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Seasonal differences in energy requirements of Garden Warblers *Sylvia borin* migrating across the Sahara desert

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The Sahara desert acts as an ecological barrier for billions of passerine birds on their way to and from their African wintering areas. The Garden Warbler *Sylvia borin* is one of the most common migrants involved. We used body mass of this species from Greece in autumn and spring to simulate the desert crossing and to assess how body mass relates to fuel requirement. The flight range estimates were adjusted to the seasonal extent of the desert, 2200 km in autumn and about 2800 km in spring. In autumn, with an average fuel load of about 100% of body mass without fuel, birds were not able to cross the desert in still air, but northerly winds prevail during September and with the average wind assistance only one in 14 was predicted to fail to make the crossing. Body mass data from spring, after the desert crossing, was used to estimate departure body mass from south of the desert. The average wind assistance in spring is close to zero and departure body mass of the average bird arriving at Antikythira, a small Greek island, under such conditions was estimated to be 34.6 g, which corresponded to a fuel load of 116%. Calculations based on 1% body mass loss per hour of flight showed slightly larger body mass loss than that calculated from flight range estimates. The results suggest that passerine birds about to cross the eastern part of the Sahara desert need to attain a larger fuel load in spring than in autumn.

Keywords: barrier crossing, bird migration, eastern Mediterranean, flight range, fuel load, *Sylvia borin*.

Within the Afro-Palaearctic bird migration system, many birds face the challenge of passing a huge ecological barrier, the Sahara desert. Moreau (1961, 1972) suggested that the desert could be crossed in a 40–60 h non-stop flight, based on the density of migrants found at oases and in the desert during daytime. An intermittent strategy involving regular stopovers in the desert was later proposed by Bairlein (1985, 1992) and Biebach *et al.* (1986). Recent radar studies confirm that most passerine migrants seem to use an intermittent flight strategy when crossing the desert, flying during the night and resting during the day (Biebach *et al.* 2000, Schmaljohann *et al.* 2007a). Furthermore, birds stopping-over in the western Sahara during the day are not considered to be fall-outs, as they carry sufficient fuel loads to complete the crossing (Salewski *et al.* 2010b). The number of passerine and near-passerine birds crossing the desert in autumn has been estimated at 2.1 billion (Hahn *et al.* 2009). The distance to be covered can exceed 2000 km, with few foraging opportunities, and in the east includes crossing the Mediterranean Sea. Movements of the equatorial Intertropical Convergence Zone (ITCZ) bring rain to areas just south

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of the desert during the northern summer (Zwarts *et al.* 2009), and this phenomenon makes the distance to cross longer in spring than in autumn. It is clear that most birds have to accumulate enough energy in the form of fat and protein before starting to cross the desert (Fry *et al.* 1970, Piersma 1990, Biebach 1998, Jenni & Jenni-Eiermann 1998).

One of the best-studied species to perform this biannual barrier crossing is the Garden Warbler *Sylvia borin* (Bairlein 1991, Spina *et al.* 1993, Grattarola *et al.* 1999), which breeds in the temperate zone throughout Eurasia and winters in central and southern Africa (Cramp 1992). All known populations of the Garden Warbler are obligate long-distance migrants and it is one of the most numerous long-distance migrants in the Palaearctic (Hahn *et al.* 2009). A recent study in Crete, southern Greece, showed that first-year Garden Warblers arrive in autumn with relatively small fuel loads, stay 14–20 days and then depart with a fuel load close to 100% of body mass without fuel (Fransson *et al.* 2008).

In this study, we used flight range estimates to understand how the estimated departure fuel load in Crete (Fransson *et al.* 2008) relates to the energy needed for the desert crossing for birds following an intermittent flight strategy in autumn. Using spring body mass data of Garden Warblers from a small Greek island, Antikythira, we also simulated the desert crossing and hence estimated the departure body mass needed from south of the desert. The simulations were adjusted to the seasonal extent of the desert and to the seasonal differences in prevailing wind conditions over the desert. Calculations based on 1% body mass loss per hour of flight were performed to compare the outcome with that received from the flight range estimates.

