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1 An efficient survey method for estimating populations of Marsh Tits *Poecile palustris*, a low-  
2 density woodland passerine

3

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28 **Capsule** A playback survey comprising two visits to woodland in early spring can reliably  
29 detect Marsh Tits, and permit reasonable estimation of the number of territories.

30 **Aims** To assess the efficacy of an efficient survey method for detecting and estimating  
31 populations of Marsh Tits.

32 **Methods** Detection probability of colour-marked Marsh Tits, surveyed using playback, was  
33 assessed with Cormack-Jolly-Seber models. Reliability of territory estimates was compared  
34 between colour-marked and largely or wholly unmarked populations.

35 **Results** Playback surveys over two visits in early spring was highly effective in detecting  
36 individual Marsh Tits. Territory estimates were similar for woods in years where fewer than  
37 20% of the population was marked compared to years when a higher proportion of birds  
38 were colour-marked, although territories may be underestimated in larger woods with  
39 unmarked populations.

40 **Conclusion** A playback survey comprising two visits in early spring is recommended as an  
41 efficient method of surveying Marsh Tit populations and locating individuals. A survey  
42 protocol is suggested.

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## 56 **Introduction**

57 Field surveys that reliably quantify the number of birds inhabiting a given area are  
58 fundamental to most population studies and species conservation initiatives (Thompson  
59 2002, Gregory et al. 2004). In forested habitats, where visibility is generally restricted,  
60 several well-established sampling methodologies can generate an index of bird abundance,  
61 including point counts, line transects and mist-netting (Gilbert et al. 1998, Bibby et al. 2000).  
62 However, these sampling methods can be poorly suited to woodland species that occur at  
63 low density, have large territories, and forage among dense vegetation or in tall treetops,  
64 such as some woodpeckers (Picidae), orioles (Oriolidae) and tits (Paridae) (Gilbert et al.  
65 1998, Bibby et al. 2000, Charman et al. 2010).

66 A common strategy for overcoming such limitations is to estimate the absolute population by  
67 undertaking intensive repeated surveys of all wooded habitat in the study area using a  
68 mapping methodology (e.g. Dagley 1994, Vitkander et al. 1994, Wesolowski 2015). Such an  
69 approach ensures that individuals are more likely to be encountered, but is generally labour-  
70 intensive. Surveys requiring only confirmation of presence or absence can be achieved with  
71 fewer visits than territory mapping, but passive surveys may still require many hours of effort  
72 to detect the target species (Charman et al. 2010)

73 For some species, the additional use of playback of recorded song or calls during surveys  
74 can increase efficiency and detection probability by eliciting counter-singing from territorial  
75 birds (Bibby et al. 2000, Allen 2004). Playback mapping surveys have been used to census  
76 or detect the presence of Willow Tits *Poecile montanus* (Orell et al. 1994, Lewis et al. 2009a)  
77 and Marsh Tits *P. palustris* (Broughton et al. 2012a), both of which occupy large territories at  
78 low density in wooded habitats; this technique has become favoured for surveying these two  
79 species in Britain, where their respective abundance has declined substantially (Lewis et al.  
80 2009b, Broughton & Hinsley 2015).

81 Despite their widespread use, assessment of the accuracy of survey methods is uncommon  
82 in the ornithological literature (Gilbert et al. 1998, Bibby et al. 2000, Thompson 2002).  
83 Specifically, there has been no validation of the efficacy of the playback method for detecting

84 or quantifying Marsh Tits, which could support its use for mapping and monitoring of this  
85 species. In this paper we assess the reliability of a standardised playback method for the  
86 efficient census of Marsh Tits in woodland patches, using colour-marked (leg rings) birds for  
87 validation of detection and population estimates. An accurate and reliable method of  
88 surveying this species would be valuable for monitoring and research that supports the  
89 species' conservation, and may have wider applicability to similar low-density species.

