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1   Winter habitat selection by Marsh Tits *Poecile palustris* in a British woodland

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29   Summary

30   Capsule Radio-tracking and remote sensing showed Marsh Tits selected for English Oak

31   *Quercus robur* trees within large winter home-ranges.

32   Aims To investigate winter habitat selection by Marsh Tits in a British wood, testing for

33   preferences in tree species and woodland structure.

34   Methods Thirteen Marsh Tits were radio-tracked during the winter, and home-ranges were

35   derived. Lidar and hyperspectral data were used to compare the vegetation structure and

36   tree species composition of entire home-ranges and the core areas of intensive use within.

37   Instantaneous sampling observations provided further information for tree species utilisation.

38   Results The mean home-range was very large (39 ha, n = 13). There were no significant

39   differences in mean tree height or canopy closure, or in understorey height and volume,

40   between full home-ranges and the core areas of use. Core areas contained a significantly

41   greater proportion of English Oak relative to availability in the full home-ranges.

42   Instantaneous sampling confirmed that English Oak was used significantly more than other

43   trees.

44   Conclusion Selection for English Oak during winter contrasted with previous studies of

45   breeding territories, indicating that habitat usage varies seasonally, and Marsh Tits require

46   extensive areas of woodland habitat during winter. These results help to explain the

47   sensitivity of Marsh Tits to habitat fragmentation, and demonstrate the need for habitat

48   selection studies throughout the year.

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57 INTRODUCTION

58 Habitat selection is a dominant theme in ornithology, and the distribution of birds relative to

59 availability of habitat is a common method of investigating such patterns (Johnson 2007;

60 Fuller 2012). Quantifying the use of differing habitat composition or structures is important

61 for understanding whether and how a bird's requirements are met by available resources in

62 the environment. This, in turn, can inform species conservation to ensure that sufficient

63 habitat exists for bird populations to be maintained. For woodland or forest birds, studies of

64 habitat selection frequently focus on breeding habitat (Amar et al. 2006; summary in

65 Wesołowski & Fuller 2012). Less attention has been given to habitat selection by resident

66 birds during the non-breeding period, when harsh weather and reduced food availability

67 could result in greater resource limitation than in spring/summer, and so selection may be

68 more acute (e.g. Matthysen 1998).

69

70 Among the relatively well-studied parids *Paridae* of wooded habitats, some species form

71 stable winter flocks in discrete home-ranges (Ekman 1989), and this behaviour can aid the

72 delineation of available habitat and analysis of the composition of utilised areas (Siffczyk et

73 al. 2003; Hadley & Desrochers 2008), similar to methods used for breeding territories (e.g.

74 Broughton et al. 2006). Recording the movements and defining the home-ranges of parids is

75 relatively straightforward, using standard methods such as colour-ringing or radio-telemetry

76 (Naef-Daenzer 1994; Hadley & Desrochers 2008), or recent advancements such as passive

77 integrated transponder (PIT) tags (Farine & Lang 2013). However, characterising woodland

78 habitat over the scale of a parid home-range can be more problematic, due to the strongly

79 heterogeneous and three-dimensional nature of such vegetation (Hinsley et al. 2002;

80 Broughton et al. 2012a). Remote sensing methods, such as light detection and ranging

81 (lidar), can overcome some of the limitations of ground-based sampling methods by

82 providing high-resolution, three-dimensional habitat data of entire home-ranges and study

83 areas (Bradbury et al. 2005; Vierling et al. 2008). The combination of remote sensing habitat

84   data with high-resolution data of bird locations, territories or home-ranges allows powerful

85   analyses of habitat selection (e.g. Broughton et al. 2012a, 2012b; Smart et al. 2012).

86

87   The Marsh Tit *Poecile palustris* is a non-migratory parid of temperate deciduous woodlands

88   in Europe and Asia. In Britain, Marsh Tit abundance fell by 73% between 1967 and 2011

89   (Baillie et al. 2014), with a 22% range contraction over the same period (Balmer et al. 2013).

90   The causes of this decline are not fully understood, but may relate to habitat fragmentation

91   and inter-specific competition with increasing numbers of Great Tits *Parus major* and Blue

92   Tits *Cyanistes caeruleus* (Broughton 2012). Marsh Tit pairs are strictly territorial in spring,

93   and the composition of their large (5-6 ha) breeding territories is well-described in Britain,

94   with a preference for a tall, near-closed tree canopy above a dense understorey shrub layer,

95   characteristic of mature woodland (Hinsley et al. 2007; Broughton et al. 2012a, 2012b).

96   However, little information is available on habitat selection during the non-breeding season,

97   including the composition of winter home-ranges.

