



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

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Ageing and sexing Marsh Tits *Poecile palustris* presents some difficulties for ringers. Wing length has previously been found to be useful for sexing English Marsh Tits, although the replacement of all juvenile rectrices and greater coverts by first-year birds made ageing difficult. We examined Marsh Tits of known age and sex and found that 93.5% of birds could be sexed correctly using wing lengths of ≤ 62 mm for females and ≥ 63 mm for males. Wing length was also an indicator of age: many first-years had shorter wings, but most also retained some juvenile rectrices and greater coverts after the post-juvenile moult, and could be readily aged using these features. We found a primary moult period of 67 days for adult Marsh Tits, with a mean onset of 27 May.

The Marsh Tit *Poecile palustris* is a problematic species for ringers; males and females are similar in plumage (Svensson 1992) and current ageing techniques are subtle and unreliable (King & Muddeman 1995).

Nilsson (1992) found wing length to be a reliable method of sexing nominate-race Marsh Tits in Sweden, with males having longer wings. Gosler & King (1989) found a strongly bimodal distribution for wing length, due to sexual dimorphism, in a small sample of birds in south-central England. Using a larger sample, King & Muddeman (1995) were later able to validate the use of wing length for sexing birds from this same population, but they were unable to confirm the reliability of sexually dimorphic plumage characters, such as bib size, suggested by Gosler & King (1989). Svensson (1992) listed two criteria for distinguishing adult Marsh Tits from first-year birds after the post-juvenile moult (referred to as 'first-years' hereafter), these being shape of the rectrices (rounded and fresher in adults, pointed and worn in first-years) and retention of juvenile greater coverts (JGCs) in some first-years, creating a subtle moult limit. Nilsson (1992) found that first-years had shorter wing lengths than adults, although there was substantial overlap. Rectrix shape is used to age several tits (Svensson 1992), including the closely related Willow Tit *P. montana* (Laaksonen & Lehtikoinen 1976) and Black-capped Chickadee *P. atricapilla* (Smith 1991), although King & Muddeman (1995) found it to be unreliable for their Marsh Tit population due to differences in wear and the tendency of some juveniles to replace the whole tail during the post-juvenile moult. King & Muddeman (1995) also found JGCs in only 2% of their sample (one

bird), suggesting that this criterion may be of limited value. Current knowledge therefore suggests that, in England, only adult Marsh Tits undergoing wing moult during the summer (Ginn & Melville 1983) may be separated reliably from the majority of first-years.

The aims of this study were, firstly, to test King & Muddeman's (1995) main findings on the use of wing length, JGCs and rectrix shape to age and sex Marsh Tits, using a large sample of birds of known age and sex. Secondly, the relationship of wing length to age and sex, and the period of adult primary moult and post-juvenile moult, were investigated.

METHODS

Study sites and data collection

Research in the Monks Wood area (Cambridgeshire, eastern England, 52°24'N 0°14'W) between 1993 and 2008, and Wytham Woods (Oxfordshire, central England, 51°46'N, 1°19'W) between 2004 and 2007, generated morphometric data for 182 Marsh Tits of known age and sex over 663 handlings. Birds were caught using baited traps or mist nets, including 70 birds first ringed as pulli, and fitted with a unique combination of colour rings and a BTO aluminium ring. A total of 154 individuals were examined at Monks Wood and 28 at Wytham Woods. Breeding data, including laying and hatching dates, were collected from the Monks Wood population for 11 nests in 2005, 15 in 2006, 20 in 2007 and 17 in 2008. A weather station at Monks Wood provided data for the calculation of warmth sum values (the

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sum of daily maximum temperatures) from 1 March to 25 April (McCleery & Perrins 1998) each year until 2007.

