

ORIGINAL PAPER

MIGRATION OF THE SKYLARK *ALAUDA ARVENSIS* ALONG THE SOUTHERN FRENCH ATLANTIC COAST

R. Hargues^{1,2}, P. Girardot¹, F. Ibañez¹, P. Mourguiart^{3,4*} & J. Recarte¹

¹ FDC40 - Fédération Départementale des Chasseurs des Landes, 111 chemin de l'Herté, BP 10, F-40465 Pontonx-sur-l'Adour.

Tel : (33) 5 58 90 18 69. Fax: (33) 5 58 74 12 00. E-mail: contact@fedechasseurslandes.asso.fr

² FNC - Fédération Nationale des Chasseurs, 13 rue du Général Leclerc, F-92130 Issy-les-Moulineaux. Tel : (33) 1 41 09 65 10. Fax: (33) 1 41 09 65 20. E-mail: rhargues@chasseurde france.com

³ IRD - Université de Pau et des Pays de l'Adour, UFR Sciences et Techniques, allée du Parc Montaury, F-64600 Anglet.

Tel : (33) 5 59 57 44 43. Fax: (33) 5 59 57 44 02.

⁴ Present address: IRD - 213 rue La Fayette, F-75480 Paris cedex 10.

E-mail: philippe.mourguiart@neuf.fr

* Corresponding author.

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Abstract

Mist-nettings of Eurasian skylarks (*Alauda arvensis*) were conducted throughout the day near the coastline in south-western France during the fall migratory period. The main objective of this work was to document some aspects of body condition (mass and fat stores) in skylarks. Between 1997 and 2004, a total of 8903 birds were captured in October-November. The median capture dates of fall migrations for females and males were October 24 and October 26, respectively. About 58.4% and 34.0% of birds were females and males respectively, the remaining 7.6% corresponding to unsexed birds. Skylarks arrived to our study site with low fat stores, 42% of the individuals showing no visible fat deposits. Rates of mass changes were found to be positively related to the time of day: individuals captured during the night before 07:00 were 3-4% heavier than individuals captured during daylight between 07:00 and 20:00. On the daytime, the average rate of body mass gain was about 5% for both sexes, suggesting that migratory birds were not only able to gain energy for their regular metabolism, but they were also able to store fat for migration. According to allometric equations to estimate the energetic cost of flight, flight ranges for the majority of birds were estimated to be less than 180 - 240 km for females and lower than 160 - 220 for males. As migratory stopover sites are used for refuelling by many migrant land birds, our data suggest that most of the skylarks might exhibit a « feed-by-day, fly-by night » strategy in our region, highlighting the need for preserving stopover sites, such as those encountered in south-western France, for successful migration. Considering that many migrant birds such as skylarks feed heavily on seeds, changes in agricultural practices might affect survival capabilities of skylarks during their fall migration and in winter.

Introduction

Numerous birds fly long distances to achieve their annual migrations from breeding sites to wintering areas. Migration is the most expensive activity per unit of time for birds [1,2]. Among body fuel reserves, fat is the most advantageous energy resource [e.g. 3,4]. However, for many passerine birds, the energy required to achieve long-

distance migrations usually exceeds the amount these individuals are able to build up. Consequently, the amount of fat stored varies greatly according to migratory strategy. Odum *et al.* [5] have proposed a classification based on the strategy adopted by migrant birds: (1) short-range migrants that become moderately obese but begin migration before peak deposition; (2) short-range migrants that begin migration after peak deposition, and (3) long-range migrants that become extremely obese (fat up to 50 per cent of body weight) just prior to long flights. Therefore, migrants from categories 1 and 2 undertake a series of flights interrupted by staging stops in order to replenish their energy stores for the next stage [6,7].