METHODS

We simulated migration of Garden Warblers from central Crete over the Mediterranean Sea and the Sahara desert during autumn (Fig. 1). The simulations for spring took birds on a route from the southern edge of the desert to the island of Antikythira. In all cases, birds in the simulations followed an intermittent flight strategy (Schmaljohann *et al.* 2007a) with departure 1 h after sunset (Åkesson *et al.* 1996, Fortin *et al.* 1999). During the day, simulations included stop-overs with a loss of 0.5% of body mass per hour (Meijer *et al.* 1994, Schmaljohann *et al.* 2008). Each flight was simulated separately starting with the body mass after the daytime rest. The seasonal variation in the distance to be covered when passing the Sahara desert was taken into consideration for calculations of the total flight distance using normalized difference vegetation index (NDVI) maps (http://www.seaturtle.org, Fig. 1). NDVI maps for September 2005–2008 were used to estimate that the shortest distance from Crete to the southern edge of the desert, which was about 2200 km in autumn, and the position where vegetation started in the south varied by about 100 km for those years. The minimum distance for the return flight in spring between the edge of the Sahara and Antikythira was estimated to be about 2800 km, estimated from NDVI maps for April 2005–2008, and showed less variation in the southern border compared with the autumn.

Flight range estimates

The calculation of maximum flight ranges was based on aerodynamic theory (Pennycuick 1989) using the software FLIGHT 1.18 (Pennycuick 2008). This aerodynamic approach has the advantage that it allows birds with different wing spans and wing areas to have different flight efficiencies (Thomas 1996, Pennycuick 2008). The basic input parameters include the take-off body mass, wing span, wing area, flying altitude, air density and aspect ratio, the last being the ratio of the wing span to the mean wing chord (Pennycuick 2008). Other important parameters include the airframe fraction (the ratio of the total body mass, minus the sum of the fat mass and the flight muscle mass, and the total body mass), fat fraction (the ratio of the mass of stored fat that is available to be used as fuel and the total body mass) and the flight muscle fraction (the ratio of the flight muscle and the total body mass). The computation allows for protein from the flight muscles to be consumed, so as to reflect the decreasing demands on the muscles as overall mass declines. The computations also recognize that metabolic processes require some minimum percentage of the energy to be derived from oxidizing protein (Jenni & Jenni-Eiermann 1998).

Linear regressions were applied to determine the relationship between wing length and wing span (wing span = 0.204 × wing + 6.294; $F_{1,45} = 788.9$, $P < 0.001$, $r^2 = 0.946$) and between wing length

