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Contrasting strategies for wing-moult and pre-migratory fuelling in western and eastern populations of Common Whitethroat *Sylvia communis*

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Trade-offs between moult and fuelling in migrant birds vary with migration distance and the environmental conditions they encounter. We compared wing moult and fuelling at the northern and southern ends of migration in two populations of adult Common Whitethroats *Sylvia communis*. The western population moults most remiges at the breeding grounds in Europe (e.g. Poland) and migrates 4000–5000 km to western Africa (e.g. Nigeria). The eastern population moults all remiges at the non-breeding grounds and migrates 7000–10 000 km from western Asia (e.g. southwestern Siberia) to eastern and southern Africa. We tested the hypotheses that: (1) Whitethroats moult their wing feathers slowly in South Africa, where they face fewer time constraints than in Poland, and (2) fuelling is slower when it coincides with moulting (Poland, South Africa) than when it occurs alone (Siberia, Nigeria). We estimated moult timing of primaries, secondaries and tertials from moult records of Polish and South African Whitethroats ringed in 1987–2017 and determined fuelling patterns from the body mass of Whitethroats ringed in all four regions. The western population moulted wing feathers in Poland over 55 days (2 July–26 August) at a varying rate, up to 13 feathers simultaneously, but fuelled slowly until departure in August–mid-September. In Nigeria, during the drier period of mid-February–March they fuelled slowly, but the fuelling rate increased threefold in April–May after the rains before mid-April–May departure. The eastern population did not moult in Siberia but fuelled three times faster before mid-July–early August departure than did the western birds moulting in Poland. In South Africa, the

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Whitethroats moulted over 57 days (2 January–28 February) at a constant rate of up to nine feathers simultaneously and fuelled slowly from mid-December until mid-April–May departure. These results suggest the two populations use contrasting strategies to capitalize on food supplies before departure from breeding and non-breeding grounds.

Keywords: Africa, Europe, fuelling, migration, moult, southwestern Siberia, Sylviidae.

Moult of flight feathers demands a large energy expenditure and is usually separated from other costly activities such as breeding and migration (Murphy & King 1992, Lindström *et al.* 1993). Migrants adopt different strategies to fit moult between breeding and migration, even within a species: they can moult at the breeding grounds, at the non-breeding grounds or at stopover sites, or split the process between these areas (Ginn & Melville 1983, Newton 2009). Fuelling for migration ('fuelling') is another energy-intensive process (Jenni-Eiermann & Jenni 1996). Thus the timing of fuelling in relation to wing moult might vary between populations under different time and energy constraints, often imposed by their migration distance (Newton 2009). Relationships between moult and fuelling have been studied in migrant passerines at the northern breeding grounds (Lindström *et al.* 1994, Jenni-Eiermann & Jenni 1996) and in captivity (Morton & Welton 1973) but little is known about these relationships in the southern hemisphere.

Adult *Sylvia* warblers undergo complete moult once a year, but the location and the timing of the moult of different plumage tracts varies between species and between populations of the same species (Jenni & Winkler 1994, Shirihai *et al.* 2001). Adult Common Whitethroats ('Whitethroats') migrating from Europe to west Africa moult their primaries, secondaries and tertials ('wing moult') at the breeding grounds (Jenni & Winkler 1994); a small proportion undertake an additional partial moult of a few secondaries, tertials, and of primaries, at the non-breeding grounds (Waldenström & Ottosson 2002). This pattern contrasts with their eastern conspecifics, which moult wing flight feathers at the non-breeding grounds in southern Africa (Jenni & Winkler 1994, Shirihai *et al.* 2001). The timing and sequence of adult wing moult remain largely unknown for the eastern population, as does the relationship between moult and fuelling beyond east Africa (Yohannes *et al.* 2009). In some species, the strategy for moult and pre-migratory fuelling is related to the population's migration distance, and fuelling *en route* supplements stores accumulated before migration (Ginn & Melville 1983, Schaub & Jenni 2000, Newton 2009, Ożarowska 2015). Regardless of where birds moult, they also need to fuel before migrating from the breeding and the non-breeding grounds. The trade-off between moult and pre-migratory fuelling also depends on temperature and rainfall, which determine food availability (Katti & Price 1999).

We hypothesized that Whitethroats moult their wing feathers more slowly during the long austral summer at their non-breeding grounds in South Africa than on their breeding grounds in central Europe, where they are constrained by time to breed and moult during the brief northern spring and summer. Moult and fuelling are both energetically costly processes, so we hypothesized that fuelling would be slower during moult (Poland, South Africa) than when it occurred alone (Siberia, Nigeria). To test these hypotheses, we compared the patterns of wing moult and fuelling in two populations of Whitethroats: (1) migrants from central Europe to west Africa that migrate about 4000–5000 km within the northern hemisphere and moult on the breeding grounds ('western population') and (2) migrants from Siberia and western Asia to South Africa that cross about 7000–10 000 km between the two hemispheres and moult on the non-breeding grounds ('eastern population'). We discuss how the moult and fuelling of different populations are limited by physiological constraints and are shaped by their migration distance and environmental conditions at both ends of their migrations.

METHODS

Study species

Whitethroats that breed in western, central and northern Europe belong to the subspecies *Sylvia communis communis* (Cramp & Brooks 1992). They arrive in Europe mid-April, breed May–June and depart August–September (Nowakowski 1999, Tomiałojć & Stawarczyk 2003, Cepák *et al.* 2008, Bairlein *et al.* 2014). These Whitethroats migrate to western, central and eastern Africa, and most remain north of the equator (Cramp & Brooks 1992). Their main non-breeding destinations are in the Sahel, and the farthest recoveries come from Nigeria and Chad, about 4000–5000 km from their breeding grounds (Cepák *et al.* 2008, Fransson & Hall-Karlsson 2008, Zwarts *et al.* 2009, Valkama *et al.* 2014). These western populations remain on the Sahelian non-breeding grounds from mid-November to mid-March (Zwarts *et al.* 2009). One Whitethroat ringed in Nigeria and recovered in Poland (Polish Ringing Centre unpubl. data) confirms the migratory connection between these breeding and non-breeding grounds. Most adults of the central European populations moult wing flight feathers at the breeding grounds; some suspend this moult before migration (Jenni & Winkler 1994, Schaub & Jenni 2000, Hall & Fransson 2001, Shirihai *et al.* 2001). Whitethroats feed mainly on invertebrates (Cramp & Brooks 1992) but the best food for fuelling is a combination of insects and berries (Bairlein 1998).