98

99   Nilsson & Smith (1988) reported that Swedish Marsh Tits established group home-ranges

100   during winter, occupied by an adult pair and several non-related juveniles, similar to other

101   boreal parids (Ekman 1989). However, other work indicates that Marsh Tits elsewhere

102   occupy large, overlapping winter home-ranges in which individuals forage and associate in

103   changeable groups (Amann 1997; Broughton et al. 2010). Early studies by Hartley (1953),

104   Gibb (1954), and later Morse (1978), described aspects of Marsh Tit foraging behaviour

105   throughout the year in Wytham Woods, southern England. A variety of trees and shrubs

106   were recorded being used during the winter, but particularly English Oak *Quercus robur*,

107   European Elder *Sambucus nigra* and Common Beech *Fagus sylvatica*. This was revisited by

108   Carpenter (2008), partly at the same site, but no preference was found for any tree or shrub

109   species in winter. Similarly, Broughton et al. (2006, 2012a) found no evidence of selection

110   for particular trees or shrubs in Marsh Tit breeding territories in Monks Wood, eastern

111   England. However, unlike the winter studies, the analyses of breeding habitat could relate

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112   tree species selection to their availability to individual birds, by characterising territory

113   composition. This approach has yet to be applied to winter studies, and so uncertainties

114   remain regarding habitat selection during this significant part of Marsh Tit's annual cycle,

115   including how this may differ from the breeding period.

116

117   We investigated the winter habitat selection of Marsh Tits by defining winter home-ranges

118   using radio-tracking, characterising habitat availability using remote sensing methods, and

119   then comparing the habitat composition of home-ranges against that of the areas of most

120   intensive use within. This was supported by field observations of vegetation utilisation. We

121   then put winter habitat selection into the context of studies of breeding territory composition,

122   to determine how habitat selection varies throughout the year and how this may influence

123   Marsh Tit conservation.

124

125   MATERIALS AND METHODS

126   The study was centred on 160 ha of mature deciduous woodland at Monks Wood National

127   Nature Reserve in Cambridgeshire, UK (52° 24' N, 0° 14' W), which is dominated by

128   Common Ash *Fraxinus excelsior*, English Oak and Field Maple *Acer campestre* in the tree

129   canopy, with smaller amounts of Silver Birch *Betula pendula*, European Aspen *Populus*

130   *tremula* and elm *Ulmus* spp. (Hill et al. 2010). The understorey is dominated by hawthorns

131   *Crataegus* spp., Blackthorn *Prunus spinosa* and Common Hazel *Corylus avellana*

132   (Broughton et al. 2006). Since 2003, almost all Marsh Tits have been marked with a unique

133   combination of colour-rings, and aged and sexed using biometrics, moult and breeding

134   behaviour (Broughton et al. 2008, 2010).

135

136   Home-range delineation

137   Aebischer et al. (1993) recommend a sample size above ten individuals for radio-tracking

138   analyses of habitat utilisation, and for this study we radio-tracked 13 Marsh Tits during two

139   winter periods: four birds in November-December 2006 and nine birds in December-January

140   2007-2008. Climate was similar in both winter periods, with a regional (East Anglia) mean

141   temperature of 6-7 °C and 10-11 days of air frost during the months of sampling (Met Office

142   2013). Radio-tracked birds were comprised of one juvenile female and four adult and eight

143   juvenile males, with males being preferred due to their larger size meeting recommendations

144   for the maximum load of radio-transmitters (Caccamise & Hedin 1985). We used Pip Ag317

145   radio-transmitters (Biotrack, Wareham, Dorset, UK) attached by gluing and tying to the

146   central tail feathers in the first winter period, and fitted to the rump using a 'Rappole harness'

147   (Rappole & Tipton 1991) in the second period.

148

149   Radio-tracking of each bird began on the day after transmitter attachment, and took place on

150   4-11 days (mean = 7, s.d. = 2) over a 4-27 day period (mean = 11, s.d. = 6). The period of

151   data collection overlapped by one week for all four birds in the first winter, and in the second

152   winter up to three birds at a time overlapped by up to four days. Artificial food was not

153   available except to capture birds on specific days, when data were not collected, and birds

154   were recaptured for tag-removal after their radio-tracking period. During each radio-tracking

155   session, focal birds were located by an observer using a Yagi antenna and followed at a

156   typical range of 10-30 m, attempting to keep the bird under continuous observation where

157   possible. We used instantaneous sampling (Martin & Bateson 2007) from the initial location

158   to record the coordinates of focal birds on large-scale maps at 10 min intervals during radio-

159   tracking sessions of 0.5-2.5 h (median = 1.25 h). Post-hoc analysis showed that 10 min

160   intervals were sufficient for birds to move up to three times the median distance between any

161   two recorded locations between sampling points.

162

163   When in view, the species of tree or shrub in which the focal bird was situated was recorded

164   at each sampling point. In a study of winter behaviour, Carpenter (2008) has previously

165   shown that Marsh Tits at this site spend the majority of their time (65%) actively foraging in

166   trees and shrubs, while at another English site Gibb (1954) reported that birds were feeding

167   in *c.* 90% of winter observations, and so we assumed that Marsh Tit use of vegetation during

168   our sampling would primarily be driven by this activity. Location coordinates were digitised in

169   ArcGIS 9 (ESRI, Redlands, CA, USA), and maximum home-ranges were calculated in

170   Animal Space Use 1.3 (Horne & Garton 2009) using kernel estimation with a smoothing

171   parameter derived from likelihood cross-validation and a 10 m cell size. Asymptote analysis

172   identified the minimum number of locations required for home-range calculations, by plotting

173   number against the cumulative area of each home-range (Kenward 2001). The asymptote

174   was reached when home-range area increased by less than 5% with the addition of five or

175   more new locations, indicating that the full extent had essentially been reached. For 11 birds

176   the asymptote was reached at 23-94 locations, although it was not reached for the remaining

177   two birds. However, as the 73-74 locations for these two individuals exceeded the mean

178   asymptote of 60 (s.d. = 20) for other birds, we considered that largely representative home-

179   ranges would be derived, and so included all birds in analyses.

