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1 **Morphology, geographical variation and the subspecies of Marsh Tit *Poecile palustris***  
2 **in Britain and central Europe**

3

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29 **SUMMARY**

30 **Capsule** All British Marsh Tits belong to subspecies *Poecile palustris dresseri*, being smaller  
31 than nominate *P. p. palustris* of central Europe.

32

33 **Aims** Determining the subspecies of Marsh Tit in Britain to test whether ssp. *P. p. palustris*  
34 occurs in northern England and Scotland, by assessing regional variation in size compared  
35 with central European birds.

36

37 **Methods** 1147 wing length and 250 tail length measurements from 953 Marsh Tits were  
38 compared between eight British locations to test for regional variation. Biometrics were  
39 compared between birds from Britain and six locations within the continental European  
40 range of ssp. *palustris*.

41

42 **Results** There was no regional variation in wing or tail lengths among British Marsh Tits,  
43 indicating that all resident birds belong to ssp. *dresseri*. There was no evidence supporting  
44 the existence of ssp. *palustris* in northern England. British birds were significantly smaller  
45 than those from continental Europe, with proportionately shorter tails, consistent across all  
46 age and sex classes.

47

48 **Conclusion** All British Marsh Tits should be considered as ssp. *dresseri*, with ssp. *palustris*  
49 being limited to continental Europe. With no evidence of regional variation in size within  
50 Britain, reliable sexing methods based on biometrics could be applied in demographic  
51 studies throughout the country.

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56 The taxonomy of tits (Paridae) has long been a subject of intense study among ornithologists  
57 (Eck 2006). A refinement of species and subspecies classifications during the late 19<sup>th</sup> and  
58 early 20<sup>th</sup> Centuries, based on morphology and vocalisations (Vaurie & Snow 1957), had led  
59 to stability until new techniques of molecular genetic analysis initiated a new era of  
60 taxonomic change in the last two decades (e.g. Gill *et al.* 2005, Johansson *et al.* 2013).  
61 Despite these advances the taxonomic status or validity of most of the claimed subspecies  
62 of tits remains unclear, due to the large variation between and within populations, and also  
63 the changing trends and concepts within taxonomy (Eck 2006).

64 For some well-studied species in the Western Palearctic, such as the Willow Tit *Poecile*  
65 *montanus* and Coal Tit *Periparus ater*, historical classifications of subspecies based on  
66 apparent differences in plumage, size and vocalisations were not detected in the genetic  
67 structure of populations (Kvist *et al.* 2001, Pentzold *et al.* 2013). Such contradictions  
68 underline the continuing role of morphology, behaviour and bioacoustics in the taxonomic  
69 classification of phenologically or biologically distinct populations.

70 The Marsh Tit *Poecile palustris* is a species of Paridae where the classification of  
71 subspecies has remained unresolved since the early 20<sup>th</sup> Century (Cramp & Perrins 1993,  
72 Eck 2006). A clinal increase in size (wing and tail length) and decrease in colour saturation  
73 of the plumage is reported to occur from west to east across their Western Palearctic range  
74 (Cramp & Perrins 1993). Numerous subspecies have been proposed on this cline, but at  
75 present the only widely recognised forms are nominate ssp. *palustris* in central and northern  
76 Europe, which ranges from southern Scandinavia to northern Iberia and east to Poland and  
77 Greece, being replaced by ssp. *stagnatilis* in eastern Europe, *karbadensis* in the northern  
78 Caucasus, and *italiacus* in the French Alps and Italy (Cramp & Perrins 1993, Harrap & Quinn  
79 1995, Eck 2006, Gosler & Clement 2007).

80 There is particular confusion over the Marsh Tit subspecies present in Britain, at the western  
81 end of the European cline, where the species has undergone a 73% decline in abundance  
82 between 1966 and 2013 (Broughton & Hinsley 2015). Stejneger (1886) and Hartert (1907)  
83 assigned all British birds to ssp. *dresseri*, the smallest and darkest European form, but

84 Clancey (1947) proposed that birds at the northern edge of the British range, in northern  
85 England (Northumberland and Cumbria) and southeast Scotland (East Lothian and eastern  
86 Borders) should be treated as ssp. *palustris* based on the plumage colouration of skins  
87 examined.

