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DO BLACKCAPS *SYLVIA ATRICAPILLA* STOPPING OVER AT A LOCALITY FROM SOUTHERN IBERIA REFUEL FOR CROSSING THE SAHARA?

¿SE PREPARAN LAS CURRUCAS CAPIROTADAS *SYLVIA ATRICAPILLA* DURANTE EL PERIODO DE PASO MIGRATORIO POSNUPCIAL EN UNA LOCALIDAD DEL SUR DE ESPAÑA PARA CRUZAR EL SAHARA?

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Summary.—*Do blackcaps* Sylvia atricapilla *stopping over at a locality from Southern Iberia refuel for crossing the Sahara?*

Migrants that cross large inhospitable areas must accumulate large loads of fuel to reach their destinations successfully. The stopover strategies of European long-distance migrants are relatively well studied for species that overwinter in tropical Africa, but less so for those that overwinter mainly around the Mediterranean and of which only a fraction reach tropical Africa. Our aim here was to analyse whether blackcaps *Sylvia atricapilla* stopping over in southern Iberia gain sufficient fuel in this region to be able to reach tropical Africa. Blackcaps were mistnetted during the autumn migration period of 2005 at a locality in Northern Iberia (Loza) and another in Southern Iberia (Doñana). Blackcaps at Doñana had lower fuel loads and a slower fuel deposition rate than at Loza, and the estimated flight ranges from both sites were insufficient to reach tropical Africa. The stopover duration was similar at both localities. If trans-Saharan birds occurred at Doñana, they would need to refuel at other stopover sites in Southern Iberia or in Northern Africa before crossing the Sahara. The circum-Mediterranean region may hence be of great importance for the fraction of the blackcap population that overwinters in tropical Africa.

Key words: ecological barriers, fuel load, Mediterranean region, migration distances, migration strategies, stopover.

Resumen.—*Se preparan las currucas capirotadas* Sylvia atricapilla *durante el periodo de paso migratorio postnupcial en una localidad del sur de España para cruzar el Sahara?*

Al cruzar barreras geográficas importantes, las aves han de acumular gran cantidad de reservas para alcanzar con éxito sus áreas de destino. La estrategia migratoria de las especies que cruzan este tipo de

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barreras es bastante bien conocida para muchas especies europeas que invernan en África tropical, aunque no tanto en las que pasan el invierno principalmente en la cuenca mediterránea pero que cuentan con individuos/poblaciones que cruzan el Sahara. Es el caso de la curruca capirotada *Sylvia atricapilla*. El objetivo de este artículo es analizar si las currucas capirotadas presentes en el sur de la Península durante el periodo de paso posnupcial cargan suficiente cantidad de reservas como para alcanzar África tropical. Se capturaron currucas con redes de niebla en el otoño de 2005 en Loza (N de España) y Doñana (S de España). En Doñana, las currucas mostraron reservas y tasas de ganancia de peso inferiores a las del N de España, y el rango de vuelo estimado para los dos puntos de muestreo fue insuficiente para llegar a África tropical. El tiempo de estancia no varió entre localidades. Si las currucas que llegan a África tropical paran en otoño en Doñana, necesitarían parar para ganar reservas en algún punto antes de cruzar el Sahara, bien en otras zonas del sur peninsular o en África septentrional. La región circum-mediterránea, en consecuencia, puede jugar un papel clave para la fracción de currucas capirotadas que invernan en África tropical.

Palabras clave: barreras ecológicas, distancia migratoria, estrategias migratorias, puntos de descanso y alimentación en migración, región mediterránea, reservas.

INTRODUCTION

The circum-Mediterranean region is a target wintering area for many European bird species (e.g. Cramp, 1992, 1998). However, a fraction of populations of those species which overwinter mainly in Southern Europe or Northern Africa continue their migration to overwinter in tropical Africa (e.g. Cramp, 1992, 1998). Migrants that cross large inhospitable areas must accumulate large fuel loads to reach their destinations successfully (reviewed by Newton, 2008). In this scenario, Southern Iberia offers one of the last opportunities to refuel before the Sahara during the autumn migration period (Hilgerloh and Wiltschko, 2000). The stopover strategies of European long-distance migrants are relatively well studied for species that overwinter in tropical Africa (Schaub and Jenni, 2000a, 2001a), but are less well known for those species that overwinter mainly within the circum-Mediterranean region, only a fraction of which reach tropical Africa.

European migrants that overwinter in tropical Africa could accumulate large fuel loads in:

(i) Northern Iberia (Grandío, 1998).
(ii) Southern Iberia, before crossing the Mediterranean (Rubolini *et al.*, 2002).
(iii) Northwestern Africa, immediately before crossing the desert (Izhaki and Maitav, 1998; Fransson *et al.*, 2008).