180

181   Core home-ranges were identified by plotting the cumulative area of home-range kernel

182   contours in 5% increments, which revealed inflection points for each bird at the 65-80%

183   contour (containing 65-80% of locations). Beyond this, further outlying locations led to a

184   more rapid increase in home-range size. To standardise spatial analyses between

185   individuals, we applied the mean 70% contour to define core home-ranges for all birds,

186   which contained 70% of the locations for each individual. The remaining area between the

187   70% contour and the 100% perimeter contour defined the home-range peripheries.

188

189   Analysis of the social organisation of this Marsh Tit population (in prep.) showed that birds

190   did not show winter territoriality, but instead had individual, sometimes partially-overlapping

191   home-ranges, with only casual associations between most birds. The home-ranges

192   examined here covered *c.*80% of the study area in total, and the maximum overlap of core

193   home-ranges between any two individuals was only 65%. This indicated that sampling of

194   woodland vegetation would not be significantly biased by location or social interactions and

195   that the movements of each bird could be treated as independent, as birds were not

196   constrained in their utilisation of the available habitat.

197

198   Remote sensing of habitat data

199   Data describing the woodland vegetation structure and composition of home-ranges were

200   collected using airborne remote sensing. Discrete return lidar data were acquired for Monks

201   Wood in June 2005, and used to generate a raster canopy-height model. This described the

202   height of each 0.5 x 0.5 m grid cell of the woodland canopy surface to 1 cm precision, with

203   the tree canopy layer defined as vegetation taller than 8 m and the understorey layer as

204   vegetation 1-8 m in height (see Hill & Broughton 2009 for full details). However, due to

205   obscuration of much of the understorey by tree canopy foliage in the summer 2005 model,

206   additional lidar data from April 2003 were employed. At this stage of early spring, lidar could

207   penetrate more fully through the dormant tree canopy and onto the understorey below. This

208   provided additional height and coverage data for understorey shrubs that were combined

209   with the 2005 data to create a model of the total understorey layer (Hill & Broughton 2009;

210   Broughton et al. 2012b). Previous work (Broughton et al. 2012b) has shown that the mature

211   woodland in the study area is essentially stable, with little dynamic change in vegetation

212   being apparent during the 3-5 year lag between the remote sensing data collection and

213   radio-tracking fieldwork.

214   The mean height and closure (spatial coverage) of the tree canopy were calculated for the

215   core and periphery of each home-range in ArcGIS 9. The mean height and volume of the

216   understorey layer were also extracted for each home-range division, with volume calculated

217   as the vegetation height multiplied by the area of each grid cell.

218

219   A 1 m resolution raster map of tree species coverage in the canopy layer was derived from a

220   supervised classification of time-series Airborne Thematic Mapper data, acquired in 2003

221   (see Hill et al. 2010 for technical details). This had a surveyed accuracy of 88%, and was

222   used to calculate the coverage of the home-range cores and peripheries by each of the six

8

223   tree species (listed above). Grid cells in the understorey and field layers (vegetation < 8 m in

224   height) were assigned to an unclassified category.

225

226   Statistical analysis

227   Selection for vegetation structure was tested by comparing the lidar-derived variables of

228   canopy and understorey structure between the home-range cores and peripheries, using

229   Wilcoxon signed rank tests (W statistic). We also used Mann-Whitney U tests to look for

230   differences between age classes of birds.

231

232   Selection for preferred tree species was tested by comparing the proportions of each tree in

233   the full home-ranges (100% maximum extent) and the 70% core home-range areas, using a

234   compositional analysis (Aebischer et al. 1993). This was implemented using the 'compana'

235   functionality in the 'adehabitat' package (Calenge 2014), in R version 2.9.1 (the R

236   Foundation for Statistical Computing). In this analysis, the tree species composition in the

237   full home-range represents the habitat available to each bird, while the composition of the

238   core area reflects preferred species utilisation or selection by the bird. If the utilisation of tree

239   species differs from random, then they can be ranked according to their proportion in each

240   area, and any significant between-rank differences can be identified (Aebischer et al. 1993).

241

242   During instantaneous sampling it became apparent that the focal bird was sometimes out of

243   direct observation, leading to incomplete data for usage of tree and shrub species. This was

244   biased towards sampling points when the focal bird was in dense understorey thickets,

245   meaning that usage of canopy tree species was easier to record than understorey shrubs.

246   As such, we limited analysis to observations in canopy trees, for which any bias of non-

247   observation would be similar across tree species, and which would assist interpretation of

248   the compositional analyses. Instantaneous sampling scores for tree species use were

249   calculated for each Marsh Tit with a minimum of 15 observations (pooled across radio-

250   tracking sessions), and a Kruskal-Wallis test was applied to determine preferential use.

