

Fuel load and flight ranges of blackcaps *Sylvia atricapilla* in northern Iberia during autumn and spring migrations

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Abstract Fuel accumulation, mainly as fatty acids, is one of the main characteristics of migratory birds. Studying to what extent each population or species manages fuel load and how it varies along routes of migration or between seasons (autumn and spring migrations) is crucial to our understanding of bird migration strategies. Our aim here was to analyse whether migratory blackcaps *Sylvia atricapilla* passing through northern Iberia differ in their mean fuel loads, rate of fuel accumulation and ‘potential’ flight ranges between migration seasons. Blackcaps were mist netted for 4 h-periods beginning at dawn from 16 September to 15 November 2003–2005, and from 1 March to 30 April 2004–2006 in a European Atlantic hedgerow at Loza, northern Iberia. Both fuel load and fuel deposition rate (this latter assessed with difference in body mass of within-season recaptured individuals) were higher in autumn than in spring. Possible hypotheses explaining these results could be seasonal-associated variations in food availability (likely lower during spring than during autumn), the fact that a fraction of the migrants captured in spring could breed close to the study area and different selective pressures for breeding and wintering [Current Zoology 55(6): 401–410, 2009].

Key words Blackcap, *Sylvia atricapilla*, Fuel load, Iberia, Migration, Stopover

Fuel accumulation is one of the main characteristics of migratory birds (Newton, 2008). It is mainly stored as fats, that release higher amounts of energy compared with proteins or carbohydrates (Klaassen et al., 1997a). This energy is needed to support long flights that usually take several hours, as well as to survive when landing in unfamiliar areas where migrants need some time to find or to be able to access food (Newton, 2008). Studying to what extent each population or species manages the fuel load and how it varies along routes or among seasons can provide basic insights into the strategies of migration (Schaub and Jenni, 2000a).

The blackcap *Sylvia atricapilla* is a widespread Palearctic songbird, breeding in most of Europe, Asia (up to 85°E), northern Africa and the Macaronesian region (Shirihai et al., 2001). The West European Blackcap population is formed by both birds that overwinter within the circum-Mediterranean region (principally in southern Iberia; Cantos, 1995) and in the tropical savannas from West Africa; this latter population is likely much less numerous (Shirihai et al., 2001). Thus, during autumn and spring, northern Iberia receives an influx of Blackcaps moving, respectively, to or from their wintering areas farther south. As a border region of one of the main wintering regions for the species, northern Iberia offers a good location for analyses of Blackcap migration strategies.

In autumn, mean body mass for Blackcaps decreases from north to south in West Europe: southern Britain,

20 g (Langslow, 1976); northern Iberia, 18.5 g (Grandío, 1997; Arizaga et al., 2008), southern Iberia, 18.5 g (Langslow, 1976). As Blackcaps crossing West Europe belong to a single western European population (Shirihai et al., 2001), body mass here represents (or can be used as a surrogate of) fuel load, that is mainly stored as fats (Newton, 2008). This suggests that Blackcaps gain enough fuel in or near their breeding areas to reach southern Europe, likely without needing to gain much fuel at stopover localities (Ellegren and Fransson, 1992). In contrast, literature relative to Blackcap’s fuel load and fuel deposition rate during the spring migration period is chiefly focused on stopover localities placed just before and after the Sahara Desert (Maitav and Izhaki, 1994; Hjort et al., 1996; Izhaki and Maitav, 1998; Gannes, 2002), and only one study deals with fuel analyses for mainland West Europe (Langslow, 1976). This latter study showed that just before the spring migration period, resident wintering migrants gained a high body mass in southern Europe (normally up to 24 g), arriving in northern Europe with a mean body mass between 16.5 and 19.5 g (Langslow, 1976). This suggests that the Blackcap may accumulate as much fuel as needed in southern Europe to arrive in the breeding quarters in northern Europe without needing to stopover to refuel. However, we have no data from intermediate regions to support this hypothesis. Compared with autumn, the spring migration period has been reported to be faster (Fransson, 1995), supporting the

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hypothesis that the urge to arrive as soon as possible to their goal areas is higher in spring. Assuming that a high fuel load allows maintenance of higher migration speeds, two hypotheses are proposed: a higher fuel load in spring relative to autumn is expected if this region is used to consistently refuel before crossing Europe or, conversely, fuel load is mainly stored in winter as evidenced by lower fuel loads during spring (Langslow, 1976) before the return to breeding quarters.

In autumn, blackcaps change to a diet of fruits, a very abundant food source across Europe during this time that allows them to gain fuel very fast. Although this diet is likely to allow high rates of fuel accumulation across Europe, existing data indicate that the rate of fuel deposition diminishes from northern (0.72 g/day; Langslow, 1976) to southern Europe (0.20 g/day; Arizaga et al., 2008). Rate of fuel accumulation is unknown for the spring migration period in West Europe.