88 Vaurie & Snow (1957) ignored Clancey's (1947) proposal and treated all British Marsh Tits  
89 as ssp. *dresseri*, extending the range of this form to northwest France based on size and  
90 colouration. Some authors, however, later accepted the claim of ssp. *palustris* in northern  
91 Britain (Cramp & Perrins 1993, Harrap & Quinn 1995) or the absence of ssp. *dresseri* from  
92 that area (Gosler & Clement 2007). In contrast, the British Ornithologists' Union (2013)  
93 currently recognise *dresseri* as the only subspecies of Marsh Tit on the 'British List', the  
94 official record of wild birds occurring in Britain. Yet, both *palustris* and *dresseri* are still  
95 designated as native forms in the UK government's biodiversity action plan for priority  
96 species (JNCC 2010, Burns & Eaton 2014), while Parkin & Knox (2010) acknowledged that  
97 the presence of ssp. *palustris* requires confirmation.

98 There appears to be no subsequent evidence for Clancey's (1947) claim of the Marsh Tit  
99 ssp. *palustris* occurring in Britain. Although size is cited as a key distinguishing feature  
100 between ssp. *palustris* and the smaller *dresseri* (Hartert 1907, Mayaud 1933) there has been  
101 no adequate statistical comparison between birds from northern and southern Britain and  
102 continental Europe. Wing length is the most consistent measure of body size in passerines  
103 (Gosler *et al.* 1998), and Broughton (2009) used this to compare live ssp. *dresseri* birds from  
104 eastern England with ssp. *palustris* birds from Sweden, but the test was limited by different  
105 measurement techniques (minimum wing chord for Swedish birds, maximum chord for  
106 English; see Svensson (1992) for differences between the methods).

107 It has also been hypothesised that geographical variation in Marsh Tit wing length may occur  
108 within subspecies in Britain, which would undermine its use as a sexing criterion (du Feu &  
109 du Feu 2014). Although McCollin *et al.* (2015) found only limited evidence for variation in  
110 wing length with latitude among four species of passerine in Britain, such variation in Marsh  
111 Tits, if it occurs, could also support Clancey's (1947) proposal of British Marsh Tits being

112 polytypic. The suggestions of Clancey (1947) and du Feu & du Feu (2014) require formal  
113 testing to assess the geographical variation in size and clarify the subspecies occurring in  
114 Britain, and also to clarify the range of the nominate ssp. *palustris* in Europe.  
115 We aimed to address these questions by comparing Marsh Tit biometrics within and  
116 between Britain and continental Europe. A lack of variation within Britain, but a contrast with  
117 ssp. *palustris* birds from elsewhere, would indicate that *dresseri* is the only resident British  
118 subspecies and that the range of *palustris* is restricted to the continental mainland.  
119 Consistent size within Britain would also support the use by analysts of biometrics for sexing  
120 Marsh Tits throughout the country, and the ability to apply a universal sexing method would  
121 be valuable for estimating population structure for demographic studies aiming to understand  
122 the causes of the species' population decline (Broughton & Hinsley 2015).

123

## 124 **METHODS**

### 125 **Measurements of British Marsh Tits**

126 The maximum-chord wing measurement (1 mm precision) of live Marsh Tits was used to  
127 compare geographical variation in body size between British populations. A total of 1147  
128 measurements of 953 individuals (42-451 measurements per site) were available from eight  
129 regions across England and Wales, spanning 538 km from north to south and 365 km from  
130 west to east, comprising 1) Devon: Yarner Wood (50°35'N, 3°43'W) and Peck Farm  
131 (50°37'N, 3°46'W); 2) Berkshire (Berks): Combe Wood (51°20'N, 1°29'W); 3) Oxfordshire  
132 (Oxon): Wytham Woods (51°46'N, 1°20'W) and Bagley Wood (51°43'N, 1°16'W); 4)  
133 Cambridgeshire (Cams): Monks Wood (52°24'N, 0°14'W) and adjacent woods within 5 km;  
134 5) Suffolk: Bradfield Wood (52°10'N, 0°82'E); 6) Cumbria: Roudsea Wood (54°13'N, 3°0'W);  
135 7) Northumberland (Northumbs): within 20 km of Alnwick (55°41'N, 1°70'W); 8) Powys:  
136 Llangorse (51°56'N, 3°15'W) (Fig. 1). The minimum distance between regions (Oxon and  
137 Berks) was 50 km.