251

RESULTS

The mean maximum extent of the 13 Marsh Tit home-ranges was 39.3 ha (s.d. = 20.1), with

a range of 10.4-82.7 ha. These incorporated a mean core area, as defined by the 70%

contour, of 8.4 ha (s.d. = 4.5) and a range of 2.4-15.6 ha.

The home-ranges of 12 birds fell wholly or largely (> 90%) within the area of remotely

sensed vegetation data, and so were included in habitat analyses. In this group, there was

no difference in home-range area between the four adult and seven juvenile males ($U =$

20.5, $P = 1.00$), while that of the single juvenile female was also similar (36.4 ha). We also

found no difference between adults and juveniles in any of the structural habitat metrics in

the home-range cores or peripheries (Mann-Whitney tests, all P values > 0.23), and so all

birds were pooled for further analyses. This showed that, within all home-ranges, there was

no significant difference in the height or volume of understorey shrubs between the 70%

core areas and the home-range peripheries, and also no difference in tree canopy height or

tree canopy closure in the home-range peripheries (Table 1).

Following the order of abundance in the study area, Common Ash was the dominant tree

canopy species in home-ranges, followed by English Oak and then Field Maple, with other

species being rare (Table 2). Except for Common Ash, all tree species occurred in greater

proportions in the home-ranges than in the wider study area, as did unclassified vegetation

below 8 m in height.

Within home-ranges, compositional analysis indicated that selection of canopy tree species

differed significantly from random (weighted mean $\Lambda = 0.07$, $P = 0.01$). English Oak was

ranked highest in the order of Marsh Tit selection (Table 3), with a disproportionately greater

coverage in the 70% core home-range areas than in the peripheries, an average difference

of 15%. English Oak and unclassified vegetation were favoured to a significantly greater

279   extent than Common Ash or Field Maple, which had a low rank of habitat selection. The

280   selection for unclassified vegetation may have represented greater use of understorey

281   shrubs under areas of relatively open tree canopy in the home-range cores (Table 1). There

282   was a weak, non-significant, negative correlation between home-range area and the

283   proportion of English Oak (Fig. 1).

284

285   Sufficient data for canopy tree species use from instantaneous sampling were available for

286   ten birds, totalling 268 sampling point records, with an average of 27 observations (s.d. = 8)

287   contributing to summary sampling scores for each bird (Table 4). Tree species use was not

288   uniform (Kruskal-Wallis χ^2 = 24.4, d.f. = 3, P < 0.01), and pair-wise Wilcoxon tests showed

289   that English Oak was used significantly more than Common Ash (W = 99.0, P < 0.01), Field

290   Maple (W = 100.0, P < 0.01), and combined European Aspen, Silver Birch and elm (W =

291   89.0, P < 0.01). There was also weaker support for a greater use of English Oak over all tree

292   species combined (W = 74.5, P = 0.07), but adults did not use oak to greater extent than

293   juveniles (U = 23.0, P = 0.17). A further 108 observations (29% of the total) were of Marsh

294   Tits using understorey shrubs, but this cannot be used as an accurate reflection of the

295   proportional usage of the understorey versus the tree canopy due to observational bias (see

296   methods).

297

298   DISCUSSION

299   To date, all studies of Marsh Tit habitat selection within individual ranges have focussed on

300   breeding territories in spring, identifying a preference for a tall tree canopy and dense

301   understorey in relatively large territories averaging 5-6 ha (reviewed in Broughton 2012). In

302   previous work on Marsh Tit habitat selection in breeding territories, also at Monks Wood, no

303   selection for any particular tree species was detected (Broughton et al. 2006, 2012a).

304   However, analysis of microhabitat selection of nesting locations within territories found some

305   preference for Common Ash and Field Maple, with possible avoidance of English Oak,

306   although this could not be differentiated from selection for habitat structure rather than tree

307   species (Broughton et al. 2012b).

308

309   The current study is the first to investigate habitat composition and selection within defined

310   Marsh Tit home-ranges during winter, and the results contrast with those for spring breeding

311   territories. Marsh Tit winter home-ranges averaged 5-6 times larger than spring territories at

312   the same site, and, unlike results for spring territories (Broughton et al. 2006, 2012a), clear

313   selection was shown for English Oak in the core areas of intensive use within the winter

314   home-ranges. The difference in the percentage cover of English Oak in the home-range

315   cores was not substantially greater than in the full home-ranges (Table 2), and this may be

316   due to the dispersed distribution of oak trees in the study area. However, as a percentage of

317   the proportional cover in the study area, the coverage of English Oak in the home-range

318   cores was some 21% greater than that generally available in the wood.