Whitethroats breeding near Omsk in southwestern Siberia (Russia) are of the *Sylvia c. volgensis* and *S. c. icterops* subspecies (Cramp & Brooks 1992, Shirihai *et al.* 2001). They arrive at their breeding grounds in late April–early May, breed May–June and depart in August–early September (Soloviev 2005, Ryabitsev 2014). Siberian Whitethroats migrate to east and southern Africa (Cramp & Brooks 1992, Pearson *et al.* 2014). Whitethroats that visit South Africa during mid-November–mid-April are mostly *S. c. icterops* and *S. c. volgensis*, which suggests they come from southwestern Siberia, although occasional *S. c. communis* from Europe and *S. c. rubicola* from east Asia do occur in South Africa (Curry-Lindahl 1981, Raijmakers & Raijmakers 1994, Earle 2005). These eastern populations cross at least 7000–10 000 km from their breeding grounds, which extend from SW Siberia to western Turkmenistan and west Asia, to reach South Africa (Cramp & Brooks 1992). *Sylvia c. icterops* moult all their wing feathers in Africa, but moult patterns of the other subspecies occurring in South Africa remain unknown (Raijmakers & Raijmakers 1994, Earle 2005).

Locations and sampling

For the western population, we used data on Whitethroats mist-netted and ringed at five sites on their breeding grounds in Poland during July–October 2013–2017, and at six locations at their non-breeding grounds in Nigeria during September–May 2001–2017 (Fig. 1, Table 1). All Polish study sites were in pine or mixed forests with an understorey of berry bushes, where fruits and invertebrates were abundant in August–mid-October (Nowakowski *et al.* 2012). The study period in Poland spanned the end of breeding until after the post-breeding migration (Nowakowski 1999). In central Nigeria, the birds were caught in bushes and woodlands abundant in fruits and insects, especially after rains began in March–April. In northern Nigeria, where shrubs are the dominant vegetation, Whitethroats were trapped during *ad hoc* field trips from September to February.

For the eastern population, we used data on Whitethroats ringed at the breeding grounds in southwestern Siberia near Omsk, Russia, in August–September (end of breeding to start of migration) in 2005–2011, and at 16 non-breeding sites in northeastern South Africa (North West, Gauteng, Mpumalanga and Limpopo provinces) in November–April 1987–2017 (Fig. 1, Table 1). In Siberia, Whitethroats were found in fruit trees and berry bushes, while insects were also plentiful during the capture period. In South Africa, Whitethroats were caught in bushes and woodlands during the summer rainfall season when insects and fruit are abundant (Allan *et al.* 1997).

At Polish and Siberian ringing stations, mist-netting took place daily from morning to evening. In Nigeria and South Africa, mist-netting occurred in the cool morning and afternoon hours. Most ringed birds were aged as adults or immatures, with a few subadults (Svensson 1984). In Poland, Nigeria and South Africa moult was scored as 0–5 (Ginn & Melville 1983, de Beer *et al.* 2001) for each primary. For a sub-sample of birds, the 18 flight feathers (nine full-sized primaries P1–P9, six secondaries S1–S6 and three tertials T1–T3) were scored. In Siberia, birds moulting wing feathers were noted. The birds were weighed (to 0.1 g) and wing lengths were measured (to 1 mm) in birds that were not moulting the outermost primaries (Svensson 1984, Earle 2005, Busse & Meissner 2015).

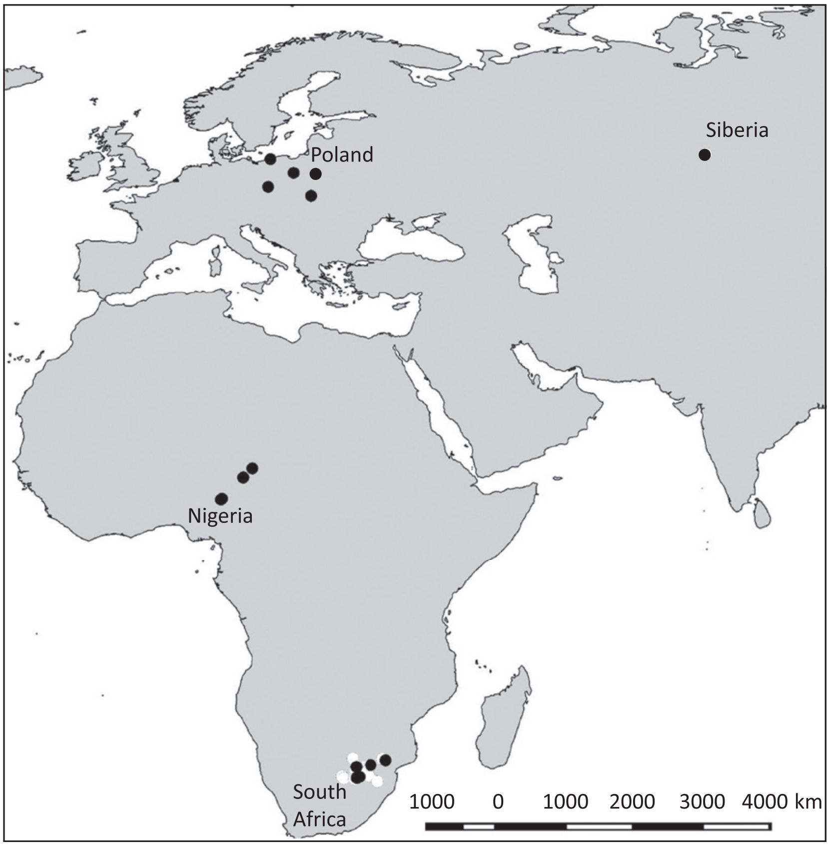

Figure 1. Ringing locations of the western (Poland–Nigeria) and eastern (Siberia–South Africa) migrant populations of Whitethroats used in this study. Filled circles = locations that provided records on moult status and body mass; open circles = locations that provided only body mass. The location names and coordinates are listed in Appendix S2.

Table 1. Numbers of birds in each stage of moult, with wing length and body mass, of the western (Poland–Nigeria) and eastern (Siberia–South Africa) populations of Common Whitethroats.

