

Fuel management and stopover duration of Blackcaps *Sylvia atricapilla* stopping over in northern Spain during autumn migration period

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Capsule Fuel load is correlated with fuel deposition rate; stopover duration is affected by arrival fuel load.

Aims To determine the stopover duration, fuel management and flight ranges at departure of Blackcaps stopping over in northern Spain.

Methods Systematic mist-netting and ringing allowed the use of mark–recapture Cormack–Jolly–Seber models for the estimation of stopover duration. Trapped birds were measured and weighed in order to estimate mass gain. FLIGHT software was used to estimate flight ranges.

Results Stopover duration ranged from 3.6 to 13.6 days, and was negatively correlated with arrival body mass (assessed by body mass at the first capture event). On average, arrival body mass was 18.4 g, whilst body mass at departure was 19.8 g. No significant differences in arrival body mass and departure body mass were observed between age or sex classes. Mass deposition rate did not differ between age or sex classes (mean = 0.20 g/day). Birds recaptured one day after the first capture event lost mass, whilst recaptures from the second day onwards had a mean gain of mass; mass was observed to increase linearly with the stopover duration. Mass deposition rate was positively correlated with departure body mass. Finally, with a mean departure body mass of 19.8 g, a Blackcap stopping over in northern Spain should be able to fly up to 1100 km.

Conclusions Stopover duration assessed by Cormack–Jolly–Seber models was longer than that observed in birds recaptured more than once ('minimum stopover duration'). Stopover was longer for birds arriving with less fuel. The positive relationship between departure body mass and mass deposition rate suggests a time-minimizing strategy. The lack of difference in fuel deposition rate between age and sex classes suggests a relatively abundant food supply at the study site, but other explanations might also account for the lack of age and sex differences, for example if competition for food was not determined by social hierarchies but by scramble competition. Departing fuel load would allow these birds to arrive at their wintering areas in southern Spain under still-air conditions, without needing to refuel.

In bird migration most time and energy are consumed during stopovers (Hedenström & Ålerstam 1997). Therefore, stopover analysis has great importance for understanding the strategies of migrant species. Relevant components of stopover strategies are stopover duration, fuel deposition rate (gained fuel per unit time) and departure fuel load (fuel load when leaving a stopover site, Ålerstam & Lindström 1990, Lindström & Ålerstam 1992, Ålerstam & Hedenström 1998, Schaub & Jenni 2001).

The first relevant issue in stopover analysis, from both biological and conservation perspectives, is to know how long a bird stops over at a particular site (Schaub & Jenni 2001, Balança & Schaub 2005). Unless stopover duration is measured directly (e.g. by radiotelemetry or satellite tracking, Meyburg *et al.* 1996, Chernetsov & Mukhin 2006), it must be estimated from data on captures and recaptures or resighting. A widely used method in this second case is to calculate the minimum or observed stopover duration (Kaiser 1999) by subtracting the date of last capture from that of first capture at the stopover site (one day among nocturnal migrants). However, this

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method involves two biases: (1) dates of arrival and departure are unknown; and (2) it only uses data from birds captured at least twice, so a very small part of the population is considered. By contrast, Cormack–Jolly–Seber models give a better estimation of stopover duration, taking into account all the available data, and estimating probabilities that birds were at a site before the first capture event and after the last one (Schaub *et al.* 2001).

Within a species, stopover duration is reported to vary with a number of factors: year and site (Schaub & Jenni 2001, Gannes 2002), time within the period of passage (Schaub & Jenni 2001, Balança & Schaub 2005), moult stage (Schaub & Jenni 2001), sex and age-class (Balança & Schaub 2005). Also, migrants arriving with more fuel generally stop over for shorter periods because, given a fuel deposition rate, these individuals would more quickly store the amount of fuel needed to reach the next goal area (Bairlein 1985, Pettersson & Hasselquist 1985, Biebach *et al.* 1986, Moore & Kerlinger 1987, Kuenzi *et al.* 1991). However, it is also reported that migrants arriving with more fuel may stop over for as long as birds with lower fuel loads (Safriel & Lavee 1988, Kuenzi *et al.* 1991, Ottosson *et al.* 2002).

Fuel management (and particularly fuel deposition rate) when stopping over is expected to be affected by several factors, such as social status, food availability and arrival fuel load. Social status determines priority of access to food, especially when individuals with the same food requirements are concentrated at a stopover site (Moore *et al.* 2003). In this case, refuelling rates could be influenced by competition for available food resources, and are expected to be higher among dominant birds (Lindström *et al.* 1990), i.e. adults over young, males over females (Carpenter *et al.* 1993, Moore *et al.* 2003). Alternatively, it is possible that access to food will be determined by scramble competition (i.e. more aggressive or hungry birds would access food with higher probabilities). Food availability determines how fast and to what extent refuelling takes place (Ellegren 1991, Fransson 1998, Dänhardt & Lindström 2001): when food is abundant, the effect of social status or scramble competition could be negligible (Moore & Yong 1991). Fuel deposition rate might be faster in birds arriving with low fuel, independent of their social status (Yong & Moore 2005).