Alerstam and Lindström (1990) proposed that migrants tend to minimize time, global energy cost, flight cost or predation during migration. In time or in global energy minimisers, fuel deposition rate is hypothesised to be positively correlated with fuel load when birds leave a stopover site. By contrast, when flight energy cost or predation are minimised, a bird would take more benefits by reducing the over-load associated cost, so in this case departure fuel load is independent from the fuel deposition rate. To test this hypothesis adequately, fuel at the day of departure must be known (Alerstam and Lindström, 1990; see for examples Bayly, 2006; Delingat et al., 2006). This cannot be obtained from ordinary ringing sessions due to the fact that the birds can remain at a stopover site after the last capture (Schaub et al., 2001) and the rate of fuel accumulation can be non-linear (Fransson, 1998). In blackcaps stopping-over in northern Iberia, however, rate of mass deposition was observed to increase linearly with time (Arizaga et al., 2008), so in this case data from ordinary ringing sessions could be valid to estimate an optimal strategy.

To summarise, we analyse here whether migratory Blackcaps at a stopover site in northern Iberia show different fuel loads and deposition rates between the autumn and spring periods of passage.

1 Materials and Methods

1.1 Sampling site, protocol

The sampling location was an approximately 50 ha fenced-area at Loza (42°50' N 01°43' W, 415 m a. s. l.), 5 km west of Pamplona city (Navarra). Vegetation in this area is formed by reed-beds (a small patch of c. a. 5 ha) surrounded by prairies with Eurosiberian shrubs, mainly *Rosaceae* (genus *Prunus*, *Rosa*, *Rubus*, *Crataegus*) and *Sambucus* spp., as well as some elms *Ulmus* spp. In summer and autumn, shrubs contain abundant fleshy fruits such as elderberries and

blackberries, commonly consumed by several passerine species to refuel. Such fruits are absent in spring, a period when leaves are also absent until the middle of season and when floods, cold spells, or even small snow falls that hamper the occurrence of high numbers of insects (JA per. obs.) are frequent. During this period, Blackcaps feed chiefly on flowers from *Prunus* shrubs (JA per. obs.). Loza is used by Blackcaps mainly as a stopover site, though also by a small local breeding population that leaves this area during the autumn (Arizaga et al. unpubl. data). Regardless, this population is marginal in size compared with the huge number of migrants that appear in autumn and spring. No wintering blackcaps occur at Loza.

Blackcaps were captured with mist nets (60 linear m disposed in four sets) placed across a hedgerow-line, both during autumn (from 16 September to 15 November 2003 – 2005) and spring migrations (from 1 March to 30 April 2004 – 2006), either 4 days a week (autumn 2003 – 2004, spring 2004 – 2005) or in daily trapping sessions (autumn 2005, spring 2006), for 4 h-periods beginning at dawn. Hereafter, we refer to time elapsed from September to April as a 'year'.

Once captured, each bird was ringed and its sex and age were determined (Svensson, 1996), using two age categories: immature (with juvenile primary feathers; birds in their first autumn or spring; EURING code 3/5), and adult birds (birds captured after their complete moult; EURING code 4/6). We recorded wing length (± 0.5 mm), tarsus length (± 0.1 mm), body mass (± 0.1 g), moult state (checking if birds showed active moult, both for body and flight feathers) and fat score (scaled from 0 to 8; ± 0.5) (Kaiser, 1993; Svensson, 1996). All measurements were recorded by JA.

Concerning the non-moulting birds with their sex and age known and all measurements recorded (body mass, tarsus length), we obtained 2774 captures of 2635 specimens (autumn: 1973; spring: 662) and 139 recaptures (autumn: 122; spring: 17).

1.2 Fuel load

Captures from trapping sessions at a stopover site entail some restrictions that must be considered. In particular, both the first and last captures are often not obtained at exact dates of arrival or departure (Schaub et al., 2001), so detailed patterns of individual time-associated fuel variations cannot be obtained for the entire stopover period for each bird. Thus, we are aiming for a general insight into the mean fuel load and fuel deposition rate for our population (Schaub and Jenni, 2000 a, b, 2001).

To assess fuel load we considered: (1) body mass controlled for body size and (2) fuel load (in percentage) over lean body mass. This last variable was not included into the models but calculated due to its usefulness for comparison with other bird species.

To determine the best variable to estimate body size , we used a subset of our data that only considered those birds without any visible fat content (fat = 0 ; $n = 84$) and regressed body mass on wing and tarsus length . We did not consider moulting birds since they could show proportionally higher body masses (Newton , 1968 ; Chilgren , 1977). Tarsus length was better than wing length to assess body size (tarsus length : $r = 0.514$, $P < 0.001$; wing length : $r = 0.306$, $P = 0.005$), and not less predictive than a multivariate regression that included both wing and tarsus length ($r = 0.546$, $P < 0.001$). Thus , we used tarsus length to assess body size (Senar and Pascual , 1997).