		Moult status						
Region	Measurements	Pre-moult	In moult	Suspended	Post-moult	Total	Body mass (g)	Wing length (mm)
Poland	All tracts	3	122	10	15	150	363	121
	Primaries only	3	111	2	34	150		
South Africa	All tracts	7	27	0	21	56	206	65
	Primaries only	15	58	0	50	123		
Nigeria							342	337
Siberia							77	72

Moult stages are listed for all tracts of wing flight feathers combined (primaries, secondaries and tertials) and in primaries only. The same birds are not necessarily included in each dataset. For study regions see Figure 1.

Moult and fuel estimations

To determine moult patterns, we analysed 150 moult records of 114 adults ringed in Poland and 123 moult records of 115 adults ringed in South Africa (Table 1). The wing feathers scored for moult were numbered as in de Beer *et al.* (2001). In Poland, moult was scored for primaries, secondaries and tertials. In South Africa, moult was scored for all these feathers at 56 captures

(Table 1). To improve the accuracy of moult estimates for primaries, we supplemented the 56 full moult cards with 67 records of primary moult only (Table 1) of Whitethroats caught at the same or nearby locations (Fig. 1) over the same period as the main dataset. Few subadults were recorded, so we combined them with adults for analyses.

To estimate fuelling patterns, we used 988 records of body mass (Table 1). We combined data from all years for each region. The datasets for moult, mass and wing length partly overlapped (Table 1). For Nigeria and South Africa, we supplemented our data with published data on Whitethroat moult and body mass (Raijmakers & Raijmakers 1994, Waldenström & Ottosson 2002) and analysed it using our methods. We compared 595 records of wing length among groups to assess differences in body size. Mean minimum monthly temperatures and mean monthly rainfall in the study regions (www.wetterkontor.de/de/klima/) served as a proxy for conditions that determine the occurrence of food (Salewski *et al.* 2004, Lingbeek *et al.* 2017).

Analysing moult in populations

We distinguished four groups of birds by their moult records: (1) pre-moulters, with moult scores of 0 for all feathers; (2) birds during moult, with a sequence of growing feathers; (3) birds with suspended moult in any tract of wing feathers, indicated by adjacent feathers having scores of 5 (new) and 0 (old); and (4) post-moulters, with scores of 5 for all feathers. Birds with suspended moult in the primary, secondary or tertial feather tracts were excluded from analyses of continuous moult. To estimate moult parameters for all wing flight feathers jointly, we used the proportion of feather mass grown (PFMG; Summers *et al.* 1983) for each bird as a wing moult index (Underhill & Zucchini 1988, Underhill *et al.* 1990). Calculation of PFMG requires the mean relative mass of each feather (Underhill & Summers 1993). To obtain this, we weighed the dried feathers from both wings of one dead adult Whitethroat, a casualty at a Polish station (Table S1). We averaged the masses for the corresponding feathers from both wings and calculated the mass of each primary, secondary and tertial, relative to the combined mass of all these feathers (Table S1; Underhill & Joubert 1995). We counted the date of capture as the number of days from 1 June.

We estimated moult parameters for all wing feathers combined ('whole wing method'), feather by feather (Underhill 2003) and for all primaries combined (Underhill & Zucchini 1988, Underhill *et al.* 1990) for the Polish and South African populations, using the R package *moult* (Erni *et al.* 2013). The estimates for primaries (Tables S1–S3) enabled comparison with other species. We applied the Underhill–Zucchini moult model (Underhill & Zucchini 1988) not only to the primaries, but also to the secondaries and tertials. This novel application enabled us to estimate moult timing of all the three tracts at once – accounting for simultaneous growth of primaries, secondaries and tertials – to reflect the investment of resources in the replacement of all large wing feathers.

To estimate moult duration, mean start date and its standard deviation for Poland, we applied the moult model with data type 4 (for definitions of data types, see Underhill & Zucchini 1988 and Underhill *et al.* 1990), which was the dataset including moulting and post-moult birds, but excluding the few pre-moult birds. In South Africa, we used data type 2 (Underhill & Zucchini 1988), including pre-moult, in-moult and post-moult birds, which were sufficiently sampled. To compare moult parameters for the whole wing between Poland and South Africa, we used data type 4 and included the geographical region as a covariate for each of three moult parameters (Erni *et al.* 2013, Remisiewicz *et al.* 2014), then ranked the models using the Akaike information criterion corrected for small samples (AICc) (Burnham & Anderson 2002).

To improve the estimates from a small sample of birds moulting P1–P4 in Poland, and T1–T3 in both regions, we estimated moult parameters of each feather by combining the data for each of these groups of feathers and using the feather number as a covariate in moult models (Remisiewicz *et al.* 2010). We calculated 'intershedding' intervals (Serra & Underhill 2006) as the difference between the estimated moult start dates of subsequently moulted feathers.

We compared growth rates of each feather between the Polish and the South African populations using the *Z*-test in STATISTICA 13.1 (Statsoft Inc. 2014). Daily feather growth rates were derived by dividing the relative mass of a feather by the estimated moult duration for that feather. We modelled the overall cumulative daily production of wing feather material using the daily growth rates and moult timing estimated per feather (Remisiewicz *et al.* 2009). Finally, we compared mean daily rates of feather mass production during each quartile of moult (Q1–Q4), dividing the total feather mass produced (100%) into four equal parts (25% stages). To test for different growth rates between groups, we applied the permutation test for ANOVA and *post-hoc* pairwise permutation tests (Manly 2007, R code by Howell 2009, 2015), as in Remisiewicz *et al.* (2017). We adopted $P < 0.05$ as indicating statistical significance.

Estimation of timing and rate of pre-migratory fuelling

To analyse fuelling rates, we pooled the body masses for moulting, pre- and post-moult birds with those for birds of unknown moult status. To determine whether feather wear could affect our analyses of body mass, we compared wing lengths of birds having worn feathers (pre-moult) with birds with fresh feathers (post-moult) in Poland and South Africa. Differences in body size can confound comparisons of body mass and fuelling rates (Piersma & Davidson 1991). To assess differences in body size, we compared wing lengths among pre-moult birds from Poland, Siberia and South Africa, and among post-moult birds from Poland, Nigeria and South Africa, using the Kruskal–Wallis test and *U*-test, because the distributions of wing lengths departed from normality.

