Contrasting fattening strategies in related migratory species: the blackcap, garden warbler, common whitethroat and lesser whitethroat

Agnieszka Ożarowska

Avian Ecophysiology Unit, Department of Vertebrate Ecology and Zoology, University of Gdańsk, ul. Wita Stwosza 59, PL-80-308 Gdańsk, Poland (e-mail: agnieszka.ozarowska@biol.ug.edu.pl); and Bird Migration Research Station, University of Gdańsk, ul. Wita Stwosza 59, PL-80-308 Gdańsk, Poland; and SE European Bird Migration Network, PL-84-210 Przebendowo, Poland

Related species showed different strategies when migrating south towards wintering grounds in the Sahel and southern Africa: the garden warbler steadily increased fuel reserves along the migration route, the blackcap showed mixed fattening strategy with high fat reserves just before the Sahara crossing, the common whitethroat accumulated large fat reserves well in advance (North Mediterranean) before crossing this barrier, while the lesser whitethroat starting from the northern part of the Mediterranean showed a stable level of fat reserves. Results of this study support the hypothesis that species-specific ecology, rather than phylogenetic relationships, plays the major role in the evolution and form of bird migration. There were also population-specific differences in the strategy of species based on migration distance (blackcap), as well as individual differences where some individuals of the same species were potentially able to cover larger distance than conspecifics (blackcap, common whitethroat).

Introduction

Migratory birds heading towards eastern Africa have to cross or circumvent the Mediterranean Sea, pass through the Middle East which, to a large extent, is a desert region, and finally cross the Sahara (Shirihai 1996, Bruderer & Liechti 1999). The fuel load, including fat and protein reserves, is a key element in the strategy adopted by migrating birds, particularly when overcoming large geographical barriers, like the sea, high mountain ranges or desert areas (Schaub & Jenni 2000a, Newton 2008, Chernetsov 2012). When focusing on fuel reserves exclusively, long-distance migrants show several different strategies of the accumulation of these reserves (Schaub & Jenni 2000a). Migration strategy can also differ in related species, like in the reed and sedge warbler (*Acrocephalus scirpaceus, A. schoenobaenus*) (Bibby & Green 1981, Yosef & Chernetsov 2004, 2005). These differences are attributed to the varied availability and predictability of food resources the two species rely upon. However, such studies are limited (Bibby & Green 1981, Schaub & Jenni 2000b, Bayly 2007), and the question remains how related species, morphologically and ecologically similar, facing the same conditions and utilizing

common resources, i.e. having a similar diet, "organize" their travel when moving southwards along their route to sub-Saharan Africa.

I analysed four common species in the genus *Sylvia*: the blackcap *S. atricapilla*, garden warbler *S. borin*, common whitethroat *S. communis* and lesser whitethroat *S. curruca*; the first two are sister species, while the other two are related species (Blondel *et al.* 1996, Voelker & Light 2011). These species are trans-Saharan migrants spending winter in the Sahel or as far south as South Africa (garden warbler), except some blackcap populations wintering in southern Europe. The blackcaps, which originate east of 12–13°E, are long-distance migrants and migrate southeast, mostly through the Middle East and spend winter in eastern Africa (Shirihai *et al.* 2001). Ringing recoveries of the garden warbler also indicate an east–west segregation of the species as individuals of more easterly breeding populations (*S. b. woodwardi*) winter in eastern and southern Africa (Shirihai *et al.* 2001). The breeding ground intergradation zone of the nominate subspecies and the eastern *woodwardi* is wide, and extends from Poland to Bulgaria (Bairlein 1991, Hagemeijer & Blair 1997). A weakly defined migratory divide exists in the common whitethroat as well. Birds originating east of 10°E migrate southeast and spend winter in eastern and southern Africa (Shirihai *et al.* 2001). The whole European population of the lesser whitethroat moves southeast and winters entirely in the northern tropics (north of 5°N) of eastern and northeastern Africa (Pearson & Lack 1992).

There are a number of studies on the migration strategy of some species, like the garden warbler (e.g. Bairlein 1991, Schaub & Jenni 2000a, 2000b) and blackcap (e.g. Rolshausen *et al.* 2010, Arizaga & Barba 2011, Kopiec & Ożarowska 2012) with a growing body of information detailing the migration of these species in West Africa (Ottosson *et al.* 2005, Smith 2007, Bayly & Rumsey 2010, Iwajomo *et al.* 2011). Research on bird migration in East Africa is far more limited (e.g. Pearson & Lack 1992, Yosef 1997, Yohannes *et al.* 2009) and studies on Asian populations are almost non-existent (e.g. Zduniak & Yosef 2012). The aim of this study was to compare the fat reserve accumulation of four *Sylvia* species migrating along the eastern flyway and to evaluate which factor plays the major role: phylogenetic relationships leading to similar fattening strategies of related species or rather species-specific ecology resulting in different patterns. If the latter is the case, a further question involves whether this pattern is conservative or flexible within the species.