To estimate fuel load over the lean body mass , we used this equation : $100 \times [(\text{actual body mass} - \text{lean body mass}) / \text{lean body mass}]$ (Alerstam and Lindström , 1990). Technically , lean mass is defined as total mass minus fat mass . However , fuel accumulation in migrants is also due to the accumulation of proteins , and this can change lean mass . Therefore , we defined lean mass as body mass before starting fuel accumulation . To assess lean body mass we used a function obtained after

regressing body mass on tarsus length for those birds without any visible fat content : $r = 0.514$, $F_{1,83} = 29.535$, $P < 0.001$; lean body mass = $(0.853 \times \text{tarsus length}) - 0.977$.

1.3 Fuel deposition rate

We recaptured 139 birds (both age and sex known and body mass and tarsus length measured) to assess rate of mass accumulation . We calculated mass deposition rate by dividing the difference in mass by the difference in days from the last to first capture event . To assess whether the capture time (hours 1st to 4th) affected body mass (Cherry , 1982 ; Carlisle et al . , 2005) , we regressed body mass on catching hour and tarsus length and determined that capture time did not affect body mass ($r = 0.160$, $F_{1,857} = 11.268$, $P < 0.001$; standardized B parameters : tarsus length , 0.145 , $P < 0.001$; hour , 0.067 , $P = 0.048$). Thus , body mass was not controlled for catching time . Two outliers were removed from the data set owing to their very long stopover duration (time elapsed between the first and last captures : 24 days during autumn , Fig. 1).

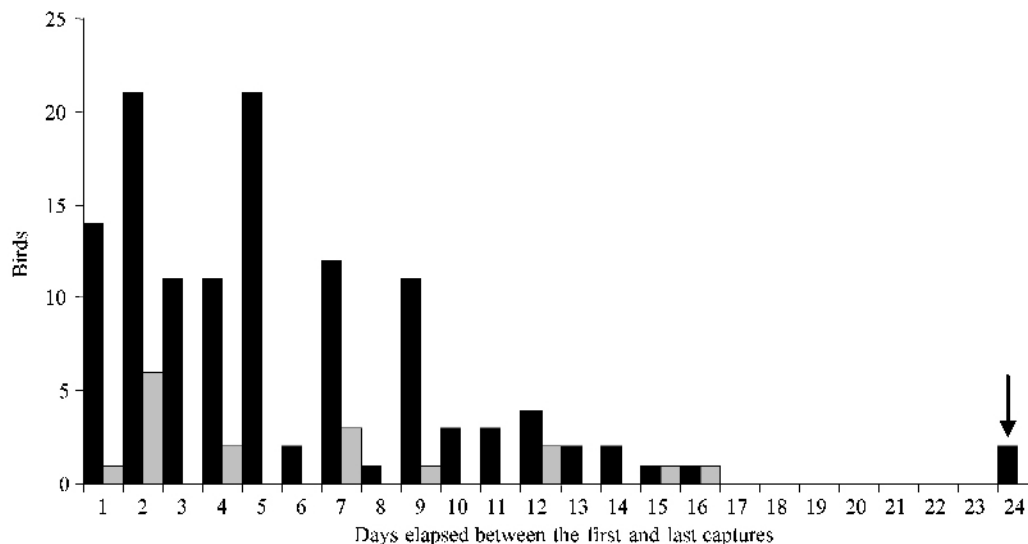


Fig.1 Minimum stopover durations (time elapsed between the first and last captures) of blackcaps at Loza , during autumn and spring (grey)

Arrow shows two birds (extreme outliers) with a very long stopover .

1.4 Modelling

Rate of mass accumulation fit the normal distribution (Kolmogorov test , $P > 0.05$) and , though body mass showed a slight positive skew from this distribution (Kolmogorov test : $P < 0.05$), its SD was low ($SD/\text{mean} : 0.104$). Thus , parametric Univariate Linear Models , that accept slight biases from a normal distribution , with normal errors were used to test for the effect of period , year , age and sex on body mass and mass deposition rate (year was only considered for body mass due to a constraint in sample size for mass deposition rate) (Sokal and Rohlf , 1995). Concerning models of

body mass , only the data on the first capture event for each bird were considered ($n = 2635$).

We employed a model-fitting approach using Akaike Information Criterion corrected for small sample sizes (AICc) to examine factors influencing body mass (Atkinson et al . , 2007). Thus , models were ranked by AICc , and the one with the lowest AICc was selected as the final best-fit model . Models with a difference in AICc < 2 from the first model did not differ statistically (Burnham and Anderson , 1998).

The software SPSS v. 15.0 for Windows was used to calculate the models and means are shown with \pm SE .

1.5 Flight ranges

To estimate the flight ranges in relation to fuel load we used the FLIGHT software v. 1.17 (Pennycuik, 1998). We considered zero crop mass (when a bird leaves a stopover site its crop is assumed to be empty), 0.2 m of wing span and 0.0078 m² of wing area (average values obtained from a sample of 11 Blackcaps, JA unpubl. data), flying at 1000 m a. s. l. (c. a. 585 m above ground level at Loza) (Newton, 2008), in a standard atmosphere at this height of 8.5 °C, 898 hPa, and 1.11 kg/m³ (Pennycuik, 1998). To estimate flight ranges, FLIGHT states that body mass is formed by fats (mass of stored fats usable as fuel during flight), flight muscle mass and the airframe mass (skeletal, feathers and organs mass). Fraction of flight muscle and airframe mass over total mass are determined by the software and, hence, only the fat mass remains to be introduced. An increase of body mass over lean mass is mainly due to fat, though also to proteins (Klaassen et al., 1997). As proteins release less energy than fats, an over-estimation of flight ranges is expected if fuel load over lean body mass is considered to be formed by only fats. Thus, to estimate the fat mass we considered that a 18% of the fuel load was formed by proteins (Klaassen et al., 1997b): proportion of fats over body mass = $1 - [1 / ([0.82 \times \text{proportion of fuel load over lean body mass}] + 1)]$.