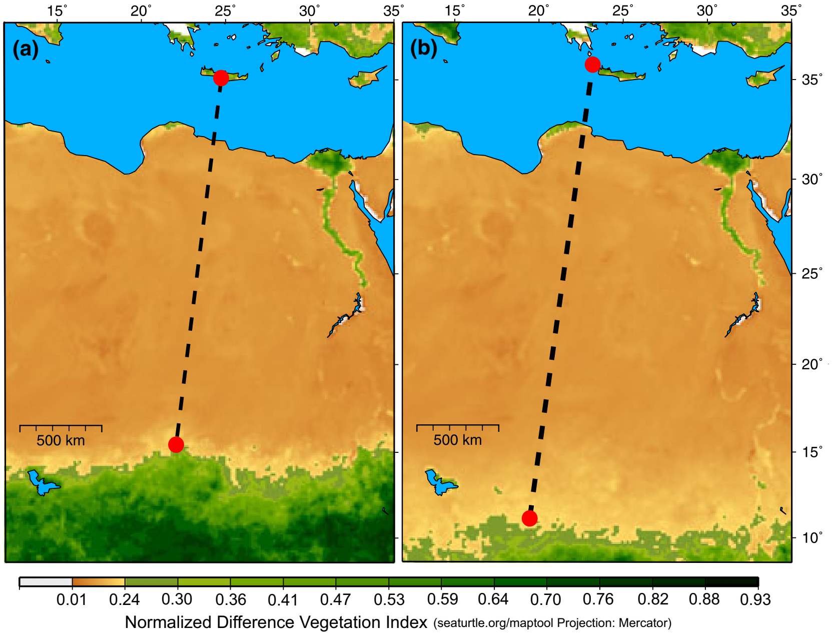

Figure 1. Examples of normalized difference vegetation index (NDVI) maps of the study area used to calculate the distance to be crossed over the desert during (a) autumn and (b) spring 2008. The dashed lines show the distance from Crete to south of the desert in autumn and from the southern edge of the desert to Antikythira in spring.

and wing area (wing area = 1.616 × wing – 30.167; $F_{1,44} = 128.4$, $P < 0.001$, $r^2 = 0.744$) for Garden Warblers caught on Crete. The formulae estimated were used to estimate the wing span and wing area of every bird simulated. Departure body mass and wing length data of 14 first-year Garden Warblers used for the simulated southward migration were taken from Fransson *et al.* (2008), where birds attached with radio-transmitters were followed during complete stopover periods. For the northward migration, five simulations were based on mean body mass and wing length of birds trapped at Antikythira Bird Observatory within the standardized ringing of migrants run by the Hellenic Ornithological Society and the Hellenic Bird Ringing Centre from the beginning of April until the end of May during 2007 and 2008. The simulations included three model birds with mean wing length and each with a different body mass (mean ± sd). In two other cases, we included birds with mean body mass but with different wing lengths (± sd). For more details on the calculation of the departure body mass and the study sites, see Fransson *et al.* (2008) and Dimaki *et al.* (2006).

As fat and muscle scores were not available, the flight muscle and fat mass fraction were estimated separately for each bird based on the relationship between the flight muscle mass and airframe mass of Garden Warblers measured close to the barrier crossing in autumn (Bauchinger & Biebach 2001). The default value (5%) of minimum energy used from protein was used when birds had sufficient fat load remaining. When fat load dropped below 5% of body mass without fuel, the minimum energy used from protein was set to 30% to resemble phase III of fasting, which seems to occur during endurance flight (Jenni *et al.* 2000, Schwilch *et al.* 2002). Default values in the software were used for other variables.

During autumn simulations, birds were set to fly at an altitude of 500 m when they were crossing the desert (Klaassen & Biebach 2000, Schmaljohann *et al.* 2007a) and at 1500 m when crossing the Mediterranean Sea (Bruderer & Liechti 1998). The duration of night flights was set to 10 h (Schmaljohann *et al.* 2007a, 2008) and only for the last migration step was the flight allowed to be prolonged for up to 50 km to reach the southern edge of the desert. Throughout the northward spring simulations, the birds were set to migrate at an altitude of 2000 m over the desert (Liechti & Schmaljohann 2007) and at 1500 m over the sea (Bruderer & Liechti 1998) for 12 h per flight (Schmaljohann *et al.* 2007a). For the final flight step, if birds had reached or passed the African coast, they were set to prolong their flight until they reached Antikythira.

Calculation of body mass loss

Body mass loss during migration has recently been calculated as 1% of the body mass per hour of flight (Delingat *et al.* 2008). We have used this method to make a comparison with the results received from the FLIGHT program. In both methods we used the same distances, time budgets and body mass loss during daytime rests. The body mass loss was calculated for every hour separately and the flight speed used in these calculations was set to 12 m/s (Alerstam *et al.* 2007).