Material and methods

I analysed data on four species of the genus *Sylvia* captured during autumn migration (12 August–17 November) at eight ringing stations located in four main regions along the southeastern migration flyway (Table 1), during various autumn seasons in 2000–2006. The stations were located on the southern coast of the Baltic Sea (Bukowo-Kopań in Poland), close to the northeastern coast of the Mediterranean (Manyas in Turkey), in the eastern region of the Mediterranean (Dhleil in Jordan), and the northeastern part of Africa (Burullus, Wadi El Rayan, Sharm El Sheikh, Saluga/Ghazal and Wadi Gemal in Egypt). Due to the low number of birds captured at most of the Egyptian stations (Table 1), the data from these sites were pooled. Sampling effort differed between the studied regions (Table 1); still the data covered the whole migration of the species at the stations located in the Mediterranean and northeastern African regions. However, when analysing the data from the southern Baltic coast, the studied period covered the whole migration of the blackcap, while for the garden warbler, whitethroat and lesser whitethroat it covered most of it (over 90%) and the migration peak (Nowakowski 1999).

Standard SE European Bird Migration Network methodology including constant effort mist-netting and a standard set of biometric measurements (wing and tail lengths, wing formula; weight (accuracy 0.1 g), fat score; Busse 2000), was applied during the fieldwork. This methodology was developed on the basis of the Operation Baltic schedule — the program which started in the early 1960s. The applied fat score scale consists of 9 classes (Busse 2000). The number of nets and their location throughout the whole migration season were constant.

Table 1. Location and characteristics of the ringing sites and sampling effort in the analysed regions. Country codes: PL = Poland, TR = Turkey, JO = Jordan, EG = Egypt; species codes: SAT = blackcap. SBO = garden warbler, SCO = common whitethroat, SCU = lesser whitethroat.

Stations, country code coordinates	Habitat	Studied years	Region	Average number of studied days in a region per year	Species code	Total number of captured birds in a region
Bukowo-Kopań, PL (16°25′E, 54°28′N)	typical coastal temperate habitats: rather scattered, mostly pine forests, some alder in wet parts of the site; bushes, including elder dense hedgerows of blackberry and raspberry	2000–2006	S Baltic	95	SAT SBO SCO SCU	4583 1277 330 720
Manyas, TR (28°04′E, 40°13′N)	oak grove of height 3–5 m with many clearings of grassy patches, surrounded by agricultural fields	2002–2003	N Mediterranean	61	SAT SBO SCO SCU	569 47 67 149
Dhleil, JO (36°07′E, 32°08′N)	located in the valley (ca. 3 km long, 500–1000 m wide) at the edge of vast, sparsely inhabited territory and the desert; most of the area covered by an olive plantation, mixed with orchards	2001–2002	E Mediterranean	68	SAT SBO SCO SCU	2128 203 32 226
Burullus, EG (30°55′E, 31°31′N)	located in the Nile delta close to lake Burullus; dominant reedbed habitat	2005–2006	NE Africa	56 (if Sharm El Sheik excluded: 60)	SAT SBO SCO SCU	11 19 34 415
Wadi El Rayan, EG (30°19′E, 29°12′N)	typical wadi on the edge of two lakes; sparse vegetation consisting mostly of reed, tamarisks and palms adjacent to sand/stony vast desert areas	2001–2002				
Sharm El Sheikh, EG (34°17′E, 27°51′N)	located near the coast of the Red Sea; sparse vegetation consisting mostly of reed, tamarisks and palms adjacent to sand/stony vast desert areas	2003				
Saluga/Ghazal, EG (32°52′E, 24°04′N)	located on islands on the Nile; a mixture of grasslands, rocky and stony areas, sandbars and thick bushes with single low trees	2003–2005				
Wadi Gemal, EG (35°04′E, 24°38′N)	typical wadi; sparse vegetation consisting mostly of reed tamarisks and palms adjacent to sand/stony vast desert areas	2005				

For several reasons I focused exclusively on the analyses of fat reserves. Energy stores of migrating birds consist of lipids, proteins and water. Still, fat (lipids) can make up over 80% of these stores in small passerines (Klaassen & Biebach 1994, Klaassen *et al.* 1997, Wojciechowski *et al.* 2014). Fat scores are easy to measure, unobtrusive and provide a relatively accurate fat index suitable for the study of body condition of small passerines in which exact estimates of fat content of individual birds are not required (Conway *et al.* 1994). Moreover when a number of birds are captured at a single site, fat classes enable the detection of small differences in fat levels, while body mass corrected for structural size is less sensitive (Rogers 2003). As migrants were captured in different regions, I was not able to separate individuals of different breeding origin, which may differ in structural size/body mass, therefore I assumed that fat scores alone could be more suitable for assessing a migrant's fat reserves.