We described seasonal trends in body mass in these four regions using a locally weighted regression smoother (Summers *et al.* 1985, Mullers *et al.* 2009, code in Remisiewicz *et al.* 2017). Those papers used linear regression, but we used quantile regression as in Kirkman *et al.* (2013). We estimated the trend in body mass through time of the upper quartile (R package quantreg; Koenker 2017). We used this method because the variability in body mass increased during the season, especially at the breeding grounds, and light and heavy birds occurred together. The light birds were probably not fuelling yet, or were preparing to depart with a low fuel load. We regarded the trajectory of the smoother provided by the upper quartile as an objective estimate of the rate of pre-migratory fuelling by birds that were actually in the process of fuelling. We used a smoothing parameter of 38 days (the length of the study period in Siberia) in the locally weighted smoother. This is a relatively wide window during which changing masses can affect the estimates, but it helped to smooth gaps in the data. We excluded isolated individuals trapped more than 12 days before and after their main cohorts; these become unacceptably influential points in determining the trajectory of the smoother. This approach enabled us to compare body mass trends between regions with scarce and abundant data.

To obtain an estimate of the start of pre-migratory fuelling, we chose the first of three consecutive days of positive slope in each trend (Remisiewicz *et al.* 2017). To enable comparisons, we drew the smoothed trends for the periods where the pairs of regions had sufficient data: 30 July–2 September for Poland and Siberia and 23 November–28 April for Nigeria and South Africa. We then compared mean fuelling rates by region for the common periods of fuelling in Siberia and Poland (30 July–2 September) and in Nigeria and South Africa (12 February–5 April). For Nigeria, we compared the fuelling rates before and after 5 April. Finally, we compared fuelling rates between moulting and post-moult birds in Poland, South Africa and Nigeria. The fuelling rates we compared were approximate relative values, and were probably underestimated because some birds might continue fuelling at the study sites after capture. To compare fuelling rates, we used the permutation test for ANOVA and *post-hoc* pairwise permutation tests (Manly 2007, R scripts by Howell 2009, 2015). All these statistical analyses were run in R 3.2.5 (R Foundation for Statistical Computing 2016).

RESULTS

Common Whitethroats moulted their remiges over a similar time period in Poland and South Africa (Fig. 2, Tables S2 and S3). The rate was variable in the western population moulting at the breeding grounds in Poland, but almost uniform in the eastern population at their non-breeding grounds in South Africa (Table 2). In Poland, wing moult progressed rapidly after a slow start, with a maximum of 13 wing feathers growing simultaneously; in South Africa, up to nine remiges grew simultaneously, but each at a faster rate than in Poland (Figs S1 and S2, Tables S2 and S3). In Poland, fuelling coincided with wing moult and was slow, but in South Africa, fuelling was mostly undertaken after moult and was twice as fast as in Poland (Table 3). In both regions, moulting birds fuelled more slowly than post-moult birds (Table 3). Whitethroats fuelled faster in the two regions where wing moult was uncommon, i.e. in Siberia and in Nigeria during April–May, than in Poland and in South Africa, where wing moult was common (Table 3, Fig. 3).

Moult strategies

Most Whitethroats in Poland (93.3%) and South Africa (100%) replaced their remiges continuously, without suspending moult (Table 1, Fig. 3). In Nigeria, 17% of adults moulted secondaries or tertials, but not primaries (Fig. 3). Duration of complete moult (Poland 55 days; South Africa 57 days) did not differ statistically, although the starting date and its standard deviation differed (Model 1, Table S4). In Poland, after the first few feathers started moulting (T1, P1–P3), the pattern of moult onset by feather did not show a clear sequence (Fig. S1). In South Africa, Whitethroats moulted each feather tract more regularly, replacing primaries and tertials in sequence, and secondaries from S1, then S6 and proceeding centripetally; wing moult was completed with the moult of S4 (Fig. S1, Table S3).

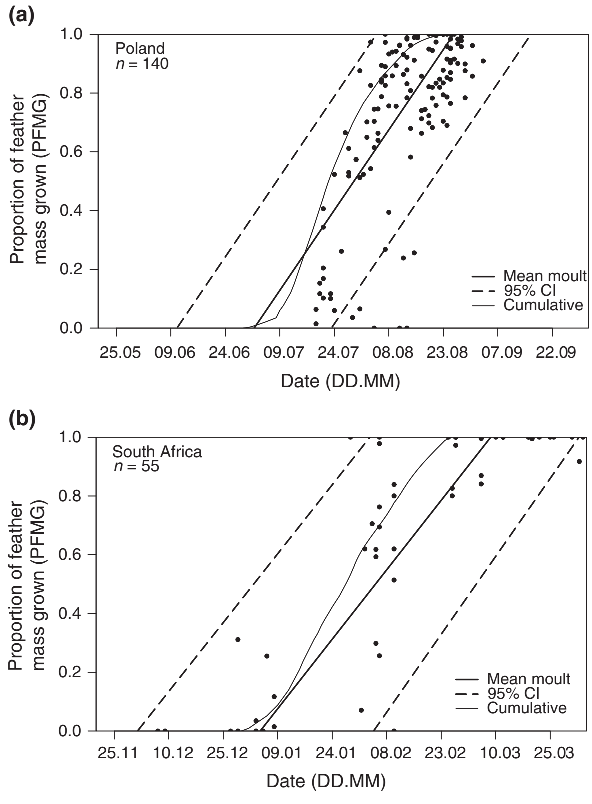

Figure 2. Temporal distribution of the proportion of feather mass grown (PFMG) moult indices for primaries, secondaries and tertials combined in relation to the capture date of Whitethroats in Poland and in South Africa. Thick black lines = mean moult progress, dashed lines = its 95% confidence interval (CI) derived using the Underhill–Zucchini moult model for data type 4 for Poland, and data type 2 for South Africa. Thin black lines = the cumulative curves of the daily feather mass production based on feather-by-feather methods (see Tables S2 and S3).

In Poland, moult rate varied by up to four times between the quartiles of PFMG; in South Africa the rate was nearly constant. The overall mean moult rate was similar in both regions (Table 2). The variable rate in Poland occurred because Whitethroats initially moulted a few remiges and then grew up to 13 simultaneously (Fig. S2); 11% of individuals were growing 10–13 feathers simultaneously. In South Africa, Whitethroats moulted up to nine feathers simultaneously (Fig. S2). Feathers were shed at shorter intervals in Poland (every 0–4 days) than in South Africa (0–8 days; *U*-test: $U = 90.0$, $P = 0.058$; Tables S2 and S3). In Poland, almost all feathers grew more slowly than the corresponding feathers in South Africa (Tables S2 and S3).