Refuelling rate may vary during the stopover period. Body mass in some migrants may decrease or remain constant for some time after reaching stopover sites

(Mehlum 1983, Carpenter *et al.* 1993, Gannes 2002). To explain this result two alternative hypotheses have been proposed. The first is that when a migrant reaches a stopover site, it has to search for food and shelter in an unfamiliar area. Consequently, there is often a search-associated cost of time, usually related to an energy cost, and a consequent mass loss (Alerstam & Lindström 1990, Hedenström & Alerstam 1997). The second hypothesis is that handling by humans is reported to have an effect on the initial mass loss in some cases (Schwilch & Jenni 2001). In these cases fuel deposition rate should be expected to be negative for some time after arrival or handling, so birds may lose mass during this time. In addition, fuel deposition rate has been reported to decrease around the day of departure (Fransson 1998). This has been associated with physiological changes in preparation for the flight (Hume & Biebach 1996), as well as to a mass-dependent cost of transport and predation. Thus, a bird carrying a relatively high amount of fuel uses relatively more energy to move itself than a less loaded bird. Additionally, it is more vulnerable to predators as it loses manoeuvrability (Witter & Cuthill 1993, Klaasen & Lindström 1996, Lind *et al.* 1999).

Alerstam & Lindström (1990) proposed that birds could show distinct strategies to optimize the migratory journey: they could tend to minimize time, energy or risk of predation. Thus, a prediction given by their models is that departure fuel load is positively correlated to fuel deposition rate in ‘time minimizers’, whilst it would be independent of fuel deposition rate in those which minimize energy. Thus, it should be possible to gain insights into which strategy is employed by a particular species by examining the relationship between departure fuel load and fuel deposition rate.

Finally, a relevant question associated with migration strategies is an estimate of flight ranges (Alerstam 1990). Many models have been proposed, obtained either from aerodynamic theory (Pennycuik 1975, 1989, Greenewalt 1975, Rayner 1979) or from analyses of measured cost of flight. According to Weber & Houston (1997), the latter models give flight ranges that can differ by an order of magnitude depending on what exponents are used in the equations. Accordingly, using models based on aerodynamic theory is more conservative.

Blackcaps *Sylvia atricapilla* are common Palearctic passerines, breeding in most of Europe, and wintering in southern Europe and north Africa and, to a lesser extent, in central and southern Africa (Shirihai *et al.*

2001). Although it is a commonly ringed bird in Europe (Berthold & Solenen 1997), detailed analyses on its fuel load and fuel deposition rate at stopover localities are insufficient to give a complete overview on its migratory strategy. Studies on its stopover behaviour in some localities in central Africa (Hjort *et al.* 1996), the Middle East (Maitav & Izhaki 1994, Izhaki & Maitav 1998, Gannes 2002) and Europe (Turrian & Jenni 1991, Ellegren & Fransson 1992, Grandío 1997) are available. Studies are particularly scarce in southern Europe (but see Grandío 1997, Leal *et al.* 2004), although the region has a high interest for both migrating and wintering Blackcaps (Tellería *et al.* 1999, Belda *et al.* 2007).

In this work we focused on the analysis of fuel management of migrating Blackcaps in northern Spain during the autumn migration period. We were interested in (1) determining the stopover duration, and how arrival fuel load affected it; (2) estimating fuel deposition rate and departure fuel load, and how they were correlated and affected by social status; and (3) estimating the flight range of birds departing from this stopover site.

STUDY AREA AND METHODS

Study site and field methods

Data were collected at Loza (42°50'N 01°43'W, 415 m asl), located 5 km west of Pamplona city, 40 km south-west of the Pyrenees, in northern Spain. Blackcaps were mist-netted daily (60 m of nets divided into four sets) during the autumn migration period in 2005 (from 12 September to 26 October, and four additional days up to 15 November). Nets were placed within a hedgerow composed of Atlantic shrubs (mainly of the family Rosaceae and *Sambucus* spp.), as well as some elms. To ensure a larger sample size of recaptured adults (see Table 1) we used additional data from 2003 and 2004, when nets were placed for three days each week, from mid-September to the end of October. In all cases the nets were open for four hours from dawn.

Once captured, each Blackcap was ringed and its sex and age determined (Svensson 1998). Two age categories were considered: juveniles (fledged that year, EURING code 3, Speek *et al.* 2001), and adults (fledged the previous year or before, EURING code 4). We recorded wing length (method III from Svensson 1998; ± 0.5 mm), body mass (using Tanita digital balance; ± 0.1 g), moult state (whether birds showed active moult) and fat score (scaled from 0 to 8 following

Table 1. Number of Blackcaps at the Loza stopover site in north Spain, during the autumn migration period^a.