Ageing and sexing

Birds ringed as pulli were of known age on subsequent capture. Other birds were attributed to age groups based on the following criteria. Juveniles (EURING code 3J) could be aged due to the loose texture of the feathers and sparseness of underwing coverts (Jenni & Winkler 1994), first-year birds (EURING codes 3 and 5) were aged on first capture using rectrix shape where possible, and adults (EURING codes 4 and 6) could be aged on first capture during summer using the presence of wing moult. In the absence of wing moult, birds with no juvenile rectrices were not aged due to the possibility of first-years having replaced the tail and thus being indistinguishable from adults. Measurements of individuals examined as both first-years and adults were included in both age classes and, along with repeat measurements from adults in subsequent years, were analysed for evidence of an increase in wing length with age. Birds were sexed using the presence of a brood patch (breeding females) and breeding behaviour, including 'courtship-feeding', incubation and singing, with song being exceptional among female Marsh Tits (Broughton 2008).

In 2007, 53 known first-year birds from Monks Wood were assessed for the extent of post-juvenile moult, including the greater coverts (GCs). The number of retained JGCs was recorded for the right wing and tails were examined for the number and position of any feathers that had been replaced (numbered from innermost feather R1), these being identified by differential wear and shape. A small number of birds examined in 2003–06 provided additional data on tail moult (15 birds) and JGCs (four birds). Fourteen birds examined in 1993–95 and 2008 provided additional data for timing of post-juvenile moult.

Wing length

Wing length (maximum chord, measured to 1 mm) was collected for 130 males and 100 females between July and March across all years, including 48 birds examined in both first-year and adult plumage and incorporated into both categories. Adults and first-years were examined in all months of the sampling period, with trapping effort deployed progressively throughout the study area until all birds of both age classes had been captured at each trap site. Bias towards trapping date and age or sex was thus avoided. Moult scores were recorded for adults undergoing primary moult (110 scores from 86 birds). Where the same adults were examined in consecutive years, only the first wing-length measurement was included in analyses. This may, however, have potentially excluded longer wing lengths from individuals as they age. To test this, the data

were analysed for any change in wing length among 18 individual adults trapped in two different years. To test the effect of wear on an individual's wing length over the annual sampling period, which may have influenced the measurement recorded due to the date of sampling, two measurements of wing length for 24 individuals were compared after a period of at least three months during the same sampling period (pooled for age and sex due to small sample sizes: nine males, 15 females; 18 first-years, six adults). Measurement error was considered negligible due to 90% of birds being examined by one of the authors (RKB) and measurements being highly consistent among and between ringers involved.

Statistical and moult analysis

Simple probability analysis and t-tests were used for the analyses of wing length. Primary moult of adults was investigated using an Underhill–Zucchini model (Underhill & Zucchini 1988) to determine moult duration and onset. We applied a Type 3 model to moult scores from birds undergoing active primary moult during the period 1993–2008 (excluding 1997 and 2002–03), converting the moult scores for each feather to mass of new feather material grown (primary moult mass score, or 'PMS'). PMS was derived by weighing each primary feather of a single Marsh Tit and expressing these values as a proportion of the total mass (Dawson 2005). The mass values for primaries 1–10 (inner–outer), as a proportion of the total, were as follows: 0.082, 0.084, 0.093, 0.110, 0.125, 0.133, 0.132, 0.122, 0.095 and 0.024. PMS was then calculated for each bird as the sum of each mass value multiplied by the moult score for the corresponding primary, and the sum divided by the number of moult score categories (5). This procedure gave a measure of moult stage that was less influenced than the standard numerical score by the variable lengths and weights of the different primary feathers (Dawson & Newton 2004), thus improving linearity.

The moult data were examined for annual differences that may have biased the overall estimates of moult onset and duration, and small sample sizes led to the exclusion of data from 1995 and 1998–99 from subsequent analyses. Excluding these years and fitting a regression on date to the PMS data for each year showed no statistically-significant difference between slopes (two-tailed F-test: $F_{9,57} = 1.61$, $P = 0.13$), but clear differences in intercepts (two-tailed F-test: $F_{9,57} = 4.03$, $P < 0.001$), consistent with a common duration of moult but with annual variation in the mean date of onset. We therefore modified the Type 3 analysis to allow for annual differences in mean onset of moult, and applied this to 77 mass-based moult scores from the 74 birds that were in active moult. The relationship between timing of moult and the breeding cycle was examined by correlating (Pearson product-moment correlation) the model output

with mean annual laying dates. As data for the timing of egg-laying were available for only a small number of years, and date of egg-laying has been found to be strongly linked to spring temperatures in the Marsh Tit (Dolenec 2006), timing of moult was also correlated with warmth sum values, which were used as a proxy for laying date and were available for a greater number of years.

