Fuel load and potential flight ranges of passerine birds migrating through the western edge of the Pyrenees

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Abstract. The estimation of fuel load and the potential flight ranges of migrant birds are crucial to understanding the ecological and evolutionary significance of bird migration strategies. The movement of migrant birds between Iberia and the rest of Western Europe is thought to be shaped by the Pyrenees and nearby seas. Because of this area's unique geography, the routes of migrants that move to (autumn migration) or from (spring migration) Iberia tend to pass through the western and eastern edges of the Pyrenees. Fuel-load analyses and the assessment of potential flight ranges from these edges can provide insights about the extent of Iberia's use as a consistent stopover and fuelling area. Using data obtained over a period of six years (2004-2009), we calculated fuel load and potential flight ranges for ten common passerines (pre-Saharan, i.e. that overwinter mainly within the circum-Mediterranean region: Robin Erithacus rubecula, Bluethroat Luscinia svecica, Chiffchaff Phylloscopus collybita, Blackcap Sylvia atricapilla; sub-Saharan, i.e. that overwinter in tropical Africa: Sedge Warbler Acrocephalus schoenobaenus, Reed Warbler Acrocephalus scirpaceus, Melodious Warbler Hippolais polyglotta, Willow Warbler Phylloscopus trochilus, Garden Warbler Sylvia borin, Common Whitethroat Sylvia communis that stopover at Txingudi marshlands, at the western edge of the Pyrenees. The fuel load for the 25% heaviest fraction of caught birds ranged from 10.6% over lean body mass to 25.5% (mean: 18.3%) in spring and from 6.7% to 39.7% (mean: 25.2%) in autumn. Thus, potential flight ranges tended to be longer during autumn than during spring, particularly for the sub-Saharan species. All pre-Saharan species except one (Bluethroat) had sufficient fuel to arrive in southern İberia or northern Africa, and three sub-Saharan species (Sedge Warbler, Garden Warbler, Common Whitethroat) had sufficient fuel to reach the north of the Sahara Desert but not its southern border. The potential flight ranges in spring were rather similar among species (ca. 1000 km from Txingudi).

Key words: body mass, fat and muscle scores, flight ranges, fuel load, Iberia, migration, stopover, Txingudi

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INTRODUCTION

The estimation of fuel load and the potential flight ranges of migrant birds are basic issues to understanding the ecological and evolutionary significance of bird migration strategies (Ellegren & Fransson 1992, Hjort et al. 1996, Izhaki & Maitav 1998, Rubolini et al. 2002). Migrants that rely on flapping flight, such as passerines, must choose between carrying small fuel loads to avoid the costs, both in terms of increasing energy expenditures or predation risk, that may accompany the increased body mass (Kullberg et al. 1996, Lind et al. 1999) or carrying large fuel loads to cover longer distances during migration. Thus, large fuel loads are normally stored only before crossing large, inhospitable ecological barriers with null or very low prospects to refuel (Grandío 1998, Schaub & Jenni 2000, Rubolini et al. 2002, Delingat et al. 2008).

Iberia is a main wintering area for several species from western Europe (e.g., Cramp 1988, 1992, Cramp & Perrins 1994) and this area is one of the last opportunities to refuel before crossing the Sahara Desert for species that overwinter in tropical Africa (Hilgerloh & Wiltschko 2000, Schaub & Jenni 2000). The movement of migrant birds between Iberia and the rest of western Europe is thought to be shaped by the Pyrenees and the nearby seas, i.e., the Mediterranean Sea to the east and the Bay of Biscay to the west (Galarza & Tellería 2003). Because of this particular geography, the routes of migrants that move to (autumn migration) or from (spring migration) Iberia tend to pass through the western and eastern edges of the Pyrenees (Galarza & Tellería 2003). Fuel-load analyses and the assessment of potential flight ranges from these sites can provide insights into the extent to which Iberia is used as a consistent stopover and fuelling area.