Age	Sex	2005		2003 and 2004
		Captures	Individuals recaptured	Individuals recaptured
Juvenile	Male	432	30	–
	Female	362	27	–
Adult	Male	92	3	7
	Female	63	3	9

Data on recaptures of adults from 2003 and 2004 are included to increase the sample size of this age-class. Data on juveniles from 2003 and 2004 were not used. Data are included only for birds that had all biometric parameters measured, and were not moulting. ^a12 September to 26 October in 2005, 12 September to 24 October in 2003 and 2004

Kaiser 1993; ± 0.5). In 2005, the time of capture, to the nearest hour (ranging from 1 to 4) was also recorded. All measurements were recorded by the same person (J.A.). In the analyses we used only data on birds for which we had measured all parameters, whose age and sex were known, and which were not moulting. Moulting is costly from an energetic viewpoint (Jenni & Winkler 1994), so a moulting bird is likely to show a different fuel management strategy compared with a non-moulting bird. Schaub & Jenni (2001) also observed that stopover duration of moulting birds tended to be different.

Estimation of stopover duration

To estimate the stopover duration and its effects on arrival body mass (ABM; assessed as body mass at the first capture event), we used the data obtained from daily captures in 2005. This resulted in 45 sampling days (from 12 September to 26 October), and 939 different birds among which 60 were recaptured. The data were analysed with Cormack–Jolly–Seber models, according to Lebreton *et al.* (1992). This method allows the estimation of apparent survival (Φ , probability of a bird captured at time t to remain at that site up to $t + 1$), seniority (γ , probability that a bird captured at time t was already at that site at $t - 1$), and recapture (p , probability of capturing a bird given that it is present) separately, as described in Schaub *et al.* (2001, see also Schaub & Jenni 2001).

We used MARK v.4.2. software (White & Burnham 1999) to estimate survival, seniority and recapture parameters. As a basic model that fitted the data from which to select models, we considered a model where

Φ (or γ) and p were constant over time [$\Phi(\cdot)$ $p(\cdot)$ or $\gamma(\cdot)$ $p(\cdot)$]. In this case, data fitted well with Cormack–Jolly–Seber assumptions (TEST 2 and 3 from RELEASE, $P > 0.05$; these test for the alternative hypotheses of heterogeneity in recapture probability and in the apparent survival among different birds, respectively). This basic model [$\Phi(\cdot)$ $p(\cdot)$ or $\gamma(\cdot)$ $p(\cdot)$] fitted the data (boot-strap, $P > 0.05$). Although time, age and sex might also affect Φ , γ or p (Schaub & Jenni 2001, Balança & Schaub 2005, Belda *et al.* 2007), our sample was not large enough to consider these possible sources of variation in the basic model.

To test for the effect of fuel load at arrival on stopover duration, ABM was used as a surrogate of arrival fuel load. Thus, ABM was included as a co-variate into the basic model, with four models being considered for Φ and γ , respectively. The logit-link function was used, as it is recommended when co-variables are included in Cormack–Jolly–Seber models:

$$\text{Logit}(\Phi \text{ or } \gamma) = B_0 B_1 (\text{co-variate})$$

where B_0 and B_1 are constants. Model selection was made using the information-theory approach (Burnham & Anderson 1998). The corrected Akaike information criterion (AICc) was used for ranking the fit of models to the data (Burnham & Anderson 1998); those with lower AIC better fitted the data. We considered that models with a difference in AIC of less than two units ($\Delta\text{AIC} < 2$) were similarly supported by the data, whilst $\Delta\text{AIC} > 2$ was considered as evidence for a real difference in the fit of the models to the data (Burnham & Anderson 1998). Finally, to estimate the stopover duration we used the software SODA (Schaub *et al.* 2001), which considers the time elapsed between the first and last capture events as well as Φ and γ .

Analyses of body mass and mass gain

Body mass in birds is mainly determined by body size and fuel load. Fuel load is mostly stored as fats (Klaassen *et al.* 1997, Jenni & Jenni-Eirmann 1998), though also as proteins (up to 5% of the energy budget, according to Jenni & Jenni-Eirmann 1998, but see Pennycuik 1989, 1998). The contribution of fuel load to body mass is especially important during migration, when fat fuel loads in excess of 100% of lean body mass (body mass without any fat content) are possible (Lovei 1989, Berthold 1993). Although birds could burn muscle mass (i.e. proteins) in flight, it is not possible to estimate the body mass without all fuel (i.e. without fat

and muscles) of a living bird without killing it. Thus, we have used the difference between body mass and lean body mass as an estimate of fuel reserves of a bird. This will be considered in the discussion.

In a number of analyses of migrants during stopover, body mass is used to assess directly the energetic condition of a bird (Turrian & Jenni 1991, Grandío 1997). In other cases, however, energetic condition is assessed by measurements that estimate fuel contents using fat score (Turrian & Jenni 1991, Maitav & Izhaki 1994, Grandío 1997), or fuel load measured as a percentage over lean body mass (Alerstam & Lindström 1990, Lindström & Alerstam 1992, Hedenström *et al.* 1993). Fuel load is normally assessed by regressing actual body mass on a variable of body size (such as wing length; Ellegren & Fransson 1992) and another assessing fat contents. Although this method produces dimensionless values, making comparisons easier, it is less accurate as the error from the regression is added to that of measurement. Thus, in a preliminary approach we observed that, for instance, the departure body mass accuracy was 1.4% over the mean (19.8 ± 0.3 g se, $n = 79$; see results for further details), whilst the departure fuel load accuracy (estimated considering a lean body mass of 16.8 g; see below for further details) was 9.2% over the mean ($17.8 \pm 1.7\%$, $n = 79$). Therefore, we have used body mass as a surrogate for fuel load.

