typical size of groups visiting feeders declined between non-breeding seasons, from

289   approximately four individuals in the first, high-density year to approximately three birds in

290   the second year of lower density, though standard deviations indicated wide variation (Table

291   1). The reduced group size coincided with a 78% decline in the number of juvenile birds

292   between non-breeding seasons, from 68 individuals to just 15, and a corresponding 84%

293   decline in the ratio of juveniles to adults (Table 1). Despite these differences in population

294   size and composition, similar metrics of social structure were derived for both non-breeding

295   seasons (Table 1).

296   The frequency distributions of association indices also revealed very similar patterns in both

297   non-breeding seasons (Fig. 2). As with gregariousness and group size (Table 1), the

298   distributions indicated that a typical Coal Tit had at least moderate associations (index ≥0.5)

299   with approximately two or three individuals, including strong association (index ≥0.8) with

300   one bird, but weak bonds (>0 and <0.5) with three or four others. The large proportion of

301   zero-value associations indicated spatial separation of individuals across the forest, but the

302   absence of bimodality in the frequency distributions was strong evidence against a discrete

303   flock or pair-territorial structure in the population.

304 Tests for the existence of preferred or strong associations between individuals within the

305 population were significant in both years (Table 1), with some dyads being observed

306 together more often than by chance. However, only a small number of significant

307 associations involved established male-female pairs from the previous or subsequent spring,

308 where both individuals were still present in the study area, comprising two of eight such

309 dyads in the first year (involving seven males and seven females) and two of 14 dyads in the

310 second year (seven females, 12 males). This indicated that breeding pairs did not generally

311 associate strongly around the feeder sites during the non-breeding season, thus providing

312 no support for a pair-based or discrete flock organisation and favouring a basic flock

313 structure.

314

315 Spring territories and site tenacity

316 A total of 28 territories were detected during the first spring season, and 24 in the second

317 spring, averaging 3.3 ha (SD = 1.8 ha) over both years (Fig. 3). There was strong evidence

318 for site tenacity carrying over from the spring to the non-breeding season, with 60% of 14

319 surviving males and six females recorded only at trap sites within a 100 m buffer of their

320 previous spring territory. All territories of these 20 surviving birds had 1-3 trap sites

321 (averaging 2) within this threshold, which accounted for 75% (range = 0-100%) of all sites

322 visited by each bird.

323 For all individuals recorded on more than one occasion at the trap and observation sites

324 across the forest, the median maximum distances between observations were 234 m (range:

325 0-1037 m, n = 79 birds) and 231 m (range: 0-737 m, n = 34 birds) in the first and second

326 non-breeding seasons respectively. Absolute maximum ranging distances exceeded 500 m

327 for only 5% and 12% of these birds in each of those respective seasons, indicating that most

328 Coal Tits ranged over a relatively limited area in the non-breeding season. Most individuals

329   were recorded at more than one site, comprising 63% in the first non-breeding period and

330   52% in the second.

331   Site tenacity also carried over between years, with 64% of 14 surviving males and all six

332   surviving females centring their consecutive spring territories within their occupied extent

333   from the previous spring. Both members of five pairs survived between years, with four

334   resuming the same pair bonds and one pair 'divorcing' to occupy territories with different

335   individuals.

336

337   Discussion

338   The Coal Tit population in the deciduous forest of Monks Wood appeared to be

339   predominantly resident and sedentary. There was a shift in social structure between

340   seasons, from generally small groupings of individuals in the autumn-winter non-breeding

341   season to territorial pairs in spring, and this pattern was consistent between the two years of

342   study. These results appear to be the first detailed description of the social structure of Coal

343   Tits in deciduous forest in Europe (Matthysen 1990; Dhondt 2007).

344   The non-breeding social structure was most similar to a basic flock organisation, with

345   individuals having many associations of varying strength in non-exclusive home-ranges

346   (Ekman 1989; Matthysen 1990; Dhondt 2007). Although the home-ranges were not

347   estimated directly, adults mostly visited trap sites within 100 m of their spring territory, with

348   median ranging distances of less than 235 m for all birds, and the large proportion of zero

349   association indices indicated that many individuals never met. Hence, the autumn-winter

350   ranging of Coal Tits appeared to generally extend only a little beyond that of spring, with

351   associations involving neighbouring adults and overlapping juveniles in variable

352   combinations.