The skylark *Alauda arvensis* is one of the most abundant birds in Europe with over 40 million estimated breeding pairs, although it is presently declining [8,9]. This species breeds extensively across most of Europe and winters in south-western Europe and Northern Africa [10-12]. Skylarks are considered as short-range migrants even though some birds fly over 3000 km from Scandinavia to Spain or Morocco. Owing to its widespread distribution, the causes of its population decline are poorly understood because population trends are not extensively known [13,14]. In fact, fall migration, which is a critical period for migrant birds [15], has been particularly poorly investigated. The present study examined fat-deposition strategies adopted by this species at a stopover location ideally situated on its western European migratory route. Our purposes are threefold: (1) To provide basic information on migration phenology of skylarks during fall migration along the southern French Atlantic coast, (2) To investigate geographic patterns of fat storage in migrants, and, (3) To give an insight into the stopover ecology of this bird species.

Methods

Field data were collected in fall from 1997 to 2004 on sites along the French Bay of Biscay between 45° 15' and 43° 45' N and between 0° 58' and 1° 19' W. This region is ideally situated to receive a large number of skylarks [16]. Mist netting was conducted on 15 to 25 days in October-November. We divided the day into 22 units, each corresponding to an hour between 22:00 and 20:00. Between 20:00 and 22:00 nets were not running. The proportion of birds caught in each of these units was then calculated.

The birds were captured using standard nylon mist nests (2.5 m height x 12 m long), with a mesh size of 20 - 27 mm. During daylight, three horizontal mist nets were opened at 7:00 and functioned until 20:00. At night, from 22:00 to 7:00, three vertical mist nets were used and were checked every 20 minutes. To ensure a maximum capture success, nets were placed at the top of dunes near forest edges and a tape recorder with specific sounds was used to attract birds [17].

Each skylark was banded with a numbered aluminium leg band. Wing length measured from the ulna to the longest tip (± 1 mm) and body weight (± 1 g) were recorded. Wing length, which is bi-modally distributed, was used for sex determination [18]. To confirm or refute the possibility of hourly fluctuations in skylark body mass, differences in body mass changes were compared over daytime for the two sexes separately.

The amount of subcutaneous fat deposits in the interclavicular fossa was visually quantified according to a four-point scale (adiposity index classes) [19]: 1 = nearly no fat observed; 2. thin layer of fat on furcula; 3. fat filling the furcula but not mounded; 4. fat greatly bulging in furcula and covering part of the abdomen. Estimates of body fat mass change were calculated by subtracting the average weight of birds belonging to fat score of group 1 from the average weight of birds with fat scores 2, 3 and 4.

Considering that fat provides nearly all of the fuel for extended migratory flights [3, 20], the energy available for flight can be calculated if the total available body fat is known. Since metabolic rate per gram of fat-free weight appears to be similar among passerines of 10 - 40 g [5], the flight range of a bird with a given amount of fat can be estimated. Several authors [21,22] agree that, during stopover all of the mass gain results from fat storage. Therefore, this increase in body mass (g) was first converted into energy equivalents by considering the energy value of fat to be 39.8 kJ g⁻¹ [23]. Secondly, different empirical data were used to estimate flight metabolism in skylarks [22-27]. The most basic estimate was given by Nisbet *et al.* [24] with a consumption of fat by passerines at a rate of about 1% of their body mass per hour during migratory flight. Another approach uses the basal metabolic rate (BMR) of birds: the cost of flight would be a simple multiple of BMR, varying between 6 and 12 times the BMR for passerines [e.g. 19,20,24]. Unfortunately, we found only 2 references regarding the metabolism of skylarks [28,29]. It was estimated at 0.722 W for a 31.7 g bird [28] and 0.562 W for a 46.1 g bird [29]. This estimate was then converted into the amount of fat built down by dividing the value by the caloric density of fat. There are also indirect methods to measure the energetic cost of flight, including body mass loss. Different regressions have been proposed from distinct measurements on birds, including body mass, wing length or wing area [26,27]. The different approaches were tested.

Finally, flight ranges, which are particularly valuable for generating migratory strategy predictions [7], were calculated assuming a mean speed for skylarks in migration of about 30 to 40 km h⁻¹ [30].

All statistical analyses were performed with Minitab (Minitab for Windows v. 12.2). Data were analyzed by the Anderson-Darling Test to determine distribution and are expressed as mean \pm SD. Comparisons between groups were performed by a one way-ANOVA, and an unpaired t-test was used to detect significant differences ($p < 0.05$) among groups.