In the autumn migration period, long-distance migrants that overwinter in tropical Africa (hereafter, sub-Saharans; pre-Saharans are migrants that overwinter mainly within the circum-Mediterranean region) must gain the large fuel loads that are necessary for crossing the Sahara Desert either in Europe or in northern Africa. The different strategies performed by each species are thought to be caused by species-specific foraging prospects to consistently refuel immediately before the desert (Bibby & Green 1981, Schaub & Jenni 2000). Thus, some species with low expectations of gaining large fuel loads in southern Europe should accumulate as much fuel as possible in northern Europe, while other species with higher prospects of gaining fat in the south could delay a large fuel accumulation until reaching southern Europe or even northern Africa (Schaub & Jenni 2000). However, data on how birds use Iberia to refuel are scarce for both pre- and sub-Saharan migrants. We predict that whether northern Iberia is relevant as a refuelling area, pre-Saharan birds could gain in this region as much fuel as necessary to arrive in their wintering areas within the circum-Mediterranean region, whilst sub-Saharan birds would gain fuel loads as high as to arrive in tropical Africa. As a result, pre-Saharan migrants in autumn should be expected to have lower fuel loads than sub-Saharan migrants. However, species-specific differences are expected for sub-Saharan migrants. Thus, whereas some species such as the Sedge Warbler Acrocephalus schoenobaenus have been reported to accumulate as much fuel as needed to reach the south border of the Sahara far from the circum-Mediterranean region (Bibby & Green 1981, Grandío 1998), others like Reed Warbler Acrocephalus scirpaceus and Garden Warbler Sylvia borin seem to post-pone such a high fuel accumulation up to reaching southern Iberia or northern Africa (Bibby & Green 1981, Bairlein 1991, Schaub & Jenni 2000, Fransson et al. 2008).

In spring, it is important for birds to reach the breeding areas as quick as possible because early arrival increases their chance of finding a mate and good territory (Potti & Montalvo 1991, Spina et al. 1994). The strategies of migrants across Europe during the spring are still unclear since most studies have focused on the autumn migration period, especially studies concerning passerines (Ellegren & Fransson 1992, Pilastro et al. 1998, Schaub & Jenni 2000, 2001, but see Delingat et al. 2006, Fransson et al. 2006). In western Europe, some species, such as Blackcap Sylvia atricapilla have been suggested to accumulate as much fuel as needed at or close to their wintering areas to arrive in their breeding sites without needing to stopover to refuel (Langslow 1976, but see Arizaga & Barba 2009). Such a hypothesis, however, has not ever been contrasted and it is virtually unknown to what extent such a strategy may be general or specific for most passerines. We tested here whether migrants passing through the western edge of the Pyrenees had sufficient fuel to reach their breeding areas in Europe. In addition, due to the lack of relevant geographic barriers and hence the possibility to refuel virtually everywhere, both pre- and sub-Saharan migrants are expected to carry similar loads of fuel.

Using data obtained over a period of six years (2004–2009), we calculated fuel load and potential flight ranges for a selected number of common passerines that stopover at Txingudi marshlands, a Ramsar site (i.e. a wetland declared to be of international importance according to the Ramsar Convention) located in the western edge of the Pyrenees. We hypothesized that, in autumn, sub-Saharan birds should carry higher fuel loads than pre-Saharan ones, whilst in spring both groups should carry similar loads of fuel.

MATERIAL AND METHODS

Data collection

We used data from the most common passerines (six sub-Saharans and four pre-Saharans) captured with mist nets at the Txingudi Ringing Station (Table 1), which operates in the Txingudi marshlands in northern Iberia (Fig. 1). The habitats in this area mainly consisted of reed beds, wet prairies and a forest of alders (*Alnus* spp.) (Arizaga et al. 2007). Txingudi is located between the western Pyrenees and the south-eastern corner of the Bay of Biscay. Because of this area's particular geographic location, a "funnel effect" is caused at

Table 1. Common stopping-over passerines captured at Txingudi during the autumn and spring migrations. Status at Txingudi
(P — passage migrant; B — breeding; W — wintering), the location of main wintering areas (M — Mediterranean region;
A — tropical Africa), sample size (N) and months considered for the study are listed.