To analyse both body mass and mass deposition rate, data on recaptures obtained in 2005 (juvenile and adult birds) and in 2003 and 2004 (adult birds) were used ($n = 79$; Table 1). Thus, body mass at the first (ABM) and last capture event (departure body mass, DBM) were available for each bird. Mass difference between DBM and ABM, divided by number of days elapsed between them, was used to assess the mass deposition rate (MDR). Considering data from 2005, body mass did not differ among the birds captured at different times during the four hours of trapping ($F_{3,861} = 1.969$; $P = 0.117$; co-variate [wing length], $F_{1,861} = 32.581$, $P < 0.001$), so time of capture was not considered in further analyses. To analyse ABM and DBM in relation to age and sex, we performed two-way ANOVAs on mass with sex and age as selection variables, and wing length (used here as an estimate of body size, Gosler *et al.* 1998) as a co-variate (F_{Levene} , $P > 0.05$ for all cases). A two-way ANOVA on MDR with sex and age as selection variables was also performed ($F_{\text{Levene}} = 1.833$, $P = 0.148$).

In order to make comparisons with other studies, we also assessed the departure fuel load as a percentage over lean body mass (LBM). To estimate this we took

into account those birds captured in 2003 to 2005 that did not have any fat content (fat scores = 0), resulting in a mean body mass of 16.8 ± 0.3 g ($n = 15$). Thus, fuel load was calculated according to:

$$\text{Departure fuel load} = \frac{[\text{DBM} - \text{LBM}]/\text{LBM}] \times 100}{(1)}$$

Both MDR and DBM followed normal curves of distribution (K-S test, $P > 0.05$), so to study the relationship between them we used Pearson's coefficient of correlation (r). To contrast data on counts, χ^2 tests were used. The P -exact value was considered in 2×2 tables (Agresti 1996). Means are given \pm se. SPSS v.13.0 for Windows was used for statistics.

To explore whether mass gain was correlated with the number of days elapsed between the first and last capture events, both variables were regressed and the r from a linear (i.e. birds increased their mass linearly up to the departure day) and a log regression (assuming a decreasing mass change close to the departure day, Fransson 1998) obtained. To test whether data fitted better a linear or a logarithmic regression, the AICc was used (Motulsky & Christopoulos 2004). The model with lower AICc was considered to describe the data better if $\Delta\text{AIC} > 2$. The software GraphPad Prism was used in this case.

Estimation of flight ranges

To estimate flight ranges in relation to departure fuel load we used FLIGHT software v. 1.17 (Pennycuick 1989, 1998). We considered an average individual with a DBM of 19.8 g (see results for further details), equivalent to a departure fuel load of 17.8% over the lean body mass, zero crop mass (when a bird leaves a stopover site its crop is assumed to be empty), wing span of 0.2 m, wing area of 0.0078 m² (J.A. unpubl. data), flying at 1000 m asl (about 585 m above ground level at Loza) (Alerstam 1990), in a standard atmosphere at this height of 8.5°C, 898 hPa and 1.11 kg/m³ (Pennycuick 1989, 1998).

RESULTS

Stopover duration

Models considering both Φ and γ fitted data better when the ABM of migrants was included as a co-variate of Φ and γ (lowest AICc values; Table 2). For survival, difference in AICc with the next model, which

considered both Φ and p constant, was less than two ($\Delta\text{AICc} < 2$), suggesting that there were no differences in the fit of the models. In this case, these first two models were averaged (Anderson & Burnham 2000), for which the AICc weight (Table 2) of both models was considered to obtain the estimation of survival. For seniority, however, the difference between the first model and the second one was $\Delta\text{AICc} > 2$, supporting statistical differences in the fit of the first model to data. Thus, birds with lower ABM were more likely to have been settled at the study site for longer than birds with higher ABM. Accordingly, there is evidence of an effect of ABM on stopover duration (Fig. 1). Models with p affected by ABM did not fit the data as well as the models previously mentioned (Table 2).

In both parameters, the models showed that ABM had a negative effect on both Φ and γ (equations 2 and 3, once the ABM was standardized; we show B values \pm se), so, when arriving at Loza, the higher the body mass of a bird, the shorter the stopover duration:

$$\text{Logit}(\Phi) = (1.344 \pm 0.155) - [(0.224 \pm 0.115) (\text{ABM})] \quad (2)$$

$$\text{Logit}(\gamma) = (1.424 \pm 0.168) - [(0.281 \pm 0.123) (\text{ABM})] \quad (3)$$

Thus, considering a range of ABM from 28.6 g to 15.0 g, stopover duration varied from 3.6 ± 1.0 to 13.6 ± 0.6 days, respectively (Fig. 1). A bird with an ABM of 18.4 g (mean ABM of Blackcaps captured at least twice in our study area; see below) would have a mean stopover duration of 9.6 ± 0.6 days. Mean minimum stopover duration (Kaiser 1993) was 6.4 ± 0.5 days.