Results

Temporal variation

During the fall migration of our 8-year study (1997 - 2004), we trapped and ringed 8903 skylarks: 81.8% in Mimizan (44° 12' N / 1° 13' W), 8% in Tocane (45° 15' N / 0° 29' W), 6% in Soustons (43° 45' N / 1° 19' W), 4% in Lit-et-Mixe (44° 02' N / 1° 15' W), and 0.2% in Ychoux (44° 13' N / 0° 58' W). None of the 8903 individuals was recaptured. Sex was determined in 8861 individuals: 58.4% and 34.0% were identified as females and males, respectively; 7.6% were undetermined. Migratory stopovers occurred in autumn, with the first and last captures occurring in October

the 13th and November the 8th, respectively (Fig. 1). The median Julian capture dates of fall migrations for females and males correspond to day 298 (October 24) and day 300 (October 26), respectively.

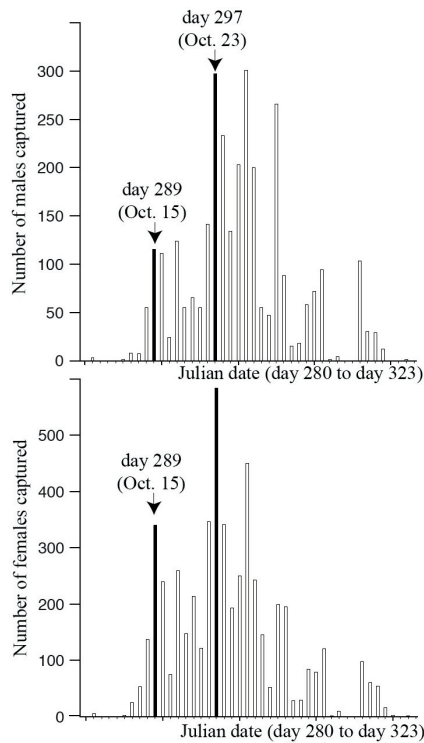


Fig. 1. Autumn migration phenology based on the number of male and female skylarks that were caught, ringed and sexed along the southern French Atlantic coast between 1997 and 2004.

The daily capture rate peaked during the nocturnal hours. About 50% of birds were captured between 00:00 and 06:59, representing a mean of about 567 birds per hour representing a two-fold increase of the capture rate (261 birds per hour) obtained during the 7:00 to 23:59 period (Fig. 2). Sample sizes of skylarks captured before 23:00 and between 18:00 and 19:59 represented less than 50% of the daily capture rate for both sexes.

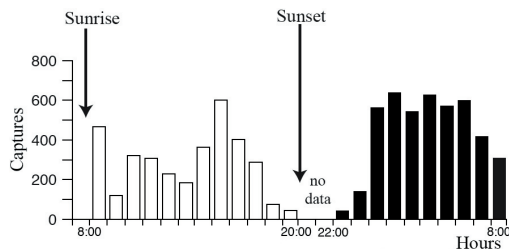


Fig. 2. Temporal distribution of daily captures of skylarks during fall migration along the southern French Atlantic coast.

Wing length

As shown in Fig. 3, a clear bi-modality in wing length due to sexual dimorphism was detected in our data set. Mean wing lengths for females and males were 105.0 ± 2.09 and 115.6 ± 2.41 mm, respectively (Table 1). Individuals presenting intermediate values (corresponding to 7.6% of the birds) were considered as unsexed birds.

