FUEL LOAD AND FLIGHT RANGE ESTIMATION OF MIGRATING PASSERINES IN THE WESTERN PART OF THE CARPATHIAN BASIN DURING THE AUTUMN MIGRATION

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Estimating fuel load and potential flight ranges of migrant passerines are basic issues in understanding bird migration strategies. Thirteen sub-Saharan and three pre-Saharan migrant passerine species were analysed in this study. The birds were captured at the Tömörd Bird Ringing Station in the western part of the Carpathian Basin. A general linear model with body mass as the dependent variable and fat score, muscle score and wing length as independent variables were used to estimate lean body mass (body mass without fuel deposits) and fuel load. In ten of the species studied, models considering interactions between factors fit the data better than the main-effect models. Body mass was positively correlated with the fat score in all species, with muscle score in ten species and wing length in 14 species. During autumn, fuel load tended to be larger in the sub-Saharan migrants, especially in four species which pass over the Mediterranean Sea, Common Nightingale (*Luscinia megarhynchos*), Icterine Warbler (*Hippolais icterina*), Garden Warbler (*Sylvia borin*) and Barred Warbler (*Curruca nisoria*). Nine sub-Saharan migrants, Marsh Warbler (*Acrocephalus palustris*), Sedge Warbler (*A. schoenobaenus*), Eurasian Reed Warbler (*A. scirpaceus*), European Pied Flycatcher (*Ficedula hypoleuca*), Spotted Flycatcher (*Muscicapa striata*), Wood Warbler (*Phylloscopus sibilatrix*), Willow Warbler (*Ph. trochilus*), Common Whitethroat (*C. communis*) and Lesser Whitethroat (*C. curruca*) had estimated flight ranges similar (<1300 km) to two pre-Saharans, European Robin (*Erithacus rubecula*) and Eurasian Blackap (*S. atricapilla*). The three short-distance migrants, including the Common Chiffchaff (*Ph. collybita*) with the shortest distance, had sufficient fuel load to reach their southern European wintering sites without needing to refuel at stopover sites.

Keywords: passerine, fuel load, flight range, western Hungary.

INTRODUCTION

Estimating fuel load and the potential flight ranges of migrating passerines are crucial to understanding the ecological and evolutionary aspects of their migration strategies (Ellegren & Fransson 1992, Hjort *et al*. 1996, Rubolini *et al*. 2002). Small passerine migrants are under-represented in long-term recapture studies, despite being ringed in large numbers (Spina *et al*. 2022).

For example, only 125 of the 36,556 European Robins ringed in Hungary were recovered abroad (0.04%) between 1951 and 2022 (MME 2022). In the absence of recaptures and the high cost of geolocators, other methods are needed to identify migration routes and stopover or wintering sites. The most cost-effective method is to estimate flight ranges and fuel loads based on biometric parameters such as wing length, body mass and body fat (Csörgő & Halmos 2002, Delingat *et al*. 2008, Arizaga *et al*. 2013, Sander *et al*. 2017, Bozó *et al*. 2019). Body fat is the primary and best metabolic reserve for migratory birds (McWilliams *et al*. 2004): maintaining adipose tissue requires much less energy than maintaining skeletal muscle and liver tissue (Scott & Evens 1992). Birds can obtain 95% of their total energy expenditure during the flight from fat (Jenni & Jenni-Eiermann 1998). Accordingly, the amount of fat stored determines the distances birds can cover in a single flight (Csörgő *et al*. 2009).

Most migrants accumulate large fat reserves before crossing the unfavourable ecogeographical barriers with no or very low prospects of refuelling (Schaub & Jenni 2000a, b, Ottosson *et al*. 2002, Rubolini *et al*. 2002, Fransson *et al*. 2008). Migratory passerines must choose between carrying small fuel loads to avoid the increased energy expenditure or predation risk (Kullberg *et al*. 1996, Lind *et al*. 1999) and carrying large fuel loads to cover longer distances. According to several studies, pre-Saharan migrants, i.e., species that overwinter mainly within the circum-Mediterranean region, should be expected to have lower fuel loads in autumn than sub-Saharan migrants, i.e., species that overwinter in tropical Africa (Alerstam 1990, Schaub & Jenni 2000b, Gyurácz *et al*. 2017b, 2019). However, species-specific differences are expected for both migrant strategies (Arizaga *et al*. 2011). Thus, whereas some species, such as the Sedge Warbler have been reported to accumulate as much fuel as it needed to reach northern Africa from the Carpathian Basin, others, like the Reed Warbler seem to postpone such a high fuel accumulation until reaching southern Europe (Gyurácz *et al*. 2004).