Pre-migratory fuelling

Whitethroats fuelled during moult in Poland, South Africa and Nigeria. However, birds that had completed moult fuelled faster than those fuelling during moult: 4.3 times faster in Poland and 2.4 times faster in South Africa (Table 3). Body mass increased three times faster in Siberia than in Poland during the same period (Table 3, Fig. 3). In South Africa, we estimated fuelling to begin on 12 December and it continued until departure in April. Fuelling in Nigeria began on 12 February by our estimates (Fig. 3). We compared the fuelling rates between these two regions from the start of fuelling in Nigeria on 12 February to 5 April, the latest date when Whitethroats occurred in sufficient numbers in South Africa (Fig. 3). The fuelling rate in Nigeria during mid-February–early April was similar to that in South Africa but it doubled closer to departure (Table 3, Fig. 3).

Wing lengths, a proxy for the body size, did not differ between pre-moult and post-moult birds or between most regions (Table S5). Wing lengths of

Table 2. The timing and rates (PFMG/day, %) of feather mass production for all 18 wing feathers in Poland and South Africa (permutation test for ANOVA: Poland, $P = 0.001$, South Africa, $P = 0.008$).

		Poland		South Africa	
Quarter stages of PFMG	% feather mass produced	Mean moult dates (days)	Mean moult rate (%PFMG/day)	Mean moult dates (days)	Mean moult rate (%PFMG/day)
Q1	0.0–25.0	30 Jun–15 Jul (16)	1.395	31 Dec–16 Jan (17)	1.401
Q2	25.1–50.0	16–22 Jul (7)	3.722**	17–27 Jan (11)	2.229*
Q3	50.1–75.0	23–31 Jul (9)	2.876**	28 Jan–8 Feb (12)	2.104
Q4	75.1–100.0	1–24 Aug (24)	1.072**	9–27 Feb (18)	1.467*
Average ranges and rate	0.0–100.0	30 Jun–24 Aug (56)	1.785	31 Dec–27 Feb (58)	1.724

PFMG, proportion of feather mass grown. *$P < 0.001$, **$P < 0.0001$ for pairwise permutation tests comparing moult rate at stages Q2–Q4 with the previous stage in each region.

Table 3. Mean fuelling periods and rates in moulting and post-moult Whitethroats, and in all birds combined (moulting, post-moult and of unknown moult status) for western (Poland–Nigeria) and eastern (Siberia–South Africa (SA)) populations.

Region and moult status	No. of days compared	Compared periods	Mean fuelling rate, g/day (sd)	Comparisons of moulting and post-moult birds in a region	Comparisons for all birds between regions	
Poland						
Moulting	19	8–25 Aug	0.036 (0.001)			
Post-moult	19	8–25 Aug	0.153 (0.163)	**$P < 0.0001$**		
All birds	38	30 July–2 Sep	0.027 (0.010)		Poland/Siberia	**$P < 0.0001$**
Siberia					Siberia/SA	**$P < 0.0001$**
All birds	38	30 July–2 Sep	$0.109\ (0.003\times10^{-10})$		Siberia/Nigeria p1	**$P < 0.0001$**
Nigeria						
Moulting	76	12 Feb–28 Apr	0.072 (0.052)			
Post-moult	76	12 Feb–28 Apr	0.082 (0.074)	**$P = 0.359$**		
All birds (p1)	53	12 Feb–5 Apr	0.053 (0.034)		Nigeria p1/SA	$P = 0.252$
					Nigeria p1/Poland	**$P < 0.0001$**
All birds (p2)	28	6 Apr–28 Apr	0.139 (0.051)*		Nigeria p2/Siberia	**$P < 0.0001$**
					Nigeria p2/Poland	**$P < 0.0001$**
South Africa						
Moulting	62	29 Jan–31 Mar	0.023 (0.012)			
Post-moult	62	29 Jan–31 Mar	0.054 (0.053)	**$P < 0.0001$**		
All birds	53	12 Feb–5 Apr	0.045 (0.039)		SA/Poland	**$P < 0.0001$**

Fuelling rates for 'all birds' calculated in the common periods for Siberia and Poland (30 July–2 September) and for Nigeria and South Africa (12 February–5 April). For Nigeria, we also compared fuelling rates in this period (p1) and after 5 April (p2). Fuelling rates for 'all birds' differed among the regions (ANOVA for permutation test: $F_{3,288} = 0.72$, $P < 0.001$). The last two columns give *P*-values from pairwise permutation tests, with significant values in bold. *$P < 0.0001$ for comparison between p1 and p2 in Nigeria.

pre-moult birds were on average shorter in Siberia than in South Africa (Table S5). Three birds in Siberia had shorter wings than elsewhere (< 65 mm) and were light (< 13 g; Table S5, Appendix S2); they were among the lightest 25% of birds in Siberia and so were excluded from estimating the fuelling curve. Thus, we conclude that the differences in fuelling rates between regions are real, rather than reflecting differences in body size.

DISCUSSION

Migration distance is a key factor affecting the annual cycles of migrants, including the time they remain at the breeding and non-breeding grounds (Ginn & Melville 1983, Newton 2009). Moult rate in migrants might vary depending on the time available before departure (Lindström *et al.* 1994). Thus, we expected different moult