Species	Code	Status at	Wintering	Spring	Autumn	Sampling Months
				(11)	(IN)	
Sedge Warbler Acrocephalus schoenobaenus	Acrsch	Р	A	55	602	Apr.–May, Aug.–Sep.
Reed Warbler Acrocephalus scirpaceus	Acrsci	BP	A	117	1193	Apr.–May, Aug.–Sep.
Robin Erithacus rubecula	Erirub	BPW	Μ	158	426	MarApr., SepOct.
Melodious Warbler Hipolais polyglotta	Hippol	BP	А	68	80	Apr.–May, Aug.–Sep.
Bluethroat Luscinia svecica	Lussve	Р	M/A	-	198	Aug.–Sep.
Common Chiffchaff Phylloscopus collybita	Phycol	Р	Μ	187	230	MarApr., SepOct.
Willow Warbler Phylloscopus trochilus	Phytro	Р	А	57	571	Mar.–Apr., Aug.–Sep.
Blackcap Sylvia atricapilla	Sylatr	BP	Μ	167	149	Mar.–Apr., Sep.–Oct.
Garden Warbler Sylvia borin	Sylbor	BP	А	20	53	Apr.–May, Aug.–Sep.
Common Whitethroat Sylvia communis	Sylcom	Р	А	29	58	Apr.–May, Aug.–Sep.

Txingudi because several bird species avoid crossing the sea and the Pyrenees during their migration. Therefore, Txingudi is one of the main "natural windows" to either enter Iberia during the autumn migration period or leave it during the spring migration.

Birds were captured with mist nets (16-mm mesh), ringed, aged (juvenile, i.e. birds of first- calendar year captured with all juvenile feathers; older birds, i.e. birds of first- or more calendar year, but captured after at least their first moult) and measured for body mass (0.1-g accuracy), wing length (0.5-mm accuracy, method III by Svensson 1996), flight muscle (scaled from 0 to 3, as shown in Bairlein 1994) and subcutaneous fat scores (scaled from 0 to 8, Kaiser 1993). We additionally noted if birds were moulting (yes/no) or breeding (i.e. were captured with a brood patch in females and cloacal protuberance in males). Birds with missing records (wing length, body mass, fat and muscle scores not recorded), in moult or that were breeding were excluded from the data set. Juvenile birds (local birds hatched in or near the area) were also excluded. Because our study was focused on the species level, age and sex classes were pooled. In addition, considering age and/or sex categories would diminish the sample size too much is some species (Table 1).

Statistical analyses

After reaching a stopover site, a bird can stay in the area for one day and resume the journey the subsequent day/night, indicating that fuel load at departure does not vary substantially from fuel load at arrival. Alternatively, a bird can stay in the area for a period of time to refuel, causing a substantial increase in fuel load. Therefore, the fuel load of migrants captured at a given stopover



Fig. 1. Left: Atlantic flyway in southwestern Europe (recreated by thick lines) and the location of Txingudi (narrow arrow) between the southeastern Bay of Biscay and the western Pyrenees. Right: Sampling points (black dots) at Txingudi marshlands.

point is close to departure fuel load in the first case but not in the second one. Indeed, an inherent problem with capture data from conventional bird-trapping stations is that departure fuel load is unknown because a given individual could be already present before the first capture event or stay for a prolonged period after the final capture (Schaub et al. 2001). Furthermore, only a few of captured birds were recaptured in the same area and season (Arizaga et al. 2008, Arizaga & Barba 2009). A possible solution for such a problem is assuming that birds from the 25% heaviest fraction of the captures are more likely to be birds just about to depart (Ellegren & Fransson 1992). Accordingly, we considered the birds above the 75th percentile of fat and muscle scores to be those about to depart.

The body mass of a bird normally consists of the sum of the structural mass (mass of live birds with no subcutaneous fat stores and without breast muscles) and fuel load. The fuel load is stored mainly as lipids and, to a lesser extent, proteins (Jenni & Jenni-Eiermann 1998). Therefore, body mass (*m*) is due to structural body mass (here assessed with wing length, WL, Gosler et al. 1998), fat (FS; scaled from 0 to 8; 0 is no subcutaneous fat) and flight muscle scores (MS). Following Salewski et al. (2009), the equation to estimate body mass in relation to structural body mass, fat and flight muscle scores is:

$$m = \beta_0 + \beta_1(WL) + \beta_2(FS) + \beta_3(MS) + \varepsilon.$$

 ε is the residual term with a normal distribution, mean zero and constant variance. For each species, we used a general linear model for body mass with WL as a covariate and FS and MS as factors. Structural body mass was assessed by considering FS and MS = 0. However, in two out of ten species all MS recorded were > 0, and in the rest of the species the mean proportion of birds with MS = 0 was 1.3% (range: 0.3-2.8%). Migrants with a MS = 0 were very rare at Txingudi, and this scarcity forced us to remove these birds from our data set to obtain sufficiently reliable statistics to estimate structural mass. Consequently, we considered FS = 0 and MS = 1to assess structural mass. Thus, we must notice that structural mass could have been overestimated, causing fuel load to be underestimated. Overall, our species did gain a mean of 0.22 g/ unit of MS (from MS = 1 to MS = 2). In an individual of 15 g of lean body mass, this would give a flight no longer than 80 km (see below for calculation).

We used ANOVAs to test whether fuel load differed between periods (autumn/winter) and species with different migration distances (preand sub-Saharans).

Flight ranges were calculated assuming that flying passerines lose mass at a constant rate of 1%/hour of flight (Hussel & Lambert 1980, Kvist et al. 1998). Using Delingat et al. (2008), potential flight ranges, Υ (in km), can be assessed as:

$$Y = 100 \times U \times \ln(1+f)$$

where U = groundspeed, (here considered to be 60 km/h; Salewski et al. 2010); $f = (m-m_0)/m_{0'}$, m = actual body mass, and m_0 = mass without fuel (i.e., with zero fat and flight muscle scores). The SE of potential flight ranges, *Y* is: SE_Y = 100 × U × (SE/(1-f))

The software SPSS 18.0 was used for the statistical analyses.

RESULTS

Generalized linear models that best explained the variation of body mass were those with no interactions among FS, MS and WL (Table 2). The proportion of variance explained by the models ranged from 32% to 74% (Robin and Sedge Warbler, respectively; mean = 51%).

Body mass was positively correlated with WL and varied in relation to FS in all species and to MS in six out of the ten species (Table 3). FS accounted for most of variance (from 16 to 70%,

Table 2. Corrected Akaike values (AICc), R²-values and difference in AICc values (Δ AICc) for the general linear models conducted to explain body mass in relation to wing length (WL), fat (FS) and muscle scores (MS). Models with the lowest AICc values better fit the data and had a difference in AICc > 2, indicating a significant difference in the fit of the models to the data (Burnham & Anderson 1998). (+) represents models in which only the main effects were considered and (×) represents models including all possible interactions. Codes of species — see Table 1.

Species	WL+FS+MS		WL×FS	×MS	
	AICc	R ²	AICc	R ²	ΔAICc
Acrsch	1669.643	0.74	1677.932	0.75	8.289
Acrsci	3839.322	0.47	3857.718	0.48	18.496
Erirub	1738.032	0.32	1752.575	0.32	14.543
Hippol	341.174	0.65	360.446	0.64	19.272
Lussve	574.547	0.42	582.409	0.42	7.862
Phycol	649.360	0.45	662.845	0.45	13.485
Phytro	1433.263	0.50	1435.322	0.52	2.059
Sylatr	1135.875	0.49	1145.421	0.51	9.546
Sylbor	283.504	0.55	317.397	0.51	33.893
Sylcom	288.468	0.46	291.121	0.59	2.653

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Table 3. Effects of wing length (WL), fat (FS) and muscle (MS) scores on body mass. Models did not consider interactions between WL, FS and MS (see for further details in Table 2). Values with asterisk had a significant effect on body mass. Codes of the species — see Table 1.

Species	W	L	FS	6	M	S	Resi	idual
	SS	df	SS	Df	SS	df	SS	df
Acrsch	32.440*	1	1176.897*	8	5.818*	2	469.039	645
Acrsci	116.021*	1	928.334*	7	2.251	2	1411.179	1299
Erirub	71.731*	1	218.913*	6	8.704*	2	645.254	574
Hippol	13.757*	1	122.196*	6	3.933*	2	73.906	138
Lussve	80.882*	1	51.711*	4	0.395	1	193.928	191
Phycol	51.600*	1	43.686*	5	0.561	2	110.296	408
Phytro	94.215*	1	274.787*	6	3.696*	2	347.657	618
Sylatr	42.282*	1	393.678*	6	16.695*	2	626.430	306
Sylbor	21.216*	1	126.814*	6	14.321*	1	150.449	64
Sylcom	7.836*	1	88.486*	6	1.728	2	104.629	77

mean = 38%), followed by WL (from 2 to 25%, mean = 10%) and MS (from less than 1 to 5%; mean = 1%).