2 Results

2.1 Fuel load and flight ranges

The model best fitting the data was one in which fuel load varied between periods, between age classes and among years (Table 1; ANOVA: tarsus length, $F_{1,2634} = 77.542$, $P < 0.001$; period, $F_{1,2634} = 51.781$, $P < 0.001$; year, $F_{3,2634} = 20.163$, $P < 0.001$; age, $F_{1,2634}$

= 21.910, $P < 0.001$; period \times year, $F_{3,2634} = 13.492$, $P < 0.001$; rest of interactions: $P > 0.05$). After controlling for body size, body mass was higher in autumn in adults, and during 2004–2005 and 2005–2006 (Fig. 2). Lean body mass did not vary between age classes ($t_{2633} = 1.779$; $P = 0.075$), supporting the hypothesis that difference in body mass between age classes was due to a difference in fuel stores. Histograms of body mass for spring and autumn are shown with more detail in Fig. 3.

Table 1 AICc scores for models examining variations in body mass in blackcaps passing through a stopover site in northern Iberia

Models	AICc	Δ AICc
Period, Year, Age	10689.934	0.000
Period, Year, Age, Sex	10702.040	12.106
Period, Year	10709.288	19.354
Period, Year, Sex	10712.401	22.467
Period, Age	10744.336	54.402
Period, Age, Sex	10748.476	58.542
Period	10760.595	70.661
Period, Sex	10762.131	72.197
Year, Age	10787.517	97.583
Year, Age, Sex	10797.989	108.055

Within models, we considered both the main effects and all the possible interactions among the factors considered. Thus, the first model included the effect of period, year, and age, as well as the double and triple interactions. We included tarsus length as a covariate in all models. From 15 models tested, only the ten with the lowest AICc values (i. e. best fitting data) have been included.

Fuel over lean body mass in the autumn was $13.8 \pm 0.3\%$, and in the spring was $8.6 \pm 0.5\%$, giving flight ranges (under still air conditions) of 684 and 417 km in