The analyses of fat scores of captured migrants were based only on immature (first year) birds. Some studies have indicated a difference in fat reserves between adult and immature individuals, the former showing higher fat reserves (Ellegren 1991, Woodrey & Moore 1997, Jones *et al.* 2002, Jakubas & Wojczulanis-Jakubas 2010). However, due to a low number of adult birds of most species in the data set, I had to limit the analyses exclusively to immatures. Moreover, I only analysed birds captured for the first time at the studied regions (i.e. retraps were excluded). Due to the low number of warblers (except the lesser whitethroats) captured in northeastern Africa, I also excluded this region from most analyses. Since in the blackcap there are several populations that differ in migration strategy, including migration distance, a good proxy for distinguishing between short-distance blackcaps wintering in the Mediterranean region and those individuals wintering in Africa is wing length (Fiedler 2005), as this parameter reflects the distance migratory species/population covers (Berthold & Querner 1982, Lo Valvo *et al.* 1988, Telleria & Carbonell 1999, Fiedler 2005). First-year male and female blackcaps are about the same size (Holloway & Edwards 1989, Svensson 1992, Gustin *et al.* 1999, Ottosson *et al.* 2001, Shirihai *et al.* 2001, Arizaga & Barba 2011), so birds of both sexes

were pooled in the material. Based on the first and third quartiles in the wing length distribution of blackcaps captured at the Polish Baltic coast (A. Ożarowska & G. Zaniewicz unpubl. data based on a 40-years-long time series), as well as results of studies by Fiedler (2005), birds were grouped according to wing length (in parentheses) as follows: short-winged (70–74 mm), medium-winged (75–76 mm) and long-winged individuals (77–81 mm). Only long-winged birds (wing length > 76 mm) captured at the study sites were included in the analyses. Currently, it is not possible to distinguish blackcap populations originating from different regions with molecular methods (Perez-Tris *et al.* 2004, Mettler *et al.* 2013). Nevertheless, since there is some phenotypic variation, the criterion of wing length was applied based on the study by Fiedler (2005) on the breeding populations of blackcaps of different migratory behaviour.

Statistical analyses were performed using the STATISTICA 10 software (StatSoft 2011). Since all distributions of fat scores differed significantly from normal (Lilliefors test: $p < 0.05$ in all cases), non-parametric tests were used.

The Flight ver. 1.24 programme by Pennycuick (2008) was used to assess the theoretical, maximum flight range of the analysed species captured in different regions, assuming the passage at an altitude of 1000 m in still air of density 1.11 kg m^{-3}. The fat fraction, i.e. the ratio of the mass of consumable fat to body mass at departure (not to lean body mass; Pennycuick 2008) is necessary to run the simulations. The average body mass of the leanest birds provided an estimate of the average minimum body mass, which was used as a baseline to calculate the difference between the average body mass of the fattest/heaviest individuals, and finally the fat fraction. The calculations were run separately for each analysed region. The lowest body mass was estimated either as the mean body mass of all individuals of the lowest fat score (i.e. $F = 0$) or if the sample size of birds with the lowest fat score was very low ($n < 10$), as the average body mass of 25% of the individuals of the lowest weight, which represented fat scores of $F \leq 2$ (garden warbler and common whitethroat in the N and E Mediterranean; lesser whitethroat in the N and E Mediterranean, and NE Africa). The highest body mass was
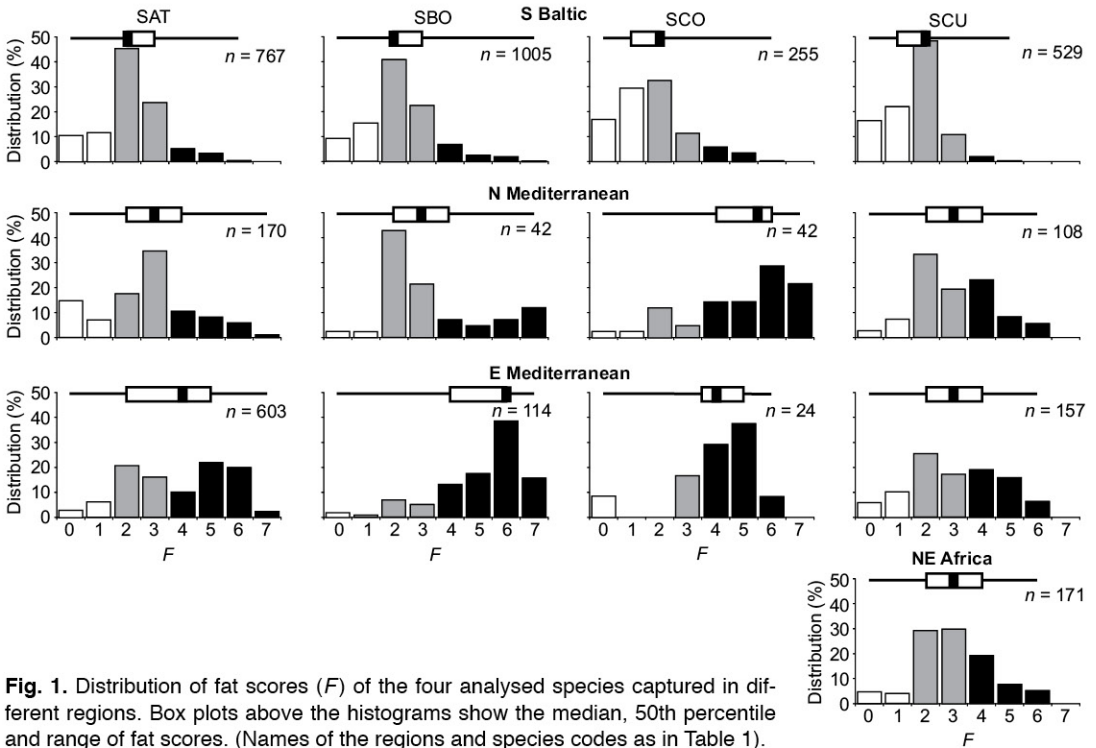
Fig. 1. Distribution of fat scores (F) of the four analysed species captured in different regions. Box plots above the histograms show the median, 50th percentile and range of fat scores. (Names of the regions and species codes as in Table 1).