353   This social structure was similar to that of resident Coal Tits in Spain (Brotons 2000), where

354   juvenile home-ranges overlapped with settled adults during winter, with no apparent

355   territorial behaviour. British Great Tits and Marsh Tits also show similar groupings in basic

356   flocks, although their ranging movements appear more extensive than those recorded for

357   Coal Tits in Monks Wood (Broughton et al. 2015; Firth and Sheldon 2016).

358   Typical groups of Coal Tits in Monks Wood comprised 3-4 individuals, but the few strong

359   associations indicated that group membership was inconsistent. The absence of a stable

360   flock membership and, by extension, exclusive home-ranges of groups during the non-

361   breeding season clearly discounted a discrete flock structure. Similarly, despite remaining in

362   the vicinity of their spring territory, known pairs did not generally associate strongly at the

363   feeding sites during autumn and winter, which also undermined a pair-based social structure

364   (Ekman 1989; Matthysen 1990; Dhondt 2007).

365   The absence of clear pair bonds detected between Coal Tits in the non-breeding season

366   differs from the results of Brotons (2000), who demonstrated the maintenance of over-winter

367   pair bonds in Spain. In Japan, Nakamura (1975) also concluded that winter groups of Coal

368   Tits were based around pair units. Löhrl (1974) and Brotons (2000) observed repeated

369   pairing of the same individuals in consecutive springs, which was also found amongst most

370   surviving birds in Monks Wood, indicating some long-term associations. However, it is

371   possible that such pairings may have been re-established annually, resulting from the

372   sedentary behaviour of both birds placing them in close proximity each spring, rather than

373   maintenance of continuous pair bonds throughout the year. Alternatively, pair associations

374   may been obscured due to intra- or inter-specific dominance hierarchies around the feeders,

375   though any birds excluded from feeders but present in the immediate vicinity would still have

376   been detectable.

377   The pattern of small, variable groups of resident Coal Tits in limited, but overlapping, ranges

378   was consistent with observations of this species in mixed species flocks elsewhere in

15

English deciduous forest, where birds associated with relatively few conspecifics in large groups of heterospecifics (Farine et al. 2012). In both cases there was little evidence of the abundant transients reported from coniferous forest in Spain (Brotons 2000), although almost half of the birds detected during the first non-breeding season were recorded fewer than five times. This could reflect transient birds or a change in the attraction of artificial food, but may have also reflected mortality during the longer time interval between the two sampling periods in the first non-breeding season compared to the second.

Determining social behaviour from observations at artificial feeding stations has long been a standard and widely used technique in the study of parids (e.g. Ficken et al. 1981; Farine et al. 2015a; Firth et al. 2016), although limitations could include coincidental attraction to feeders of individuals that are not otherwise socially connected. Continuous availability of food at a single site over many months (e.g. Ficken et al. 1981) could also potentially influence settlement or territorial behaviour in defence of a rich food source. However, other studies have employed a network of feeding sites that were active only for short periods (Farine et al. 2012; Firth and Sheldon 2016), including the current study where food was also allowed to run out at alternate feeders on different days, and this could counter any artefacts of artificial food sources by disrupting coincidental location-based groupings of birds. In addition to detecting social units moving over geographical space, the sampling protocol that we used could also detect their appearance at the same or different locations over time, as they were recorded during different 0.5 h sampling periods. As such, we consider that the results are a reliable reflection of the true social structure of the Coal Tit population.