Fuel load for the 25% heaviest fraction ranged from 0.106 (i.e, 10.6% over lean body mass) to 0.255 (Robin and Sedge Warbler, respectively; mean = 0.183) in the spring and from 0.067 to 0.397 (Bluethroat and Reed Warbler, respectively; mean = 0.252) in autumn (Table 4). Overall, mean fuel load ranged from 0.15 to 0.20 during the spring (without differences between pre- and sub-Saharans during the spring, but not during the autumn; period: $F_{1,17} = 5.885$, p = 0.029; distance: $F_{1,17} = 7.745$, p= 0.015; period×distance: $F_{1.17} = 5.212$, p = 0.039; data on the Bluethroat were excluded due to the lack of captures in spring; Fig. 2). Fuel load during autumn did not differ from the spring for the pre-Saharans, but a mean fuel load of nearly 0.30 was reported in autumn for the sub-Saharans (Fig. 2).

Potential flight ranges tended to be longer during the autumn than during the spring migration period, particularly for the sub-Saharan migrants (Fig. 3). In the spring, however, flight ranges tended to be similar between the pre- and sub-Saharans (mean = 1000 km). In autumn, all pre-Saharans except the Bluethroat had sufficient fuel to arrive in southern Iberia or northern Africa. Bluethroats had lower fuel loads and, consequently, their flight range was shorter (< 400 km). The sub-Saharans in autumn had sufficient fuel to reach the north of Africa and the Sedge Warbler, Garden Warbler and Common Whitethroat could reach the northern border of the Sahara Desert.

DISCUSSION

Fuel load and thus flight ranges tended to be longer during autumn than during spring,

Table 4. Median (and 25^{th} – 75^{th} percentiles) fat (FS) and muscle (MS) scores and mean (± SE) fuel load (FL) over structural mass (i.e., body mass of a bird with FS = 0 and MS = 1; see methods for further details). Mean fuel load was calculated for the 25% heaviest fraction, which is more likely to be representative of birds about to depart than mean fuel load for the entire population. The p values are from t-tests where the spring and autumn fuel loads were compared. Codes of the species — see Table 1.

Species		Spring			Autumn		p values of t
	FS	MS	FL25%	FS	MS	FL25%	test (for FL)
Acrsch	2.0 (2.0-4.0)	2.0 (2.0–2.0)	0.255 ± 0.014	2.0 (1.0–4.0)	2.0 (1.0–2.0)	0.397 ± 0.012	< 0.001
Acrsci	2.0 (1.0–3.0)	2.0 (1.0–2.0)	0.176 ± 0.037	2.0 (1.0–3.0)	1.0 (1.0–2.0)	0.278 ± 0.007	< 0.001
Erirub	1.0 (0.0–1.0)	2.0 (1.0–2.0)	0.106 ± 0.009	1.0 (0.0–2.0)	1.0 (1.0–2.0)	0.160 ± 0.006	< 0.001
Hippol	2.0 (1.0–2.0)	2.0 (2.0–2.0)	0.141 ± 0.013	1.0 (0.0–2.0)	1.0 (1.0–2.0)	0.254 ± 0.043	0.021
Lussve	-	-	-	1.0 (0.0–1.0)	1.0 (1.0–2.0)	0.067 ± 0.006	-
Phycol	1.0 (1.0–2.0)	2.0 (1.0–2.0)	0.192 ± 0.010	1.0 (0.0–2.0)	1.0 (1.0–2.0)	0.169 ± 0.010	0.101
Phytro	2.0 (1.0–2.0)	1.0 (1.0–2.0)	0.223 ± 0.052	2.0 (1.0–2.0)	1.0 (1.0–2.0)	0.237 ± 0.010	0.704
Sylatr	2.0 (1.0-3.0)	2.0 (1.0–2.0)	0.223 ± 0.014	2.0 (1.0-3.0)	2.0 (1.0-2.0)	0.204 ± 0.008	0.242
Sylbor	1.0 (0.0–3.0)	1.5 (1.0–2.0)	0.144 ± 0.016	3.0 (1.5–4.0)	2.0 (1.0–2.0)	0.389 ± 0.023	< 0.001
Sylcom	2.0 (1.0–3.0)	2.0 (1.0–2.0)	0.187 ± 0.013	3.0 (2.0–3.0)	2.0 (1.0–2.0)	0.362 ± 0.029	< 0.001