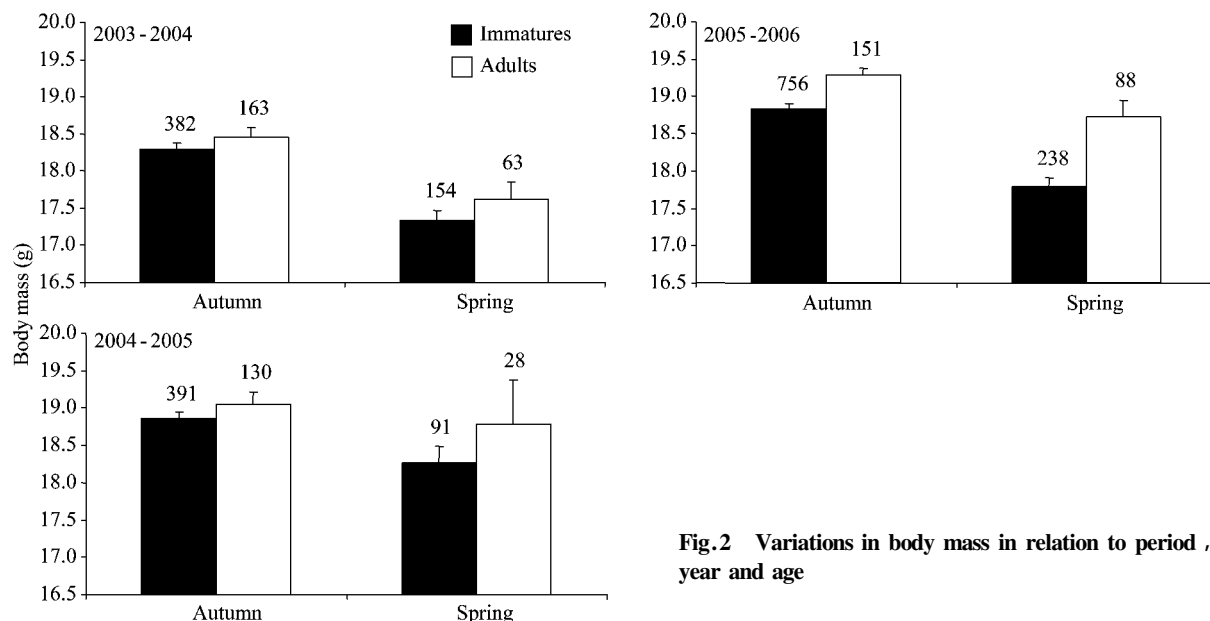


Fig. 2 Variations in body mass in relation to period, year and age

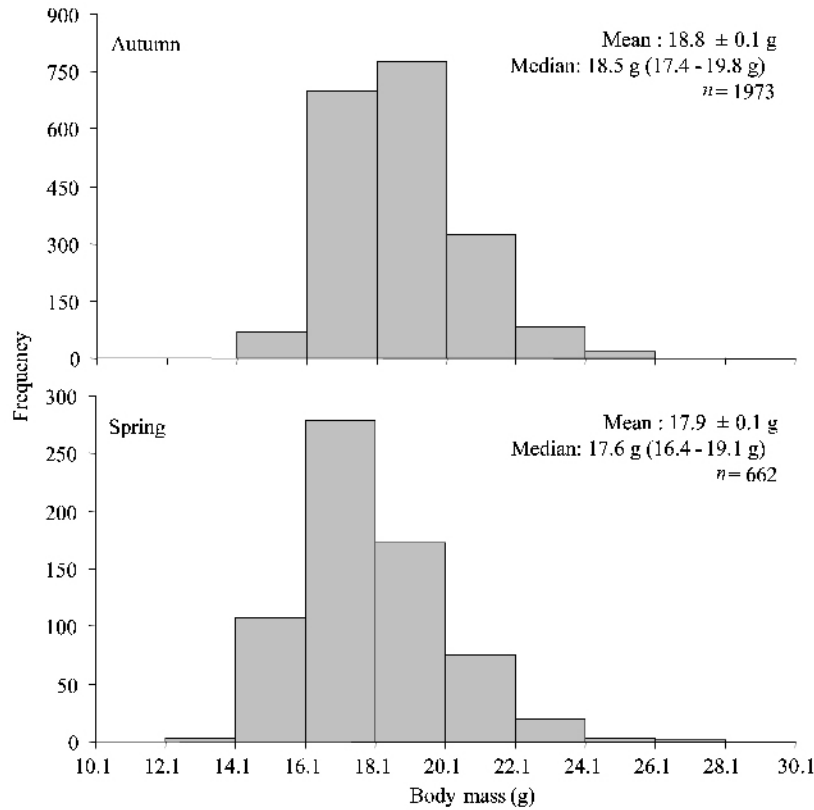


Fig.3 Distribution of body mass within the population during the autumn and spring migrations
 Mean (± SE) and median (with percentile 25 and 75) values have been also included.

autumn and spring , respectively. It is likely that these samples would include birds ranging from those just arrived to birds just about to depart. Thus , we recalculated the flight ranges for the 25% heaviest fraction within each period (Ellegren and Fransson 1992) , and the new fuel loads over the lean body mass were $28.2 \pm 0.4\%$ ($n = 494$) in the autumn and $25.1 \pm 0.7\%$ ($n = 166$) in spring , giving flight ranges of 1410 and 1249 km during the autumn and spring migrations , respectively.

Table 2 Relationship between body mass , body size (tarsus length) and date

Period	Statistics and Parameters	2003 – 2004	2004 – 2005	2005 – 2006
Autumn	<i>r</i>	0.251***	0.309***	0.258***
	<i>N</i>	545	521	907
	<i>B</i> (tarsus length)	0.235***	0.240***	0.116***
	<i>B</i> (date)	0.097*	0.213***	0.224***
Spring	<i>r</i>	0.337***	0.490	0.307
	<i>N</i>	217	119	326
	<i>B</i> (tarsus length)	0.201**	0.114	0.138**
	<i>B</i> (date)	- 0.258***	- 0.477***	- 0.286***

We show Pearson’s correlation coefficient (*r*) , sample size and the standardised *B* parameters of the function and their corresponding *P* values (*** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$).

Body mass was positively correlated with the date during autumn , and negatively during spring (Table 2) ,

suggesting that late-migrants in autumn were more fuel loaded than migrants passing over earlier , and the opposite trend occurred during spring.

2.2 Fuel deposition rate

The best-fit model only considered the effect of period on mass deposition rate (Table 3). Thus , the mass deposition rate was higher during autumn (0.14 ± 0.03 g/day ; range : - 1.10 to 1.15 ; $n = 120$) than during spring ($- 0.17 \pm 0.05$ g/day ; range : - 1.13 to 0.20 ; $n = 17$; ANOVA : Period , $F_{1,136} = 10.153$, $P = 0.002$; Tarsus length , $F_{1,136} = 0.475$, $P = 0.492$) . The proportion of migrants with negative mass deposition rates was lower in autumn (35.0%) than in spring (70.6% ; $\chi^2_1 = 7.898$, $P = 0.005$) , hence the low rate observed during spring was due to a higher proportion of migrants that lost mass. To gain a more accurate picture of fuelling patterns , we modelled body mass change against days between captures , mass and date at first capture event. In autumn , the only significant effect was the number of days from the first capture event (function : $r = 0.289$, $P = 0.017$; standardised *B* parameters : mass , - 0.152 , $P = 0.098$; date , - 0.030 , $P = 0.739$; days , 0.211 , $P = 0.023$; Fig.4). Conversely , in spring we did not find a significant correlation between mass deposition rate and days between captures , mass and date (function : $r = 0.614$, $P = 0.095$; standardized *B* parameters : mass , - 0.597 , $P = 0.028$; date , 0.004 ,