The migration strategies of birds, especially passerines, across the western European flyway during the autumn are relatively well known since many studies have focused on the stopover ecology (Ellegren & Fransson 1992, Pilastro *et al*. 1998, Schaub & Jenni 2000a, 2001, Delingat *et al*. 2006, Fransson *et al*. 2006, Halupka *et al*. 2017, Fourcade 2022). Less is known about the stopover strategies and sites of most passerines using the central and eastern European flyways (Spina *et al*. 2022). Since many of these species are threatened by habitat loss, fragmentation and degradation (Szép *et al*. 2021), knowledge of migration strategies is important for effective conservation actions.

Many common migratory passerines originating from central and northern Europe stop over during autumn in western Hungary (Gyurácz *et al*. 2017a). Using data obtained during the autumn migration for 20 years, we calculated fuel load and potential flight ranges for 16 common passerines that

stopover in part of the Carpathian Basin. We hypothesised that sub-Saharan, long-distance migrants should carry higher fuel loads than pre-Saharan, short-distance ones and should have a longer range.

MATERIAL AND METHODS

Study area – We used data from 13 sub-Saharan, and three pre-Saharan migrant passerines (Table 1) captured at the Tömörd Bird Ringing Station in western Hungary (47°21′N 16°40′E), located 15 km from Szombathely (Fig. 1). There are four natural habitat types around the station. Shrubland: bushes and herbs forming compact, dense vegetation, which is dissected by small grass patches. Its characteristic plant is Blackthorn (*Prunus spinosa*). Forest: broadleaf trees and bushes forming compact, dense edge vegetation and an ecotone community with Turkey Oak (*Quercus cerris*) as the characteristic plant. There are dense shrubs and normal forestry management (e.g., periodic felling of trees) in the forest. Grassland with shrubs: this habitat type is a transition between the wet habitats of

Table 1. Common stopping-over passerines captured at Tömörd during the autumn migration. Status at Tömörd (STÖ) (P = passage migrant; B = breeding; W = overwintering), the location of main overwintering region (OR) (M = Mediterranean region; A = tropical Africa), sample size (N) and months considered for the study are listed

Species	Species code	STÖ	OR	N	Months
Marsh Warbler – *Acrocephalus palustris*	ACRRIS	BP	A	383	Aug.-Sep.
Sedge Warbler – *Acrocephalus schoenobaenus*	ACRSCH	P	A	571	Aug.-Sep.
Eurasian Reed Warbler – *Acrocephalus scirpaceus*	ACRSCI	P	A	223	Aug.-Sep.
European Robin – *Erithacus rubecula*	ERIRUB	BPW	M	15,857	Sep.-Oct.
European Pied Flycatcher – *Ficedula hypoleuca*	FICHYP	P	A	1350	Aug.-Sep.
Icterine Warbler – *Hippolais icterina*	HIPICT	P	A	323	Aug.-Sep.
Common Nightingale – *Luscinia megarhynchos*	LUSMEG	BP	A	281	Aug.-Sep.
Spotted Flycatcher – *Muscicapa striata*	MUSTRI	BP	A	707	Aug.-Sep.
Common Chiffchaff – *Phylloscopus collybita*	PHYCOL	BP	M	7087	Sep.-Oct.
Wood Warbler – *Phylloscous sibilatrix*	PHYSIB	BP	A	252	Aug.-Sep.
Willow Warbler – *Phylloscopus trochilus*	PHYTRO	BP	A	745	Aug.-Sep.
Eurasian Blackcap – *Sylvia atricapilla*	SYLATR	BP	M	11,153	Sep.-Oct.
Garden Warbler – *Sylvia borin*	SYLBOR	BP	A	699	Aug.-Sep.
Common Whitethroat – *Curruca communis*	SYLCOM	BP	A	1475	Aug.-Sep.
Lesser Whitethroat – *Curruca curruca*	SYLCUR	BP	A	2023	Aug.-Sep.
Barred Warbler – *Curruca nisoria*	SYLNIS	BP	A	66	Aug.-Sep.