estimated as the average body mass of 25% of the heaviest individuals, which represented fat scores of $F \geq 3$. A similar procedure was used by e.g., Iwajomo *et al*. (2011) and Meissner *et al*. (2011). I used data on wing span (WS)/wing area (WA) either provided in the Flight programme or from the literature (blackcap: WS = 0.224 m, WA = 0.0096 m², n = 21; garden warbler: WS = 0.24 m, WA = 0.011 m², n = 10; common whitethroat: WS = 0.21 m, WA = 0.0087 m²; lesser whitethroat WS = 0.19 m, WA = 0.0073 m²). The use of different assumptions and models for flight cost strongly affects the estimates of flight range (McWilliams *et al*. 2004), thus the obtained results are only a rough estimate of potential flight range, but as the key point in the present study was to obtain a relative estimate of the distance covered by the studied species in order to establish differences or similarities among them, such an approach was considered adequate.

Results

In all studied species, birds captured in dif-

ferent regions differed significantly in fat reserves (Kruskal-Wallis test: the blackcap $H_{2,1540} = 301.60$, $p < 0.001$; garden warbler $H_{2,1161} = 222.67$, $p < 0.001$; common whitethroat $H_{2,321} = 98.24$, $p < 0.001$; lesser whitethroat $H_{3,965} = 238.02$, $p < 0.001$; Fig. 1). Blackcaps significantly increased their fat reserves when moving southwards (Dunn's *post-hoc* test: $p < 0.001$ in all cases; Fig. 1). Fat scores recorded in these birds ranged from 0 for no fat, to the highest score 7, in which the furculum and belly were completely covered with fat, while pectoral muscles were covered partly. A bimodal distribution of fat scores of individuals captured in the eastern Mediterranean region is noteworthy (Fig. 1), as medium ($F = 2$–3) and higher scores ($F > 5$) dominated the observed pattern. Similarly to the blackcap, the garden warbler also showed significant increase in fat reserves towards southern regions (Dunn's *post-hoc* test: $p < 0.001$ in all cases; Fig. 1). In the common whitethroat, the difference was observed in birds captured on the southern coast of the Baltic Sea and two other regions, i.e. the northern and eastern Mediterranean (Dunn's *post-hoc* test: $p < 0.001$ in both
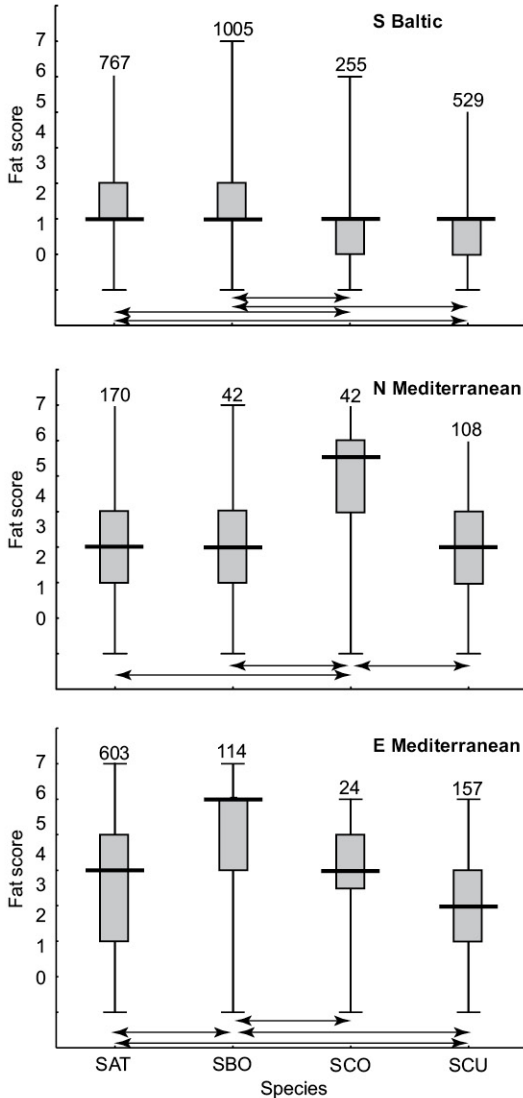
Fig. 2. Comparison of fat scores of the four analysed species captured in different regions. The box plots show medians, 50th percentiles, range of fat scores, and sample sizes; arrows indicate significant differences in fat scores (Dunn's *post-hoc* test: *p* < 0.01). (Names of the regions and species codes as in Table 1).