Body mass and mass deposition rate (MDR)

Migrants at Loza showed a mean ABM of 18.4 ± 0.2 g ($n = 79$), whilst DBM was on average 19.8 ± 0.3 g ($n = 79$) (paired sample t -test, $t_{78} = 5.704$, $P < 0.001$). In a Blackcap with a mean lean body mass of 16.8 g (obtained from birds with fat = 0), this is equivalent to having a departure fuel load of $17.8 \pm 1.7\%$ over the lean body mass. Blackcaps captured only once had a higher body mass than recaptured birds at their first capture event ($F_{1,964} = 5.267$, $P = 0.021$; co-variate, wing length, $F_{1,964} = 42.899$, $P < 0.001$; 18.9 ± 0.1 g, $n = 886$ versus 18.4 ± 0.2 g, $n = 79$).

No significant differences in ABM and DBM were observed between age or sex classes (Table 3). Both ABM and DBM increased with body size (Table 3).

Table 2. Models used to estimate the stopover duration of Blackcaps at the Loza stopover site in north Spain, during the autumn migration period.

Models	AICc	Δ AICc	AICc weight	Parameters	Deviance	Significance
$\Phi(\text{ABM}) p(\cdot)$	777.101	0.000	0.712	3	771.077	Survival is affected by body mass when arriving, whilst the probability of recapture is constant
$\Phi(\cdot) p(\cdot)$	778.915	1.814	0.288	2	774.903	Survival and recapture probability are constant
$\Phi(\text{ABM}) p(\text{ABM})$	1337.327	560.226	0.000	3	1331.303	Both survival and recapture probability are affected by body mass when arriving
$\Phi(\cdot) p(\text{ABM})$	1423.911	646.810	0.000	2	1419.899	Survival is constant, whilst the probability of recapture is affected by body mass when arriving
$\gamma(\text{ABM}) p(\cdot)$	772.971	0.000	0.856	3	766.947	Seniority is affected by body mass when arriving, whilst the probability of recapture is constant
$\gamma(\cdot) p(\cdot)$	776.539	3.568	0.144	2	772.527	Seniority and recapture probability are constant
$\gamma(\text{ABM}) p(\text{ABM})$	1336.316	563.345	0.000	3	1330.292	Both seniority and the probability of recapture are affected by body mass when arriving
$\gamma(\cdot) p(\text{ABM})$	1422.526	649.555	0.000	2	1418.514	Seniority is constant whilst the probability of recapture is affected by body mass when arriving.

Data used were obtained in 2005 (12 September to 26 October). Abbreviations: Φ , apparent survival; γ , apparent seniority; p , probability of recapture; ABM, arrival body mass (g). Δ AICc = $\text{AICc}_i - \text{AICc}_{\text{minimum}}$.

Mass deposition rate did not differ significantly between age or sex classes (Table 3), resulting in a mean MDR of 0.20 ± 0.05 g/day ($n = 79$, equivalent to a fuel deposition rate of 1.20%/day over lean body mass). The proportion of individuals accumulating fuel was much higher than those losing it (including in this group two birds with MDR = 0, $\chi^2_1 = 10.65$, P -exact = 0.001).

The change of mass from the first to the last capture events was not constant in relation to the number of days between them (Fig. 2). Data fitted better a log ($r = 0.534$, $F_{1,78} = 30.677$, $P < 0.001$) than a linear function ($r = 0.486$, $F_{1,78} = 23.863$, $P < 0.001$; difference in

AICc = 5.165). Nonetheless, when the outliers (see Fig. 2) were removed both models were similar (log function, $r = 0.533$, $F_{1,76} = 29.687$, $P < 0.001$; linear function, $r = 0.525$, $F_{1,76} = 28.531$, $P < 0.001$; difference in AICc = 0.855), so data fitted well to a linear function. Thus, for the normal ranges of stopover duration at our study site, mass gain increased linearly with stopover duration.

The maximum change of mass was observed in an individual that gained 9.7 g in 13 days. On average a bird would gain no more than 4 g. We also observed that birds recaptured one day after the first capture

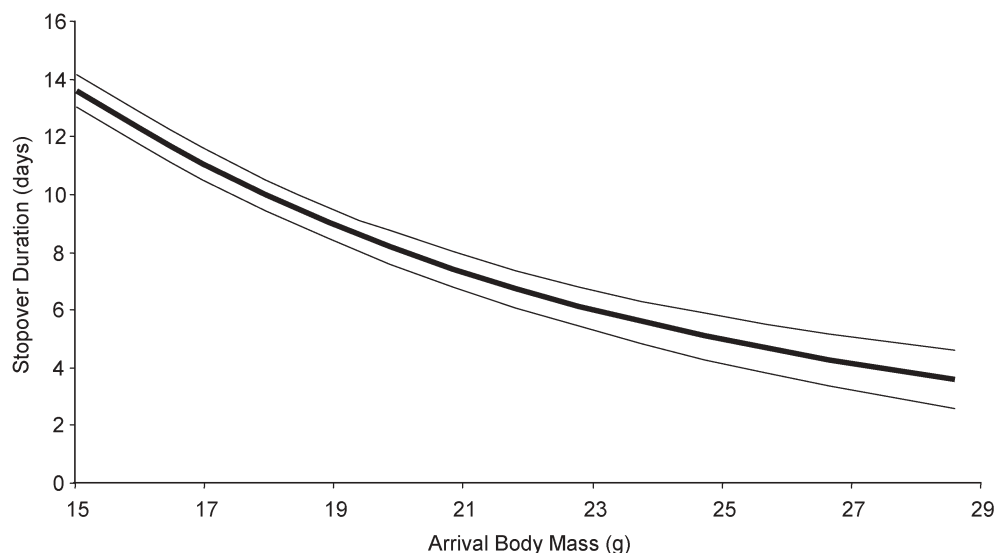
**Figure 1.** Mean stopover duration (\pm se) of migrating Blackcaps at the Loza site in northern Spain, during the autumn migration period, as a function of arrival body mass. This function is based on model averaging estimates for Φ and best-fitting models for γ .