138 Where possible, birds were aged as juveniles (prior to the first full moult at one year old) or  
139 as adults (one year or older) according to ageing criteria in Svensson (1992) and Broughton

140 *et al.* (2008). Marsh Tit wing lengths generally show a significant increase for the same  
141 individual after the first full moult from juvenile to adult plumage in their second summer  
142 (Nilsson 1992), but not thereafter (Broughton *et al.* 2008), and so measurements of the  
143 same individual as a juvenile and an adult were included in both age classes for analysis  
144 (Broughton *et al.* 2008, du Feu & du Feu 2014). Data collection took place throughout the  
145 year between 1996 and 2015. Additional wing length data from Oxon were derived from King  
146 & Muddeman (1995) and pooled with local data to increase sample sizes. Data were  
147 collected by experienced ringers (banders) at all sites, mostly professional  
148 ecologists/ornithologists or ringing trainers, and measurement techniques from all locations  
149 except Devon, Powys and Northumbs were validated (by RKB) during at least one ringing  
150 session.

151 Sexing data based on behaviour, cloacal protuberance or presence of a brood patch  
152 (Svensson 1992, King & Muddeman 1995, Broughton *et al.* 2008) were available for Cambs,  
153 Oxon and Suffolk, and indicated broadly equal proportions of males (54-58%) and females in  
154 samples. Tail length measurements (Svensson 1992) at 0.5 mm precision were available for  
155 250 birds from Cambs, Suffolk and Berks. Tail length and its relative proportion to wing  
156 length is cited as a distinguishing feature of Marsh Tit subspecies across Eurasia (Cramp &  
157 Perrins 1993, Eck 2006), and these measurements were used to support the wing length  
158 analyses.

159

## 160 **Measurements from continental Europe**

161 For comparison with British birds, 575 maximum-chord wing length measurements from live  
162 Marsh Tits were derived from the literature for five sites within the reported range of ssp.  
163 *palustris* within central Europe (and southern Scandinavia): Kaliningrad (Markovets 1998),  
164 southwest Germany (Ludescher 1973), northwest Germany (Hudde 1985), southern Sweden  
165 (Alatalo *et al.* 1985) and northern Switzerland (Amann 1980), and also original data collected  
166 from a sixth area in southwest Poland (within 30 km of Opole: 50°39'N, 17°57'E) during  
167 2002-2014 (Fig. 1). Data for individual birds were only available from Poland and

168 Switzerland, for the remaining sites only summary data were available (mean, standard  
169 deviation or standard error, and sample size). Summary data of tail lengths by age and sex  
170 class were available from Kaliningrad (139 measurements) for comparison with British birds.

171

## 172 **Statistical analysis**

173 Marsh Tit wing lengths vary with age and sex, creating a bimodal frequency distribution in  
174 unbiased population samples (Amann 1980, Nilsson 1992, Broughton *et al.* 2008), so  
175 geographical variation between British populations was tested using the Kruskal-Wallis test  
176 to accommodate non-normal frequency distributions. Pair-wise Kolmogorov-Smirnov tests  
177 were used to compare wing length frequency distributions between every population, which  
178 would indicate a difference in size or a significant bias in composition. Tail length  
179 measurements from Cambs, Berks and Suffolk were compared using a Kruskal-Wallis test,  
180 with age and sex classes combined for analysis and caution applied due to some small  
181 sample sizes. To assess the subspecies of northern English birds in more detail, Mann-  
182 Whitney tests were used to compare wing lengths of juveniles and adults between Cumbria  
183 and Cambs, both of which had adequately large and more reliably aged samples for each  
184 class due to long-running studies.

185 Mean values of wing length and 95% confidence limits from each British population were  
186 plotted alongside those from populations of ssp. *palustris*, where non-overlapping confidence  
187 limits between groups would indicate statistically significant differentiation at the  $\alpha$  level of  
188 0.05. The position of the northern English (Cumbria and Northumbs) populations in this plot,  
189 relative to southern English or continental populations, would support the subspecies  
190 identification as *palustris* or *dresseri*. Where summary data for combined age and sex  
191 classes were not available from the literature, the weighted means were derived using  
192 sample sizes as weights, and 95% confidence limits were estimated by calculating the  
193 standard errors from the pooled variance and multiplying by 1.96.