The assessment of the non-breeding social organisation of British Coal Tits helps to inform the conflicting (Ekman 1989; Dhondt 2007) or uncertain (Matthysen 1990) classification of this species' social structure, but further questions remain. Brotons (2000) noted that, as in the current study, the basic flock structure of Spanish Coal Tits undermined the theoretical link between food-hoarding and group territoriality in wintering parids (Ekman 1989; Matthysen 1990). Ekman's (1989) suggestion that Scandinavian Coal Tits adopt a discrete

flock structure in winter requires further confirmation due to a small sample (Matthysen 1990), but such intra-specific geographical variation in social structure also exists among food-hoarding Black-capped Chickadees (Smith and Van Buskirk 1988) and Marsh Tits (Broughton et al. 2015).

The drivers of intra-specific variation in social structure are unknown, but may relate to competition avoidance, foraging efficiency and territory acquisition (Matthysen 1990; Dhondt 2007), and be influenced by long-term spatial arrangement of individuals (Firth and Sheldon 2016). The effect of inter-specific competition on social structure is rarely considered, although this can influence use of foraging microhabitat (Alatalo et al. 1985). Sympatric species that flocked with Coal Tits at Monks Wood (pers. obs.), and elsewhere in southern Britain (Farine et al. 2012), included Marsh Tit, Great Tit, Blue Tit *Cyanistes caeruleus* and Eurasian Nuthatch *Sitta europaea*, all of which are larger and socially dominant to the Coal Tit (Perrins 1979). Alerstam et al. (1974) found a higher population density and larger flocks of Coal Tits on the Swedish island of Gotland than on the mainland, where inter-specific competition was greater, but there appears to be no information for how varying competition may affect the detailed social structure of sub-dominant parids between regions and habitats.

Lens and Dhondt (1992) found that air temperature was related to flock size in Crested Tits *Lophophanes cristatus*, with birds splitting into smaller groups on warmer days (those above 0°C). We were unable to test this during our study, as the relatively mild winters in southern Britain meant that daylight temperatures were positive on all sampling days. However, the similar social structure of Coal Tits at Monks Wood during both winters indicated relative stability over time.

Population density and food abundance were suggested by Brotons (2000) as potential determinants of social structure, although no significant differences in metrics were noted in Monks Wood after a halving of the population density between years, and information was

432   lacking on the general food availability in the study area. Brotons (2000) considered

433   wintering Coal Tits in the Spanish Pyrenees to have abundant natural food, and the relatively

434   mild climate of southern Britain may also be less costly than the harsher climate and shorter

435   day lengths experienced by wintering Coal Tits in Scandinavia; such conditions could favour

436   the group territoriality reported by Ekman (1989) as a means of resource defence and

437   enhanced foraging efficiency.

438   Although Dhondt (2007) considered group territoriality as a derived behaviour among parid

439   species, there may be little selective pressure to adopt this organisation where species are

440   year-round residents in temperate climates or resource-rich environments. This could mean

441   that food-hoarding species such as the Coal Tit and Marsh Tit in the mild climate of southern

442   Britain, or the food-rich Pyrenean forest, maintain the 'ancestral' basic flock structure, similar

443   to resident populations of Great Tits (Matthysen 1990; Dhondt 2007). Smulders (1998)

444   proposed that food hoarding could develop among a basic flock structure in birds, but would

445   be favoured in colder regions, and so climate may underlie the variation in food hoarding and

446   flocking behaviours observed among parids.

447   Despite the apparent limitations of the classification approach in accommodating intra-

448   specific variation in social organisation (Ekman 1989; Matthysen 1990; Dhondt 2007), this

449   could be improved by considering classification at the appropriate population or sub-specific

450   level rather than the species level. Knowledge and classification of the basic social structure

451   of parids remains valuable due to the numerous analyses of animal social behaviour that

452   utilise these species (e.g. Croft et al. 2016), and understanding the inter- and intra-specific

453   variation in social structure is important for the interpretation and comparison of experimental

454   or comparative studies. As variables such as gregariousness, group size and ranging

455   distances could be expected to differ between and within species depending on whether the

456   study populations form basic or discrete flocks, such differences would have implications for

457   the transmission of information, behaviours or pathogens through social networks and

458   populations by influencing social interactions (e.g. Aplin 2012; Farine et al. 2015b).