Table 1. Sample size (n), Mean and 95% Confidence Interval, Range and Standard Deviation of skylarks wing length and weights according to fat classes in south-western France, autumns 1997-2004.

		n	Mean \pm 95% CI	range	S.D.
Females	Wing length (mm)	5197	105 ± 0.06	[96 - 114]	2.09
	Total weight (g)	5191	32.7 ± 0.08	[21 - 45]	2.82
	Weight class				
	1	2234	31.3 ± 0.1	[21 - 42]	2.39
	2	2051	33.1 ± 0.1	[26 - 43]	2.32
Unsexed	3	760	35.2 ± 0.17	[27 - 43]	2.44
	4	133	36.7 ± 0.53	[30 - 45]	3.10
	Wing length (mm)	672	110.6 ± 0.11	[103 - 114]	1.43
	Total weight (g)	671	34.2 ± 0.18	[25 - 45]	2.39
	Weight class				
Males	1	322	33.4 ± 0.24	[25 - 38]	2.24
	2	254	34.4 ± 0.23	[28 - 41]	1.84
	3	83	36.2 ± 0.55	[28 - 45]	2.54
	4	9	38.7 ± 1.71	[35 - 44]	2.62
	Wing length (mm)	3024	115.6 ± 0.09	[106 - 124]	2.41
Males	Total weight (g)	3021	38.5 ± 0.1	[26 - 49]	2.91
	Weight class				
	1	1196	37 ± 0.14	[26 - 44]	2.48
	2	1310	38.9 ± 0.13	[30 - 47]	2.44
	3	428	40.9 ± 0.24	[35 - 49]	2.57
	4	80	42.3 ± 0.67	[35 - 49]	3.08

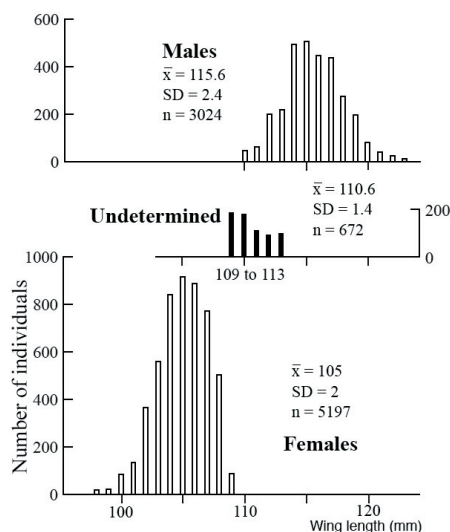


Fig. 3. Frequency distributions of wing lengths among skylarks caught during fall migration between 1997 and 2004 along the southern French Atlantic coast. Data were grouped by sex.

Weights

The mean female and male mass was 32.7 ± 2.82 and 38.5 ± 2.91 g respectively (Table 1). Fall male migrants were significantly heavier than females ($p < 0.0001$). Both female ($F_{21,4700} = 17.07$, $P < 0.001$) and male ($F_{21,2542} = 8.94$, $P < 0.001$) body mass changed significantly among hours and body mass peaked between 22:00 and 07:00 for both sexes (Fig. 4). Skylarks captured during the night before 07:00 were 3.5 % heavier (unpaired t-test, $p < 0.001$) (33.34 g and 39.11 g, in females and males, respectively) than individuals captured during daylight between 07:00 and 20:00 (32.14 g and 37.85 g in females and males, respectively).

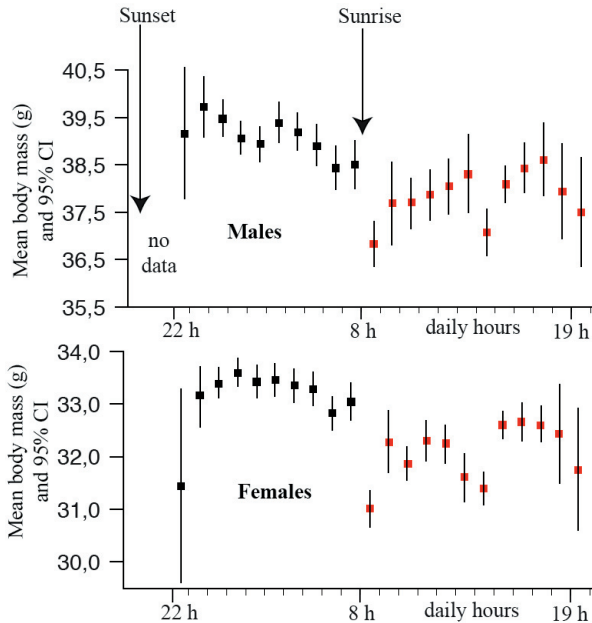


Fig. 4. Changes in mean body mass for male and female skylarks during fall migration (1997-2004 pooled) along the southern French Atlantic coast.