194 Comparisons of wing length by age and sex classes between known populations of ssp.  
195 *dresseri* and *palustris* were possible using the larger datasets from Cambs and Switzerland,

196 applying Mann-Whitney tests. A second plot of means and 95% confidence intervals  
197 compared the summary data of tail lengths between ssp. *palustris* birds from Kaliningrad and  
198 *dresseri* birds from Cambs. Tail/wing ratios were also calculated for each class to assess  
199 relative proportions (Eck 2006). All analyses were performed in R version 3.0.2 (R Core  
200 Team 2013).

201

## 202 **RESULTS**

### 203 **Comparisons within Britain**

204 The results indicated that all eight populations of British Marsh Tit were of a similar body  
205 size. There was no significant difference in median values of wing length, including for  
206 Cumbria and Northumberland in northern England (Kruskal-Wallis test:  $H = 5.77$ ,  $df = 7$ ,  $P =$   
207  $0.566$ ), and all populations shared identical values for the first and third quartile (Table 1).  
208 Pair-wise Kolmogorov-Smirnov tests showed a similar distribution of wing lengths (all tests:  
209  $D = 0.053-0.154$ ,  $P = 0.320-0.999$ ), indicating no significant deviation or compositional bias  
210 in samples. Tail lengths of birds from Suffolk, Cambs and Berks did not differ significantly  
211 (Kruskal-Wallis test:  $H = 4.70$ ,  $df = 2$ ,  $P = 0.096$ , Table 2), and the tail/wing ratios were  
212 similar at 0.82, 0.83 and 0.84 respectively. For the larger samples of wing lengths from  
213 Cambs and Cumbria, Mann-Whitney tests revealed no significant difference between adults  
214 at each site (medians = 64.0 mm, respective  $n = 206$  and  $106$ ,  $W = 16772.0$ ,  $P = 0.809$ ), or  
215 between juveniles (respective medians = 63.0 and 62.0 mm,  $n = 245$  and  $200$ ,  $W = 43227.5$ ,  
216  $P = 0.309$ ).

217

### 218 **Comparisons between Britain and continental Europe**

219 Plotting the means and 95% confidence limits for the British populations of known ssp.  
220 *dresseri* and those within the central European range of ssp. *palustris* showed no overlap  
221 between groups, denoting significant differentiation (Fig. 2). The populations from northern  
222 England (Cumbria and Northumberland) were positioned clearly within the *dresseri* group.  
223 The westernmost sample of *palustris* from northwest Germany appeared somewhat

224 intermediate between the two subspecies, possibly representing an intergrade population  
225 between *palustris* and *dresseri*.

226 The median wing lengths of Swiss ssp. *palustris* birds were significantly longer than those of  
227 Cambs ssp. *dresseri* birds for all age and sex classes, by a consistent 2 mm or 3% in every  
228 group (all pair-wise Mann-Whitney tests:  $W = 2659.5-10948.5$ ,  $P < 0.001$ ; Fig. 3).  
229 Comparisons of tail length between ssp. *palustris* birds from Kaliningrad and ssp. *dresseri*  
230 birds from Cambs also showed a significant difference at the  $\alpha$  level of 0.05 for all age and  
231 sex classes (Fig. 4), with the tails of continental birds being approximately 4-5 mm (8-10%)  
232 longer in every group. The tail/wing ratio for Kaliningrad birds was 0.87 in each age and sex  
233 class, compared to 0.82 (juvenile females) or 0.83 (other ages/sexes) for Cambs birds,  
234 showing that the tails of the ssp. *palustris* birds were also proportionately longer than those  
235 of *dresseri*.

236

## 237 **DISCUSSION**

238 Marsh Tits from the British populations examined shared very similar wing and tail lengths,  
239 and tail/wing proportions, indicating that they were all from the same subspecies (ssp.  
240 *dresseri*). These measurements were significantly shorter than the wings and tails of birds  
241 within the continental European range of ssp. *palustris*. These results confirm that *dresseri* is  
242 the only Marsh Tit subspecies present throughout the British range, with no evidence for the  
243 existence of ssp. *palustris* in northern England (cf. Clancey 1947, JNCC 2010).

244 Despite wing length being a key distinction between Marsh Tit subspecies, the  
245 measurements of 12 skins from Northumberland classified by Clancey (1947) as ssp.  
246 *palustris* actually fall within the range of ssp. *dresseri* (Cramp & Perrins 1993). Furthermore,  
247 Kniprath (1967) showed that the plumage colour saturation of Marsh Tits can vary with age  
248 and wear, which may bias the assessment of small samples such as Clancey's (1947). As  
249 such, the original claim by Clancey (1947) of ssp. *palustris* in northern England and Scotland  
250 appears unsubstantiated, perhaps being an example of "enthusiastic...micro-taxonomy"

251 based on “...extraordinarily subtle...differences in small, unrepresentative samples” which  
252 had earlier drawn criticism (see Knox 2007).