Table 3. Two-way ANOVAs on arrival body mass (ABM), departure body mass (DBM) and mass deposition rate (MDR) in relation to age and sex.

	Factor	$F_{1,78}$	P
ABM	Age	1.472	0.229
	Sex	0.077	0.782
	Age × Sex	0.596	0.442
	Co-variate: wing length	6.633	0.012
DBM	Age	3.804	0.055
	Sex	0.016	0.900
	Age × Sex	0.105	0.747
	Co-variate: wing length	4.088	0.047
MDR	Age	0.423	0.518
	Sex	0.088	0.768
	Age × Sex	0.206	0.651

event showed a negative mean mass change (-0.1 ± 0.1 g, $n = 16$), supporting an associated cost of settlement. By contrast, recaptures from the second day after the first capture event showed a mean gain of body mass.

An overall significant correlation between MDR and DBM ($r = 0.520$, $F_{1,78} = 28.556$, $P < 0.001$, $n = 79$; Fig. 3) was observed, so birds with lower MDR tended to depart with less fuel. Two categories of birds are shown in Fig. 3: birds with positive, and birds with negative mass gain. When only individuals with negative MDR were considered, the relationship between MDR and DBM disappeared, whilst it became slightly stronger when considering only individuals with positive MDR (Fig. 3). Furthermore, no significant differences in proportions between age or sex classes were observed among birds with negative or no gain of mass and those

with positive MDR (age, $\chi^2_1 = 0.314$, P -exact = 0.614; sex, $\chi^2_1 = 0.102$, P -exact = 0.818). Rate of refuelling was not affected by body mass at arrival ($r = 0.203$, $F_{1,78} = 3.297$, $P = 0.073$, $n = 79$).

Estimation of flight ranges

With a mean DBM of 17.8% over the lean body mass, a Blackcap stopping over at our study site should be able to fly to a new stopover (or wintering) area as far as 1096 km away. Thus, a bird departing from Loza would carry enough fuel to reach southern Spain, a very important wintering area for many populations from northern and central Europe (Cantos 1995, Tellería *et al.* 1999) (distance from Loza to Gibraltar is about 1000 km).

DISCUSSION

Stopover duration

According to Cormack–Jolly–Seber models, the stopover duration of Blackcaps at Loza varied in relation to body mass at arrival (ABM). Stopover duration ranged from 3.6 to 13.6 days. Birds with higher ABM stopped for a shorter time. Most of this relationship arises from the fact that birds having lower mass at their first capture event stayed longer; the effect of ABM on survival was not significant.

We demonstrated that birds with higher body mass at their first capture were less likely to stay than those with lower body mass. This is supported by the fact that

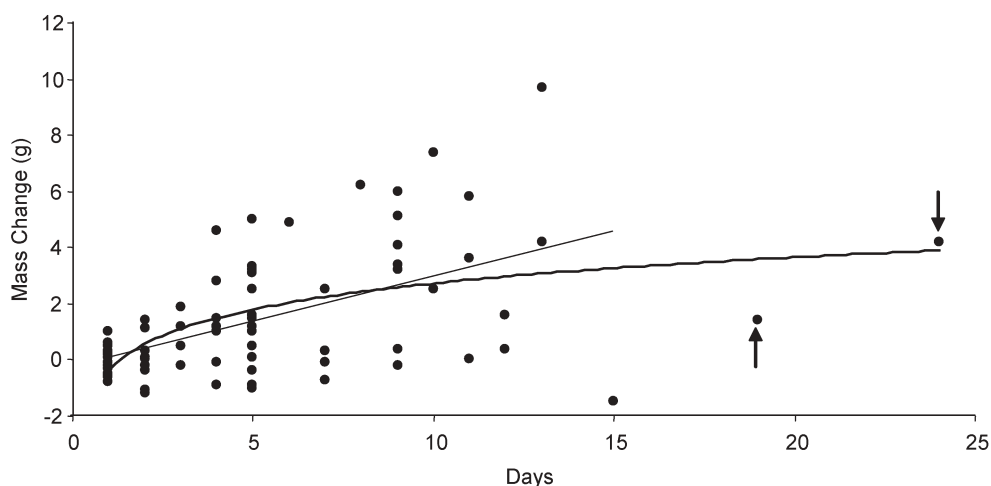


Figure 2. Mass change in migrating Blackcaps at the Loza stopover site in northern Spain, in relation to the number of days elapsed between the first and last capture events. A log function gave the best fit to data (see text for further details) when the whole data set was considered. However, when the two outliers (shown by arrows) were removed, a linear function gave the best fit (mass change = $-0.1988 + 0.3208$ days).