the swamp and the steppe communities that cover the croplands around the marsh. There are a few bushes in the grassland with two small patches of Dwarf Elder (*Sambucus ebulus*). The grassland is not managed. Marsh: a small (6 ha), permanent and isolated wetland. The characteristic plant is Reedmace (*Typha latifolia*).

Table 2. Best-fit GLM models. BM: independent variable, WL: covariate, FS and MS : factors. All one or two-way interactions were considered. Only the top models (ΔAICc < 3) are shown.

Model	AICc	AICcWeights
ACRRIS		
BM ~ 1 + FS + MS + WL + MS:FS + FS:WL	1039.06	5.62e-01
BM ~ 1 + FS + MS + WL + MS:FS + FS:WL + MS:WL	1039.60	4.29e-01
BM ~ 1 + FS + MS + WL + FS:WL + MS:WL	1049.12	3.67e-03
ACRSCH		
BM ~ 1 + FS + MS + WL + MS:FS + FS:WL	1749.35	5.95e-01
BM ~ 1 + FS + MS + WL + MS:FS + FS:WL + MS:WL	1751.21	2.35e-01
BM ~ 1 + FS + WL + FS:WL + MS:WL	1754.07	5.61e-02
ACRSCI		
BM ~ 1 + WL + FS:WL	533.31	2.63e-01
BM ~ 1 + FS + WL	533.70	2.17e-01
BM ~ 1 + MS + WL + FS:WL	533.53	8.69e-03
ERIRUB		
BM ~ 1 + FS + MS + WL + MS:FS	46047.72	6.69e-01
BM ~ 1 + FS + MS + WL + MS:FS + MS:WL	46049.80	2.37e-01
BM ~ 1 + FS + MS + WL + MS:FS + FS:WL	46052.54	6.01e-02
FICHYP		
BM ~ 1 + FS + MS + WL + MS:FS + MS:WL	3168.54	7.91e-01
BM ~ 1 + FS + MS + WL + MS:FS + FS:WL + MS:WL	3171.38	1.91e-01
BM ~ 1 + FS + MS + WL + MS:WL	3177.27	1.01e-02
HIPICT		
BM ~ 1 + FS + MS + WL + MS:FS + FS:WL + MS:WL	842.77	9.89e-01
BM ~ 1 + FS + MS + WL + MS:FS + FS:WL	852.16	9.05e-03
BM ~ 1 + FS + MS + WL + MS:FS + MS:WL	855.99	1.33e-03
LUSMEG		
BM ~ 1 + FS + MS + WL + MS:FS + FS:WL	1063.86	5.69e-01
BM ~ 1 + FS + MS + WL + FS:WL	1066.91	1.24e-01
BM ~ 1 + FS + MS + WL + MS:FS + FS:WL + MS:WL	1067.01	1.18e-01