Wind data

To obtain a view of the prevailing wind conditions in the area of passage as well as the seasonal variation, we used information from NCEP Reanalysis data provided by the NOAA/OAR/ESRL PSD, Boulder, CO, USA (http://www.cdc.noaa.gov/). Wind data were extracted for the years 2005–2008 and divided into spring (10 April–9 May) and autumn (1–30 September). We chose values for midnight (0 h universal time UTC) for three different sites: close to the coast in Libya (32°00′N, 23°30′E), central Sahara (24°00′N, 22°00E) and close to the southern border of the Sahara (15°00′N, 20°00′E). We extracted both v-wind and u-wind, which are the north–south component and the west–east component, respectively. These values were used to estimate the actual wind speed and direction. To estimate the wind assistance, we estimated the average tailwind component. Based on recoveries in the Mediterranean area (Spina & Volponi 2009) we estimated and used a migratory direction of 200° (SSW) in autumn and 20° (NNE) in spring. The tailwind component was calculated as: cos (wind direction − migratory direction) × wind speed (Liechti *et al.* 2000). We also included wind conditions at different altitudes by using three different air pressure levels (925, 850 and 700 mb), representing *c.* 750, 1500 and 3000 m asl, available in the NCEP Reanalysis data from the altitude range where nocturnal flights may occur.

RESULTS

In the Sahara during autumn, wind conditions are known to be fairly stable and northeasterly winds prevail over most of the area (Moreau 1961, 1972). For Garden Warblers passing from Crete and southward, the average tail wind component in September 2005–2008 varied between 3.28 and 3.83 m/s depending on altitude (Table 1). In spring, wind conditions varied much more and headwind conditions occurred on average at lower altitudes, while the average tailwind component was close to zero at high altitude during the period 10 April–9 May 2005–2008 (Table 1). Wind directions regularly differed between altitudes and in spring both headwinds and tailwinds occurred in 41% of the nights at different altitudes in the locations where wind data were sampled.

The mean wing length of the 14 first-year Garden Warblers, with estimated departure fuel loads on Crete in autumn, was 79.7 ± 1.3 mm. The mean wing length and body mass of Garden Warblers caught on Antikythira during spring was 81.4 ± 1.9 mm (*n* = 1365) and 16.0 ± 1.6 g (*n* = 1359), respectively. Body mass in spring varied between 10.1 and 21.8 g, and the estimated departure body mass from Crete in autumn varied between 27.3 and 32.7 g (Fig. 2).

Simulated Garden Warblers crossing the Sahara during autumn in still air ran out of fuel after five nights without reaching the southern edge of the desert. The majority of these birds were, however, between 65 and 200 km from the desert edge as defined by the NDVI map, with two exceptions having 390 and 550 km remaining. When including the average wind assistance found during autumn of 3.5 m/s, only one bird, which had a departure fuel load (in relation to body mass with-

Table 1. Average tailwind component (m/s) at three different sites in eastern Sahara (see Methods for locations) during autumn (1–30 September) and spring (10 April–9 May) 2005–2008 and at three different altitudes (m asl).

		Autumn			Spring		
		750	1500	3000	750	1500	3000
2005	Coast	3.25	3.40	1.83	0.14	0.14	1.70
	Central	6.98	6.81	5.05	−4.72	−1.88	1.23
	South	−1.22	2.29	3.71	−4.89	−4.99	−0.77
2006	Coast	3.49	2.05	0.36	−1.19	3.55	1.41
	Central	6.76	6.08	3.40	−6.22	−4.42	−0.03
	South	−2.06	1.93	6.39	−6.84	−6.49	−0.35
2007	Coast	3.59	2.74	1.89	−0.72	−0.22	1.31
	Central	7.59	7.27	6.06	−3.88	−1.83	0.70
	South	3.11	3.80	4.12	−4.54	−5.17	−2.69
2008	Coast	2.70	1.91	1.28	0.88	1.26	1.56
	Central	5.58	4.44	1.97	−7.28	−5.95	−3.10
	South	−0.16	3.29	5.99	−7.17	−7.20	−0.69
Mean		3.28	3.83	3.50	−3.87	−2.77	0.00

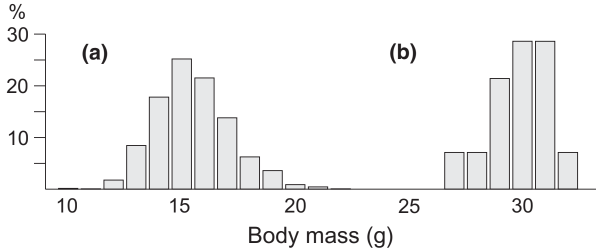

Figure 2. Distribution of body mass data of (a) 1359 Garden Warblers trapped on Antikythira in spring 2007 and 2008, and (b) autumn departure body mass for 14 Garden Warblers in Crete 2004.