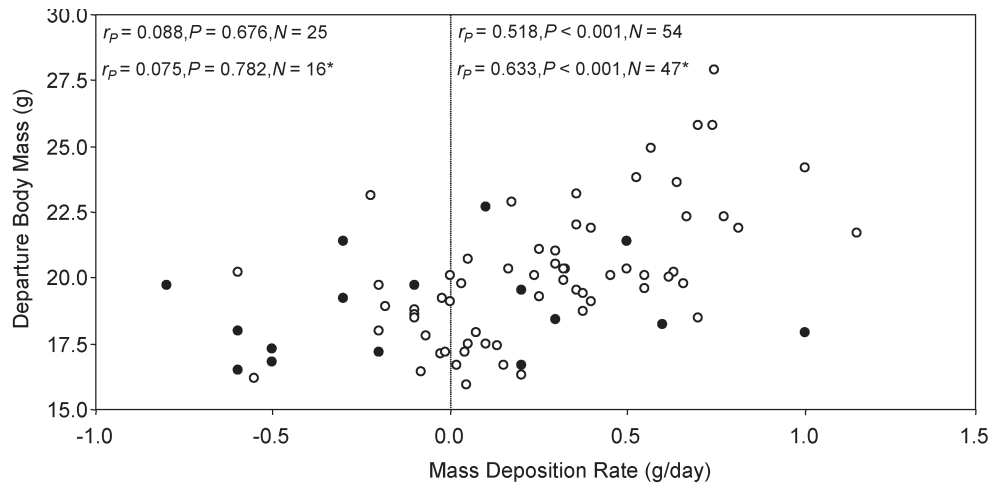


Figure 3. Body mass and mass deposition rate for a sample ($n = 79$) of migrating Blackcaps in northern Spain. Pearson's correlation coefficient is calculated separately for the group of birds with negative and positive mass deposition rate. White circles refer to birds recaptured after a day following the first capture event. Additionally, Pearson's correlation coefficient is recalculated in each case concerning only the bird population recaptured more than one day after the first capture event (*).

Blackcaps caught only once showed a higher body mass than those captured more than once. This has been reported in other birds, during both the autumn (Bairlein 1985, Pettersson & Hasselquist 1985, Biebach *et al.* 1986) and spring migrations (Moore & Kerlinger 1987, Kuenzi *et al.* 1991). Nonetheless, Blackcaps stopping over at the desert edge in Israel during spring did not show any correlation between stopover duration and ABM (Maitav & Izhaki 1994). These authors also observed that a high percentage of Blackcaps at their study area stopped over for fewer times, suggesting that birds tended to continue their migration until reaching more fertile areas further north.

Stopover duration varied from 3.6 ± 1.0 to 13.6 ± 0.6 days. For a bird with an ABM of 18.4 g the stopover duration is estimated to be 9.6 ± 0.6 days, which is higher than the observed minimum stopover (6.4 ± 0.5 days). A longer stopover duration is commonly observed when it is assessed by Cormack–Jolly–Seber models than when it is directly obtained from differences between the capture and recapture day (Kaiser 1999, Schaub *et al.* 2001).

Body mass, mass deposition rate and flight ranges

When migratory Blackcaps landed at Loza in autumn, they showed a mean body mass of 18.4 g (about 9.5% over their lean body mass), and after stopover reached a mean body mass of 19.8 g (about 17.8% over their lean body mass). A similar mean fuel load (about 15%)

was reported by Ellegren & Fransson (1992) for a population of migrating Blackcaps in Scandinavia, during autumn. This result agrees with the mean fuel load observed in passerines that overwinter in temperate latitudes (Alerstam & Lindström 1990), and it is lower than that observed in long-distance passerines (such as those that overwinter in central or southern Africa), whose fuel loads often have mean values of over 50% of lean body mass (Alerstam & Lindström 1990, Alerstam 1990).

A high fuel load increases the energetic cost of transport and impairs the ability to escape from predators (Lind *et al.* 1999, Kullberg *et al.* 2000). In autumn, Europe offers many suitable stopover areas in which both shelter and food can be found. Therefore, western European populations do not have to fly over large inhospitable areas and do not need to store a large amount of fuel. Nevertheless, our data agree with those of Ellegren & Fransson (1992), and give flight ranges of over 1000 km without needing to refuel. Furthermore, these results might be underestimated as we considered that only fat contents may be used as fuel, whereas birds are also able to use muscle mass to retrieve energy for flying (Jenni & Jenni-Eirmann 1998).