253 The results also provide compelling evidence against clinal or regional variation in Marsh Tit  
254 size within Britain, as postulated by du Feu & du Feu (2014), and no support for an increase  
255 in wing length with latitude (McCollin *et al.* 2015). These findings are important in  
256 demonstrating that reliable methods of sexing Marsh Tits based on biometrics from one  
257 population could be applied by analysts to other populations across the British range, given  
258 representative samples, with an insignificant risk of regional variation introducing unknown  
259 bias into analyses (Broughton *et al.* 2008, du Feu & du Feu 2014).

260 The present study is the first to fully demonstrate a consistent body size in Marsh Tits across  
261 a subspecies, and the first to perform an adequate statistical comparison of differences in  
262 morphology between different populations (cf. Mayaud 1933). Despite being highly  
263 sedentary, with relatively short dispersal distances and a sensitivity to habitat fragmentation  
264 (Broughton *et al.* 2010, Wesolowski 2015), our results offer no evidence of founder effects or  
265 reproductive isolation influencing body size between Marsh Tit populations within Britain (cf.  
266 du Feu & du Feu 2014). This implies that some genetic flow has been maintained, or a lack  
267 of selective pressure on body size, despite extreme fragmentation of woodland habitat  
268 (Broughton & Hinsley 2015).

269 Several key implications for Marsh Tit taxonomy and conservation can also be derived from  
270 these results. Firstly, the existence of only one native subspecies in Britain means that the  
271 geographical range of *ssp. dresseri* can be confidently stated to extend to southern  
272 Scotland, with a corresponding British population of 41,000 territories (Musgrove *et al.*  
273 2013). Conversely, it can be stated that the European range of *ssp. palustris* does not  
274 extend to Britain and this taxon should be considered as restricted to continental Europe.

275 A second issue concerns the validity of subspecies classification. Based on photoelectric  
276 measurements of colouration, Kniprath (1967) suggested that Marsh Tits may be considered  
277 as a monotypic species that shows a high degree of variation throughout Europe but cannot  
278 be reliably categorized into subspecies. Our results of wing and tail lengths contradict this

279 interpretation, as British Marsh Tits are clearly and consistently divisible from populations in  
280 central Europe and Scandinavia on the basis of size. Populations of Marsh Tits in western  
281 continental Europe are more problematic, and our results showed that birds from northwest  
282 Germany (Essen) were somewhat intermediate in size between ssp. *palustris* and *dresseri*.  
283 The inclusion by Vaurie & Snow (1957) of Marsh Tits from western France into the *dresseri*  
284 subspecies was based on similarities in the plumage colouration (visually assessed) and  
285 wing length of skins, but sample sizes were very small (ten birds or fewer). Mayaud (1933)  
286 maintained that Marsh Tits in western France were distinctly smaller than ssp. *dresseri* and  
287 belonged to local ssp. *darti* (Jouard 1929), but this taxon is not currently recognised (Cramp  
288 & Perrins 1993, Gosler & Clement 2007).

289 The subspecies identification of Marsh Tits in France is important in determining whether  
290 British Marsh Tits are, in fact, an island endemic subspecies as is currently recognised for  
291 British Willow Tits *P. m. kleinschmidti*; British populations of both species probably became  
292 isolated from conspecifics at the same time, approximately 8,000 years ago, when the  
293 English Channel flooded. There appears to be little morphological data available for French  
294 Marsh Tits, however, and no published material derived from live birds, which can differ from  
295 skins due to shrinkage and de-fleshing of the latter (Kelm 1970, Svensson 1992).  
296 Comparison of wing length measurements taken from 59 skins in western France (Mayaud  
297 1933) with those of 22 skins from England (Cramp & Perrins 1993) shows a significant  
298 overlap for females but not males, leaving the question unresolved.

299 Detailed morphological comparisons between large samples of live birds, preferably of  
300 known age and sex, appear necessary to classify the subspecies of Marsh Tit present in  
301 France, and hence the potentially unique status of ssp. *dresseri* in Britain. Future genetic  
302 analyses may also contribute to the taxonomy of Marsh Tit subspecies, although a study of  
303 Willow Tits failed to detect any genetic differentiation between European subspecies (Kvist  
304 *et al.* 2001).