459　To conclude, Coal Tits in temperate deciduous forest in southern Britain displayed a basic

460　flock structure in the non-breeding season, comprising variable small groups of neighbouring

461　sedentary birds, with individuals typically ranging over several hundred metres, and pairs

462　occupying exclusive territories in spring. This pattern was similar to that observed among

463　Coal Tits in coniferous habitat further south, in Spain (Brotons 2000), but differed from that

464　reported from a small sample of a northern population in Sweden (Ekman 1989), suggesting

465　potential intra-specific variation of social structure in different areas of Europe. Further

466　studies of northern populations of Coal Tits would be valuable in confirming the extent of any

467　such variation. . Detailed baseline studies of the social structure of populations of other

468　parid species across their ranges would also assist the robust assessment of social

469　organisation in this group, including variation within and between species, and aid the

470　development a more detailed understanding of the evolutionary and ecological basis of

471　social behaviour.

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572   Table 1. Metrics of social structure and population composition of Coal Tits in two non-

573   breeding (autumn-winter) seasons, comprising 89 individuals in 2015/2016 and 44 in

574   2016/2017. Subsets of 33 birds in 2015/2016 and 22 in 2016/2017 with five or more

575   observations were used to generate metrics of modularity (where Q = the extent of clustering

576   within the population on a scale of 0-1), gregariousness (a bird's mean number of associates

577   of any age class) and preferred (i.e. strong) association between birds. Association indices

578   reflected the strength of association between dyads and were based on the proportion of

579   coincidental and non-coincidental sightings of each bird in an association matrix (see

580   Methods).

Variable	2015/2016	2016/2017
Non-breeding density, birds/10 ha	5.6	2.8
juvenile:adult ratio	4.5	0.7
Group size, mean (SD)	4.2 (2.0)	3.0 (1.7)
Gregariousness:		
All birds, mean (SD)	2.7 (0.8)	2.2 (1.1)
Juveniles, mean (SD)	2.8 (0.8)	2.6 (1.0)
Adults, mean (SD)	2.6 (0.7)	1.9 (1.1)
Test of preferred association[1]:		
CV of actual association indices (CV_a)	3.04	3.99
CV of randomised association indices (CV_r)	1.54	1.51
Significance of $CV_a > CV_r$, one-sided P value	< 0.001	< 0.001
Modularity Q	0.5	0.6

581   1. Using 10000 random permutations of association indices, and 1000 trials per permutation,

582   to generate a coefficient of variation (CV)