which were also the highest out of all analysed species (median 6; Fig. 1). Fat reserves were significantly lower in lesser whitethroats captured in the southern Baltic as compared with those of whitethroats captured in other regions (Dunn's *post-hoc* test: *p* < 0.001 in all cases); while no difference was found among birds captured either in the northern and eastern Mediterranean or the northeastern African region (Dunn's *post-hoc* test, *p* = 1.000 in all cases) — in all these regions median fat score was 3 (Fig. 1).

There was a significant difference in fat score between the four species captured in the southern Baltic, and the northern and eastern Mediterranean (Fig. 2; S Baltic: Kruskal-Wallis test $H_{3,2556}$ = 115.04, *p* < 0.001; N Mediterranean: Kruskal-Wallis test $H_{3,362}$ = 38.60, *p* < 0.001; E Mediterranean: Kruskal-Wallis test: $H_{3,898}$ = 90.50, *p* < 0.001). In the southern Baltic region no significant difference was observed either between the blackcap and garden warbler (Dunn's *post-hoc* test: *p* = 1.000) or the common and lesser whitethroat (Dunn's *post-hoc* test: *p* = 1.000). Larger species showed higher fat reserves as compared with those of smaller ones, i.e. the common and lesser whitethroats (Dunn's *post-hoc* test: *p* < 0.001 in each case; Fig. 2). In the northern Mediterranean region, the common whitethroat showed the highest fat scores (median 5.5; Fig. 2) out of the four analysed species (Dunn's *post-hoc* test, *p* < 0.001 in all cases; Fig. 2), while there was no difference between the other species (Dunn's *post-hoc* test: *p* = 1.000 in all cases; Fig. 2). The last region, where all species except the common whitethroat (*n* = 24), were captured in considerable numbers was the eastern Mediterranean. The garden warbler showed the highest fat reserves and significantly differed from the other species (Dunn's *post-hoc* test: *p* < 0.04 in all cases; Fig. 2). The blackcap had higher fat reserves than the lesser whitethroat (Dunn's *post-hoc* test: *p* < 0.001; Fig. 2), while it did not differ when compared with the common whitethroat (Dunn's *post-hoc* test: *p* = 1.000; Fig. 2); likewise, there was no difference between the common whitethroat and the lesser whitethroat (Dunn's *post-hoc* test: *p* = 0.088; Fig. 2).