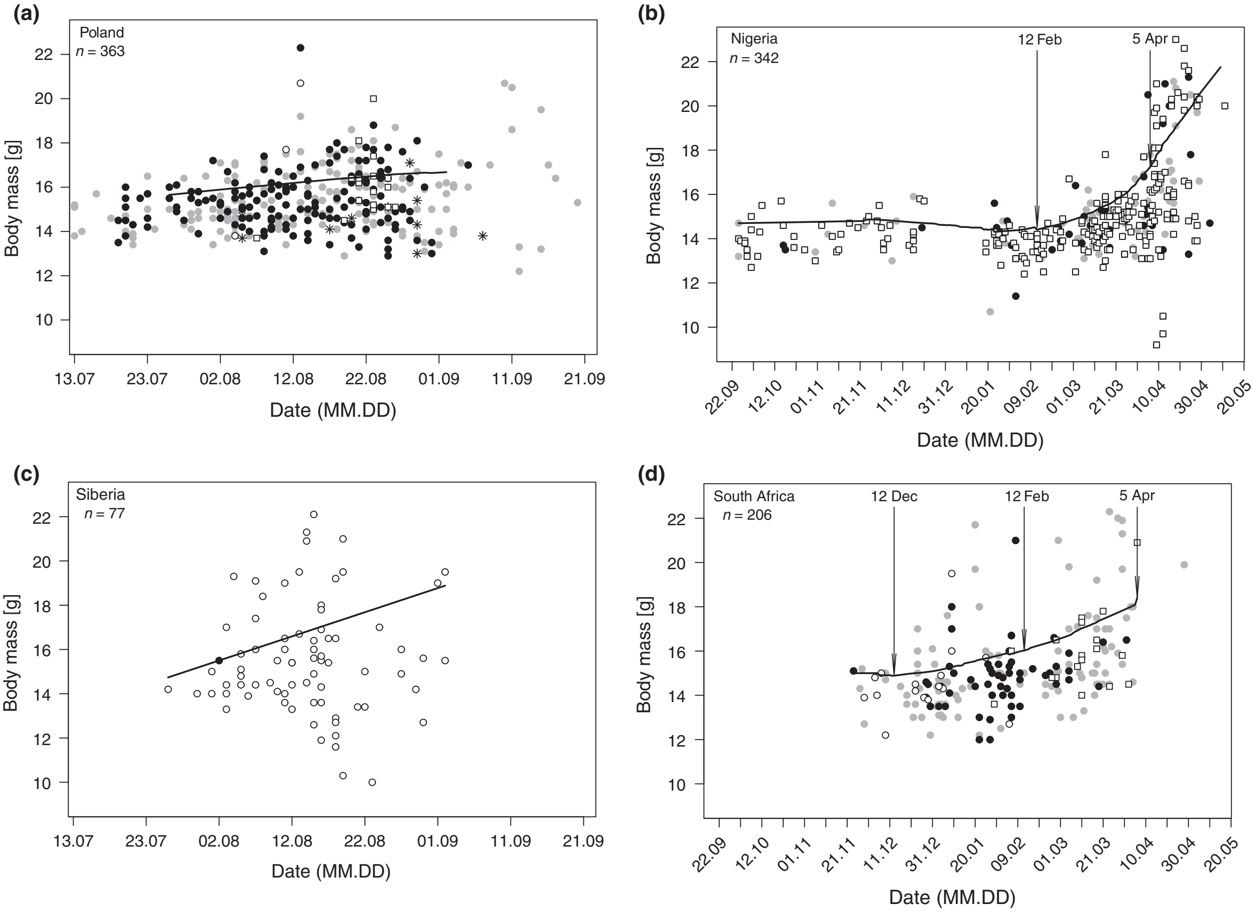

Figure 3. Body mass in relation to the date of capture for the western (Poland–Nigeria) and eastern (Siberia–South Africa) populations of Whitethroats. Black lines reflect body mass trends (locally weighted quantile regression) of the 75th percentile of body mass, drawn for all the birds in a region combined in the common periods 26 July–2 September for Poland and Siberia, and 23 November–28 April for Nigeria and South Africa. Open circles = pre-moult birds; black circles = moulting birds; white squares = post-moult birds; asterisks = birds with suspended moult; grey circles = birds of unknown moult status. Arrows with dates indicate periods of fuelling at non-breeding grounds: 12 December = beginning of fuelling in South Africa, 12 February–5 April = period 1 common for Nigeria and South Africa, after 5 April = period 2 in Nigeria, not represented by birds in South Africa (Table 3).

and fuelling strategies in the two populations of Whitethroats: the eastern population migrates almost twice as far as the western population and stays longer at its moulting grounds. The different moult and fuelling strategies were striking, but more complex than we had predicted. First, contrary to our expectations, the western Whitethroats in Poland and the eastern ones in South Africa moulted for similar durations and at a similar overall rate. However, the two populations achieved similar moult rates differently: in Poland, Whitethroats moulted at a varying rate and more feathers at a time, but in South Africa, they moulted at a uniform rate by growing fewer feathers simultaneously. Secondly, as we expected, at the breeding grounds Whitethroats fuelled faster when they did not moult (in Siberia) than when they did (in Poland). Similarly, at the non-breeding grounds, Whitethroats fuelled slowly when moulting, even during the rainy season in South Africa. In Nigeria, they fuelled slowly in mid-February–March, probably constrained more by drought than by an infrequent additional partial moult of tertials and odd secondaries, but three times faster in April–May after the rains and close to departure. Additionally, moulting birds fuelled more slowly than post-moult cohorts in each region where moult occurred. These findings confirmed our second hypothesis that fuelling would be impeded during moult.

These findings raise further questions about the life history of the two populations of a species, with contrasting migration and moult strategies: (1) Why do western Whitethroats moult most remiges rapidly during their short post-breeding period in Poland, rather than in the Sahel, where they spend about 6 months? (2) Why do eastern Whitethroats moult their wing feathers over only 2 of their 4½-month sojourn in South Africa? We address these questions in the context of migration distances and the conditions these populations encounter at their breeding and non-breeding grounds.

Patterns of moult

After breeding in May–mid-July (Cramp & Brooks 1992), Whitethroats moulted their wing feathers in Poland on average over 2 months, in the 2- to 3-month gap between the end of breeding and departing in August–mid-September (Nowakowski 1999, Tomiałojć & Stawarczyk 2003). The timing of the post-breeding moult in Poland is within the range of Whitethroat moult in northern and western Europe, July–September (Ginn & Melville 1983, Jenni & Winkler 1994, Hall & Fransson 2001, Shirihai *et al.* 2001, Morrisson *et al.* 2015). The eastern Whitethroats in South Africa moulted over 2 months of their stay from the end of November to early April (Earle 2005). The moult timing we estimated falls within the published December–March moult period for Whitethroats in South Africa (Raijmakers & Raijmakers 1994, Earle 2005). The few adults moulting tertials and infrequently odd secondaries in Nigeria in September–December (Fig. 3) were probably finishing their complete wing moult (Jenni & Winkler 1994). The moult of a few secondaries and tertials in several Whitethroats in late January–April was probably the next moult sequence, an additional pre-breeding partial moult of a few remiges, which infrequently occurs in Whitethroats in west Africa (Jenni & Winkler 1994, Waldenström & Ottosson 2002).