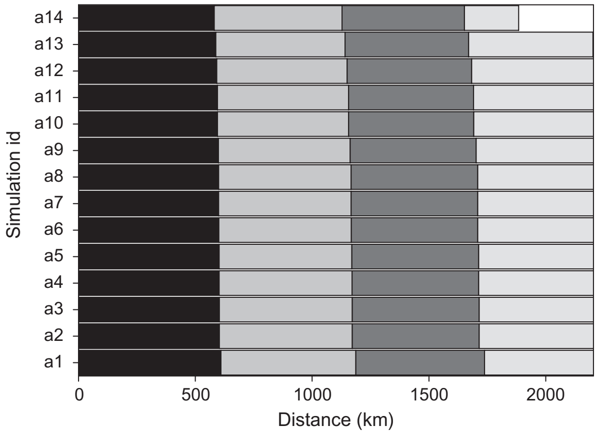

Figure 3. Distance covered by 14 simulated Garden Warblers during autumn, showing the length of each flight step with a wind assistance of 2.7 m/s (simulation id refers to Table 2).

out fuel) of 74.9% and an equivalent body mass of 27.28 g, was predicted to fail to cross the barrier (Table 2). The number of flight steps necessary for crossing the barrier with wind assistance included was reduced from five to four nights of flying (Fig. 3).

For the spring simulation, when birds were assumed to fly for 2 h more each night than during autumn, birds needed five nights of flying to cross the Sahara in still air and also if they had an average wind assistance of 0.5 m/s. The number of nights of flying was reduced to four when increasing the average wind assistance to 2.7 m/s. For a bird with an average size and body mass, the departure fuel load needed for crossing the desert in spring without wind assistance, which seems likely to be common, and arriving in Antikythira was estimated at 116.3%, corresponding to a departure body mass of 34.6 g (Table 3). Birds larger in size were estimated to need smaller fuel loads and smaller birds a larger fuel load. With an average wind assistance of 2.7 m/s, the departure fuel load of an average bird arriving in Antikythira was calculated to be around 84%, corresponding to a body mass of 29.4 g (Table 3). If a bird had at least some wind assistance during the desert crossing, a lower fuel load would be needed.

The calculations based on 1% body mass loss per hour of flight were consistent with those obtained using FLIGHT, even if the loss of body mass was larger by this method (Tables 2 and 3). For example, a bird starting off in autumn with a body mass of 32.7 g is estimated to arrive after four nights weighing 17.8 g, compared with 18.8 g according to FLIGHT. A bird departing in spring weighing 32.2 g without wind assistance is estimated to arrive after six nights with a body mass of 13.2 g, and the arrival body mass according to FLIGHT was 14.4 g. One difference between the two methods is that in the program FLIGHT, a bird will eventually run out of fuel depending on the input.

Table 2. Departure and arrival body mass and departure fuel loads of Garden Warblers simulated to cross the Sahara desert from Crete during autumn, with an average wind assistance of 3.5 m/s calculated with the FLIGHT program and with the empirical method of 1% body mass loss. Arrival body masses under still air conditions are also shown for the empirical method, while this was not possible for the other method since all birds run out of fuel before reaching the southern edge of the desert.

		FLIGHT			1% body mass loss	
id	Departure body mass (g)	Wing length (mm)	Departure fuel load (%)	Arrival body mass (g)	Arrival body mass (g)	Arrival body mass (g, still air)
1	32.7	79	115.1	18.8	17.8	14.8
2	30.6	78	105.6	17.6	16.7	13.8
3	31.0	79	104.2	17.9	16.9	14.0
4	30.4	78	104.0	17.5	16.6	13.8
5	30.2	78	102.6	17.4	16.5	13.7
6	31.8	81	100.1	18.4	17.3	14.4
8	31.1	81	95.5	17.8	17.0	14.1
9	31.5	82	94.4	18.1	17.2	14.3
7	30.9	80	97.9	17.8	16.8	14.0
11	29.7	80	90.3	16.8	16.2	13.4
10	29.2	79	92.2	16.5	15.9	13.2
12	29.0	80	85.9	16.3	15.8	13.1
13	28.7	81	80.3	16.1	15.6	13.0
14	27.3	80	74.9	–	14.9	12.4

–, Bird not able to cross the desert.