90

## 91 **Methods**

### 92 Study species

93 The Marsh Tit is a small (9-12 g) passerine that is largely restricted to mature broadleaved or  
94 mixed woodland habitats in temperate Europe and east Asia (Cramp & Perrins 1993). Marsh  
95 Tits are non-migratory and highly sedentary, undertaking relatively short post-natal dispersal  
96 distances (several km) before permanent settlement in a home-range as socially-  
97 monogamous pairs (Broughton et al. 2010, Wesolowski 2015). Winter home-ranges have  
98 been estimated at an average 31 ha (Broughton et al. 2015), and overlap with those of  
99 neighbours, but at the end of winter birds establish extensive (5-6 ha, Broughton et al.  
100 2012a), strictly-defended spring territories from March to June, in which nesting takes place  
101 from mid-April to June (Broughton & Hinsley 2015).

102

### 103 Study areas

104 During 2004-2018, as part of a long-running study of Marsh Tit ecology and behaviour  
105 (Broughton 2012, Broughton & Hinsley 2015), surveys were conducted in 16 woods in  
106 Cambridgeshire, eastern England. The woods comprised patches of mature trees set in an  
107 arable landscape matrix, ranging from 4-160 ha in area and located within a 5 km radius  
108 centred on Monks Wood (52°11' N, 0°50' E). Additional surveying took place at the 70 ha  
109 Bradfield Woods in Suffolk (52°11' N, 0°50' E) during 2014-2018. Most (14) woods, including  
110 Monks, comprised native broadleaved trees dominated by Pedunculate Oak *Quercus robur*  
111 and Common Ash *Fraxinus excelsior*, with the remaining three woods containing substantial

112 areas of non-native conifer (*Picea-Pinus*) plantation that was admixed with native  
113 broadleaves.

114

#### 115 Territory mapping benchmark surveys

116 To create a benchmark of typical densities of Marsh Tit territories, we used data from an  
117 intensive colour-ringing and territory mapping study at Monks Wood during 2003-2018. This  
118 study involved approximately 65 h of systematic annual trapping effort over at least six days  
119 each autumn, resulting in 83-100% of individuals detected in subsequent springs bearing  
120 unique combinations of colour-rings for field identification. Spring territories were quantified  
121 with a further 100 h of annual fieldwork over at least ten days during a time window from the  
122 beginning of March to mid April, after exclusive territory establishment but prior to the  
123 beginning of nesting, using the territory mapping method (Bibby et al. 2000, Broughton et al.  
124 2012). This corresponded to approximately 1 h of survey effort per 1.6 ha of habitat  
125 surveyed, allowing an efficiency comparison with other methods. Results from territory  
126 mapping were used to directly compare territory densities from assessments of other woods.

127

#### 128 Playback surveys

129 Due to limited resources, a less intensive method was required to monitor Marsh Tit  
130 populations in the 16 woods other than Monks Wood. Intermittent autumn-winter trapping in  
131 the Cambridgeshire woods during 2008-2018, and annual trapping in Bradfield Woods  
132 during 2014-2018, resulted in 15-40 (mean 27) colour-marked birds distributed across these  
133 woods in subsequent springs. Populations were entirely unmarked in at least four woods per  
134 year, and all woods (except Bradfield) experienced at least one year when all birds were  
135 unmarked.

136 To estimate numbers of spring territories without the labour-intensive territory mapping used  
137 at Monks Wood, a simplified playback survey was adopted in each wood for 4-10  
138 consecutive years between 2009 and 2018 (Table 1). Playback surveys comprised two  
139 morning visits (initiated from between 0.5 h after dawn until midday, during which time birds

140 were found to be most active and responsive in the Monks Wood surveys) to each wood in  
141 calm weather during March or early April, using the mp3 player on a Nokia C1-01 mobile  
142 telephone handset (Nokia Corporation, Espoo, Finland) loaded with mp3 sound files of  
143 Marsh Tit songs and calls.