The fat fraction of the 25% heaviest and fattest individuals differed among all species. For all species, the region with the highest value was
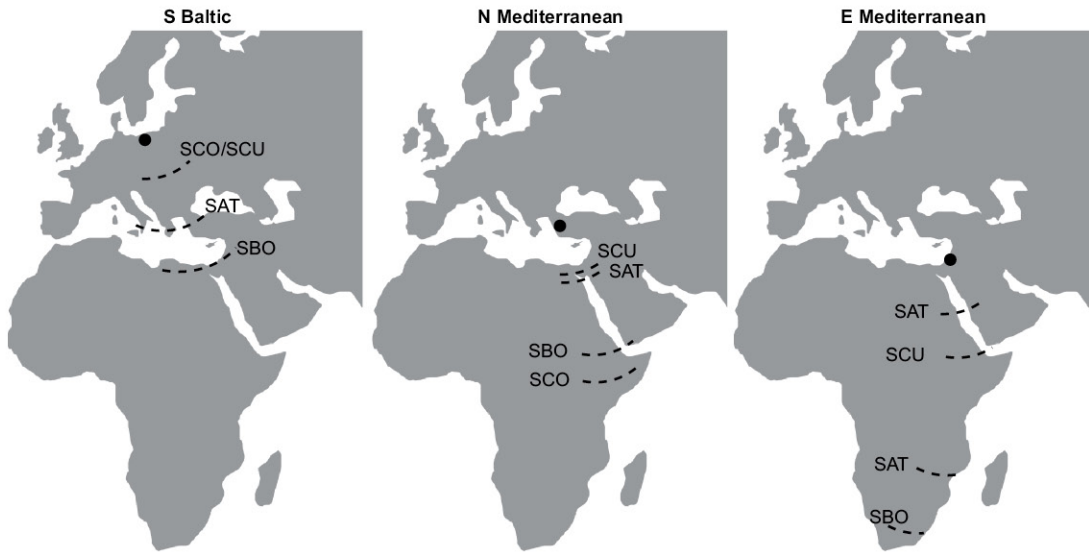
cases; Fig. 1); however the low sample size of birds captured in the latter region should be taken into account. The common whitethroat was the only species showing exceptionally high fat reserves already in the northern Mediterranean region (median 5.5; Fig. 1). These fat reserves were nearly as high as those of garden warblers captured in the eastern Mediterranean region,

Fig. 3. Maximum potential flight range of the analysed species captured in different regions: southern Baltic, northern and eastern Mediterranean calculated according to the Flight ver. 1.24 programme (Pennycuick 2008). Black dots indicate the ringing sites in the analysed regions (cf. Table 1).

the eastern Mediterranean, reaching 50% in the common whitethroat and 49% in the garden warbler (Table 2). As the blackcap captured in the eastern Mediterranean region showed a bimodal distribution of fat scores (Fig. 1), I analysed individuals in two groups: (1) medium scores of fat reserves ($F = 2$–3), and (2) higher scores ($F > 5$). Estimation of the theoretical maximum flight range of individuals with the highest fat reserves indicated differences in migration strategy between analysed species. During autumn migration, when starting from the southern Baltic region, both the common whitethroat and lesser whitethroat are potentially able to reach southern Ukraine (ca. 970 km and 870 km, respectively), the blackcap — the northwestern part of Turkey (almost 2000 km), while the garden warbler is able to reach the Middle East (over 2800 km).

The difference between the latter pair of species seems to be even greater when analysing individuals captured in the northern Mediterranean: blackcaps are theoretically able to reach the coast of the Red Sea (over 1800 km), while garden warblers can cross the Sahara and reach southern Sudan (over 3900 km; Fig. 3). The lesser whitethroat could fly to the southern part of Sinai (over 1600 km; Fig. 3), while fat reserves of common whitethroats captured in this region were exceptionally high as compared with other sites and species (Figs. 1–2). Individuals with the highest fat reserves are potentially able to cross two large barriers, i.e. the Mediterranean Sea and the Sahara Desert, and reach their winter quarters in Tanzania (ca. 5100 km).

In the eastern Mediterranean, the number of captured common whitethroats was very low,

Table 2. Fat fraction of the 25% heaviest and fattest individuals captured in different regions. In the blackcap, two values were given in the eastern Mediterranean region: the former refers to fat scores 2 and 3, the latter to fat scores 5–7.

Region	Blackcap	Garden warbler	Common whitethroat	Lesser whitethroat
S Baltic	23% ($n = 185$)	29% ($n = 240$)	13% ($n = 50$)	13% ($n = 67$)
N Mediterranean	22% ($n = 43$)	36% ($n = 10$)	44% ($n = 10$)	21% ($n = 27$)
E Mediterranean	14% ($n = 218$)/45% ($n = 263$)	49% ($n = 28$)	50% ($n = 6$)	38% ($n = 38$)
NE Africa	–	–	–	30% ($n = 43$)

so the estimation of theoretical maximum flight range was not possible. In the lesser whitethroat, the estimated theoretical flight range is extremely high (ca. 3800 km), which would enable birds to reach Kenya (Fig. 3). However, there are no records on this species wintering so far to the south (Shirihai *et al.* 2001). Individuals of this species captured in Egypt (NE Africa) were potentially able to reach their final winter quarters in Ethiopia and Sudan (ca. 2600 km). The fattest garden warblers captured in the eastern Mediterranean were potentially able to cover the farthest distance (ca. 6700 km) of all species captured in this region and fly as far as its southernmost wintering grounds (Republic of South Africa; Fig. 3). In the blackcap, birds representing two dominating groups of fat scores, were potentially able to reach wintering grounds in Ethiopia ($F = 2–3$, maximum distance over 1000 km) or as far as Malawi, Mozambique, Zambia and Zimbabwe ($F > 5$, maximum distance ca. 5300 km; Fig. 3).