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Figure legends
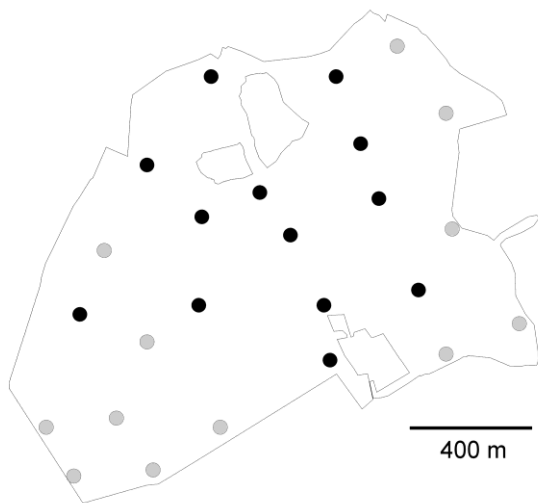
Figure 1. Location of the Coal Tit trapping sites (grey and black circles) used at the 160 ha forest patch of Monks Wood (external boundary of the forest, and internal open spaces, are outlined in grey). Sites of intensive observation of social structure sampled over two non-breeding seasons are shown by the black circles.
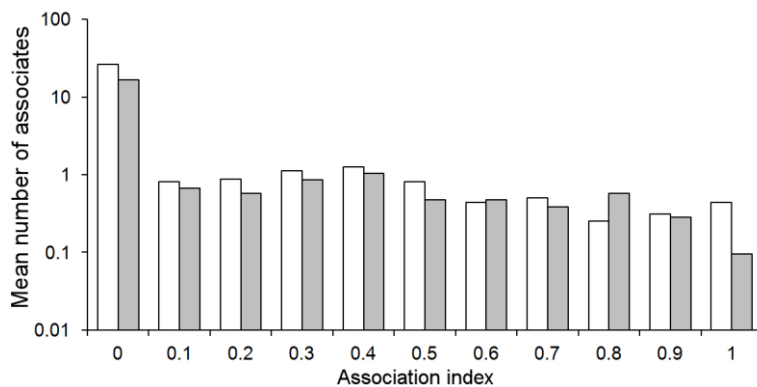
Figure 2. Frequency distribution of the mean number of associates at varying levels of association index for Coal Tits in two non-breeding seasons (autumn-winter), derived from 33 birds in the first season (open bars) and 22 birds in the second (grey bars). In both seasons, a typical Coal Tit formed strong associations with one other individual (sum of associates with index values ≥ 0.8) but had no association (index = 0) with approximately 26 other birds in the first season and 17 in the second season.
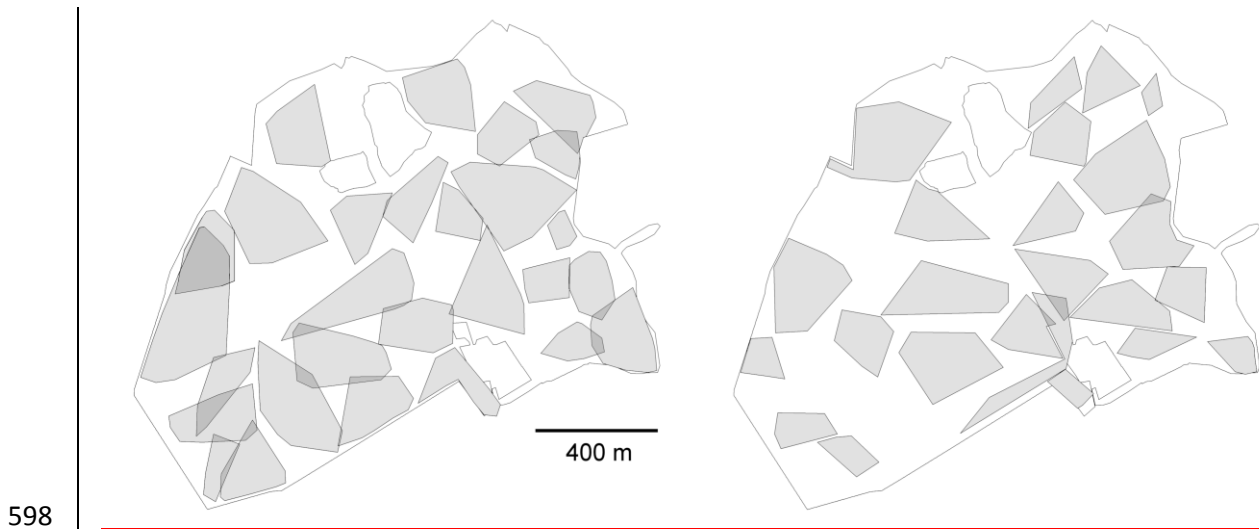
Figure 3. Distribution of 28 Coal Tit territories (shaded areas) during the spring season of 2016 (left), and 24 territories during spring 2017 (right). Areas of territory overlap are indicated by the areas of darker shading.