144 During surveys, the observer walked at a slow pace along a pre-defined route that passed  
145 within 100 m of all parts of the wood, as tests in Monks Wood found that playback from the  
146 handset was audible to humans over this distance (pers. obs.) and counter-singing between  
147 birds had been observed over a distance of approximately 250 m in the study area (visually  
148 and audibly confirmed from a location between song-posts, pers. obs.). Playback was  
149 broadcast at full volume, with no audible distortion, at stops approximately every 100 m  
150 along the survey route for around two minutes, including short (5-10 s) pauses of the  
151 recording for the observer to listen for a response of song or calls. Where no birds were  
152 detected the observer continued along the route and repeated the playback. Where a  
153 response was heard the observer remained stationary if the bird approached and appeared  
154 close by, or otherwise left the route to locate it, in both cases checking for the presence of  
155 accompanying (paired) birds and any colour-rings.

156 Responding birds were plotted on site maps, with song considered to indicate a male (song  
157 is very rare in female Marsh Tits; Broughton 2008) and a female was inferred by  
158 accompanying a singing bird and/or responding only with agitated calls but not song. Birds  
159 that followed the observer to consecutive locations in response to playback were detected by  
160 direct observation and/or colour-rings, and these plotted movements aided territory  
161 identification by providing additional mapped registrations. Frequent counter-singing  
162 between multiple responding birds also aided the mapping of individual territories.

163 The mapped observations of presumed (unmarked) or known (colour-marked) unique  
164 individuals or pairs were distinguished and grouped in the manner of standard territory  
165 mapping (Bibby et al. 2000). Previously published metrics of Marsh Tit territories (largely  
166 derived from the Monks Wood surveys) guided the groupings, including a minimum territory  
167 area of 1.5 ha and expected mean of 5-6 ha (Broughton et al. 2012a). Unless observation

168 indicated otherwise, registrations of unmarked birds more than 150 m apart were considered  
169 to relate to different individuals, as experience of marked birds in Monks Wood indicated that  
170 birds were unlikely to travel such a distance undetected in the short period in which an  
171 observer passed during a playback survey (pers. obs.). A distance of 150 m was also slightly  
172 greater than the radius of a typical 5-6 ha territory (125-138 m), and so an individual could  
173 be detected within the territory core or periphery on either visit, but without the threshold  
174 being so large as to encompass more than one typical territory (and different birds).  
175 A territory was inferred from singing or an aggressive response to playback on either survey  
176 visit. This single registration threshold was adopted because Marsh Tits are highly sedentary  
177 and most individuals have settled in defended territories by March (Broughton et al. 2010).  
178 Consequently, single records at a given location during this period were considered more  
179 likely to be residents detected only once rather than transients that were present only briefly  
180 (cf. Bibby et al. 2000). Playback surveys lasted approximately 1 h per 30 ha of habitat on  
181 each visit, or 1 h per 15 ha for the full survey (two visits), requiring a total of approximately  
182 4.7 h of effort for full surveys of the largest (70 ha) woods.

183

#### 184 Statistical analyses

185 The efficacy of playback surveys in detecting Marsh Tits and accurately estimating territory  
186 numbers was tested in two ways. First, the probability of detecting individual birds in the  
187 annual two surveys was estimated by fitting a Cormack-Jolly-Seber (CJS) model (with a logit  
188 link function) to records of marked birds across all woods (excluding Monks Wood) in  
189 Program MARK v.7.1 (Cooch & White 2017). The initial model included time-varying  
190 (annual) estimates for re-sighting probability and apparent survival, while a second model  
191 fixed the re-sighting probability at 0.99 to replicate a near-perfect encounter history for  
192 comparison. Highly correlated estimates of apparent survival between both models would  
193 indicate that the time-varying model was performing as expected and the resulting re-  
194 sighting probabilities were realistic. Both models were compared using differences in the  
195 corrected Akaike Information Criterion (AICc).