RESULTS

Ageing and moult

Only 29.4% (20/68) of first-year Marsh Tits had replaced one or more rectrices. Only six birds displayed symmetrical moult of at least one pair of rectrices (Fig 1), two of which had replaced most of the tail, except R6 on one bird and R4–R6 on the other. One bird had replaced the whole tail. Fifteen birds showed asymmetrical replacement of rectrices, with at least one rectrix replaced but not the corresponding feather on the other side of the tail. Of these, nine birds had replaced just one rectrix, most commonly R1 or R6, with asymmetrical replacement most often involving the outer tail feathers (Fig 1). Replaced feathers were not fully grown on birds examined between 11 July and 11 August across all years, except for one bird with a full-grown replacement on 14 July 2005 and one with shed feathers on 23 October 2005.

Retained JGCs were found in 93.0% of first-years (53/57). Only four birds (7.0%) were judged to have moulted all JGCs. Retained JGCs were distinctive due to an obvious moult limit in the feather tract, and were characterised by pale buffish tips and a slightly greater length than the new inner GC. Up to five JGCs were detected on some birds, although four was the most frequent (Fig 2). Juveniles were

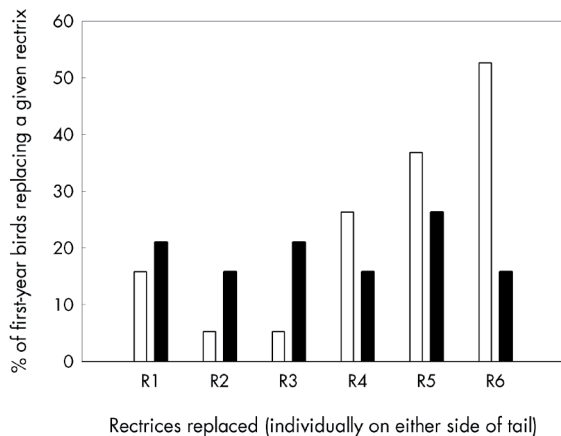


Figure 1. Percentage of those first-year Marsh Tits that replaced at least one given rectrix (R) on either side of the tail ($n = 20$ birds), showing whether each rectrix was replaced symmetrically in pairs (black, $n = 6$ birds) or asymmetrically and not in pairs (white, $n = 15$ birds). Only one bird (5%) replaced the whole tail.

already undergoing post-juvenile body moult in 2007 by the time of first capture on 19 July, and the last birds had not completed until 10 October. The period of active growth observed in the rectrices was therefore consistent with true moult for most birds, although the extent of replacements due to accidental feather loss could not be determined. The timing of the onset of post-juvenile moult was difficult to determine due to lack of data, although juveniles examined up to 3 July in other years had not yet begun (14 birds). One of these birds had dropped or lost two outer tail feathers between 1 and 3 July, but this was attributed to accidental loss as juvenile rectrices are generally only moulted after body moult has begun (Jenni & Winkler 1994). Post-juvenile moult was therefore estimated to have generally begun in early to mid July and ended in early October, this period being somewhat later than the June–Sept window given by Ginn & Melville (1983).

For adult primary moult, Fig 3 shows PMS against date, fitted with the Type 3 Underhill & Zucchini (1988) model that shows the mean progression of adult primary moult in the Monks Wood Marsh Tit population. The mean (\pm se) date of onset of primary moult was 27 May \pm 1.6 days, with a mean duration of 67.4 \pm 3.8 days ($n = 10$ years). The entire population had completed primary moult by the end of August each year, marking the end of the period where wing moult could easily be used to separate adults and first-years. The mean date for completion of primary moult was 2 August, however, indicating that many adults could not be aged using moult after the end of July, and some from as early as mid July.