MUSTRI		
BM ~ 1 + MS + WL + FS:WL	2277.88	2.09e-01
BM ~ 1 + WL + FS:WL+ MS:WL	2277.90	2.08e-01
BM ~ 1 + FS + MS	2278.37	1.64e-01
PHYCOL		
BM ~ 1 + FS + MS + WL + MS:FS	10300.68	8.13e-01
BM ~ 1 + FS + MS + WL + MS:FS + MS:WL	10304.50	1.21e-01
BM ~ 1 + FS + MS + WL + MS:FS + FS:WL	10305.98	5.74e-02
PHYSIB		
BM ~ 1 + FS + WL	559.99	1.90e-01
BM ~ 1 + WL + FS:WL	10304.50	1.49e-01
BM ~ 1 + FS + MS + WL	10305.98	1.34e-01
PHYTRO		
BM ~ 1 + FS + WL+ FS:WL	1749.61	3.28e-01
BM ~ 1 + FS + WL + FS:WL + MS:WL	1750.83	1.78e-01
BM ~ 1 + FS + MS + WL + FS:WL	1750.99	1.65e-01
SYLATR		
BM ~ 1 + FS + MS + WL+ MS:FS + FS:WL	34045.25	6.14e-01
BM ~ 1 + FS + MS + WL + MS:FS + FS:WL + MS:WL	34047.74	1.77e-01
BM ~ 1 + FS + MS + WL + FS:WL	34048.87	1.01e-01
SYLBOR		
BM ~ 1 + FS + MS + WL+ FS:WL+ MS:WL	2454.08	9.13e-01
BM ~ 1 + FS + MS + WL + MS:FS + FS:WL + MS:WL	2459.56	5.89e-02
BM ~ 1 + FS + MS + WL + FS:WL	2462.98	1.07e-02
SYLCOM		
BM ~ 1 + FS + WL+ MS:WL	4670.97	2.34e-01
BM ~ 1 + FS + MS + WL	4671.56	1.94e-01
BM ~ 1 +WL + FS:WL+ MS:WL	4671.46	1.83e-01
SYLCUR		
BM ~ 1 + FS + MS + WL + MS:FS + MS:WL	4648.70	8.36e-01
BM ~ 1 + FS + MS + WL+ MS:FS + FS:WL + MS:WL	4652.14	1.49e-01
BM ~ 1 + FS + MS + WL + MS:FS	4658.52	6.16e-03
SYLNIS		
BM ~ 1 + FS + WL	244.96	2.21e-01
BM ~ 1 + WL+ FS:WL	245.13	2.02e-01
BM ~ 1 + FS	246.14	1.22e-01

Data collection and analyses – Birds were captured-marked-recaptured during the autumn migration from 2002 to 2021. We used 28 numbered Ecotone mist nets (12 m long and 2.5 m high, with 5 shelves and a mesh size of 16 mm) for trapping. The nets were placed equally in the four habitat types. Birds were captured from dawn to dusk, except on rainy and stormy days when the nets were closed. All birds were ringed, sexed and aged, according to Svensson (1992). Flattened maximum wing length (WL) was measured to the nearest mm using a graded wing ruler. The birds were weighed to the nearest 0.1 g using a digital balance. The fat reserves (fat score, FS, 0–8) and flight muscle (muscle score, MS, 0–3) were determined visually according to the SE European Bird Migration Network protocol (Busse & Meissner 2015).

We calculated individual lean body mass (m_0, body mass without fuel deposits) to quantify the fuel load each bird was carrying. A general linear model (GLM; m: dependent variable, WL : covariate, FS and MS : factors) was fitted to the data of each species and m_0 was calculated for each individual assuming MS = 1 and FS = 0 (zero fuel load). All possible one or two-way interactions were considered in the GLM models. The models were ordered based on their AICc values and were averaged using the glmulti package of R (Table 2). Birds with MS = 0 were omitted because there were very few. The difference between body mass, m, at capture and calculated lean body mass, m_0, was defined as the fuel load (FL) ($m - m_0$). Relative fuel load was calculated as $f = (m - m_0) / m_0$ (Delingat *et al.* 2008), representing the energy resources of the bird (Sander *et al.* 2017). Fat scores 5–8 were grouped due to small sample sizes.

To estimate the flight range (Y in km), we used the dataset of individuals with FS ≥ 3, which were presumed to be ready to resume their migration, applying two different formulas.