196 Surveys could provide greater accuracy where a significant proportion of the population is  
197 colour-marked, because of the ability to distinguish between individuals. However, surveys  
198 of unmarked populations would be more efficient and widely applicable, by avoiding the  
199 need for labour-intensive trapping and marking. As such, a second test assessed whether  
200 surveys of woods containing no or few (< 20%) colour-marked birds differed from surveys of  
201 the same woods in years where 20% or more of the population was marked. Eight woods  
202 were selected where at least two years of territory estimates were available for each marking  
203 category (<20% or ≥20% of birds colour-marked) in 2009-2018, and the mean territory  
204 estimate of each category for each wood were used as paired data and compared in a  
205 Wilcoxon signed-rank test. This test assumed no significant changes in population between  
206 survey years, although variation would be smoothed by the averaging of values.

207 Reliability of the territory estimates of unmarked populations was further assessed using a  
208 sample from two large woods (70 ha and 27 ha) in five years (2012, 2014-16, 2018) when at  
209 least 50% of detected territories contained a marked bird. This sample was selected due to  
210 relatively large populations of Marsh Tits (providing a good test of territory estimation), high  
211 proportions of marked individuals (occupying ≥50% of territories, providing reliable territory  
212 estimates), and the availability of archived field maps. For each of the annual field maps for  
213 these two woods, the assessments of territory numbers were repeated after the colour-mark  
214 information was removed, and so the birds were 'anonymized' to replicate a survey of  
215 unmarked birds. The territory estimates based on data of marked and anonymized birds  
216 were generated by different assessors to avoid bias. Sample sizes of five matched pairs  
217 (some tied) for each wood were insufficient for a statistical test, such as the Wilcoxon signed  
218 rank, so the two sets of five pairs of marked and anonymized territory estimates for each  
219 were compared to simply determine the percentage differences.

220

## 221 **Results**

222 The annual surveys in Monks Wood identified a mean 19 territories (range: 10-23) in 2004-  
223 2018, giving an overall mean density of 0.12 (sd = 0.03, range: 0.06-0.15) territories/ha.

224 Playback surveys of the other 16 woods gave an identical overall mean density of 0.12 (sd =  
225 0.05) territories/ha, by averaging the means for each wood over the respective number of  
226 years of available data, but with a wider range of 0.05-0.24. There was no significant  
227 correlation between woodland area and the maximum territory density (Pearson's  $r = -0.31$ ,  
228  $P = 0.24$ ; Table 1).

229 Playback surveys detected a total of 130 individual colour-marked Marsh Tits across the  
230 woods, excluding Monks Wood, in 2009-2018. A mean 48% (range 28-62%) of birds  
231 identified in each year were detected during only one of the two surveys visits. The time-  
232 varying CJS model estimated the annual probability of re-sighting these individuals at 0.78-  
233 1.00 (mean = 0.96, sd = 0.08) over eight annual intervals, excluding the ninth interval as  
234 such models are unable to determine a terminal re-sighting rate (Cooch & White 2017). The  
235 lowest annual estimate (0.78) resulted from the failure to detect two birds that were later  
236 known to be alive, and the effect that this had among a relatively small sample of 23 birds.

237 Survival estimates from the time-varying model were closely correlated with those derived  
238 from the model with annual detection probabilities fixed at 0.99 (Spearman's  $r_s = 0.82$ ,  $P =$   
239 0.01), indicating that the time-varying model output for detection probability was realistically  
240 high. However, the AICc value of the fixed probability model (Table 2) was higher than the  
241 time varying model, suggesting the latter was the best fit to the data.

242 There was no significant difference in the mean territory estimates derived from playback  
243 surveys in woods during years when at least 20% of the population was colour-marked  
244 compared to years when fewer or no birds were marked (Wilcoxon  $W = 4.0$ ,  $P = 0.22$ ,  $n = 6$   
245 excluding two ties; Fig. 1). However, comparisons of territory estimates based on colour-  
246 marked and anonymized data from two of the larger woods found a mean underestimate of  
247 10% for an average 6.6 (range: 6-8) territories present in the 27 ha wood, and 15% for an  
248 average 10.8 (range: 9-12) territories in the 70 ha wood for five years of estimates, with an  
249 annual maximum of 25% (9 territories estimated out of an actual 12 present). Nevertheless,  
250 estimates were the same for 30% of the ten comparisons across both woods.