Furthermore, there is a clear increase of body mass (average 1.65 and 1.77 g for females and males respectively; $p < 0.01$) in the afternoon, with a secondary peak between 16:00 and 18:00 (Fig. 4).

Fat scores

More than eighty percent (80%) of the captured skylarks had subcutaneous fat scores belonging to classes 1 and 2 and only about 2% had a fat score corresponding to class 4 (Fig. 5 and 6). Body mass differed significantly ($p < 0.001$) among fat classes (Table 1).

The average body mass of females and males with fat score 1 was 31.3 g (95% CI 31.2 - 31.4) and 37.0 g (95% CI 36.86 - 37.14), respectively. These values can be considered as an estimate of the mean fat-free mass of female and male skylarks.

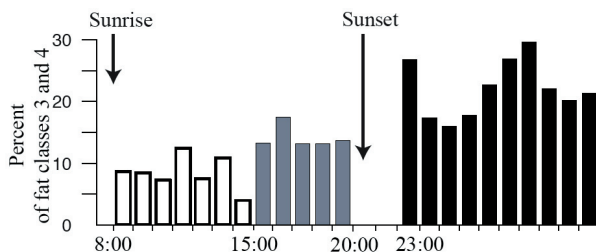


Fig. 5. Hourly distributions of fat scores among skylarks caught during fall migration between 1997 and 2004 along the southern French Atlantic coast.

Considering the body mass values referring to fat class 1, mean body fat content was estimated to be 1.8 g (5.8% fat-free body-mass) for fat class 2, 3.9 g (12.5% fat-free body-mass) for fat class 3 and 5.4 g (17.3% fat-free body-mass) for fat class 4, respectively. Average (\pm SD) body mass of male skylarks in fat classes 2, 3 and 4 were 38.9 ± 2.44 g ($n = 1310$), 40.9 ± 2.57 g ($n = 428$) and 42.3 ± 3.08 g ($n = 80$), respectively (Table 1). This would correspond to a mean body fat content of 1.9 g (5.1% fat-free body-mass), 3.9 g (10.5% fat-free body-mass) and 5.3 g (14.3% fat-free body-mass), respectively. The rate of mass gain (in grams) did not differ ($p > 0.1$) between males and females.