Although the mean date of onset of primary moult varied between years, there was no consistent trend for a progressively earlier or later onset across years ($r = 0.05$, $P = 0.90$, $n = 10$). Mean onset of primary moult was, however, highly associated with mean onset of egg-laying for the same population in those years with breeding data (2005–08)

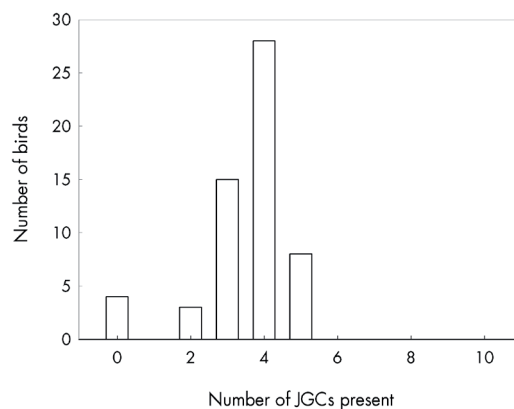


Figure 2. Frequency of the number of unmoulted juvenile greater coverts (JGCs) retained by first-year Marsh Tits ($n = 58$ birds).

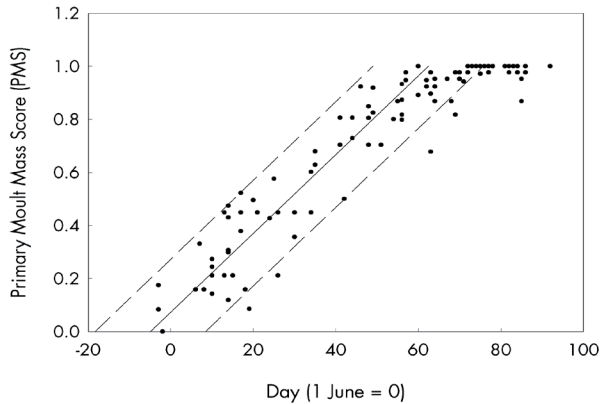


Figure 3. Marsh Tit primary feather moult across all years in the Monks Wood area (110 scores from 86 birds), expressed as primary moult mass score (PMS) against day, with a fitted model showing mean progression of moult (solid line) and the 2.5 and 97.5 percentiles (dashed lines). The model used was a Type 3 Underhill & Zucchini (1988) model, allowing for annual differences in mean onset of moult, and was derived from a subset of 77 scores from 74 birds in active moult.

($r = 0.97$, $P = 0.03$, $n = 4$), although the sample size was small. There was a moderate negative relationship between earlier mean onset of moult and higher annual warmth sum values for the nine years for which data were available (1993–94, 1996, 2000–01, 2004–07), although this was not statistically significant ($r = -0.54$, $P = 0.13$, $n = 9$).

Wing length for ageing and sexing

The wing lengths of 24 Marsh Tits with multiple measurements during one autumn–winter period showed a statistically significant decrease over that duration. However, the absolute difference between the means (\pm se) of the first and second measurements was negligible (respectively $62.5 \text{ mm} \pm 0.32$, and $62.2 \text{ mm} \pm 0.35$, $n = 24$; one-tailed paired t -test, $t_{23} = 2.77$, $P < 0.01$). The effect of wear and sampling date on wing-length measurement was therefore thought to be minimal, enabling measurements from throughout the sampling periods to be included in the analyses. In addition, repeat wing-length measurements of adults over subsequent years showed no clear evidence of a consistent change in wing length with age after the first complete moult (two-tailed t -test, $t_{17} = 1.59$, $P = 0.07$, $n = 18$). Although the P value was suggestive of a possible effect with such a small sample, and despite six of the 18 birds showing an increase in wing length (mean = $1.67 \text{ mm} \pm 0.21$), three birds showed a decrease in wing length (all of -1 mm) and nine birds showed no change. Thus wing-length measurements of adults of all ages were included in analyses.

