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

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SUMMARY

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

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

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

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

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

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 19th and
58 early 20th 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 20th 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

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

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

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

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

polytypic. The suggestions of Clancey (1947) and du Feu & du Feu (2014) require formal testing to assess the geographical variation in size and clarify the subspecies occurring in Britain, and also to clarify the range of the nominate ssp. *palustris* in Europe.

We aimed to address these questions by comparing Marsh Tit biometrics within and between Britain and continental Europe. A lack of variation within Britain, but a contrast with ssp. *palustris* birds from elsewhere, would indicate that *dresseri* is the only resident British subspecies and that the range of *palustris* is restricted to the continental mainland. Consistent size within Britain would also support the use by analysts of biometrics for sexing Marsh Tits throughout the country, and the ability to apply a universal sexing method would be valuable for estimating population structure for demographic studies aiming to understand the causes of the species' population decline (Broughton & Hinsley 2015).

METHODS

Measurements of British Marsh Tits

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

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

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

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

Measurements from continental Europe

For comparison with British birds, 575 maximum-chord wing length measurements from live Marsh Tits were derived from the literature for five sites within the reported range of ssp. *palustris* within central Europe (and southern Scandinavia): Kaliningrad (Markovets 1998), southwest Germany (Ludescher 1973), northwest Germany (Hudde 1985), southern Sweden (Alatalo *et al*. 1985) and northern Switzerland (Amann 1980), and also original data collected from a sixth area in southwest Poland (within 30 km of Opole: 50°39'N, 17°57'E) during 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 α 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 $D = 0.053\text{-}0.154$, $P = 0.320\text{-}0.999$), 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

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

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

DISCUSSION

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

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

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

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

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

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

A second issue concerns the validity of subspecies classification. Based on photoelectric measurements of colouration, Kniprath (1967) suggested that Marsh Tits may be considered as a monotypic species that shows a high degree of variation throughout Europe but cannot 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