251

## 252 **Discussion**

253 The probability of re-sighting individual Marsh Tits using the playback survey method was  
254 very high, averaging 96%, showing that almost all birds present would be detected in most  
255 years. Although intensive colour-marking and standard territory mapping in Monks Wood  
256 likely provided highly accurate data describing the number and extent of Marsh Tit territories  
257 and their occupants, this required time-consuming fieldwork over at least 16 days. Other  
258 studies employing field surveys to quantify Marsh Tit territories, without playback, have also  
259 required a large number (10-12) of site visits (Siriwardena 2006, Wesolowski et al. 2015). By  
260 contrast, in order to quantify the number of territories and indicate their approximate location,  
261 the playback method required only two visits per site and used only 11% of the time required  
262 for the intensive territory mapping survey at Monks Wood. However, unlike intensive colour-  
263 marking and territory mapping, the playback survey was unable to define territory boundaries  
264 or extent.

265 The overall territory density estimated from playback surveys in all woods (0.12  
266 territories/ha) was similar to that obtained from more intensive fieldwork during territory  
267 mapping at Monks Wood, with the greater variation in range from playback surveys likely  
268 reflecting population differences between woods of varying size and habitat type. The  
269 similarity in territory densities validated the use data from the larger Monks Wood (160 ha)  
270 as a basis for parameters of expected territory size in the smaller woods (4-70 ha), and the  
271 demonstration that territory density was not related to woodland area further justified this  
272 approach.

273 Mean territory estimates derived from the playback surveys of woods in years when many  
274 birds were marked were similar to those from years in which few or no birds were marked,  
275 showing that broadly similar results could be obtained without labour-intensive trapping and  
276 colour-marking of many birds in a population.

277 For two larger woods, however, assessment of anonymized data tended to underestimate  
278 the number of territories identified using colour-mark information. The underestimations  
279 resulted from a conservative grouping of registrations into territories, rather than detection

280 error, and averaged 10-15% overall. Error was lower for territory estimates in the smaller of  
281 the two woods, suggesting that the more complex territory configurations of larger  
282 populations in more extensive woods could lead to greater difficulty in estimating the number  
283 of territories of unmarked birds. However, the discrepancies between estimates derived from  
284 colour-marked and anonymized data were generally not substantial (maximum 2-3 territories  
285 over a total population of 15-18 territories), and were offset by the gain in efficiency and  
286 reduced survey effort.

287 Overall, the results indicate that territory estimates derived from playback surveys of Marsh  
288 Tits were of sufficient reliability for population monitoring, at least for the range of woodland  
289 patches (4-70 ha) and populations (1-13 territories/pairs) covered in this study. The accuracy  
290 of the territory estimates of unmarked populations was generally comparable to that of  
291 marked populations, though with the potential for some underestimation. Colour-marking  
292 would increase the reliability of territory estimates in larger woods, though in highly modified  
293 landscapes woodland patches tend to be fragmented and relatively small; 74% of woods  
294 across the Marsh Tit's range in England and Wales are less than 10 ha (Forestry  
295 Commission 2001, 2002), and so each is capable of supporting only a few territories. The  
296 accuracy of territory estimates in larger woods may also be improved by additional survey  
297 visits to increase the number of registrations available during assessment.

298 A suggested protocol for the efficient surveying of Marsh Tits using the playback method is  
299 given in Appendix 1, and is recommended for determining presence or absence and deriving  
300 territory or population estimates for woods with unmarked populations. For more detailed  
301 demographic studies, combining the survey methodology with colour-marking would facilitate  
302 systematic analyses of survival and dispersal (e.g. Broughton et al. 2010), as the playback  
303 methodology is effective in locating individuals with a high degree of probability and  
304 efficiency.