305 The taxonomic status of British Marsh Tits has practical implications for the species'  
306 conservation in this country. British Marsh Tits have undergone a significant decline in

307 population and contraction in range since the 1970s, particularly in northern England, and it  
308 may shortly become extinct altogether in Scotland (Balmer *et al.* 2013, Broughton & Hinsley  
309 2015). As we have shown that northern Marsh Tits do not differ from those elsewhere in  
310 Britain, there is no obvious ecological or taxonomic barrier to using birds from southern  
311 Britain as source populations for potential future reintroductions to Scotland or northern  
312 England if habitat and conditions are considered suitable (Broughton & Hinsley 2015). By  
313 extension, if the morphology, behaviour and ecology of British Marsh Tits were shown not to  
314 differ from those in western France, this would create a larger pool of source birds for  
315 reintroduction if populations in southern Britain also continued to decline.

316

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471 **TABLES**

472 Table 1. Wing length measurements of British Marsh Tits from populations in different  
 473 regions (see Fig. 1 for location details). A Kruskal-Wallis test showed no significant  
 474 difference between populations at an  $\alpha$  level of 0.05 (see Methods).

475

Location	n	Min	Q1	Median	Q3	Max
Northumberland	42	58	61	63	64	66
Cumbria	306	58	61	63	64	67
Cambridgeshire	451	59	61	63	64	67
Suffolk	73	59	61	63	64	66
Oxfordshire	105	59	61	63	64	66
Berkshire	49	60	61	64	64	65
Devon	77	60	61	63	64	66
Powys	44	59	61	63	64	68
All locations	1147	58	61	63	64	68

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477

478 Table 2. Tail length measurements of British Marsh Tits from three regions (see Fig. 1 for  
 479 details). A Kruskal-Wallis test showed no significant difference between populations at an  $\alpha$   
 480 level of 0.05 (see Methods).