The mean (\pm se) wing length of male Marsh Tits was significantly longer than that of females (age classes

combined, males: $64.2 \text{ mm} \pm 0.09$, $n = 130$; females: $61.2 \text{ mm} \pm 0.10$, $n = 100$; two-tailed t -test, $t_{217} = 21.94$, $P < 0.001$), and significantly longer for adults than for first-year birds (sexes combined, adults: $63.6 \text{ mm} \pm 0.17$, $n = 103$; first-years: $62.4 \text{ mm} \pm 0.15$, $n = 127$; two-tailed t -test, $t_{213} = 5.44$, $P < 0.001$).

The frequency distributions of wing lengths for the age and sex classes are shown in Fig 4. Empirical probability analyses indicated that, by classifying birds with wing lengths of $\leq 62 \text{ mm}$ as females and those of $\geq 63 \text{ mm}$ as males, only 8.0% of females and 5.4% of males would be wrongly classified. Such a classification would, therefore, assign 93.5% of unknown birds to the correct sex. Table 1 shows the probability of a bird of a given wing length belonging to a specific age/sex class, and the probability of an individual in that class having a specific wing length. This shows, for example, that while a bird with a wing length of 66 mm had a very high probability of being an adult male (91.7%), the probability of an adult male having a wing length of 66 mm was rather low (17.7%). Table 1 indicates that approximately half of all individuals in each

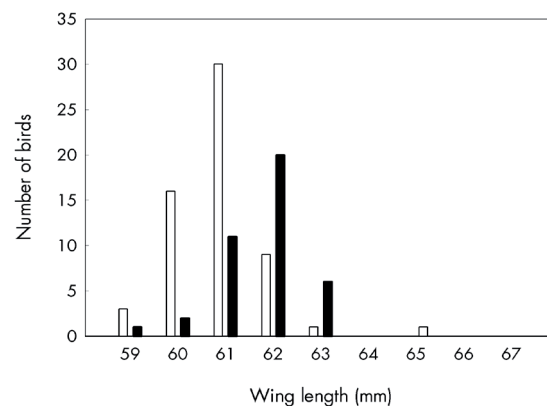
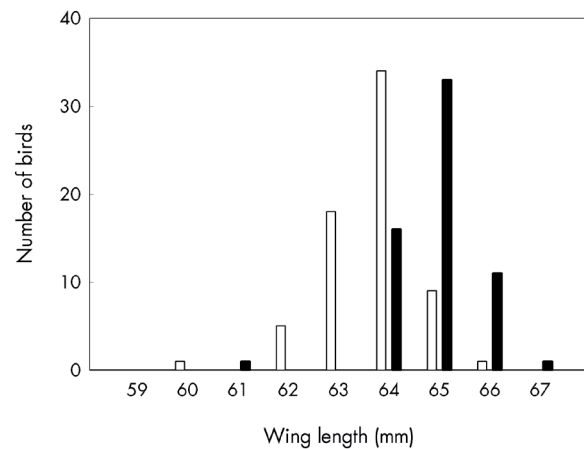


Figure 4. Wing lengths of first-year (white) and adult (black) Marsh Tits: (a) males, (b) females.

age/sex category displayed the same wing length: first-year female = 61 mm (50.8%), adult female = 62 mm (48.8%), first-year male = 64 mm (50.0%) and adult male = 65 mm (53.2%). In addition, the probability of assigning an individual to the correct age/sex class using wing length alone was between 58.8% and 100%, depending on class. These age and sex classifications and cut-off points may, therefore, be applied to birds displaying these wing lengths, albeit with varying degrees of caution.

The low incidence of rectrix replacement among first-years, with only one bird having replaced the whole tail, and the high incidence of a moult limit in the greater coverts, meant that all individuals could be aged independently of wing length. Table 2 indicates that most birds of known age and specified wing length could be sexed with an enhanced probability of success, due to birds of the wrong age class being excluded from consideration. Only first-years with a wing length of 62 mm remained problematic; first-years displaying any other wing length could be correctly assigned to the appropriate sex with a probability of 94.1% or more. Known adults could be correctly sexed with a probability of 91.7% or more, using wing length alone. Where sex was known but age was undetermined, however, the probability of assigning individuals to the correct age class was generally lower (Table 3). This was particularly true for females, where the maximum probability of correct ageing was 88.9% when discounting the outlying individual (with a wing length of 65 mm). The probability of a male or female being an adult nevertheless increased with wing length, though outliers were present in both sex categories.