305 In the current assessment, approximately half of the birds known to be present from the full  
306 playback surveys were detected on only one of the annual visits, underlining the need for a  
307 second visit per year to locate the remainder. However, for small woods (e.g. 20 ha or less)

308 a single survey visit may be sufficient if this detects that the habitat is saturated with  
309 territories (based on the average or minimum territory area, Broughton et al. 2012a), or if  
310 marked birds that occupied all potential territories in the previous year are confirmed to still  
311 be present. In such cases a second survey visit would be superfluous. However, although a  
312 single visit can confirm the presence of birds, a second survey would provide a more robust  
313 indication of absence (lower likelihood of a false negative) and will be appropriate in most  
314 cases, as habitat is unlikely to be saturated with territories, particularly in declining  
315 populations such as that in Britain.

316 The playback survey protocol adopted in this study may also be suitable or modified for the  
317 efficient census of other forest birds with similarly large territories or low density, such as the  
318 Willow Tit *P. montana*, Crested Tit *Lophophanes cristatus* and Lesser Spotted Woodpecker  
319 *Dendrocopos minor*. All of these species are scarce and/or declining in several parts of their  
320 range, including Britain. Information on the timing of territoriality and spacing of individuals,  
321 acquired through marking or tagging, would assist with estimating the number of territories  
322 from surveys of these species, as territory parameters are likely to differ from those of Marsh  
323 Tits (Orell et al. 1994, Vitkander et al. 1994). Testing and reporting the efficacy of this and  
324 other survey methods would be valuable to assess their applicability in the field, and to  
325 develop standard protocols that could be used for large-scale monitoring of such species.

326

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332

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416 Table 1. Area of woodland patches surveyed for Marsh Tits using playback over the  
 417 specified number of springs (surveyed years) during 2009-2018. Also given are the  
 418 maximum number of occupied territories estimated from surveys, the number of surveyed  
 419 years when a percentage of the population was colour-marked, and the mean percentage  
 420 and minimum-maximum percentage range of the population that was marked in years when  
 421 such birds were present.

Woodland patch area (ha)	Surveyed years	Maximum territories	Years with marked birds	Marked birds (mean %)	Marked birds (range %)
4	8	1	3	50	50-50
6	7	2	0	0	-
7	7	1	0	0	-
8	8	2	0	0	-
12	4	2	3	75	25-100
13	10	3	5	44	20-50
16	9	3	3	42	25-50
18	5	3	2	21	17-25
27	10	8	8	62	42-86
28	10	4	8	71	25-100
29	4	3	1	25	-
31	10	3	6	49	25-80
31	5	3	3	41	33-50
58	4	9	2	10	10-10
70	10	13	8	65	38-93
70	5	13	5	64	37-91

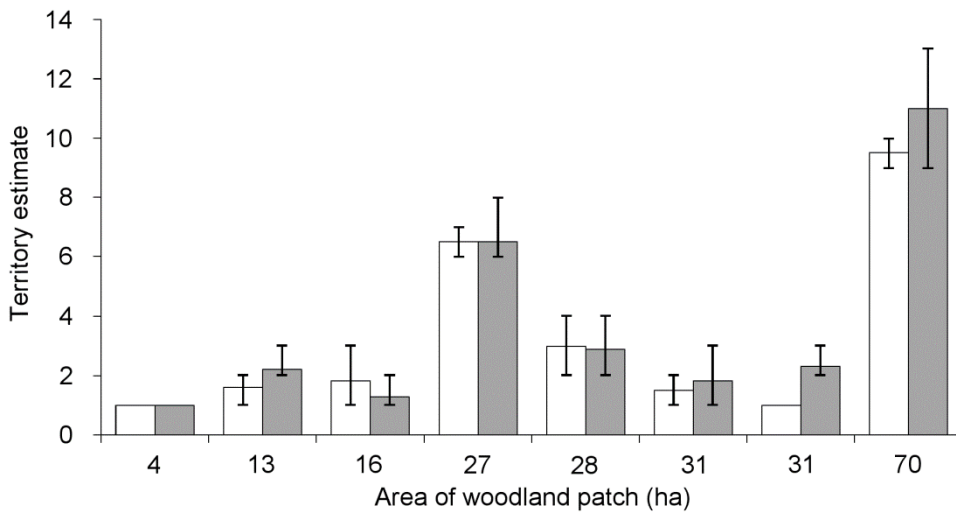
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433 Table 2. Cormack-Jolly-Seber modelling output for two candidate models estimating annual  
 434 survival ( $\Phi$ ) and detection probability ( $p$ ) of Marsh Tits over nine annual intervals, where  
 435 parameters were time-dependent ( $t$ ) annually, or fixed at a value of 0.99.