1) After Delingat *et al.* (2008), where the flight range of passerines increases with the log-scaled relative fuel load (*f*) and flight speed (U) (Equation 1): $Y = 100 \times U \times \ln(1 + f)$.
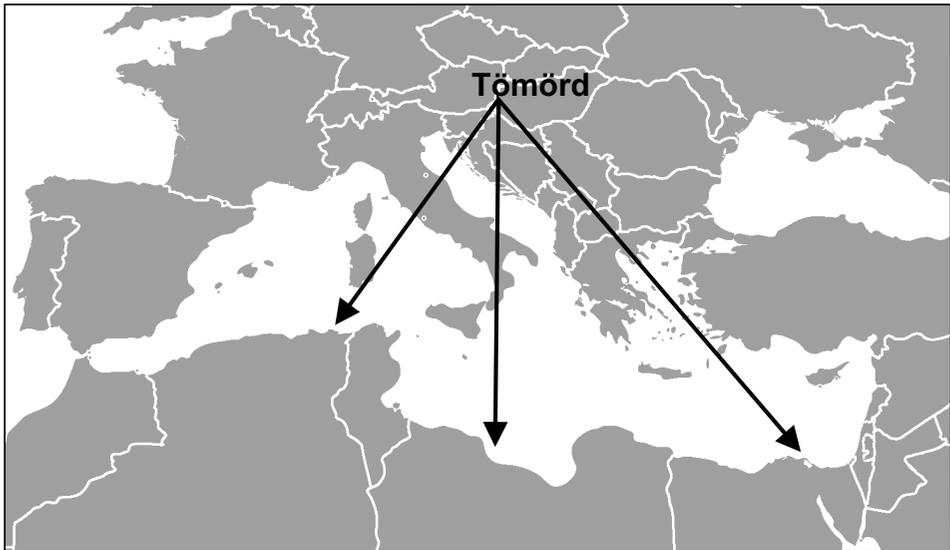
Fig. 1. Potential Mediterranean flyway in southern Europe (arrows) and the location of Tömörd

2) After ROBERTS *et al*. (2005), where flight range increases with fat mass, the energy content of fat (E_f = 9 kcal/g) and flight speed (U), and decreases with the metabolic rate during flight (FMR = 0.9 kcal/g) (Equation 2). However, as ROBERTS *et al*. (2005) used constants for all variables except fuel load (FL), flight range increases directly with fuel load (Equation 2): Y = ((fuel load (FL) × E_f)/(FMR)) × U

We compared flight ranges calculated with both equations, assuming a constant flight speed of U = 60 km/h (passerine flight speed without wind profit; SALEWSKI *et al*. 2010). The mean flight ranges of species were compared by one-way ANOVA and Tukey tests. All statistics were carried out in R version 3.3.2 (R CORE TEAM 2016) and Microsoft Office Excel 2007.

RESULTS

General linear models that best explained the variation of body mass were those with interactions between FS, MS and WL for 10 species; and those with no interactions between FS, MS and WL for five species. Both models were a good fit for the Common Nightingale (Table 3). Body mass was posi-

Table 3. Corrected Akaike values (AICc), R^2 values and difference in AICc values (ΔAICc) are shown for the general linear models calculated to explain body mass in relation to wing length (WL) and fat (FS) and muscle scores (MS). Models with the lowest AICc values are considered as the best fit to the data, and a difference in AICc > 2 indicated a significant difference in the fit of the models (BURNHAM & ANDERSON 1998). + represents models in which only the main effects were considered, and × represents models including all possible interactions. For species codes see Table 1.

Species code	WL×FS×MS			WL+FS+MS		
	AICc	ΔAICc	R^2	AICc	ΔAICc	R^2
ACRRIS	1051.14	0.00	0.50	1080.31	29.17	0.38
ACRSCH	1760.84	0.00	0.48	1764.91	4.07	0.42
ACRSCI	556.51	21.46	0.38	536.90	1.85	0.40
ERIRUB	46044.56	0.00	0.38	46057.34	12.78	0.37
FICHYP	3165.02	0.00	0.43	3187.53	22.51	0.39
HIPICT	856.51	0.00	0.65	879.17	22.66	0.57
LUSMEG	1078.21	1.13	0.47	1077.08	0.00	0.40
MUSTRI	2285.47	6.45	0.20	2279.02	0.00	0.20
PHYCOL	10304.22	0.00	0.48	10323.43	19.22	0.47
PHYSIB	504.96	0.00	0.77	561.60	56.64	0.65
PHYTRO	1772.13	13.51	0.51	1758.62	0.00	0.49
SYLATR	34042.10	0.00	0.38	34065.38	23.28	0.37
SYLBOR	2459.70	0.00	0.45	2476.31	16.61	0.39
SYLCOM	4693.34	21.86	0.42	4671.49	0.00	0.42
SYLCUR	4654.62	0.00	0.29	4667.13	12.51	0.27
SYLNIS	265.05	13.05	0.63	252.00	0.00	0.63