Discussion

The *Sylvia* species form a complex group of warblers inhabiting vast areas of the Palaearctic. Within this group I focused on common and widespread species/populations that breed on the European continent, regularly migrate and cross large geographical barriers such as the Mediterranean Sea and desert regions.

When studying the migration pattern of a widespread species, there are also some limitations of data interpretation, particularly due to different populations taking part in migration, which in most cases we cannot distinguish. This does not apply to the common and lesser whitethroats captured in the southern Baltic region. There is a migratory divide in the former species, as birds originating east of 10°E head towards the southeast, and western populations migrate southwest to winter quarters mainly in western Africa; in the latter species European populations spend winter in eastern Africa (Shirihai *et al.* 2001).

The most complex migration pattern is observed in the blackcap. The southern Baltic is the region where two main flyways of this species cross. Birds captured there represent populations following either the flyway leading towards the Apennine Peninsula from where long-distance individuals continue migration towards central Africa or the southeastern flyway leading migrants towards eastern Africa (Mokwa 2004, Bakken *et al.* 2006, Bønløkke *et al.* 2006, Fransson & Hall-Karlsson 2008).

All garden warblers are exclusively long-distance migrants, but individuals captured in the southern Baltic can represent either nominate subspecies *S. b. borin* wintering in central Africa or *S. b. woodwardi* — wintering in eastern Africa (Bairlein 1991, Hagemeijer & Blair 1997, Shirihai *et al.* 2001). In the eastern Mediterranean region, the majority of garden warblers represent the *woodwardi* subspecies, while birds of the nominate subspecies are uncommon (Shirihai 1996, Morgan & Shirihai 1997).

The eastern Mediterranean is also the region where more eastern subspecies of the common and lesser whitethroats and the blackcap are expected (Shirihai 1996, Morgan & Shirihai 1997). However, the key point of the present study was to determine the pattern of migratory fattening of related long-distance migratory species and possible organization of their way during southward migration across the European continent, the Mediterranean region and preparing for crossing the Sahara Desert. Despite their origin, these migrants share several common features, including their diet at a given site and had to tackle the same problems of preparation for the next stage of migration and overcoming large, geographical barriers. The analyses of the changes in fat stores of individuals captured in a given region enabled the study of this issue.

These four related species migrating to African winter quarters and facing two large barriers: the Mediterranean Sea and the Sahara Desert, differed in their strategy of fat reserves accumulation. It could be hypothesized that these are distance-dependent differences, as the garden warbler migrates the farthest, while the wintering grounds of the rest of the species are located in the Sahel zone and eastern Africa. Consequently, three species, i.e. the blackcap, lesser whitethroat and common whitethroat should show a similar strategy, which was not the case. The common whitethroat accumulated large fat

reserves already on the European continent, i.e. when approaching the Mediterranean Sea and well in advance of the Sahara crossing. Theoretically, these reserves were large enough to enable the birds to cross both these barriers without a need to refuel en route. This finding could also be supported by a low number of common whitethroats captured in the eastern Mediterranean compared to all the other species. It is worth remembering that this warbler is well-adapted to drier habitat of thickets and shrubs (Stoate *et al.* 2001, Wilson & Cresswell 2006, Jenni-Eiermann *et al.* 2011), so potentially it could find fauvourable foraging sites also further south. This finding is contrary to the results of Schaub and Jenni (2000a), who found that common whitethroats did not increase average body mass towards the south and accumulated the energy needed to fly over the Sahara just before it, while Jenni-Eiermann *et al.* (2011) in a study on spring migration of common whitethroats showed that birds accumulated moderate fat reserves and probably stopped and refueled regularly in oases in the Sahara. These differences might indicate different strategies of common whitethroats migrating along the southwestern and southeastern flyways (both studies focused on the western migrating populations), as well as the difference between two migrating seasons. The difference between the western and eastern migrating populations of the same species was reported by Bairlein (1991) and Schaub and Jenni (2000a) in the garden warbler. Easterly migrating birds showed a more pronounced increase in body mass. This was attributed to different conditions en route, i.e. crossing the Mediterranean in the east and less suitable stopover sites in the eastern part of North Africa prior to the Sahara, and a consequent need for larger energy stores. Still when comparing the overall fattening pattern, unlike the common whitethroat, the garden warbler showed a similar strategy migrating either along the western/central or eastern flyway — birds consistently increased their fuel load along the migration route (Bairlein 1991, Schaub & Jenni 2000a; present study). Consequently, the highest median fat load was recorded in individuals captured in the eastern Mediterranean region prior to the desert crossing, which potentially would enable birds to reach their final wintering grounds in South Africa without the need to refuel. This result is in accordance with previous studies showing high fat scores of garden warblers captured after the Sahara crossing reported from southern Uganda by Pearson (1971) or Mauritania by Salewski *et al.* (2002). The blackcap showed high fat reserves in the last stage before the Sahara crossing — in the eastern Mediterranean. The pattern of fat score distribution was bimodal, indicating two groups of birds: one, which was able to reach just the closest edge of the species wintering grounds, i.e. Ethiopia, and the second one able to reach the winter quarters in northern Zambia and Malawi. The lesser whitethroat seems to be a good example of species minimizing the costs of carrying a fuel load (Alerstam & Lindström 1990, Alerstam 2011). On the European continent, its fat reserves were enough for quite short flights to reach the next suitable stop-over site. Then, just before reaching the Mediterranean Sea, these reserves increased, but further south, unlike in the other species, they were constant. Interestingly, in spring this species is rather a time-minimizer according to Zduniak and Yosef (2012).