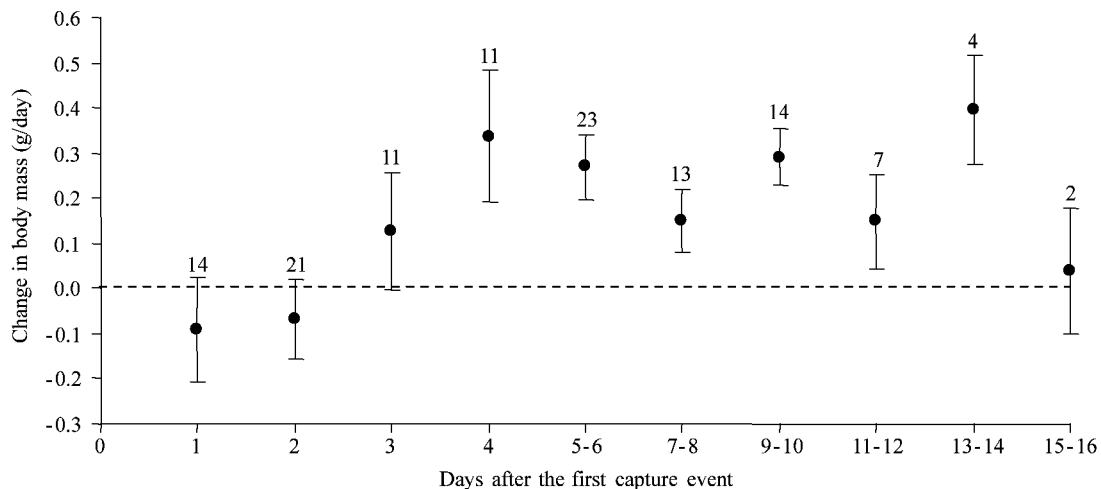


Fig. 4 Patterns of mass deposition rate in relation to number of days elapsed between the first and last captures

Data were lumped into two days for recaptures obtained after five or more days to increase sample size. Rate of mass deposition was positively correlated with days ($r = 0.243$, $P = 0.007$), this correlation became non-significant when recaptures of one or two days were not considered ($r = 0.002$, $P = 0.987$), supporting the idea that the mass deposition rate was constant and positive for recaptures of ≥ 3 days.

$P = 0.988$; days, 0.271 , $P = 0.263$).

Table 3 AICc scores for models examining variations in body mass in blackcaps passing through a stopover site in northern Iberia

Models	AICc	Δ AICc
Period	128.396	0.000
Period, Sex	131.012	2.616
Period, Age	131.700	3.304
Sex	136.451	8.055
Age	137.429	9.033
Period, Age, Sex	138.193	9.797
Age, Sex	139.477	11.081

Model structure as in Table 1. We included tarsus length as a covariate in all models.

Rate of mass deposition was positively correlated with body mass at last capture during autumn (Fig. 5). This relationship tended to be slightly more marked when only data from birds with a positive rate were analysed ($r_p = 0.581$, $P < 0.001$, $n = 78$), and was not significant when only birds with null or negative mass gain were considered ($r_p = 0.043$, $P = 0.786$, $n = 42$), or during spring ($r_p = 0.255$, $P = 0.324$, $n = 17$; Fig. 4). Nonetheless, during spring, we observed a bird with a very negative mass deposition rate (-1.13 g/day). When this individual was removed from the data set, the correlation was significant (Fig. 5).

3 Discussion

3.1 Autumn migration

Blackcaps passing through Loza in northern Iberia showed a mean body mass of 18.8 g, equivalent to a fuel load over lean body mass of nearly 15% (30% for the 25% heaviest fraction of migrants). Blackcaps captured in southern Britain during the autumn migration period showed a higher mean body mass (20 g; Langslow,

1976), supporting the hypothesis of decreasing fuel load as they approach their wintering areas. However, such a decrease does not seem to be dramatic. Although some birds could have left the area with a fuel load of around 15%, the heaviest fraction was more likely to be formed by birds just about to depart (Ellegren and Fransson, 1992). A fuel load of 35% is high enough to arrive in tropical Africa crossing the Sahara Desert and, thus, it can be stated that blackcaps are not avoiding a high fuel load when crossing Europe.

With a fuel load of 15%, a Blackcap would be able to cover a distance of more than 600 km under still air conditions and, thus, many migrants stopping-over in northern Iberia would be able to reach southern Iberia (Gibraltar is c. a. 1000 km away from Loza) without needing to refuel. Such estimation may be higher if the fuel load was formed by less than 18% of proteins (Klaassen et al., 1997a) or/and in the case of flying with tail-wind assistance (Akesson and Hedenstrom, 2000; Akesson et al., 2001, 2002; Barriocanal et al., 2002).