319

320   This selection for English Oak was supported by instantaneous sampling observations of

321   tree species use, in which Marsh Tits were recorded on oaks more than any other tree

322   species. There was also a significant selection for unclassified vegetation in the core home-

323   ranges, which probably reflected understorey vegetation exposed under an open tree

324   canopy. Limited support for this was given by the non-significant result of a slightly more

325   open tree canopy in the home-range cores, although there was no preference for a greater

326   height or volume of the understorey shrub layer. However, a limitation of this study was the

327   limited sample of Marsh Tits and the pooling of age and gender classes for analyses. While

328   the small number of birds in each class showed no significant differences between them in

329   home-range size or the habitat variables examined, it is possible that ecological differences

330   may exist between and within classes as a result of social dominance structures (Nilsson &

331   Smith 1988; Broughton et al. 2010), and this caveat applies to our results.

332

333   Notwithstanding these limitations, our results for winter habitat selection are consistent with

334   earlier studies of winter foraging sites at another English location, Wytham Woods, in which

335   English Oak was also the preferred tree species in midwinter (Hartley 1953; Gibb 1954;

336   Morse 1978). This suggests that the importance of English Oak to Marsh Tits during winter

337   may be a general characteristic, at least in southern Britain. The preference for English Oak

338   is presumably related to food availability, and Betts' (1955) analysis of Marsh Tit diet

339   recorded oak gall tissue and a range of invertebrates, including eggs and pupae, being

340   taken from twigs, buds and hanging dead leaves in oak woodland during winter. Both Gibb

341   (1954) and Betts (1955) also noted the extensive use of oaks as winter foraging sites by

342   Great, Blue and Coal Tits *Periparus ater* in English woodland.

343

344   Hartley (1953) and Gibb (1954) identified a further preference of Marsh Tits for foraging in

345   Common Beech and European Elder, but these species were virtually absent from our study

346   area and so could not be tested. In a more recent comparative study of winter habitat use at

347   Wytham Woods and Monks Wood, Carpenter (2008) recorded Marsh Tits in similar

348   proportions overall in English Oak and Common Ash. Yet, despite a similar prevalence of

349   English Oak in both woods, in Monks Wood the proportion of Marsh Tit observations in oak

350   was almost twice as high as in Wytham Woods. Carpenter suggested this may have been

351   due to competitive exclusion from preferred foraging areas by higher densities of

352   competitively dominant Great Tits and Blue Tits in Wytham. However, no previous study has

353   tested the utilisation of tree and shrub species by Marsh Tits relative to their availability

354   within individual home-ranges.

355

356   We found little evidence that Marsh Tits in our study area were selecting winter habitat

357   based on specific elements of woodland structure, unlike spring territories and nest-sites

358   (Broughton et al. 2012a, 2012b). However, the lack of preference for a taller tree canopy,

359   and the slight non-significant finding of a more open canopy in the core home-ranges, tied

360   well with the selection for unclassified (i.e. non-canopy) vegetation in the cores. Together,

13

361   this points to the importance of the understorey shrub layer to wintering Marsh Tits, a feature

362   which is also important in breeding territories (Hinsley et al. 2007; Broughton et al. 2012a).

363   Despite this, we found no evidence of selection for greater volumes of understorey shrubs in

364   the core home-ranges. At Wytham Woods, Gibb (1954) reported that 42% of Marsh Tit

365   foraging occurred in the understorey shrub layer throughout the year, compared to 47% in

366   the canopy layer, while Morse (1978) and Carpenter (2008) found that more than half of

367   winter foraging occurred in the understorey. In our study, 29% of Marsh Tit observations

368   were in shrubs, but this was likely to be a significant under-estimate. Nevertheless,

369   understorey shrubs appear to be at least as important as canopy trees as winter foraging

370   sites for Marsh Tits, offering invertebrates and also seeds/fruits as a food source (Gibb 1954;

371   Betts 1955; pers. obs.).

372

373   Although Gibb (1954) and Carpenter (2008) recorded the usage of some individual shrub

374   species by foraging Marsh Tits during winter, there has been little study of the relative

375   importance of given species or overall diversity. Addressing this question is problematic,

376   however, due to the difficulties of collecting understorey shrub data at an appropriate scale

377   and over a sufficient area to define availability, a role which remote sensing cannot yet fulfil

378   (Broughton 2012). The collection of unbiased observations of Marsh Tit shrub usage is a

379   further difficulty, even when assisted by radio-telemetry, as found during the current study.

380

381   Our results, and those from the breeding period (Broughton et al. 2006, 2012a, 2012b;

382   Hinsley et al. 2007), indicate that habitat use varies throughout the year. Elements of the

383   tree canopy and understorey shrub layers remained important in different seasons, but the

384   structural preferences of a mature canopy and understorey in spring were not replicated in

385   winter. In addition, apparent selection for Common Ash and Field Maple around nest-sites

386   (Broughton et al. 2012b) was replaced by selection for English Oak during winter. These

387   contrasts could help to explain the unusually large extent of Marsh Tit breeding territories

388   and winter home-ranges, which may need to be sufficiently large to encompass a variety of

389   habitat features to support a sedentary bird throughout the year. Such seasonal differences

390   emphasise the importance of habitat selection studies and species conservation to consider

391   the complete annual cycle, as efforts directed solely at e.g. the breeding season may

392   significantly under-estimate habitat requirements at other times of the year.