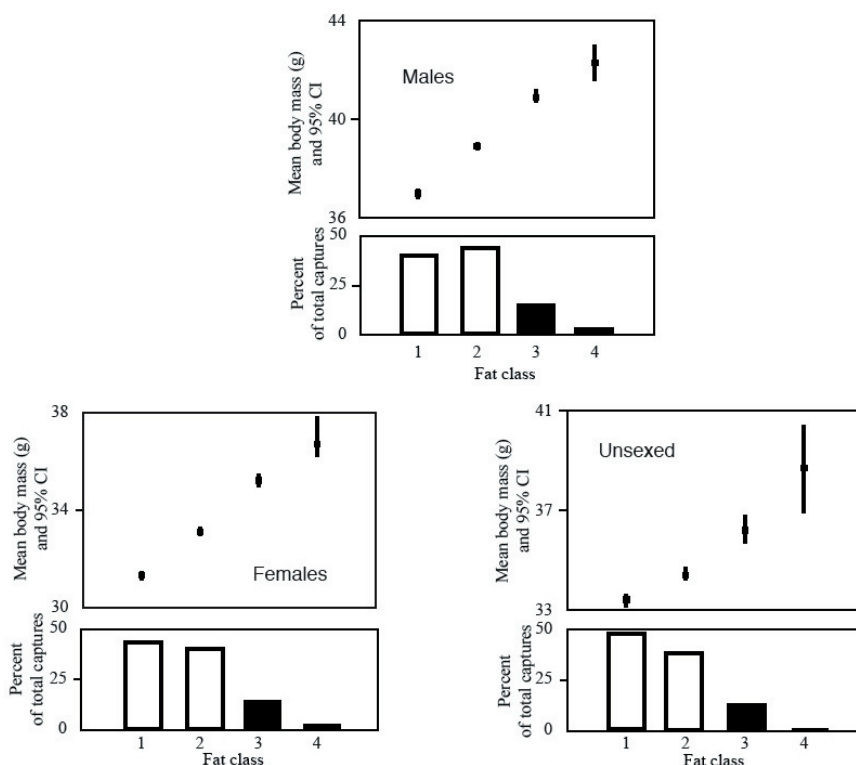


Fig. 6. Fat score classes distribution and its relationship with mean body mass of skylarks during fall migration along the southern French Atlantic coast.

Potential flight range

Differences between the flight range estimates obtained from different methods vary considerably, more than twofold (Table 2). The most realistic flight ranges were about 160 to 240 km for birds in fat class 2, 330 - 490 km for birds in fat class 3, and 415 - 650 km for individuals in class 4 (Table 2).

Discussion

The present data on wild ranging skylarks obtained during fall migration in the south-western part of France sheds light on the ecological significance of stopover habitats for the refuelling strategy used by this passerine species. To our knowledge, such results on biometrics and sex structure have, so far, never been addressed for migratory skylark populations at least for those staging in Western Europe.

Based on records from Belgium, Pirard [31] suggested that the duration of the skylark's autumnal migration lasted from October the 8th to November the 8th for the 1989 - 2002 period, peaking on October the 18th. Our data confirm that the duration of autumnal migration passage lasted about one month only, peaking on October the 24th and October 26th for females and males respectively, that is about one week later than in Belgium, located about 1000 km to the North of our study area.

In the present ranges for skylark wing lengths (96 to 124 mm) are close to those reported in a previous study [11]. The mean length for females is similar (around 105 mm) to that recorded elsewhere [32,33] and it differed by less than 1,5% for males (114.1 or 114.3 mm vs 115.6 mm in our study). The sex ratio determined in the present study, with a predominance of females, is close to that recorded along the southern Tyrrhenian coastline [34] but it differs strongly from those estimated for more northern populations, where a predominance of males (> 54%) is noted [31].

The body mass ranges recorded in our study are similar to those reported for other skylark populations for which females weighted between 26 and 44 g and males weighted between 26 and 49 g [35]. According to the general trend observed among other skylark populations, males were on average 18% heavier than females (38.5 g against 32.7 g). Fluctuations in body mass on an hourly basis have been commonly observed in nature. This phenomenon is partly due to factors such as food intake, body fuel mobilisation linked to flights, meteorological conditions (ambient temperatures), and fat storage [e.g. 36]. In general, birds with large fat stores are able to fly over longer distances than birds with smaller adiposity [6,37]. More than 40 percent of the captured birds had very low fat stores, and only 17 percent had moderate or large fat stores (fat class ≥ 3). This suggests that skylarks migrating or staging during stopover throughout our sites do not carry large fat loads, and therefore may have to restore fat periodically en route. Stopover is an important decision for many land-birds during their migration. First, migratory stopovers are used to replenish fat reserves and to avoid flying at certain times of the day or night or during unfavourable meteorological conditions [e.g. 2,38]. Generally, many passerines increase fat stores during daylight hours at stopover sites [39-41]. Lindström [42] found that maximum daily fat gains were about 4 - 5 percent fat free body mass for small passerines. On the other hand, several authors [e.g. 41] suggested that a gain of 4.5 percent body mass per day is required to offset overnight losses. If birds are mainly depositing fat, diurnal gains should exceed overnight losses, resulting

Table 2. Comparison of the different approaches used in our study for estimating flight times and flight ranges in skylarks during fall migration assuming 1. an energy equivalent of 39.8 kJ g⁻¹ of fat, and, 2. a flight speed of 30 to 40 km h⁻¹. M represents the flight metabolism in kJ h⁻¹, W the body mass in g, L the wing length in cm, and BMR the basal metabolic rate.