The relation between migration distance to the wintering grounds and fat reserves of the studied warblers was well pronounced only in the eastern Mediterranean. It is potentially one of the last stop-over regions providing conditions favourable for fat accumulation before the Sahara crossing. In this region, birds were captured in an olive plantation mixed with apple, peach and grenadine orchards. Fruits were most likely highly exploited by all *Sylvia* species as during autumn they compose a significant part of their diet (Glutz von Blotzheim & Bauer 1991, Turrian & Jenni 1991). Frugivory and a mixed diet consisting of both insects and fruits allow birds to gain mass more efficiently and extensively than exclusive insectivory (Bairlein 2002). The importance of the eastern Mediterranean as offering good stop-over and refuelling sites for *Sylvia* warblers could also be supported by the data on autumn migration in the region located to the south, i.e. Israel, where according to radar studies (Bruderer 1994), passage is intensive but migrating birds do not stop-over there (Frumkin *et al.* 1995). The pattern of autumn migration with most birds passing over the region is also

supported by fat deposits and body mass of garden warblers captured in Eilat (Israel), which were almost invariably sufficient for continuing passage and there was no evidence of staging taking place at that site (Morgan & Shirihai 1997). Higher body mass and fat deposits were also recorded in other passerine species captured in this region in autumn (Bairlein 1995, Biebach 1995, Tryjanowski & Yosef 2002). These facts correspond well to results of the present study as it seems that *Sylvia* warblers take advantage of resources available more to the north. However, an exception was the lesser whitethroat, which was captured quite numerously also in Egypt showing fat reserves high enough to reach its wintering grounds. According to the results by Biebach *et al.* (1986), 96% of lesser whitethroats grounded in the Libyan desert in Egypt had fat reserves allowing them to fly over 1500 km, i.e. 200 km more than necessary to reach the Sahel zone.

Results from this study support the concept that it is species-specific ecology rather than phylogenetic relationships that plays a major role in the evolution and form of bird migration (Salewski & Jones 2006). Helbig (2003) also showed for several Palearctic-African genera that phylogenetic relationships were not good predictors of migratory behaviour. The difference in migration strategy in related species was well documented in the reed and sedge warbler (Bibby & Green 1981, Schaub & Jenni 2000b). These researchers related it to differences in availability and predictability of food resources those two species relied on, which consequently helped to explain differences in the organization of migration. The group of *Sylvia* warblers analysed in the present study depend on similar, abundant and predictable food resources. A high fuel deposition rate (FDR) recorded in the garden warbler (Schaub & Jenni 2000b) was related to a mixed diet including a large proportion of fruits exploited by the species during autumn migration (Simons & Bairlein 1990). As the diet of the four analysed species is similar, it seems that other factors could play a crucial role. Although diet, density and predictability of the preferred food directly influence FDRs and the organization of migration (Schaub & Jenni 2000b), fattening rates probably depend also on

the degree of predation risk or resource competition (Moore & Yong 1991) and endogenous factors, like moult, actual body mass (Schaub & Jenni 2000b), and the endogenous time programme of migration (Berthold 1996).

Although there is much evidence that various strategies adopted by migratory species to cross the Sahara are endogenously pre-programmed, at least in first-year birds (Berthold 1996), still they are not fixed, and to some extent flexible within species and individuals (Biebach *et al.* 2000, Schaub & Jenni 2000a, Jenni-Eiermann *et al.* 2011). Results of the present study support this hypothesis, as species-specific and population-specific differences in migration strategy based on migration distance (blackcap) were documented, as well as individual differences when some individuals of the same species were potentially able to cover greater distance than conspecifics (blackcap, common whitethroat). These findings confirm high variation and a large spectrum of migratory behaviour in this group of related species utilizing similar resources when travelling towards their wintering grounds and facing similar ecological conditions.

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