Fig. 2. Mean (\pm SE) fuel load for the 25% heaviest fraction of the pre-Saharan (grey bars) and sub-Saharan (white) species during the autumn and spring periods at Txingudi. P values show the significant differences after t-tests. The number of species of each category is shown above bars.

particularly for the sub-Saharan species. All pre-Saharan species except one (Bluethroat) had sufficient fuel to arrive in southern Iberia or northern Africa, and three sub-Saharan species (Sedge Warbler, Garden Warbler, Common Whitethroat) had sufficient fuel to reach the north of the Sahara Desert but not its southern border. The potential flight ranges in spring were rather similar among species (c.a. 1000 km from Txingudi). In four out of the ten studied species, WL and FS, but not MS, had a significant effect on body mass. This result suggests that body mass did not change with increasing MS in these cases and could be partially due to the low variation of MS at Txingudi; most birds were found to have MS = 1 or 2, and a few birds had MS = 0 or 3 (Salewski et al. 2009). The lack of relevant geographic barriers which force birds to migrate for several consecutive nights (Schmaljohann et al. 2007) may be one of the main causes for the relatively low variation in the MS of migrant passerines passing through the western edge of the Pyrenees.

Models considering interactions between factors did not fit the data better than the main-effect models. In agreement with previous studies (Redfern et al. 2004, Salewski et al. 2009), this result supports the hypothesis that body size (assessed with WL), FS and MS are independently associated with body mass.

Mean fuel load during the spring did not substantially vary between the pre- and sub-Saharan species and reached an average value of 0.183 (i.e., 18.3% over structural mass). With this fuel load, migrants could reach a distance of ca. 1000 km from Txingudi, which would be adequate for migrants breeding in France or southern England to directly arrive in their breeding areas but not for migrants breeding in regions further to the



Fig. 3. Potential flight ranges (\pm SE) of a selected number of stopping-over passerines from Txingudi during the spring and autumn migrations (pre-Saharan, grey bars; sub-Saharan, white). Flight ranges have been calculated for the 25% heaviest fraction of each species and period. The same letters cluster species that did not have significant differences. Codes of the species — see Table 1.

north and east (Table 5). Our results support the hypothesis that migrants that stopped-over at Txingudi did not need to accumulate in this region sufficient fuel to arrive in their breeding areas without needing to refuel. In contrast, intermediate stopovers are necessary, but large fuel loads are likely not required to be stored in these sites due to the relative closeness of the breeding quarters and the chance to refuel virtually elsewhere. In this scenario, migrants stopping-over in Txingudi could reach their breeding areas in Britain, Ireland, central-western Europe and even Scandinavia (Wernham et al. 2002, Bonlokke et al. 2006) in a number of consecutive nights of flight interrupted by one-day stopovers where only small fuel loads should be gained (Delingat et al. 2006).

With a mean fuel load of nearly 0.20, the sub-Saharan species passing through the western edge of the Pyrenees had larger fuel loads than when passing through the central Mediterranean without (presumably) having stored fuel in northern Africa (Pilastro & Spina 1997). This difference suggests that the sub-Saharans would have been able to gain fuel after crossing the Sahara Desert either in northern Africa (Rguibi-Idrissi et al. 2003) or southern Iberia.

During autumn, however, fuel load tended to be larger in the sub-Saharans, especially in three species which pass over the northern border of the Sahara Desert (Sedge Warbler, Garden Warbler, Common Whitethroat), suggesting an effect of this barrier in shaping fuel load. According to other studies, a number of sub-Saharan

Table 5. Main breeding quarters of passerines commonly stopping over at Txingudi, as obtained by recovery data. Origin areas: WE — W mainland Europe, that includes mainly migrants from France, Belgium, Holland and Germany; BI — British Islands; SC — Scandinavia. Codes of the species — see Table 1.