Blackcaps with a fuel load of around 30% could theoretically reach north-western Africa from northern Iberia in a single direct flight or, more likely, in several short flights interrupted by one-day or some multi-day stopovers. Such fuel load should be particularly advantageous for the long-distance fraction of Blackcaps that overwinter in tropical Africa (Shirihai et al., 2001). Probably, most of them would need to refuel only once before the Sahara Desert, presumably in southern Iberia or in northern Africa. However, it cannot be rejected that some birds could gain in northern Iberia as much fuel as required to directly reach tropical Africa. Indeed, one of our birds was found to carry a fuel load of almost 70% over its lean mass that would allow it to cover a distance of over 4000 km, which is sufficient to reach tropical

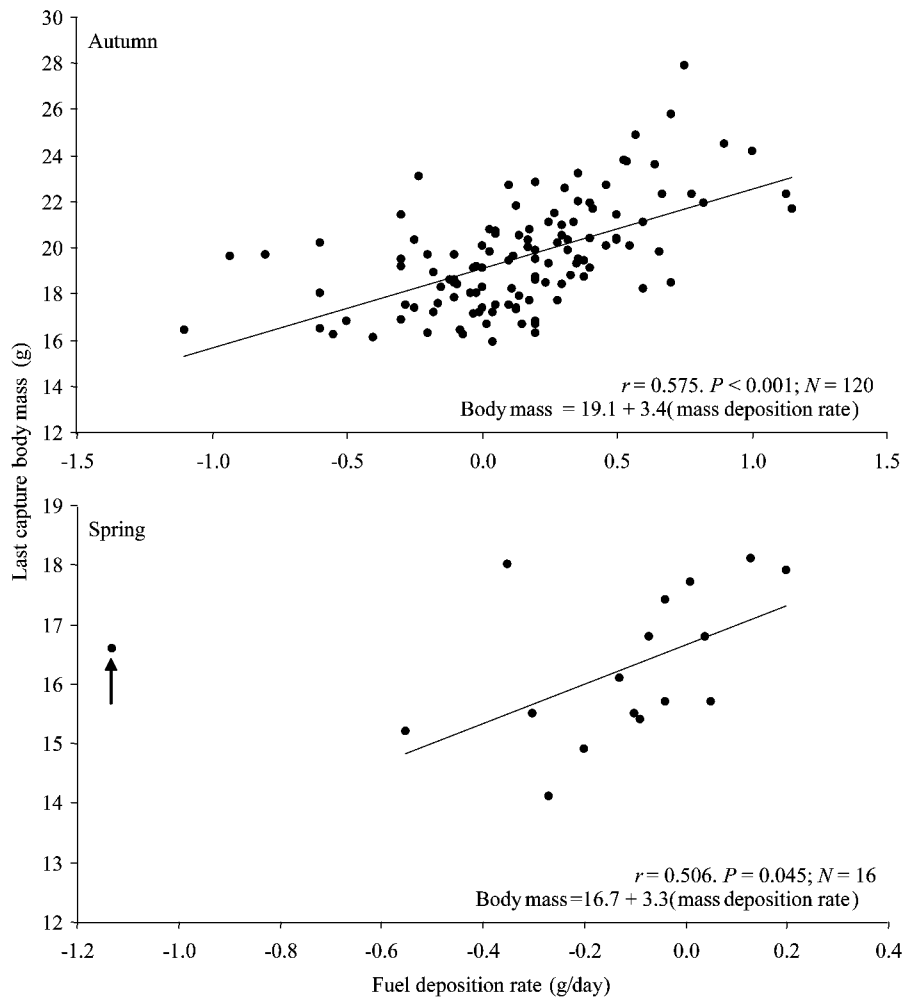


Fig.5 Relationship between last capture body mass and mass deposition rate in migratory blackcaps at Loza , during autumn and spring migrations

In spring , the arrow shows a bird (outlier) with an extremely low mass deposition rate.

Africa.

Once controlled for body size , body mass was observed to be positively correlated with the date in autumn , indicating that late migrants were more fuel loaded than earlier ones . Late migrants were more likely to suffer a higher time-constraint in order to arrive to their wintering areas in time , so a higher fuel load could allow them to keep higher speeds of migration . It seems probable that Blackcaps with higher body masses arrived at Loza before being first caught (Arizaga et al . , 2008) . However , late migrants did not refuel faster and did not stopover for longer periods (J . Arizaga , unpubl . data) . Thus , they were more likely to gain a sufficiently high fuel load before arriving in northern Iberia .