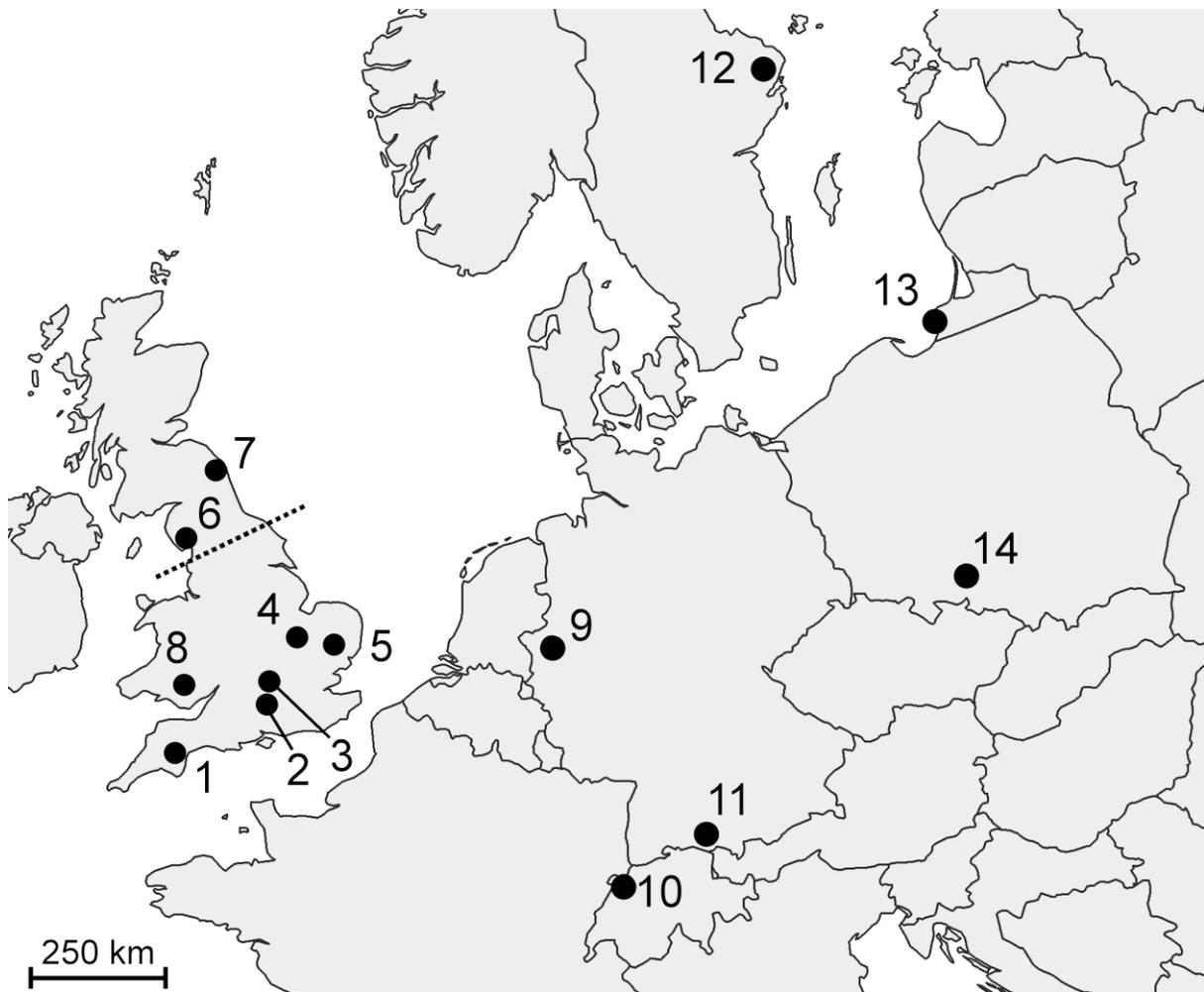
481

Location	n	Min	Q1	Median	Q3	Max
Cambridgeshire	206	47.0	50.0	52.0	53.0	57.5
Suffolk	18	46.5	49.8	51.8	53.5	56.0
Berkshire	26	49.5	51.4	54.0	54.1	56.0
All locations	250	46.5	50.4	52.0	53.5	57.5

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483 **FIGURE LEGENDS**

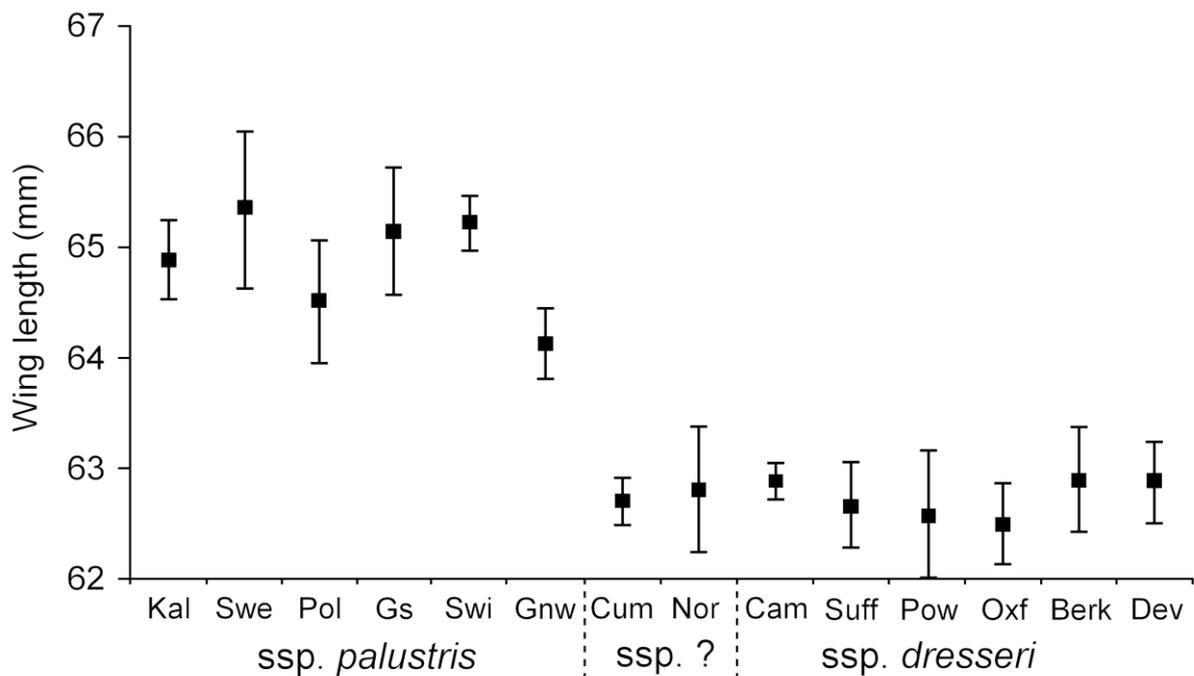
484 Figure 1. Locations of Marsh Tit biometric data. England and Wales: 1) Devon, 2) Berkshire,  
485 3) Oxfordshire, 4) Cambridgeshire, 5) Suffolk, 6) Cumbria, 7) Northumberland, 8) Powys.  
486 Dotted line in northern England marks the approximate division claimed by Clancey (1947)  
487 for Marsh Tit *ssp. palustris* to the north and *ssp. dresseri* to the south. Central Europe (and  
488 southern Scandinavia): 9) northwest Germany, 10) northern Switzerland, 11) southwest  
489 Germany, 12) southern Sweden, 13) Kaliningrad, 14) southwest Poland. See Methods for  
490 details.