Species	Origin	Source
Acrsch	BI, WE, W SC	Arizaga 2010
Acrsci	WE, BI, SC	Arizaga 2010
Erirub		Bueno 1998
Enrup	WE, BI,W SC	Remisiewicz 2002
Hippol	WE	Cantos 1992
Lucovo	W/E especially France	Bueno 1990
Lussve	WE, especially I fance	Arizaga et al. 2006
Phycol	WE, BI	Cantos 1992
Phytro	SC, WE	Cantos 1992
Sylatr	WE, BI	Cantos 1995
Sylbor	WE, SC	Cantos 1992
Sylcom	WE, SC	Cantos 1992

migrants captured at a stopover site in Israel showed higher fuel load in autumn than in spring (Izhaki & Maitav 1998, Yosef & Chernetsov 2004). As in Iberia, the difference between seasons in Israel is that during the autumn migration period migrants must cross a large desert, whilst in spring they must fly over landscapes full of opportunities to refuel. However, none of the sub-Saharan species captured at Txingudi had sufficient fuel load to reach the south margin of the Sahara, which is about 3000 km from Txingudi. Accordingly, they would need to refuel before crossing this desert in either southern Iberia or northern Africa (Rguibi-Idrissi et al. 2003, Idrissi et al. 2004). Three sub-Saharans (Reed Warbler, Willow Warbler, Melodious Warbler) had flight ranges similar (< 1500 km) to two pre-Saharans (Chiffchaff, Blackcap). This result supports the idea that these three sub-Saharan species clearly need to consistently refuel before crossing the Sahara. In this context, southern Iberia or northern Africa should be expected to play a very important role as a refuelling area. This highlights the importance of conserving these critical areas for stop over use by migrants. The identification of these areas should be a priority research goal during the next years since this could be of great importance for the conservation of such species.

The pre-Saharan species carried sufficient fuel to arrive in their wintering areas without needing to stopover to refuel. Such areas could be reached in 2–3 nights of flight (assuming a flight of 6 h and ground speeds of nearly 60 km/h). For these birds, central Iberia could play a secondary role as a refuelling region, which could be relevant only for those individuals that would have been unable to gain a sufficient amount of fuel in areas further north. An exception to this rule was the Bluethroat that had a mean potential flight range below 400 km. More than 75% of Bluethroats that pass through the western edge of Pyrenees belong to the L. s. namnetum subspecies (Arizaga et al. 2006), which is known to overwinter along the coast of Portugal and northwestern Morocco (Zucca & Jiguet 2002). Thus, Bluethroats at Txingudi could reach the northwest of Iberia (Arizaga et al. 2006) but not their chief wintering areas further south. In this scenario, northern Iberia, and particularly the wetlands along the coast, is probably a relevant fuelling area for the species. Concerning Blackcaps, it must be considered that not all Blackcaps passing through Iberia are pre-Saharan, but some continue their route in order to reach tropical Africa (Shirihai et al. 2001).

Our results thus suggest that these Blackcaps would not gain the fuel presumably required to fly over the Sahara up to reaching southern Iberia or northern Africa. Otherwise, the 25% heaviest fraction of Blackcaps should be expected to be more fuel loaded than observed at Txingudi in autumn.

In conclusion, fuel load of migrants passing through the western edge of the Pyrenees may be shaped by the ecological barriers faced en route (Rubolini et al. 2002), such as the Sahara Desert, during the autumn migration period. The lack of differences in fuel load during the spring between the species that overwinter within the circum-Mediterranean region and the species that overwinter in tropical Africa also supports this hypothesis due to the lack of relevant geographic barriers to the north of the western edge of the Pyrenees. However, our data also show that migrants crossing the Sahara Desert did not have in northern Iberia sufficient fuel as to reach the south border of this desert. This is likely to be associated to additional cost for carrying fat load and/or the impossibility to fuel in northern Iberia or even in further north regions all the fuel needed to arrive in tropical Africa.

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STRESZCZENIE

[Zapasy tłuszczowe i potencjalny zasięg przelotu podczas migracji u wróblowych wędrujących przez zachodni kraniec Pirenejów]

Dla zrozumienia ekologicznego i ewolucyjnego znaczenia strategii wędrówkowych ptaków kluczowa jest ocena zasobów tłuszczowych i potencjalnego maksymalnego zasięgu przelotu przy ich wykorzystaniu.