Table 4. Effects of wing length (WL), fat (FS) and muscle (MS) scores on body mass. The best models between WL, FS and MS (see further details in Table 2). Values with an asterisk had a significant effect on body mass (p < 0.05). For species codes see Table 1.

Species code	WL		FS		MS	
	SS	df	SS	df	SS	df
ACRRIS	21.51*	1	194.59*	5	1.57*	2
ACRSCH	22.48*	1	488.67*	5	3.99*	2
ACRSCI	26.95*	1	62.23*	5	0.16*	2
ERIRUB	1382.50*	1	8677.30*	5	39.80*	2
FICHYP	38.29*	1	493.01*	5	7.13*	2
HIPICT	11.01*	1	343.82*	5	5.10*	2
LUSMEG	48.45*	1	411.08*	5	18.99*	2
MUSTRI	2.39*	1	236.97*	5	21.84*	2
PHYCOL	1105.05*	1	468.24*	5	4.31*	2
PHYSIB	12.36*	1	224.98*	5	0.83*	2
PHYTRO	158.61*	1	268.16*	5	0.84*	2
SYLATR	1400.60*	1	6725.50*	5	71.60*	2
SYLBOR	72.71*	1	803.92*	5	19.89*	2
SYLCOM	38.42*	1	1407.59*	5	37.02*	2
SYLCUR	56.33*	1	370.37*	5	6.96*	2
SYLNIS	5.65*	1	203.39*	5	2.27*	2
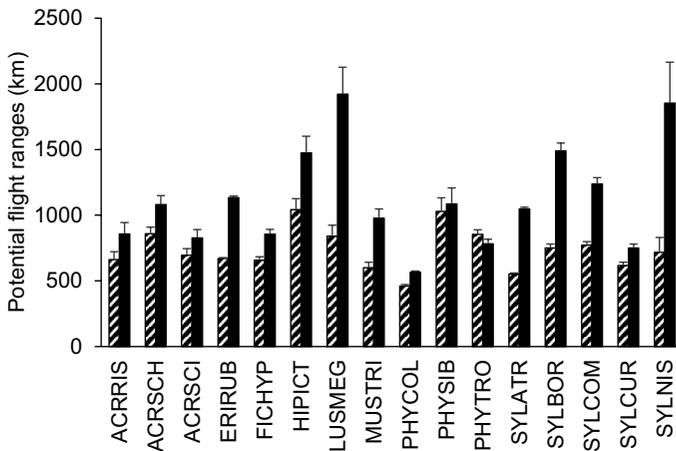
Fig. 2. Potential flight ranges (+ SE) of passerine species stopping over in Tömörd during the autumn migration. Potential flight ranges have been calculated by two methods for all birds with a fat score ≥ 3 for each species. For species codes see Table 1

Table 5. Mean ± SE fuel loads (FL; g) over lean body mass (body mass of a bird with FS = 0 and MS = 1; see methods for further details) and their percentages (*f* ; %) above lean body mass. Mean and relative fuel load were calculated for birds with FS ≥ 3, representing birds about to depart. For species codes see Table 1.