393

394   Even allowing for differences in methodology, the 39 ha mean winter home-range of Marsh

395   Tits in the current study was substantially larger than the 10-24 ha recorded for the closely-

396   related Willow Tit *Poecile montana* (Ekman 1979; Siffczyk et al. 2003), Boreal Chickadee

397   *Poecile hudsonica* (Hadley & Desrochers 2008) and Black-capped Chickadee *Poecile*

398   *atricapillus* (Smith 1991). Siffczyk et al. (2003) and Hadley & Desrochers (2008) found that

399   Willow Tits and Boreal Chickadees used large winter home-ranges to compensate for the

400   inclusion of unsuitable habitat, with birds focussing activity on widely-distributed patches of

401   preferred habitat. Marsh Tits in Monks Wood may have behaved in a similar way, by

402   establishing extensive home-ranges to encompass sufficient amounts of widely-dispersed

403   resources, such as oaks, as predicted by the resource dispersion hypothesis (Carr &

404   Macdonald 1986). Indeed, the (albeit weak) negative relationship between Marsh Tit home-

405   range size and the proportion of English Oak echoed that of Boreal Chickadee home-ranges

406   and their preferred stands of mature forest (Hadley & Desrochers 2008).

407

408   The Marsh Tit has a negative conservation status in Britain, having declined by 73%

409   between 1967 and 2011 (Baillie et al. 2014). As such, it is essential to understand the year-

410   round habitat requirements of the species in order to inform habitat management and identify

411   potential causes of decline. Differential habitat selection in spring/summer and winter may

412   provide challenges when trying to create or maintain adequate woodland habitat for Marsh

413   Tits, but further work is needed to test our findings at different sites and to fully investigate

414   the importance of understorey shrub species for winter foraging.

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424

425   REFERENCES

426   **Aebischer, N.J., Robertson, P.A. & Kenward, R.E.** 1993. Compositional analysis of habitat

427   use from animal radio-tracking data. *Ecology* **74:** 1313-1325.

428

429   **Amann, F.** 1997. Dispersal, territory establishment and behaviour of juvenile Marsh Tits

430   *Parus palustris. Orn. Beobachter* **94:** 5–18 (in German).

431

432   **Amar, A., Hewson, C.M., Thewlis, R.M., Smith, K.W., Fuller, R.J., Lindsell, J.A.,**

433   **Conway, G., Butler, S. & MacDonald, M.A.** 2006. What's happening to our woodland

434   birds? Long-term changes in the populations of woodland birds. RSPB Research Report No.

435   19, BTO Research Report No. 169. RSPB, Sandy.

436

437   **Baillie, S.R., Marchant, J.H., Leech, D.I., Massimino, D., Eglington, S.M., Johnston, A.,**

438   **Noble, D.G., Barimore, C., Kew, A.J., Downie, I.S., Risely, K. & Robinson, R.A.** 2014.

439   BirdTrends 2013: trends in numbers, breeding success and survival for UK breeding birds.

440   BTO Research Report No. 652. BTO, Thetford. http://www.bto.org/birdtrends

441

442   **Balmer, D.E., Gillings, S., Caffrey, B.J., Swann, R.L., Downie, I.S. & Fuller, R.J.** 2013.

443   *Bird Atlas 2007-11: the breeding and wintering birds of Britain and Ireland.* BTO Books,

444   Thetford, UK.

445

446   **Bradbury, R.B., Hill, R.A., Mason, D.C., Hinsley, S.A., Wilson, J.D., Balzter, H.,**

447   **Anderson, G.Q.A., Whittingham, M.J., Davenport, I.J. & Bellamy, P.E.** 2005. Modelling

448   relationships between birds and vegetation structure using airborne LiDAR data: a review

449   with case studies from agricultural and woodland environments. *Ibis* **147:** 443-452.

450

451   **Broughton, R.K. 2012.** Habitat modelling and the ecology of the Marsh Tit (*Poecile*

452   *palustris*). PhD thesis, Bournemouth University. http://nora.nerc.ac.uk/20719/ (accessed

453   March 2014).

454

455   **Broughton R.K., Hinsley S.A., Bellamy P.E., Hill R.A. & Rothery P.** 2006. Marsh Tit

456   *Poecile palustris* territories in a British broadleaved wood. *Ibis* **148:** 744-52.

457

458   **Broughton, R.K., Hinsley, S.A., Bellamy, P.E., Carpenter, J.E. and Rothery, P.** 2008.

459   Ageing and sexing Marsh Tits *Poecile palustris* using wing length and moult. *Ringing and*

460   *Migration* **24:** 88-94.

461

462   **Broughton R.K., Hill R.A., Bellamy P.E. & Hinsley S.A.** 2010. Dispersal, ranging and

463   settling behaviour of Marsh Tits *Poecile palustris* in a fragmented landscape in lowland

464   England. *Bird Study* **57:** 458-472.

465

466   **Broughton, R.K., Hill, R.A., Freeman, S.N., Bellamy, P.E. & Hinsley, S.A.** 2012a.

467   Describing habitat occupation by woodland birds with territory mapping and remotely sensed

468   data: an example using the Marsh Tit (*Poecile palustris*). *Condor* **114:** 812-822.

469

470   **Broughton, R.K., Hill, R.A., Henderson, L.J., Bellamy, P.E. & Hinsley, S.A.** 2012b.