Table 3. Departure and arrival body mass and fuel loads in Garden Warblers simulated to cross the Sahara desert and arrive in Antikythira during spring, in still air and with an average wind assistance of 2.7 m/s calculated with the FLIGHT program and with the empirical method of 1% body mass loss.

ID	Wing length (mm)	Arrival body mass (g)	Departure fuel load (%)		Departure body mass (g)	
			In still air	With wind assistance	In still air	With wind assistance
FLIGHT						
1	81.4	17.7	140.6	100.0	38.5	32.0
2	79.4	16.0	126.4	93.2	34.8	29.7
3	81.4	16.0	116.3	83.8	34.6	29.4
4	83.3	16.0	105.5	76.9	34.4	28.3
5	81.4	14.4	101.6	75.6	32.2	29.4
1% body mass loss						
1	81.4	17.7	170.6	139.4	43.3	38.3
2	79.4	16.0	153.9	125.3	39.1	34.7
3	81.4	16.0	144.4	116.9	39.1	34.7
4	83.3	16.0	134.1	107.8	39.1	34.7
5	81.4	14.4	120.0	95.0	35.2	31.2

DISCUSSION

The flight range estimates, based on an intermittent flight strategy, suggest that the departure fuel loads estimated for Garden Warblers on Crete (Fransson *et al.* 2008) in autumn would be insufficient for birds in still air conditions, although the majority of the birds in the simulations were close to the southern edge of the desert when they ran out of fuel. Wind data for September 2005–2008 showed that northerly winds occur during most nights, which means that most birds will experience wind assistance during the desert crossing in autumn. By including the average wind assistance, only one of the birds in the simulations was unable to make the crossing successfully. This bird had the lowest departure fuel load, suggesting that some birds will depart with fuel loads that are too low for a successful passage. The flight range estimates calculated in this study give support to the autumn departure fuel loads estimated for Garden Warblers captured on Crete (Fransson *et al.* 2008).

The method used for the spring simulations differed from that used for autumn by using the condition of birds arriving after the desert crossing to estimate the fuel load they had when starting migration south of the desert. If birds in the simulations cross the desert without any overall wind assistance, they have to fly for five nights with an estimated departure fuel load above 110% and a corresponding body mass close to 35 g. The wind conditions in spring are less favourable than in autumn, and during the period 10 April–9 May 2005–2008, headwind conditions occurred on average at lower altitudes whereas the average wind assistance was close to zero at higher altitudes. Interestingly, both head- and tailwind conditions were found at different altitudes in 41% of nights. However, migrants have been shown to adjust flight altitudes in response to wind conditions when crossing the Sahara (Liechti & Schmaljohann 2007, Schmaljohann *et al.* 2009) and it is therefore possible that most birds experience at least some wind assistance during the desert crossing in spring. In the western Sahara, it has also been shown that a proportion of birds under favourable wind conditions prolong their migration until midday (Schmaljohann *et al.* 2007b). Taking this into account, it is therefore possible that our estimated departure fuel load in spring may be somewhat overestimated.

Migratory birds crossing the desert are proposed to be sensitive to water loss because of high ambient temperatures and this might affect flight altitudes (e.g. Carmi *et al.* 1992, Klaassen & Biebach 2000). However, a recent study showed that migrants in the western Sahara fly at much higher temperatures than earlier predicted, indicating that the rate of water loss is not restricting birds' choice of flight altitude (Schmaljohann *et al.* 2008, 2009), so energy minimization is likely to be more important than water loss during the barrier crossing.