W związku z ukształtowaniem geograficznym szlaki wędrówek ptaków lecących z zachodniej Europy do Afryki prowadzą przez wschodnie lub zachodnie krańce Pirenejów (Fig. 1). Ocena zapasów tłuszczowych i oszacowanie jak daleko mogą przelecieć ptaki przy ich wykorzystaniu pozwala na określenie znaczenia półwyspu Iberyjskiego jako miejsca przystankowego, w którym zachodzi odbudowa zapasów przed dalszą wędrówką.

Ptaki łapane były na terenach podmokłych Txingudi (Fig. 1), chronionych w ramach konwencji Ramsar. Określano ich masę ciała, długość skrzydła, otłuszczenie (w skali 0–8) oraz opisywano wielkość mięśni służących do lotu (w skali 0–3). Do analiz wykorzystano dane zbierane w latach 2004–2009, dla ptaków złapanych w okresie wędrówki jesiennej i wiosennej (Tab. 1). Wyróżniono dwie grupy gatunków — zimujące w północnej Afryce i okolicach śródziemnomorskich (rudzik, podróżniczek, pierwiosnek, kapturka) oraz te lecące do tropikalnej Afryki (potrzos, trzcinniczek, zaganiacz, piecuszek, gajówka, cierniówka).

W przypadku ptaków łapanych na miejscu przystankowym trudno jest jednoznacznie określić ich zapasy tłuszczowe, gdyż możliwe są dwie skrajne sytuacje – zarówno, że dany ptak został złapany tuż przed dalszą wędrówką (z maksymalnymi zapasami dla gatunku i jego strategii wędrówkowej), albo tuż przed dłuższym pobytem w danym miejscu, mającym na celu ich odbudowę (a więc zapasami znacznie mniejszymi niż maksymalne). Dlatego autorzy uznali, że 25% najcięższych ze złapanych ptaków, jak również te o wartościach stanowiących powyżej 75% w skalach otłuszczenia i wielkości mięśni służących do lotu, to osobniki tuż przed odlotem i dla tej grupy ptaków przeprowadzono dalsze analizy. Określono wpływ otłuszczenia, wielkości mięśni piersiowych oraz wielkości ciała (określanej przez długość skrzydła) ma masę ciała (Tab. 2, 3) co pozwoliło także na określenie zapasów tłuszczowych (Tab. 4). Na tej podstawie wyliczano potencjalny zasięg przelotu bez konieczności odbudowy zapasów.

Podczas wędrówki wiosennej zapasy tłuszczowe stanowiły od 10,6 do 25,5% ponad normalną masę ptaka, (średnio 18,3%), oraz od 6,7 do 39,7% podczas wędrówki jesiennej (średnio 25,2%). Gatunki zimujące w tropikalnej Afryce w porównaniu do tych zimujących w północnej Afryce i okolicach śródziemnomorskich miały wyższe zapasy tłuszczowe podczas wędrówki jesiennej, zaś wiosną nie stwierdzono podobnych różnic (Fig. 2). Wydaje się także, że potencjalny zasięg przelotu z wykorzystaniem zapasów tłuszczowych jest dłuższy podczas wędrówki jesiennej niż wiosennej.

Zapasy tłuszczowe stwierdzane u gatunków zimujących w Afryce Północnej, pozwalają na przelot do południowych części Półwyspu Iberyjskiego lub północnej Afryki, bez konieczności ich uzupełniania. Tylko u podróżniczka te zapasy są znacznie mniejsze (Fig. 3). Gatunki zimujące w tropikalnej Afryce korzystając z zapasów zgromadzonych na terenach Txingudi są w stanie przelecieć maksymalnie do północnych granic Sahary. Przelot przez Saharę wymaga więc uzupełnienia zapasów.

Dla wszystkich badanych gatunków, potencjalny zasięg przelotu podczas wędrówki wiosennej jest podobny i wynosi ok. 1000 km od punktu przystankowego na zachodnich krańcach Pirenejów, na którym zbierano dane. Na tej podstawie można oceniać, że, ptaki te są w stanie dolecieć do lęgowisk we Francji czy południowej Anglii, jednak ptaki mające lęgowiska dalej na północ czy wschód wymagają kolejnych miejsc przystankowych (Tab. 5, Fig. 3).