Sex	Fat score	n	Weight (g)	Fat weight (g)	Fat energy (kJ/g)	M = 1% W	M = 12 BMR	M = 1.78 x W ^{0.64}	M = 0.91 x W ^{0.74}	M = 0.679 x W ^{0.88}	M = 2.23 x W ^{1.007} x L ^{-1.381}	M = 0.36 x W
Females	1	2234	31.3	0.0	0.00	-	-	-	-	-	-	-
						[-]	[-]	[-]	[-]	[-]	[-]	[-]
	2	2051	33.1	1.8	71.64	5h40 [170 - 270]	2h20 [70 - 90]	4h20 [130 - 170]	6h00 [180 - 240]	6h00 [180 - 240]	6h00 [180 - 240]	6h00 [180 - 240]
	3	760	35.2	3.9	155.22	12h30 [375 - 500]	5h00 [150 - 200]	9h20 [270 - 355]	12h10 [365 - 490]	12h30 [375 - 500]	12h00 [360 - 480]	12h10 [365 - 490]
Males	4	133	36.7	5.4	214.92	17h20 [520 - 695]	7h00 [200 - 275]	12h45 [360 - 480]	16h30 [495 - 660]	16h40 [500 - 670]	15h30 [470 - 625]	16h15 [490 - 650]
	1	1196	37.0	0.0	0.00	-	-	-	-	-	-	-
						[-]	[-]	[-]	[-]	[-]	[-]	[-]
	2	1310	38.9	1.9	75.62	5h00 [150 - 200]	3h10 [90 - 130]	4h00 [120 - 165]	5h30 [160 - 215]	6h00 [180 - 240]	5h45 [175 - 230]	5h30 [160 - 215]
	3	428	40.9	3.9	155.22	10h30 [315 - 420]	6h30 [190 - 260]	8h20 [245 - 325]	11h00 [330 - 440]	11h00 [330 - 440]	11h00 [330 - 440]	10h30 [315 - 420]
	4	80	42.3	5.3	210.94	14h20 [430 - 575]	8h50 [260 - 350]	11h20 [325 - 430]	14h30 [435 - 580]	14h30 [435 - 580]	14h20 [430 - 575]	13h50 [415 - 555]

in a net positive daily (24 hour) gain [41]. If body fuel reserves cannot be replenished during stopover to the level needed to compensate for the cost of delayed migration produced by stopping, then stopover sites could potentially act as “sink” habitats that reduce fitness of migrant individuals. In our study, considering that migratory flight is primarily fuelled by lipids [43,44], the average rate of diurnal body mass gain of about 5% for both females and males (Fig. 4) suggests that the daily energetic gain would at least compensate for the overnight energetic expenditure. Furthermore, none of the 8903 individuals was recaptured. These results indicate that one stopover day on our site would be sufficient for the birds to allow them to perform a sustained night’s flight. Winker *et al.* [45] suggested that Swainson’s thrushes *Catharus ustulatus* adopt a so-called “feed-by-day, fly-by night” migratory strategy. By offering stopover sites that allow a rapid body store replenishment, we can confidently advance that our region may be especially valuable for migrant passerines that need to stop en route to feed and accumulate fat (energetic reserves). During migration but also during winter, the skylark diet is based mainly on Gramineae leaves and seeds, the latter being the most energetic in terms of energy storage [e.g. 46]. Changes in European agricultural policy could have dramatic effects on bird populations depending on seed production. There is therefore a high risk that declines in breeding and wintering European skylark populations, through energetic bottlenecks, could result from agricultural intensification [47,48]. Other future probable changes in agricultural practices such as mulching or non-inversion tillage might have severe incidences on migrant skylark populations by indirect effects on seed bank accessibility [49]. The same could occur with changes in cultivated plants as skylarks and many other migrant land birds prefer seed-rich habitats such as stubble fields [50].

Finally, similar studies on fat content changes should be undertaken in other regions such as the northern part of France. These studies should assess the relative importance of different stopover sites along the migratory routes in terms of habitat quality and food supply. Also, a further analysis of the body composition of carcasses between different stopover sites will help to improve management plans for the conservation of migrant skylarks.

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