Mean rate of mass accumulation (0.14 g/day) was lower than that found in other warbler species with similar habitat- and food-requirements , such as Garden Warbler *Sylvia borin* , during the autumn migration period (0.48 g/day ; Schaub and Jenni , 2001) . Thus , these differences could be due to the fact that all west European

garden warblers are tropical migrants , so it could be advantageous for them to gain fuel at a high rate , allowing them to minimise the duration of migration (Rubolini et al . , 2002 , Fransson et al . , 2006 , Fransson et al . , 2008) . Rate of mass deposition was positively correlated with the days elapsed between captures . Thus , the initial low , negative mass deposition rate observed until the third day (Fig.4) after the first capture was likely reflecting a settlement-associated cost of energy (Alerstam and Lindström , 1990 ; Hedenström and Alerstam , 1997) or/ and a physiological constraint to rebuilding the gut following a migratory flight (Karasov et al . , 2004) . Furthermore , birds with short stopovers could be , rather than fuelling , waiting for adequate meteorological conditions before continuing . In this case , a null or even negative fuel deposition rate is normal (Fransson , 1998) . Thus , after removing birds recaptured one or two days after the first capture , the mass deposition rate was observed to increase up to 0.24 g/day , supporting the hypotheses that Blackcaps were able to accumulate fuel at

a fast rate, though this value was still lower than the one observed in some long-distance migrants that also feed on very abundant food resources (Schaub and Jenni, 2000b). By having these comparatively lower rates Blackcaps, which do not need to put on very large fuel loads, may avoid predation risks associated with higher fuel loads.

3.2 Spring migration

Contrary to autumn, mean body mass in spring (17.9 g) was lower and, consequently, the estimated potential flight ranges were shorter. Thus, with a mean fuel load of 8.6% over lean body mass, a bird would need to stopover in France to refuel before reaching its breeding areas further north if this was the case. Considering those birds in the 25% heaviest fraction, this range would increase to more than 1000 km, but even in this case, the distance was lower than that found during autumn. The mean body mass of 17.9 g is within the ranges reported in Blackcaps arriving to southern Britain during spring. Though we cannot reject the hypothesis that some birds in southern Iberia could gain sufficient fuel to arrive in northern Europe without needing to refuel (Langslow, 1976), a fraction of the population was apparently forced to migrate at a lower speed.

In accordance with the low fuel stores, mass deposition rates were also lower in spring than in autumn. Indeed, the mean rate was negative and most birds lost mass when stopping-over in Loza. Sample size was very low in spring (only 17 recaptures in three years), so this result must be cautiously considered. Such negative rates could be biased by local birds that could breed in close proximity to Loza, and which accordingly would not need to keep a high fuel load or fuel deposition rate. In line with this scenario, we observed that some males were starting to settle and establish a territory at Loza as early as late-March (JA unpubl. data). Moreover, we cannot reject the hypothesis that some migrants could follow other routes during spring compared with the ones used in autumn, as observed in other passerine birds that cross Iberia (Bueno, 1991, 1992; Cantos, 1998).

High fuel accumulation in northern Iberia in late-winter or early spring would be hampered by food-scarcity. This scarcity is likely to be a strong constraint impeding fuel accumulation during spring. Fruits are not available in spring and, until mid-spring, leaves are absent from the vegetation and cold spells are common. Insect availability, hence, is also likely to be very scarce during early spring. Whether such scenario is widespread across Europe, or is particular to Loza or northern Iberia, is a question that must be considered in future analyses.

3.3 Further considerations of fuel load and fuel deposition rate

The best-fit models for our data excluded the effect of sex on both body mass and mass deposition rate, suggesting that, during migration period, sex does not

play any relevant role in fuel management. In contrast, adults were more fuel loaded than juveniles during both autumn and spring, although they did not show a higher mass deposition rate at Loza. This suggests that the difference in fuel load originated before reaching Loza (Turrian and Jenni, 1991). Moreover, if socially mediated hierarchical patterns to access to food occur at Loza (Moore et al., 2003), they seem to be irrelevant to variation in fuel load. A superabundance of fleshy fruits in autumn could render irrelevant socially associated asymmetric contests for access to food (Moore et al., 2003). Contrary to expectations, although food was very likely scarce in spring, the result was the same as that observed in autumn when food is probably more abundant. Both the lower sample sizes and a likely bias caused by local breeding birds rather than true fuelling migrants could explain these results, but further studies are needed to clarify this question.

Rate of mass deposition was positively correlated with body mass at last capture both in autumn and spring. Assuming that mass is gained linearly with time (Arizaga et al. 2008), this result fits the time-minimizing strategy (Alerstam and Lindström, 1990). Such a strategy is probably very advantageous in spring (birds arriving early to the breeding quarters are more likely to find a mate or to establish a territory; Kokko, 1999; Kokko et al., 2006), and it has been also observed in other birds (Delingat et al., 2006). However, causes explaining a time-minimising strategy in autumn are far from completely understood. Reed warblers *Acrocephalus scirpaceus* were reported to optimise time during the autumn migration period (Bayly, 2006), a strategy that could make sense in birds that overwinter in tropical Africa, as also do some Blackcaps (Shirihai et al., 2001). However, most Blackcaps seem to overwinter within the circum-Mediterranean region, so they should not suffer from such a time-constraint unless birds arriving first to their wintering areas could be favoured for territory occupancy (Belda et al., 2007). Moreover, the slope was very similar in both periods, supporting the hypothesis that migratory Blackcaps responded similarly to time pressures during autumn and spring.

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