DISCUSSION

Nearly all (93.0%) juvenile Marsh Tits examined in the Monks Wood area had some retained JGCs, in contrast to the findings of King & Muddeman (1995) in another

English population, who found JGCs in just one bird (2.0% of their sample). The moult limit is subtle yet distinctive and was unlikely to have been missed or misinterpreted in either study. In addition, King & Muddeman (1995) found that 14% of their sample appeared to have replaced the entire tail during the post-juvenile moult, whereas our study found that only one bird (1.7%) had replaced the entire tail, and only 29.4% had replaced any rectrices at all. These differences are notable, as King & Muddeman (1995) collected their data less than 15 years before the period of our study and approximately 100 km (at similar latitude) from our study site. Both studies may, therefore, have failed to detect annual variation in the extent of greater covert and rectrix moult due to data collection occurring in a small number of years. The extent of post-juvenile moult in the greater coverts and rectrices varies for the Blue Tit *Cyanistes caeruleus* and Great Tit *Parus major*, both between years and between regions (Ginn & Melville 1983, Cramp & Perrins 1993). Some of this variation has been explained by differences in hatching dates (eg Rymkevich & Bojarinova 1996), although annual variation in hatching dates for Monks Wood Marsh Tits was low across 2005–08, and breeding is single-brooded and highly synchronised within populations (our unpublished data, Wesołowski 1998). There is evidence that laying dates for British Marsh Tits have become earlier over recent decades (Baillie *et al* 2007), which could be expected to produce an earlier and more complete post-juvenile moult in more recent birds. The suggestion from our study that post-juvenile moult is occurring later than previously recorded (Ginn & Melville 1983), and is less complete (King & Muddeman 1995), is contrary to this, and could imply that foraging conditions have deteriorated for the juvenile Marsh Tits we examined. Differences in relative hatching dates may have been present between our study and that of King & Muddeman (1995), or other factors may have been responsible for the discrepancy. Repeat studies over a longer period, and over

Table 1. Probability, as %, of assigning individual Marsh Tits to the correct age and sex class based on wing length, where age and sex are unknown. Figures in parentheses are the probability (%) of an individual in each class displaying a specified wing length.

wing length (mm)	First-year females		Adult females		First-year males		Adult males		n
59	75.0	(5.1)	25.0	(2.4)	0	(0)	0	(0)	4
60	84.2	(27.1)	10.5	(4.9)	5.3	(1.5)	0	(0)	19
61	71.4	(50.8)	26.2	(26.2)	0	(0)	2.4	(1.6)	42
62	26.5	(15.3)	58.8	(48.8)	14.7	(7.4)	0	(0)	34
63	4.2	(1.7)	24.0	(14.6)	72.0	(26.5)	0	(0)	25
64	0	(0)	0	(0)	68.0	(50.0)	32.0	(25.8)	50
65	0	(0)	2.3	(2.4)	20.9	(13.2)	76.7	(53.2)	43
66	0	(0)	0	(0)	8.3	(1.5)	91.7	(17.7)	12
67	0	(0)	0	(0)	0	(0)	100.0	(1.6)	1
n	59		41		68		62		230

Table 2. Probability, as %, of assigning individual Marsh Tits to the correct sex class based on wing length, when age is known.

Wing length (mm)	First-year females	First-year males	n (first-years)	Adult females	Adult males	n
59	100.0	0	3	100.0	0	1
60	94.1	5.9	17	100.0	0	2
61	100.0	0	30	91.7	8.3	12
62	64.3	35.7	14	100.0	0	20
63	5.3	94.7	19	100.0	0	6
64	0	100.0	34	0	100.0	16
65	0	100.0	9	2.9	97.1	34
66	0	100.0	1	0	100.0	11
67	-	-	0	0	100.0	1
n	59	68	127	41	62	103

a wider geographical area, would be required to address these questions.