Blackcaps are nocturnal migrants (Alerstam 1990), so it would be possible for birds to undertake several consecutive nights of flight, stopping over during the day to rest but not to refuel, and stop over for longer (one or two weeks) at suitable sites where they might find enough food to refuel successfully. This hypothesis may explain why in the Txingudi marshlands (100 km

north of Loza in northern Spain) Grandío (1997) obtained only 0.51% of recaptures in a relatively poor stopover area, where apart from some blackberry bushes *Rubus* spp. (which generally ripen earlier than when Blackcaps pass over that area, J.A. pers. obs.) the vegetation is dominated by reed beds *Phragmites australis* and other marsh plants. Clearly, studies of Blackcap stopover behaviour at other sites are needed to test this hypothesis.

In Robins *Erithacus rubecula* caught during the autumn migration period in southern Sweden, Dänhardt & Lindström (2001) observed a departure fuel load of 53% over the lean body mass, more than double that which we observed in Blackcaps. In this case, however, Robins were food supplemented, a fact that might promote higher fuel deposition rates and loads (Dänhardt & Lindström 2001), though species-associated differences are also possible (Alerstam 1990).

The lack of significant differences in body mass (both at arrival and departure) and in mass deposition rate among age and sex classes, suggests that, even if social status was operating at Loza as a factor determining access to food, it had no effects on mass (fuel) accumulation. At a location in Switzerland, Turrian & Jenni (1991) observed that body mass was significantly lower in young than in adults, whilst they did not find any significant difference between sex classes. In Scandinavia, Ellegren & Fransson (1992) did not find significant differences between sex classes either. A possible explanation for our result is that food availability at Loza in autumn is very high, due to the ripening of abundant blackberries and elders, a highly preferred food of migrating Blackcaps (Jordano & Herrera 1981, Jordano 1985). In this case, food abundance may render irrelevant the priority of access to food of distinct age or sex classes (Moore & Yong 1991).

Overall, mass deposition rate (MDR) was 0.2 g/day (equivalent to 1.2%/day over the lean body mass). This is much lower than the physiological maximum for passerines (7.0%/day, Lindström 1991). Nonetheless, this high rate is unlikely to be recorded in wild conditions, due to constraints imposed by food availability, unfavourable weather, or intra- or interspecific competition (Lindström & Alerstam 1992). Indeed, it is well known that fuel deposition rates in the wild tend to be lower than among birds with food supplementation, for example in Bluethroats *Luscinia svecica* (Ellegren 1991, Lindström & Alerstam 1992), Whitethroats *Sylvia communis* (Fransson 1998) and Robins (Dänhardt &

Lindström 2001). Unfortunately, Grandío (1997) did not obtain enough data on recaptures of Blackcaps at a locality in northern Spain, so we cannot compare our data with those from a nearby area. In Switzerland, Turrian & Jenni (1991) did not find any significant gain of mass in migrating Blackcaps. In contrast to long-distance warblers such as Garden Warblers *Sylvia borin*, Reed Warblers *Acrocephalus scirpaceus* and Sedge Warblers *Acrocephalus schoenobaenus* (Schaub & Jenni 2000, 2001), data on MDR and fuel load of Blackcaps in Europe, during both the autumn and the spring migration periods, are fairly scarce, so detailed analyses along their migration route are still far from complete.

The rate of refuelling varied during the period of stopover. Our data suggest a possible settlement-associated cost of energy (or physiological limits to refuel, Gannes 2002) of birds after arriving at Loza, with a mean loss of fuel of 0.1 g during the first day. This phenomenon is documented in other small passerines, such as Robins, that lost weight during the first day or two after arrival in Britain (Davis 1962) and Norway (Mehlum 1983). In Sweden, Ellegren (1991) observed in Bluethroats a mean loss of mass of 0.2 g during the first day after the first capture event. However, with a stopover duration of 15 days or less, mass gain was observed to increase linearly with increasing stopover duration. This suggests that most Blackcaps stopping over at Loza gained mass at a constant rate up to the departure day; this contrasts with other studies where, as shown above, the mass gain of migrants tends to decrease close to their departure (Klaasen & Lindström 1996, Fransson 1998). There are two alternative hypotheses that could explain these results. First, it is possible that Blackcaps simply follow a distinct strategy when they refuel during stopovers, accumulating fuel (mass) according to a linear function (Carpenter *et al.* 1983). For instance, Gannes (2002) observed in laboratory conditions that in spring Blackcaps showed a constant rate of mass accumulation. Alternatively, it is possible that under wild conditions, when food access is more restricted, most Blackcaps are not able to reach the level of fuel accumulation which could allow them to decrease the rate of refuelling close to the departure day.

Overall, migrants with higher MDR left the area with higher body mass, suggesting a time-minimizing strategy (Alerstam & Lindström 1990). Such a strategy could have a selective advantage in the occupancy of favourable places. Thus, it is reported in a number of localities in Spain that winter site fidelity in Blackcaps

is relatively high (about 30–40%, Cantos & Tellería 1994, Cuadrado *et al.* 1995, Belda *et al.* 2007), a fact that might be attributed to a strategy favouring the arrival in these wintering areas as early as possible, before competitors.

The correlation between the MDR and DBM was non-significant among individuals with a negative refuelling rate. This could in part be related to costs of settlement (see discussion above), though some birds seem unable to gain mass over several days. The reasons for this are not clear. However, we suggest that cases of birds losing fuel during stopover are more a result of constraints than part of a strategy.

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