Model	$\Delta AICc$	AICc weight	Model likelihood	No. parameters	Deviance
$\Phi_t p_t$	0	0.95	1.00	12	41.44
$\Phi_t p_{0.99}$	5.74	0.05	0.06	9	53.76

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458 Figure



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460 Figure 1. Mean (columns) and minimum-maximum (errors bars) of the estimated number of  
461 Marsh Tit territories derived from playback surveys in woodland patches of a given area.  
462 White columns represent years when the population was wholly unmarked and grey columns  
463 are years when at least 20% of birds were colour-marked.

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478 Appendix 1

479 **Playback survey protocol for detecting and quantifying Marsh Tits in spring**

480 1. Surveys should take place during the pre-nesting period of territory defence by Marsh Tits,  
481 which falls between early March and early April in England and Wales, but may vary in other  
482 regions and climates.

483 2. Two survey visits are required, on different days in fine weather, with no rain or strong  
484 wind, and preferably on mild days (no frost). Surveys should begin during the early morning,  
485 but can extend into the early afternoon if weather remains favourable.

486 3. On a large-scale site map (preferably with a scale reference or 100 x 100 m grid to assist  
487 mapping), a route should be planned that takes an observer within 100 m of all wooded  
488 habitat in the study area, while minimising overlaps on the route. Surveys visits should last a  
489 minimum of 1 hour per 30 ha of habitat.

490 4. The observer walks slowly along the route, looking and listening for Marsh Tits. At stops  
491 approximately every 100 m on the route, playback of Marsh Tit songs and calls are played  
492 for around 2 minutes, including pauses of 5-10 seconds to listen for a response. Playback  
493 should be loud enough to be audible to a human observer over 100 m, but without distortion.  
494 A mobile phone or mp3 player is suitable.

495 5. Responding Marsh Tits may approach the observer on the route and can be checked for  
496 colour-rings (if applicable). A bird may respond but not approach, and the observer may  
497 leave the route to find it and check for rings, or whether the bird is alone or paired, before  
498 returning to the route. Males typically respond more vigorously than females, with song and  
499 calls. Females may respond with agitated calls but no song, and both birds in a pair often  
500 respond together. Attention should be paid to looking for quieter females accompanying a  
501 responding male.

502 6. The locations of responding birds are registered on the site map, using standard coding  
503 conventions (e.g. [http://www.ecn.ac.uk/measurements/terrestrial/b/bi/bto3/at\\_download/file](http://www.ecn.ac.uk/measurements/terrestrial/b/bi/bto3/at_download/file)),  
504 and the observer continues with the route. Where responding birds follow the observer in

505 response to the playback, this can be marked on the map – birds may respond until the edge  
506 of their territory is reached.

507 7. Sighting registrations on survey maps from both visits can be used to estimate the number  
508 of territories by grouping or distinguishing between observations. A single registration in  
509 either visit is sufficient to indicate a territory. The absolute minimum expected area of a  
510 territory is 1.5 ha of wooded habitat, and the typical expected area is 5-6 ha, although  
511 territories may exceed 10 ha. Unless observations indicate otherwise, registrations more  
512 than 150 m apart are likely to indicate different individuals if habitat availability could  
513 accommodate a corresponding number of territories.