Species code	FL					
	Mean (g)	SE	% (*f*)	Lowest	Highest	N
ACRRIS	1.43	0.14	12.43	1.28	1.57	103
ACRSCH	1.80	0.11	16.67	1.69	1.92	222
ACRSCI	1.38	0.10	12.32	1.36	1.57	62
ERIRUB	1.89	0.02	11.96	1.89	1.93	4548
FICHYP	1.42	0.06	11.83	1.36	1.48	346
HIPICT	2.46	0.21	19.80	2.25	2.67	70
LUSMEG	3.20	0.35	15.31	2.86	3.55	63
MUSTRI	1.63	0.12	10.90	1.51	1.75	132
PHYCOL	0.60	0.01	8.30	0.58	0.61	1600
PHYSIB	1.81	0.20	19.93	1.61	2.01	64
PHYTRO	1.30	0.06	15.97	1.25	1.36	305
SYLATR	1.74	0.02	9.89	1.72	1.77	3547
SYLBOR	2.48	0.11	13.55	2.38	2.59	306
SYLCOM	2.06	0.08	14.30	1.98	2.14	507
SYLCUR	1.25	0.05	11.10	1.20	1.30	381
SYLNIS	3.09	0.52	13.09	2.57	3.60	23

tively correlated with FS in all species, MS in 10 species, and WL in 14 species (Table 4). The mean relative fuel load (*f*) for the birds with FS ≥ 3 ranged from 8.30% in the Common Chiffchaff to 19.93% in the Wood Warbler (*P. sibilatrix*) above the lean body mass; the mean over all species was 13.58% (Table 5). The mean potential flight range of all species was 736.50 ± 159.24 km (Equation 1) or 1121.56 ± 388.62 km (Equation 2) (t = 3.67, df = 31, p = 0.002). However, the potential mean flight ranges of species were significantly different (ANOVA, Equation 1: F = 41.93, df = 15, p = 0.001; Equation 2: F = 104.9, df = 15, p = 0.001). Common Chiffchaffs had the lowest fuel loads and, consequently, their shortest (< 500 km) potential flight ranges were significantly different from all the other species (Tukey test p = 0.001, Fig. 2). The mean fuel load (3.20 g) and mean potential flight range (Equation 2) of Common Nightingales were the highest (1922 km), but their mean potential flight ranges were not significantly different from those of the Icterine Warbler, Garden Warbler and Barred Warbler (all > 1400 km, Tukey test p > 0.05) (Fig. 2).

DISCUSSION

In ten of the species studied, models considering interactions between factors did fit the data better than the main-effect models. In five of the species studied, the main-effect models were better. Contrary to previous studies, our result supports the hypothesis that body size (assessed using WL), FS and MS are not independently associated with body mass for all species. In south England, the relationship between fat and pectoral muscle scores of Sedge Warblers was investigated by REDFERN *et al.* (2004). They found that although muscle and fat scores show some level of correlation, after a detailed investigation, they concluded that these parameters could vary independently. According to ARIZAGA *et al.* (2011), the general linear models that best explained the variation of body mass were those with no interactions among FS, MS and WL; the proportion of variance explained by the models was 51%. FS, MS and third primary length explained the variation in body mass of eight passerines analysed in west Africa (SALEWSKI *et al.* 2009).

Body mass was positively correlated with FS in all species, with MS in 10 species and with WL in 14 species. This result suggests that body mass changed least with increasing MS, which could be partially due to the low variation of MS at Tömörd; most birds were found to have MS = 1 or 2, and only a few birds had MS = 0 or 3. The lack of relevant ecogeographic barriers between Tömörd and the Dinaric Alps (CSÖRGŐ *et al.* 2009), which forces birds to migrate for several consecutive nights (SCHMALJOHANN *et al.* 2007), maybe one of the main causes for the relatively low variation in the MS of migrant passerines passing through western Hungary.