471   Patterns of nest placement in a population of Marsh Tits *Poecile palustris. J. Ornithol.* **153:**

472   735-746.

473

474   **Caccamise, D.F. & Hedin, R.S.** 1985. An aerodynamic basis for selecting transmitter loads

475   in birds. *Wilson Bull.* **97:** 306-318.

476

477   **Calenge, C.** 2014. compana {adehabitat}: Compositional Analysis of Habitat Use.

478   http://www.inside-r.org/packages/cran/adehabitat/docs/compana (accessed March 2014).

479

Carpenter, J.E. 2008. An investigation of causes of population decline in the marsh tit *Poecile palustris* in Britain. DPhil thesis, Oxford University.

Carr, G.M. & Macdonald, D.W. 1986. The sociality of solitary foragers – a model based on resource dispersion. *Anim. Behav.* **34:** 1540-1549.

Ekman J. 1979. Coherence, composition and territories of winter social groups of the Willow Tit *Parus montanus* and the Crested Tit *P. cristatus*. *Ornis Scand.* **10:** 56-68.

Ekman J. 1989. Ecology of non-breeding social systems of *Parus*. *Wilson Bull.* **101:** 263-288.

Farine, D.R. & Lang, S.D.J. 2013. The early bird gets the worm: foraging strategies of wild songbirds lead to the early discovery of food sources. *Biol. Lett.* **9:** 20130578.

Fuller, R.J. 2012. Habitat quality and habitat occupancy. In Fuller, R.J. (ed.) *Birds and Habitat: Relationships in Changing Landscapes*. Cambridge University Press, UK.

Gibb, J. 1954. Feeding ecology of tits, with notes on treecreeper and goldcrest. *Ibis* **96:** 513-543.

Hadley, A. & Desrochers, A. 2008. Winter habitat use by boreal chickadee flocks in a managed forest. *Wilson J. Ornithol.* **120:** 139-145.

Hartley, P.H.T. 1953. An ecological study of the feeding habits of the English titmice. *J. Anim. Ecol.* **22:** 261-288.

507 **Hill, R.A. & Broughton, R.K.** 2009. Mapping Understorey from Leaf-on and Leaf-off

508 Airborne LiDAR Data of Deciduous Woodland. *ISPRS J. Photogramm.* **64:** 223-233.

509

510 **Hill, R.A., Wilson, A.K. George, M. & Hinsley, S.A.** 2010. Mapping tree species in

511 temperate deciduous woodland using time-series multi-spectral data. *Appl. Veg. Sci.* **13:** 86–

512 99.

513

514 **Hinsley, S.A., Hill, R.A., Gaveau, D.L.A. & Bellamy, P.E.** 2002. Quantifying woodland

515 structure and habitat quality for birds using airborne laser scanning. *Funct. Ecol.* **16:** 851–

516 857.

517

518 **Hinsley, S.A., Carpenter, J.E., Broughton, R.K., Bellamy, P.E., Rothery, P., Amar, A.,**

519 **Hewson, C.A. & Gosler, A.G.** 2007. Habitat selection by Marsh Tits *Poecile palustris* in the

520 UK. *Ibis* **149 (Supplement 2):** 224-233.

521

522 **Horne, J.S. & Garton, E.O.** 2009. Animal Space Use 1.3

523 http://www.cnr.uidaho.edu/population_ecology/animal_space_use (accessed March 2014).

524

525 **Johnson, M.D.** 2007. Measuring habitat quality: a review. *Condor* **109:** 489–504.

526

527 **Kenward, R.E.** 2001. *A Manual for Wildlife Radio Tagging*. Academic Press, London.

528

529 **Martin P. & Bateson P.** 2007. Measuring Behaviour: An Introductory Guide (3rd Edition).

530 Cambridge University press, UK.

531

532 **Matthysen, E.** 1998. *The Nuthatches*. T & A D Poyser, London.

533

534   **Met Office** 2013. Climate summaries. http://www.metoffice.gov.uk/climate/uk/summaries

535   (accessed June 2014).

536

537   **Morse, D.H.** 1978. Structure and foraging patterns of flocks of tits and associated species in

538   an English woodland during winter. *Ibis* **120:** 298-312.

539

540   **Naef-Daenzer, B.** 1994. Radiotracking of Great and Blue Tits: new tools to assess

541   territoriality, home-range use and resource distribution. *Ardea* **82:** 335-347.

542

543   **Nilsson, J.-Å. & Smith, H.G.** 1988. Effects of dispersal date on winter flock establishment

544   and social dominance in marsh tits *Parus palustris. J. Anim. Ecol.* **57:** 917-928.

545

546   **Rappole, J.H. & Tipton, A.R.** 1991. New harness design for attachment of radio

547   transmitters to small passerines. *J. Field Ornithol.* **62:** 335-337.

548

549   **Siffczyk, C., Brotons, L., Kangas, K. & Orell, M.** 2003. Home range size of willow tits: a

550   response to winter habitat loss. *Oecologia* **136:** 635-642.

551

552   **Smart, L.S., Swenson, J.J., Christensen, N.L. & Sexton, J.O.** 2012. Three-dimensional

553   characterization of pine forest type and red-cockaded woodpecker habitat by small-footprint,

554   discrete-return lidar. *Forest Ecol. Manag.* **281:** 100-110.