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496 Figure 2. Mean and 95% confidence intervals for Marsh Tit wing lengths by subspecies and  
 497 location. For *ssp. palustris* on an east-west axis: Kal = Kaliningrad (n = 139), Swe = southern  
 498 Sweden (n = 29), Pol = southwest Poland (n = 29), Gs = southern Germany (n = 31), Swi =  
 499 Switzerland (n = 186), Gnw = northwest Germany (n = 161). For *ssp. dresseri* on a north-  
 500 south axis across England and Wales: Cam = Cambridgeshire (n = 451), Suff = Suffolk (n =  
 501 73), Pow = Powys (n = 44), Oxf = Oxfordshire (n = 105), Berk = Berkshire (n = 49), Dev =  
 502 Devon (n = 77). The *ssp.* in northern England is disputed: Cum = Cumbria (n = 306), Nor =  
 503 Northumberland (n = 42). For data sources see Methods.

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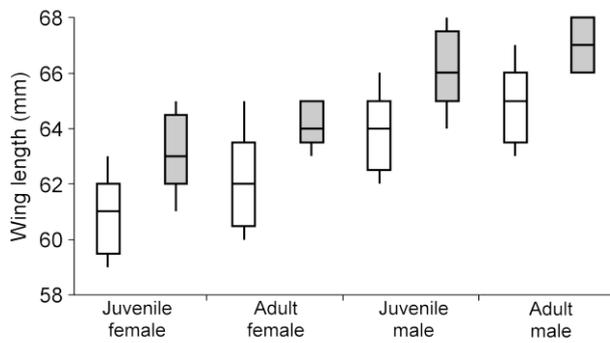
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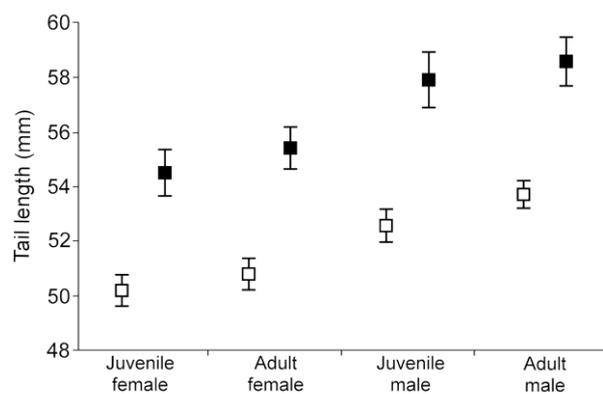
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513 Figure 3. Median, interquartile range and overall range of Marsh Tit wing lengths by age and  
 514 sex class for ssp. *dresseri* from Cambridgeshire in England (white boxes) and ssp. *palustris*  
 515 from Switzerland (grey boxes; Amann 1980). Sequential sample sizes (n) from left to right on  
 516 the x-axis: 112, 55, 95, 25, 133, 67, 111, 39. Differences between ssp. in all classes are  
 517 significant at  $P < 0.001$  (Mann-Whitney tests).



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520 Figure 4. Mean and 95% confidence intervals for Marsh Tit tail lengths by age and sex class  
 521 for ssp. *palustris* (Kaliningrad – black symbols, Markovets 1998) and ssp. *dresseri*  
 522 (Cambridgeshire, England – white symbols). Sequential sample sizes (n) from left to right on  
 523 the x-axis: 52, 39, 56, 32, 54, 28, 69, 40.



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