Bozó *et al.* (2019) estimated the flight ranges of three migrant warbler species at a stopover site next to Lake Baikal, Russia. The estimated flight ranges of the Pallas' Leaf Warbler (*Ph. proregulus*) was similar (Equation 1: 724 km) to that of the Willow Warbler and that of the Radde's Warbler (*Ph. schwarzi*) (Equation 1: 434 km) to that of the Common Chiffchaff. DELINGAT *et al.* (2008) and ARIZAGA *et al.* (2013) studied the Palaearctic-Africa migration route, where there are large geographical barriers such as the Mediterranean Sea, the Sahara Desert, the Sahel and tropical rainforests. In northern Iberia, using the same method (Equation 1), they estimated significantly longer flight ranges for both pre- and sub-Saharan migrants than our results (ARIZAGA *et al.* 2011). In western Hungary, the sub-Saharan migrants were estimated to fly no more than 900 km, whereas in Iberia, the estimates for the Garden Warbler and Sedge Warbler were 2000 km. The difference is particularly large in the case of the Eurasian Blackcap. The estimated flight distance was 1200 km in Iberia, 560 km in Tömörd. Concerning Eurasian Blackcaps, it must be considered that all Blackcaps passing through Hungary are pre-Saharan migrants,

unlike western European migrants, which migrate to tropical Africa (Shirihai *et al*. 2001, Spina *et al*. 2022).

During autumn, fuel load tended to be larger in the sub-Saharan migrants, especially in the four species which pass over the Dinaric Alps and the Mediterranean Sea (Common Nightingale, Icterine Warbler, Garden Warbler and Barred Warbler), suggesting an effect of this ecological barrier in shaping fuel load. Based on the flight distance estimated using both equations, these species can reach the nearest Tunisian shores of northern Africa without making any additional stopovers. This highlights the importance of conserving critical areas that are stopover sites for migrating passerines in southern Europe and northern Africa. However, none of the sub-Saharan species captured at Tömörd had sufficient fuel load to reach the southern margin of the Sahara, which is about 3000 km from western Hungary. Nine sub-Saharan migrants, Marsh Warbler, Sedge Warbler, Eurasian Reed Warbler, European Pied Flycatcher, Spotted Flycatcher, Wood Warbler, Willow Warbler, Common Whitethroat, Lesser Whitethroat, had estimated flight range similar (< 1300 km) to two pre-Saharans, European Robin, Eurasian Blackcap. This result supports the idea that these nine sub-Saharan species clearly need to consistently refuel before crossing the Dinari Alps and/or the Mediterranean Sea. This is possible for them because they must fly over landscapes full of opportunities to refuel. However, the sub-Saharan migrants captured in autumn at two stopover sites in Iberia and Israel showed a higher fuel load than at Tömörd. In northern Iberia, a mean fuel load of nearly 0.30 was reported in autumn migration for the sub-Saharans (Arizaga *et al*. 2011). In Eilat, the mean body mass gain as a percentage of the initial mass of Sedge Warblers was 14.1% in autumn (Yosef & Chernetsov 2004): these birds have no opportunity to refuel elsewhere before crossing the Sahara Desert to reach their wintering grounds (Cramp 1994).

The three short-distance migrants, including the Common Chiffchaff with the shortest migration distance, had sufficient fuel load to reach their southern European wintering sites without needing to refuel. The wintering areas of these species are relatively well known. The Hungarian populations of European Robin and Common Chiffchaff, together with passage migrants from northern breeding areas, migrate south-southeast and south-southwest to their wintering grounds in southern Europe and north Africa (Csörgő *et al*. 2009, Spina *et al*. 2022). These areas can be reached in 2–3 nights of flight (assuming a flight of 6 h and ground speeds of nearly 60 km/h). For these species, western Hungary could play a secondary role as a refuelling region, but only for those birds that have been unable to gain a sufficient fat reserve in areas north of the study site (Gyimóthy 2011, Gyurácz *et al*. 2017*b*).

In conclusion, the fuel load of some migrants passing through the western area of the Carpathian Basin may be shaped by the ecological barriers

faced during the autumn migration period (RUBOLINI *et al*. 2002), such as the Dinaric Alps and the Mediterranean Sea. However, our data also show that more migrants crossing the Mediterranean Sea did not have sufficient fuel in western Hungary to reach northern Africa. Therefore, stopover sites in southern Europe play a key refuelling role in these species reaching northern Africa. The three short-distance migrants studied in western Hungary have sufficient fuel to reach their southern European wintering areas.

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<div align="center">REFERENCES</div>

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