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 in 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.[1997]. 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 Grandio[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] Gaines[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, if 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 minimizers 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 Rose 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 net 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 migration 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-mouling 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 Jemni 2000 a b 2001.

To assess fuel load we considered body mass controlled for body size and 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 1997. 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 × actual body mass lean body mass Alersalm 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_{100} = 29.535 P < 0.001 lean body mass = 0.853 × 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_{100} = 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 bird 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/ 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 ± SE.
1.5 Flight ranges

To estimate the flight ranges in relation to fuel load we used the FLIGHT software v. 1.17 [Pennycuick 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 m\(^2\) of wing area average values obtained from a sample of 11 Blackcaps [JA unpubl. data] flying at 1000 m a.s. 1 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/m\(^3\) [Pennycuick 1998]. To estimate flight ranges FLIGHT states that body mass is formed by fats mass of stored fats usable as fuel during 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. 1997] a proportion of fats over body mass = 1 - 1/0.82 \times\text{proportion of fuel load over lean body mass} = 1.04.

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 [\(F_{1,364} = 77.542, P < 0.001\) period \(F_{1,364} = 51.781, P < 0.001\) year \(F_{1,364} = 20.163, P < 0.001\) age \(F_{1,364} = 21.910, P < 0.001\) period \times year \(F_{3,364} = 13.492, P < 0.001\) rest of interactions \(F_{20,364} = 3.95, P > 0.05\) . 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 \(t_{2,364} = 1.779, P = 0.075\) 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

<table>
<thead>
<tr>
<th>Models</th>
<th>AICc</th>
<th>ΔAICc</th>
</tr>
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<tbody>
<tr>
<td>Period</td>
<td>10689.934</td>
<td>0.000</td>
</tr>
<tr>
<td>Period Year Age</td>
<td>10702.040</td>
<td>12.106</td>
</tr>
<tr>
<td>Period Year</td>
<td>10709.288</td>
<td>19.354</td>
</tr>
<tr>
<td>Period Year Sex</td>
<td>10712.401</td>
<td>22.467</td>
</tr>
<tr>
<td>Period Age</td>
<td>10744.336</td>
<td>54.402</td>
</tr>
<tr>
<td>Period Age Sex</td>
<td>10748.476</td>
<td>58.542</td>
</tr>
<tr>
<td>Period</td>
<td>10760.595</td>
<td>70.661</td>
</tr>
<tr>
<td>Period Sex</td>
<td>10762.131</td>
<td>72.197</td>
</tr>
<tr>
<td>Year Age</td>
<td>10787.517</td>
<td>97.583</td>
</tr>
<tr>
<td>Year Age Sex</td>
<td>10797.989</td>
<td>108.055</td>
</tr>
</tbody>
</table>

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 value i. e. best fitting data have been included.

Fuel over lean body mass in the autumn was 13.8 ± 0.3% and in the spring was 8.6 ± 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](image-url)
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 ± 0.4% n = 494 in the autumn and 25.1 ± 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

<table>
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<tbody>
<tr>
<td>Autumn</td>
<td>r</td>
<td>0.251***</td>
<td>0.309***</td>
<td>0.258***</td>
</tr>
<tr>
<td></td>
<td>N</td>
<td>545</td>
<td>521</td>
<td>907</td>
</tr>
<tr>
<td></td>
<td>tarsus length</td>
<td>0.235***</td>
<td>0.240***</td>
<td>0.116***</td>
</tr>
<tr>
<td></td>
<td>date</td>
<td>0.097*</td>
<td>0.213***</td>
<td>0.224***</td>
</tr>
<tr>
<td>Spring</td>
<td>r</td>
<td>0.337***</td>
<td>0.490</td>
<td>0.307</td>
</tr>
<tr>
<td></td>
<td>N</td>
<td>217</td>
<td>119</td>
<td>326</td>
</tr>
<tr>
<td></td>
<td>tarsus length</td>
<td>0.201**</td>
<td>0.114</td>
<td>0.138***</td>
</tr>
<tr>
<td></td>
<td>date</td>
<td>–0.258***</td>
<td>–0.477***</td>
<td>–0.286***</td>
</tr>
</tbody>
</table>

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 ± 0.05 g/day range 1.13 to 0.20 n = 17 ANOVA Period F1,136 = 10.153 P = 0.002 Tarsus length F1,36 = 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% & $\chi^2$ = 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 $P = 0.211$ 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 0.397 $P = 0.028$ 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 day, $r = 0.234 \quad P = 0.007$, this correlation became non-significant when recaptures of one or two days were not considered, $r = 0.002 \quad P = 0.987$, supporting the idea that the mass deposition rate was constant and positive for recaptures of $\geq 3$ days.

$P = 0.988$ days $0.271 \quad P = 0.263$.  

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

<table>
<thead>
<tr>
<th>Models</th>
<th>AICc</th>
<th>ΔAICc</th>
</tr>
</thead>
<tbody>
<tr>
<td>Period</td>
<td>128.396</td>
<td>0.000</td>
</tr>
<tr>
<td>Period Sex</td>
<td>131.012</td>
<td>2.616</td>
</tr>
<tr>
<td>Period Age</td>
<td>131.700</td>
<td>3.304</td>
</tr>
<tr>
<td>Sex</td>
<td>136.451</td>
<td>8.055</td>
</tr>
<tr>
<td>Age</td>
<td>137.429</td>
<td>9.033</td>
</tr>
<tr>
<td>Period Age Sex</td>
<td>138.193</td>
<td>9.797</td>
</tr>
<tr>
<td>Age Sex</td>
<td>139.477</td>
<td>11.081</td>
</tr>
</tbody>
</table>

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 $r_p = 0.581 \quad P < 0.001 \quad n = 78$, and was not significant when only birds with null or negative mass gain were considered $r_p = 0.043 \quad P = 0.786 \quad n = 42$, or during spring $r_p = 0.255 \quad P = 0.324 \quad n = 17$, Fig. 4. Nonetheless, during spring we observed a bird with a very negative mass deposition rate $-1.13 \text{ g/day}$. 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 or 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 of 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 Lona during autumn and spring migrations
In spring, the arrow shows a bird 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 Lona before being first caught by Arizaga et al. 2008. However, late migrants did not refuel faster and did not stopover for longer periods. J. Arizaga, unpub. 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 despite its lower value was still lower than the one observed in some long-distance migrants that also feed on very abundant food resources (Schaub and Jenni 2000). 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 of 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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References


Atkinson PW, Baker AL, Bennett KA, Clark NA & Clark JA et al. 2007. Rates of mass gain and energy deposition in red knot on their final spring staging site is both time- and condition-dependent. J. Appl. Ecol. 44 885 – 895.