It is reasonable to assume that in spring, birds depart from south of the Sahara when conditions are favourable (Richardson 1990), but birds about to cross the desert probably do not know what wind conditions they will experience during the coming 4–5 days. The variation in body mass observed in birds arriving to Antikythira might reflect different conditions experienced during the desert crossing, where birds arriving with very low body mass had experienced headwinds, whereas heavier birds had more wind assistance. There are few detailed studies available from south of the desert in spring, but Ottosson *et al.* (2005) present data from several sites in West Africa showing that some birds in Nigeria reached a fuel load of about 100%. They also concluded that heavy birds might have been underestimated in their trapping and that the true departure body mass could be as high as 25–30 g. Bairlein (1991) predicted a body mass at take-off from the southern edge of the desert to be 24.7 g. Grattarola *et al.* (1999) used > 27 g as a departure body mass from south of the desert. Salewski *et al.* (2009) give an average fat score of five (on a scale ranging from zero to eight) in Garden Warblers in the western Sahara in spring, about halfway across the desert, which means that they must have departed with quite extensive fuel loads from south of the desert. Our simulation results suggest that Garden Warblers crossing the eastern part of the Sahara desert need to have a much higher departure body mass, probably close to 35 g to be on the safe side. Depending on size, this represents fuel loads between 105 and 126% of body mass without fuel. It is interesting to note that maximum spring body masses of 35.5 and 37 g have been found in Garden Warblers in two studies in Nigeria (Bairlein 1991). In five sites south of the desert in northeastern Africa, high body mass was, however, not found in Garden Warblers (Yohannes *et al.* 2009). The reason for this may be that most of the fuel load needed to cross the desert is attained at specific places, only a few days before departure and is therefore not easily detected (Schaub & Jenni 2000, Fransson *et al.* 2008).

The recently applied method to estimate body mass loss during migration as 1% of body mass per hour of flight (e.g. Delingat *et al.* 2008, Salewski *et al.* 2010a) showed qualitative agreement with the results we received using the FLIGHT program. It is, however, notable that the empirical method gave consistently larger body mass losses. More specifically in our simulations, the body mass loss of birds calculated with the 1% body mass loss method, during autumn with wind assistance, was on average 2.68% (± 0.60%) greater when crossing the desert compared with simulations using the FLIGHT program. The corresponding comparison for spring showed that birds needed on average 16.66% (± 6.28%) larger departure body mass south of the Sahara to arrive in Antikythira with the observed values, if simulations were done with the empirical method compared with results received with FLIGHT. The FLIGHT program allows body mass loss during migration to vary according to the morphometric values of each bird, which is not the case in the empirical method, and the difference in the estimated departure body mass between the two methods increases as the wing length of the simulated bird increases. On the other hand, the empirical method allows birds to continue their migration regardless their body mass, while birds might run out of fuel when simulations are carried out with the FLIGHT program. This explains why the bird with a calculated departure body mass of 27.3 g (Table 2) was not able to cross the barrier when simulated using the FLIGHT program, whereas the bird managed to cross the desert and arrive with a body mass of 12.4 g according to the empirical method. Such low body mass values are regularly present on Antikythira during spring (Fig. 2; Barboutis *et al.* 2011) as well as at sites in the western part of the desert (Salewski *et al.* 2010a).

In conclusion, our results show that passerine birds following an intermittent flight strategy need considerable fuel loads to cross the eastern Sahara desert in both autumn and spring. The barrier crossing during spring seems to be more demanding, due to the larger distance to be covered and less favourable wind conditions, also reflected in the departure fuel loads estimated in this study. Habitats close to the southern edge of the desert are most certainly of utmost importance for migratory birds when preparing for the desert crossing in spring, and changes in those areas may affect many species with breeding populations in the western part of the Palaearctic region. Finally, it is clear that wind assistance is important for a successful desert crossing and it is reasonable to believe that in years with less favourable wind conditions in the Sahara, migrants will arrive with lower body masses and that this sometimes can result in increased mortality.

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