Mechanisms of regulating moult rate

The production rate of wing feather material depends on three features of moult: the number of feathers growing simultaneously, the intershedding intervals and the growth rate of each feather (Ginn & Melville 1983). The western and eastern Whitethroats achieved a similar moult duration and rate in Poland and South Africa by different means. In Poland, Whitethroats replaced more feathers simultaneously and shed them at shorter intervals than in South Africa, where they moulted fewer feathers at a time and with less overlap, although each feather grew faster than in Poland. The varying moult rate within a season and the growth of many feathers simultaneously suggests time constraints on moult in Poland.

The timing of moult and fuelling responds to seasonal changes in photoperiod, which cue a cascade of hormonal changes (Helm & Gwinner 2006, Dawson 2008). Prolactin mediates much of the subsequent hormonal regulation of moult in response to the timing of other life-stages, parental behaviour, photoperiod and environmental factors (Dawson 2008). This mechanism would adjust the start of moult in relation to the timing of breeding at varying times, as in Poland, and adjust the end of moult to the approaching departure, as in South Africa and in Poland, as well as to current environmental conditions and the birds' physiological state (Dawson 2008). Parental behaviour affects the levels of sexual hormones, which would affect how moult is timed to the stage of development of the offspring being raised (Dawson 2008). A late start of moult necessitates rapid moult, within the birds' physiological limits (Lindström *et al.* 1994, Dawson 2008), which the birds might achieve by moulting many feathers simultaneously, as in Poland, or by growing each feather quickly, as in South Africa. Finally, moult and fuelling require access to food and water (Jenni-Eiermann & Jenni 1996, Katti & Price 1999), which might explain why the western Whitethroats moult in Poland, rather than in Nigeria.

Constraints to moult and fuelling

Wing moult and pre-migratory fuelling are energy-intensive processes, and thus one may occur at the cost of the other (Morton & Welton 1973, Lindström *et al.* 1994), and migration poses a time constraint on both. Whitethroats of both populations moulted primaries at nearly the fastest rate recorded for insectivorous passerine migrants (Table S6). Only Willow Warblers *Phylloscopus trochilus* in northwestern Europe moulted their primaries faster, probably because they are time-constrained by their early departure (Underhill *et al.* 1992). In Poland, breeding and departure restrict the time available for Whitethroats to moult, which could explain its speed, but different constraints apply in South Africa, where birds spend about 4½ months. There, pre-migratory fuelling, which begins about 3 months before departure, probably constrains moult, which is thus short and fast (Fig. 4). The maximum daily rates of feather production and fuelling are constrained by physiological and ecological factors that determine condition and metabolic rate (Lindström *et al.* 1993).

The patterns we describe in Whitethroats are consistent with the literature showing that pre-migratory fuelling during wing moult is slower and less efficient than when conducted separately (Morton & Welton 1973, Lindström *et al.* 1994). In Garden Warblers *Sylvia borin*, Lesser Whitethroats *Sylvia curruca* and Bluethroats *Luscinia svecica*, under seasonal time constraints on their breeding grounds, fuelling overlaps with moult but is retarded (Lindström *et al.* 1993, 1994, Jenni-Eiermann & Jenni 1996, Fransson & Hall-Karlsson 2000). Post-moult Whitethroats fuel faster than those moulting in Poland and in South Africa (Table 3), highlighting the benefits of separating these processes. In South Africa, Whitethroats fuelled at a similar rate to those in Nigeria, despite moulting, probably because of favourable feeding conditions, yet they fuelled even more quickly after moult.

Moult and fuelling strategy in response to environmental conditions

Environmental conditions determine the body condition of birds and affect the timing and rate of moult, fuelling and migration (Jones 1995, Allan *et al.* 1997, Katti & Price 1999, Salewski *et al.* 2004). Wing moult coincided with wet and warm periods in Poland and in South Africa, and fuelling with wet periods in all four regions (Fig. 4), when invertebrates and berries are abundant (Allan *et al.*