The pattern of rectrix moult in juvenile Marsh Tits differed depending on whether replacement was symmetrical (feathers renewed in pairs) or asymmetrical (Fig 1). Asymmetrical moult involved the outer tail feathers much more frequently than in symmetrical moult. This may indicate that asynchronous replacement of outer rectrices may be due to accidental loss and not moult. In other British tits, partial tail moult appears to be symmetrical and centrifugal and tends to involve the central rectrices (Ginn & Melville 1983, Jenni & Winkler 1994). Aggression, including physical combat, is frequent among juvenile Marsh Tits during the post-dispersal settlement phase which occurs just prior to post-juvenile moult (Nilsson 1989, pers. obs.). It is possible that outer rectrices are lost during such aggressive encounters, particularly when birds may grapple with their claws during combat, and tails are fanned with the outer feathers exposed (Cramp & Perrins 1993). Such a hypothesis is difficult to prove once true moult is under way, however, and other mechanisms of accidental loss are also possible (attacks from predators or more dominant species), as is irregular or centripetal partial moult of the rectrices. The bird with a fully grown replacement outer rectrix on 14 July, and two birds with missing outer rectrices on 3 July and 23 October, had almost certainly lost them accidentally due to the disparity with the moult sequence.

The estimated duration of adult primary wing moult in Monks Wood, 67 days, is much shorter than the 80-day period given by Ginn & Melville (1983). This could be due to Ginn & Melville's (1983) choice of model (not correcting for feather mass grown), or to data being pooled from a national database and therefore incorporating clinal or local effects on moult onset and duration (Silverin *et*

Table 3. Probability, as %, of assigning individual Marsh Tits to the correct age class based on wing length, when sex is known.

Wing length (mm)	First-year females	Adult females	n (females)	First-year males	Adult males	n (males)
59	75.0	25.0	4	-	-	0
60	88.9	11.1	18	100.0	0	1
61	73.2	26.8	41	0	100.0	1
62	31.0	69.0	29	100.0	0	5
63	14.3	85.7	7	100.0	0	18
64	-	-	0	68.0	32.0	50
65	0	100.0	1	21.4	78.6	42
66	-	-	0	8.3	91.7	12
67	-	-	0	0	100.0	1
n	59	41	100	68	62	130

al 1993). We found evidence that the onset of moult was closely linked to the timing of the breeding cycle in our population, although our sample was small, and also some indication of a link to spring temperatures. Combined data from across Britain, incorporating populations at different altitudes and latitudes, may therefore miscalculate the duration of moult. However, more information is needed to establish a firm link with spring temperatures for the timing of moult and breeding in this species.

The date of mean onset of adult wing moult, 27 May, was 6–8 weeks before the estimated onset of post-juvenile moult (early to mid July), and was during the period when successful breeders were still feeding dependent fledglings (earliest date of brood dispersal: 29 May to 9 June in 2006–08, our data). All birds caught during June until mid July could, therefore, easily be aged based on presence of wing moult or whether first-years still retained recognisable characteristics of juvenile plumage (EURING code 3J, moult code J or P). Even after the post-juvenile moult, however, virtually all first-years in our population could be aged until at least March, based on the presence of JGCs and juvenile rectrices. After March, and into the breeding period, abrasion could limit the usefulness of these features in identifying first-year birds.

Our results support those of Nilsson (1992) and Gosler & King (1989) in finding wing length to be a reliable method of sexing full-grown Marsh Tits, and validate King & Muddeman's (1995) discriminant wing length of ≤ 62 mm for females and ≥ 63 mm for males in English birds. These measurements may apply to all British birds, although large samples of birds of known age and sex from a much wider geographical range in Britain would be needed to eliminate the possibility of any clinal variation in these traits. Caution should therefore be used when applying these classifications to untested populations,

and care should be taken to avoid measurement error. If adopting the wing-length classifications reported in this paper, however, retained JGCs and retrices should also be looked for in order to refine the age and sex determination with increased reliability. Wing length was found to be useful as an additional indicator of age, with first-years having significantly shorter wings than adults, and with approximately half of all birds that shared a wing length being of the same age and sex. Although there was overlap in wing length between classes, where birds could be independently sexed using, for example, behaviour or presence of a brood patch, then ageing using wing length was much more reliable. The use of genetic sexing techniques may be of use in this context for future population studies, in enabling birds lacking JGCs or juvenile retrices to be aged retrospectively based on wing length and sex. Wing length was also indicative of sex where age was known, although the reliability of correct classification was limited.