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

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TABLES

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

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

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

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

FIGURE LEGENDS

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

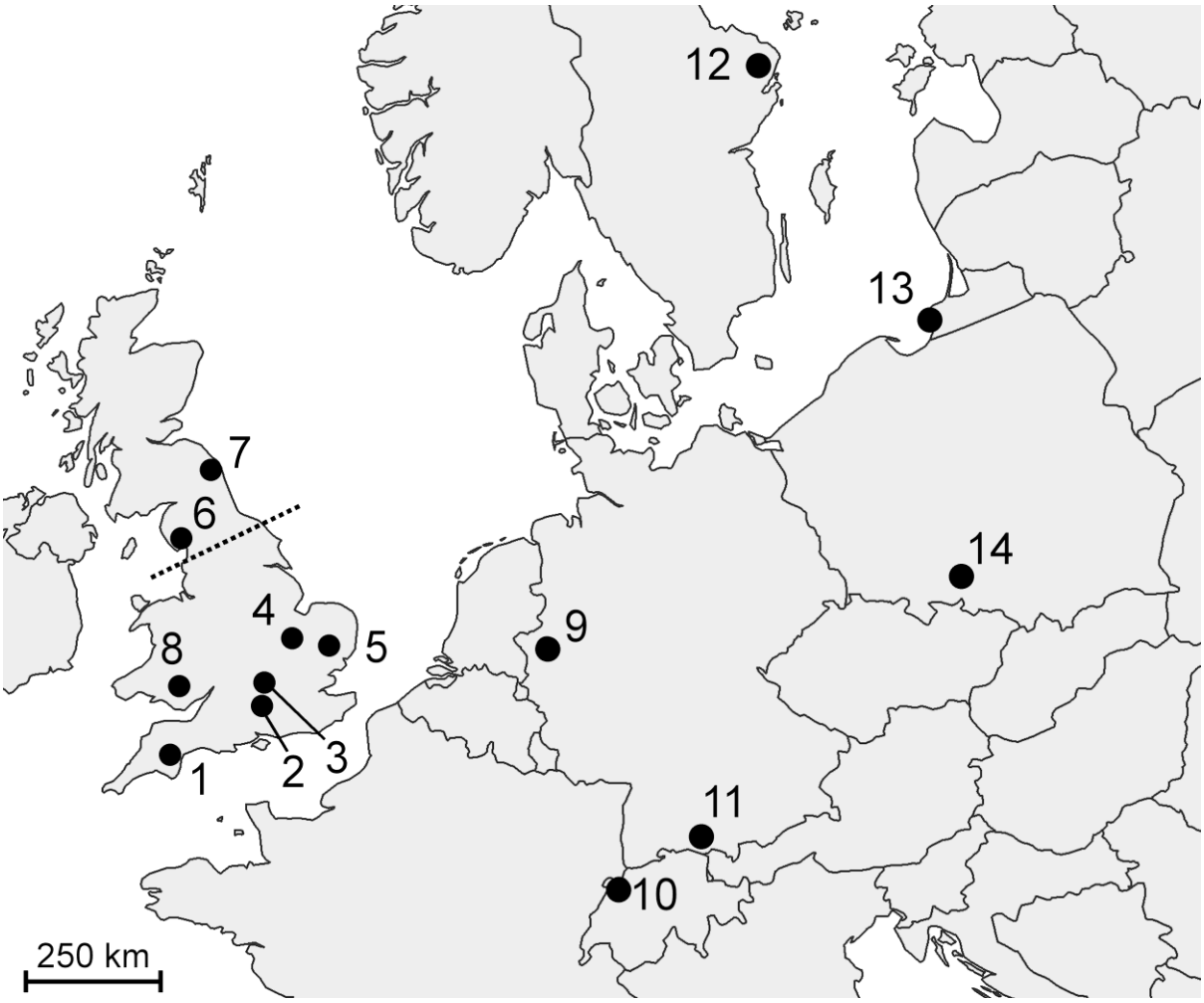
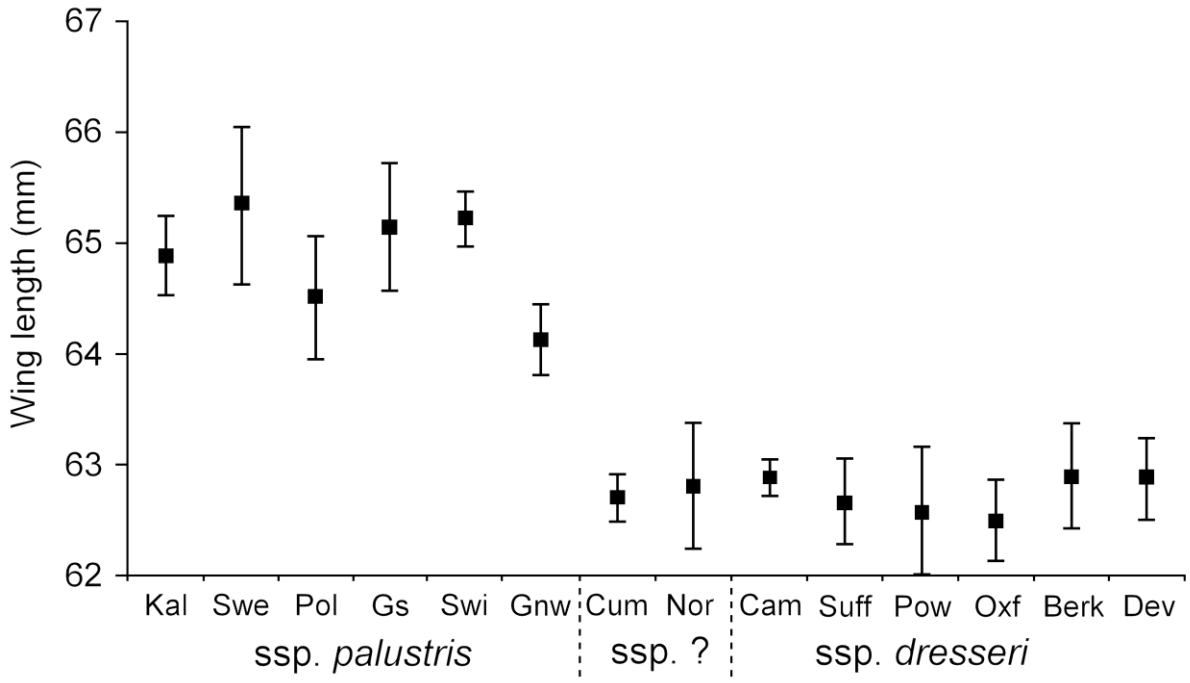
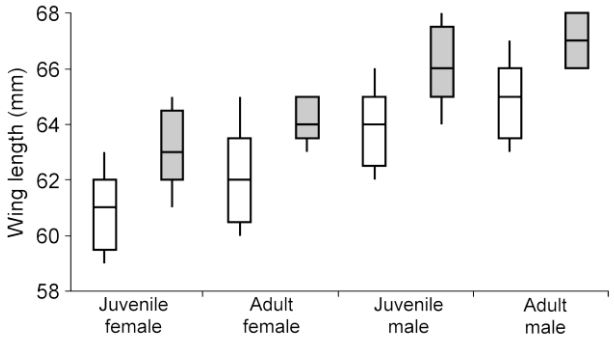


Figure 2. Mean and 95% confidence intervals for Marsh Tit wing lengths by subspecies and location. For ssp. *palustris* on an east-west axis: Kal = Kaliningrad (n = 139), Swe = southern Sweden (n = 29), Pol = southwest Poland (n = 29), Gs = southern Germany (n = 31), Swi = Switzerland (n = 186), Gnw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



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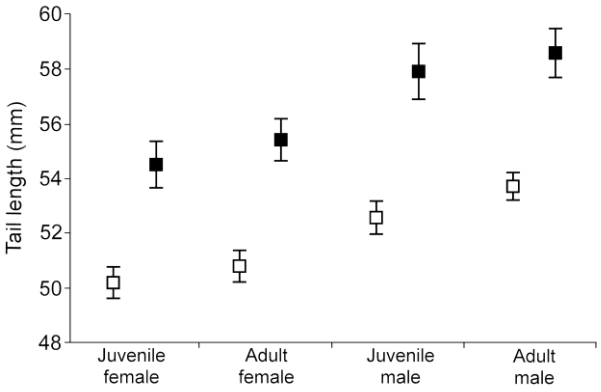
520 Figure 4. Mean and 95% confidence intervals for Marsh Tit tail lengths by age and sex class
521 for ssp. *palustris* (Kaliningrad – black symbols, Markovets 1998) and ssp. *dresseri*
522 (Cambridgeshire, England – white symbols). Sequential sample sizes (n) from left to right on
523 the *x*-axis: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



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