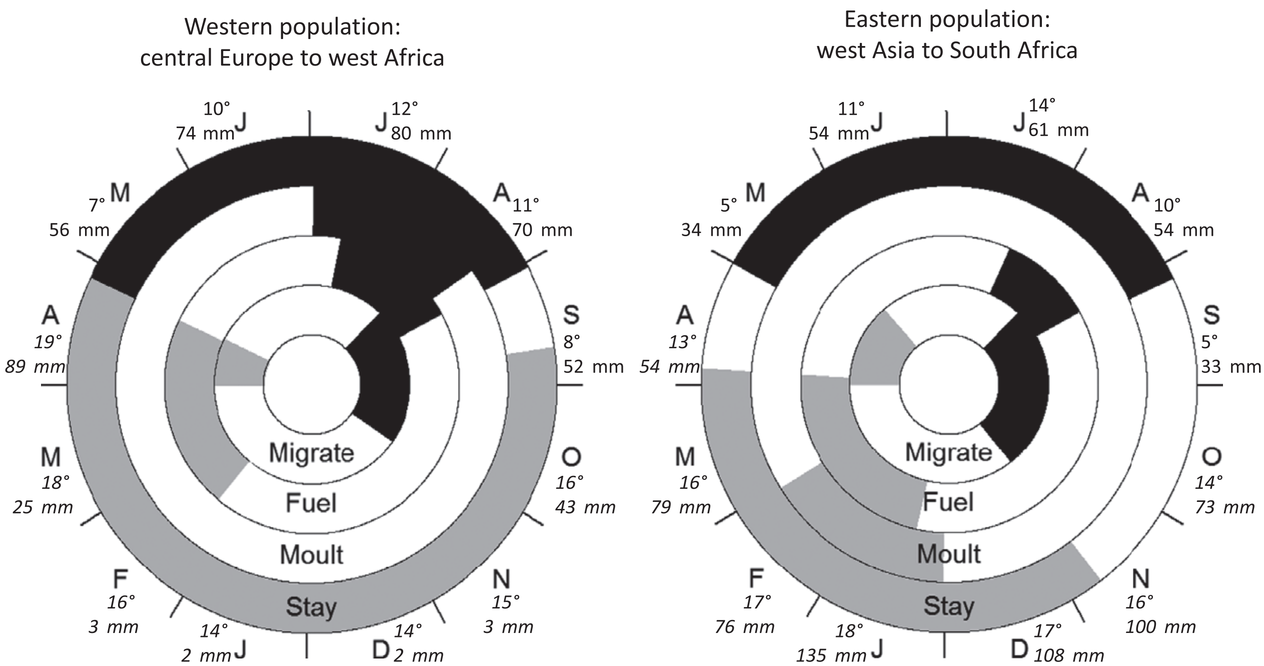

Figure 4. Timing of wing moult and fuelling in the context of other main stages of the annual cycle for the western (Poland–Nigeria) and eastern (Siberia–South Africa) populations of Whitethroats. Black = stages of the life cycle in the northern hemisphere; grey = in the southern hemisphere. Timing of moult and fuelling = our results; timing of other activities from the literature (Cramp & Brooks 1992, Nowakowski 1999, Shirihai *et al.* 2001, Tomiałojć & Stawarczyk 2003, Earle 2005). Mean minimum monthly temperatures (°C) and mean monthly rainfall (mm) beside the month symbols reflect the climate at the breeding grounds (non-italicized) and non-breeding grounds (italicized) when the birds are present. Climate data are from weather stations closest to the ringing locations where most birds in a region were ringed (see Fig. 1): Białystok in Poland, Jos in Nigeria (left figure), Omsk in Siberia (Russia), Pretoria in South Africa (right figure). From http://www.wetterkontor.de/de/klima/.

1997, Lingbeek *et al.* 2017, MR, AR, ZB, HB pers. obs.). We suggest that the contrasting patterns of wing moult and fuelling we revealed in the two Common Whitethroat populations might be the effect of adjusting to the different environmental conditions they encounter in central Europe and west Africa, and in west Asia and southern Africa.

In western Whitethroats, wing moult occurred during the rainy summer at their breeding grounds, whereas for about half of their stay in the Sahel, rainfall is usually low and food supply is limited (Fig. 4; Jones 1995, Salewski *et al.* 2004). After leaving Poland, the lean adults probably migrate south in short hops with stopovers in Europe, as immature Whitethroats do (Schaub & Jenni 2000, Ożarowska 2015). These migrants cross the Mediterranean Sea and the Sahara Desert to and from Africa. For those that head to west Africa, the Western Sahara is a *c.* 1800-km barrier before November. During the dry season, the desert extends 400–600 km southwards (Zwarts *et al.* 2009), the equivalent of two nights of flight for a Whitethroat. The increasing width of the Sahara probably selects for the early departure of Whitethroats from the breeding grounds (Hall & Fransson 2001). They arrive in the Sahel from the end of September, just before the dry season usually begins (Fig. 4), and conditions probably do not provide nutrition sufficient for moult (Zwarts *et al.* 2009). Other migrants that moult remiges in the western Sahel do so before or after the main November–December dry period (Table S6; Bensch *et al.* 1990, Salewski *et al.* 2004). When the rains come, usually between March and April (Fig. 4), Whitethroats feed intensively on insects and berries, which become abundant (Vickery *et al.* 1999, Stoate *et al.* 2001). The improved food supply would facilitate the Whitethroats' fast fuelling in April–May (Table 3) and even an additional partial moult of a few remiges (Fig. 3; Waldenström & Ottosson 2002). On the way north, they probably rely on tailwinds over the central Sahara, as do other small migrants (Schmaljohann *et al.* 2007). We suggest that large fuel loads on departure from the Sahel and wind assistance *en route* might compensate for the risk of migrating across the Sahara Desert using worn primaries.

The eastern Whitethroats in Siberia fuel fast in the warm and wet summer before their long-distance migration (Fig. 4). Their intensive fuelling before leaving the breeding grounds probably facilitates crossing the unfavourable habitats they encounter after departure, such as the steppes of Kazakhstan, compared with the more benign conditions experienced by the other population in western Europe (Schaub & Jenni 2000, Yohannes *et al.* 2009). The eastern population moults their wing feathers and fuels in southern Africa during the wet and warm season, November–April (Fig. 4), when abundant food supports both processes. We suggest these Whitethroats utilized 2 of their 4½ months in South Africa for wing moult and 2 months for fuelling because of the advantages of separating these processes, at least partially (Fig. 4).

CONCLUSIONS

The intraspecific differences in moult and fuelling in Common Whitethroats are probably determined by the climate and food supply encountered at their breeding and non-breeding grounds. We suggest that eastern Whitethroats benefit from the rich food supply of the short boreal summer to breed and fuel for their long-distance migration south, and that of the long austral summer to moult wing feathers and fuel before migration north. The western Whitethroats use the boreal summer to moult their wing feathers rapidly at the cost of limiting pre-migratory fuelling. During their long stay in the Sahel, limited food and water during the dry season probably impede wing moult, but the later rainy season enables fuelling. These contrasting strategies demonstrate that Common Whitethroats have adjusted wing moult and fuelling to the conditions they encounter each year at both ends of their migration. These flexible stages might provide a buffer against the effects of changing climate in the timing of the main events in these migrants' life cycle, such as breeding and migration, which are bound by the seasons (Helm & Gwinner 2006, Morrisson *et al.* 2015).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Fig. S1. Moult timing and sequence of each wing feather for western (Poland–Nigeria) and eastern (Siberia–South Africa) Whitethroats.

Fig. S2. The number of wing flight feathers growing simultaneously with the feather on the *X*-axis for Common Whitethroats in Poland and in South Africa.

Table S1. Mean relative mass of flight feathers in adult Common Whitethroats expressed as a percentage of the total mass of all wing feathers treated as 100%, and as percentage of the total mass of all primaries (P1–P9) treated as 100%.

Table S2. Moult sequence and moult parameters of separate wing feathers for adult Common Whitethroats caught in July–October 2013–2016 in Poland.

Table S3. Moult sequence and moult parameters of separate wing feathers for adult Common Whitethroats caught in November–April 1987–2017 in South Africa.

Table S4. Underhill–Zucchini moult models used to determine the effect of region where moult takes place (see Fig. 1) on moult parameters estimated for all primaries, secondaries and tertials jointly in adult Common Whitethroats caught in July–October 2013–2016 in Poland and in November–April 1987–2017 in South Africa.

Table S5. Mean wing lengths of Whitethroats caught in the four study regions (Fig. 1), considering the moult status of measured wings.

Table S6. Comparison of primary moult rates estimated by Underhill–Zucchini models for Whitethroats in Poland and in South Africa (Tables S2 and S3) with those for other insectivorous passerine migrants.

Appendix S2. Datasets used in the study.