These methods of ageing and sexing may also be tested on the closely related Willow Tit as, while there appears to be much more overlap of measurements for that species (Cramp & Perrins 1993), few data currently exist for birds of known age and sex of the British race.

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REFERENCES

- Baillie, S.R., Marchant, J.H., Crick, H.Q.P., Noble, D.G., Balmer, D.E., Barimore, C., Coombes, R.H., Downie, I.S., Freeman, S.N., Joys, A.C., Leech, D.I., Raven, M.J., Robinson, R.A. & Thewlis, R.M. (2007) *Breeding Birds in the Wider Countryside: their conservation status 2007*. Research Report No. 487. BTO, Thetford. (www.bto.org/birdtrends).
- Broughton, R.K. (2008) Singing in female Marsh Tits: frequency and function. *British Birds* **101**, 155–156.
- Cramp, S. & Perrins, C.M. (eds) (1993) *The Birds of the Western Palearctic*. Volume VII. Oxford University Press, Oxford.
- Dawson, A. (2005) The scaling of primary flight feather length and mass in relation to wing shape, function and habitat. *Ibis* **147**, 283–292.
- Dawson, A. & Newton, I. (2004) Use and validation of a molt score index corrected for primary feather mass. *Auk* **121**, 372–379.
- Dolenc, Z. (2006) Laying date of marsh tits *Parus palustris* in relation to climate change. *Biologia* **61**, 635–637.
- Ginn, H.B. & Melville, D.S. (1983) *Moult in Birds*. BTO Guide 19. BTO, Tring.
- Gosler, A.G. & King, J.R. (1989) A sexually dimorphic plumage character in the Coal Tit *Parus ater* with notes on the Marsh Tit *Parus palustris*. *Ringing & Migration* **10**, 53–57.
- Jenni, L. & Winkler, R. (1994) *Moult and Ageing of European Passerines*. Academic Press, London.
- King, J.R. & Muddeman, J.L. (1995) Ageing and sexing Marsh Tits *Parus palustris*. *Ringing & Migration* **16**, 172–177.
- Laaksonen, M. & Lehtikoinen, E. (1976) Age determination of Willow and Crested tits, *Parus montanus* and *P. cristatus*. *Ornis Fennica* **53**, 9–14.
- McCleery, R.H. & Perrins, C.M. (1998) Temperature and egg-laying trends. *Nature* **391**, 30–31.
- Nilsson, J.-Å. (1989) Establishment of juvenile marsh tits in winter flocks: an experimental study. *Animal Behaviour* **38**, 586–595.
- Nilsson, J.-Å. (1992) Variation in wing length in relation to sex and age of Marsh Tits *Parus palustris*. *Ornis Svecica* **2**, 7–12.
- Rymkevich, T.A. & Bojarinova, J.G. (1996) Variation in the extent of postjuvenile moult in the Great Tit near Lake Ladoga (Russia). *Bird Study* **43**, 47–59.
- Silverin, B., Massa, R. & Stokkan, K.A. (1993) Photoperiodic adaptation to breeding at different latitudes in Great Tits. *General Comparative Endocrinology* **90**, 14–22.
- Smith, S.M. (1991) *The Black-capped Chickadee: behavioral ecology and natural history*. Cornell University Press, New York.
- Svensson, L. (1992) *Identification Guide to European Passerines*. Fourth edition. Lars Svensson, Stockholm.
- Underhill, L.G. & Zucchini, W. (1988) A model for avian primary moult. *Ibis* **130**, 358–372.
- Wesołowski, T. (1998) Timing and synchronisation of breeding in a Marsh Tit *Parus palustris* population from a primaeval forest. *Ardea* **86**, 89–100.

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