555

556   **Smith, S.M.** 1991. *The Black-capped Chickadee: Behavioural Ecology and Natural History.*

557   Cornell University Press, New York.

558

559   **Vierling, K.T., Vierling, L.A., Gould, W.A., Martinuzzi, S. & Clawges, R.M.** 2008. Lidar:

560   sheding new light on habitat characterization and modelling. *Front. Ecol. Environ.* **6:** 90-98.

561

562   **Wesołowski, T. & Fuller, R.J.** 2012. Spatial variation and temporal shifts in habitat use by

563   birds at the European scale. In Fuller, R.J. (ed.) *Birds and Habitat: Relationships in*

564   *Changing Landscapes.* Cambridge University Press, UK.

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590   TABLES

591   Table 1. Woodland structural variables in the cores and peripheries of 12 Marsh Tit home-

592   ranges, compared using Wilcoxon signed rank tests (*W* statistic). Home-range cores were

593   delimited by the 70% kernel contour, and peripheries by the 70-100% contours.

594

	Home-range core, median (range)		Home-range periphery, median (range)		*W*	*P*
Canopy height (m)	13.8	(12.4-16.3)	14.3	(13.6-15.7)	19.0	0.13
Canopy closure (%)	72.1	(51.0-91.5)	77.8	(73.1-84.1)	16.0	0.08
Understorey height (m)	3.9	(3.1-4.4)	3.7	(3.3-3.9)	53.0	0.29
Understorey volume (m^3/m^2)	1.6	(0.9-2.0)	1.6	(1.4-1.7)	49.0	0.47

595

596

597   Table 2. Median percentage cover of canopy tree species in 12 Marsh Tit home-ranges and

598   home-range cores, and the wider study area. Home-range cores were delimited by the 70%

599   kernel contour within the full home-ranges (100% contour). Unclassified refers to all

600   vegetation 1-8 m in height.

601

	Home-range cores	Full home-ranges	Study area
Common Ash	26.7	31.5	41.1
English Oak	18.8	16.6	15.5
Field Maple	10.3	11.3	10.6
European Aspen	6.4	6.8	5.4
Silver Birch	2.2	2.1	1.8
Elm spp.	1.7	0.9	0.4
Unclassified	33.96	30.91	25.10

602

603

604 Table 3. Ranking matrix from compositional analysis (Aebischer et al. 1993), comparing

605 proportional use of canopy tree species in 12 Marsh Tit home-ranges (100% kernel contour)

606 vs. home-range cores (70% kernel contour). Unclassified (Unc.) refers to all vegetation 1-8

607 m in height. Single positive and negative signs indicate respective (but non-significant)

608 preference or non-preference of species in rows vs. species in columns, and triple signs

609 (+++/---) represent significant deviation from random at $P < 0.05$. The number of positive

610 associations in each row ranks tree species in increasing order of relative use, with a higher

611 rank indicating greater selection by Marsh Tits.

612

	Ash	Oak	Maple	Aspen	Birch	Elm	Unc.	Rank
Ash		---	-	-	-	+	---	1
Oak	+++		+++	+	+	+	+	6
Maple	+	---		+	-	+	---	3
Aspen	+	-	-		-	+	-	2
Birch	+	-	+	+		+	-	4
Elm	-	-	-	-	-		-	0
Unc.	+++	-	+++	+	+	+		5

613

614

615   Table 4. Summary statistics of scores from instantaneous sampling for the relative use of

616   tree species by 10 radio-tracked Marsh Tits. Values refer to the proportion of records in

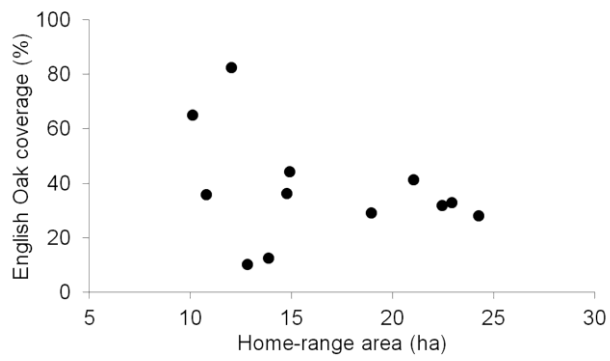617   which a bird was observed using a given tree.

	Records	Ash	Oak	Maple	Birch	Aspen	Elm	Other
Mean	26.8	0.15	0.60	0.04	0.04	0.01	0.13	0.03
s.d.	7.8	0.11	0.19	0.08	0.06	0.01	0.23	0.05
Median	25.5	0.17	0.57	0.00	0.01	0.00	0.00	0.01
Min.	15	0.00	0.33	0.00	0.00	0.00	0.00	0.00
Max.	42	0.35	0.91	0.25	0.19	0.03	0.67	0.18

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636   Legends to figures

637   Figure 1. The area of Marsh Tit home-ranges plotted against the percentage cover of

638   English Oak in the tree canopy of the home-range, showing a weak negative correlation:

639   Spearman's rank-order, r_s = -0.34, P = 0.28.

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