The blackcap *Sylvia atricapilla* is an abundant Palaearctic songbird, whose breeding range includes Western Eurasia, North-western Africa and the Macaronesian region (Cramp, 1992). The Western European populations chiefly overwinter in the Mediterranean region, although some birds reach tropical Africa (Shirihai *et al.*, 2001). The blackcap is a scarce but locally common visitor in tropical Africa, from Mauritania to Cameroon (Borrow & Demey, 2001). In Mauritania, the blackcaps occurs in large numbers on passage and during the winter (Isenmann *et al*, 2010), so there is no doubt that a significant cross-desert movement exists. Within Iberia, the main wintering area has been reported to be in the south-southwest, whereas the species is rare or absent in winter in the north (Cantos, 1995; Tellería *et al.*, 2001). Thus, blackcaps that stop over in Northern Iberia probably comprise both birds that overwinter within the circum-Mediterranean region and long-distance migrants that move up to tropical Africa. Previous studies in Northern Iberia have revealed that blackcaps there carry a mean fuel load sufficient to arrive in Southern Iberia (Arizaga *et al.*, 2008) but insufficient to arrive in tropical Africa. Long-distance migrants therefore need to stop over further south to accumulate sufficient fuel to cross the Sahara successfully (Biebach, 1990). If large fuel loads are acquired in Southern Iberia, birds there should be expected to have larger fuel loads than those in Northern Iberia. If fuel load in Southern Iberia is similar to or less than in Northern Iberia, this may indicate that long-distance blackcaps need to stop over in Northern Africa to accumulate large fuel loads before the desert crossing.

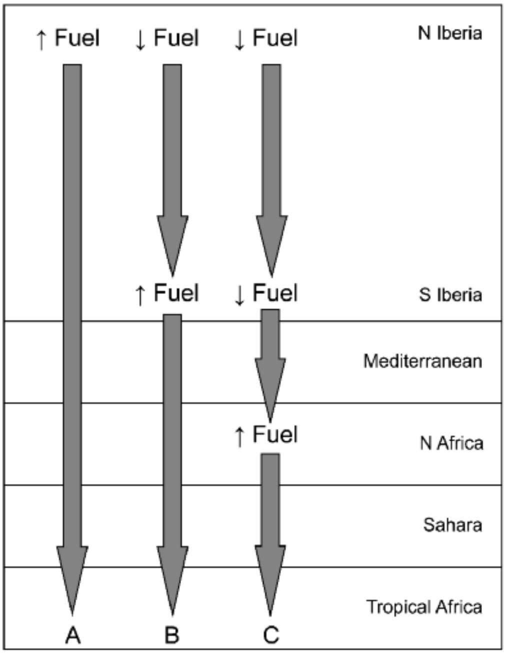

FIG. 1.—Possible strategies that may be employed by long-distance migrants that cross Iberia to overwinter in tropical Africa. A, migrants gain as much fuel in N Iberia as needed to reach their wintering areas in tropical Africa. B, high fuel reserves are obtained in S Iberia, before crossing the Mediterranean sea and reaching tropical Africa. C, high fuel reserves are obtained in North Africa on the desert margin. Adapted from Biebach (1990). *[Posibles estrategias de acumulación de reservas de las especies que cruzan España en su camino hacia sus áreas de invernada en África tropical. La ganancia de reservas suficiente para alcanzar África tropical sucede en A, N de España; B, S de España; C, N de África, justo antes de cruzar el Sahara. Adaptado de Biebach (1990).]*

The present study aimed to analyse whether blackcaps stopping over in Southern Iberia gain sufficient fuel there to reach tropical Africa without needing to refuel.

METHODS

Sampling sites

Data were collected at Loza, in the North of Spain (42º 50’ N 01º 43’ W, 415 m a.s.l.; 5 km west of Pamplona city, near the western Pyrenees) and at Manecorro Ringing Station in Doñana, in the South of Spain (37º 07’ N 06º 29’ W, 7 m a.s.l; Almonte, Huelva) (fig. 2). The vegetation at Loza consists of hedgerows of hawthorn *Crataegus* spp., elms *Ulmus minor*, elders *Sambucus* spp., brambles *Rubus* spp. and roses *Rosa* spp. At Doñana the vegetation was Mediterranean forest, with cork oaks *Quercus suber* and stone pines *Pinus pinea* and a rich evergreen undergrowth of mastic *Pistacea lentiscus* and kermes oak *Q. coccifera*, and a second zone of flooded prairie, formed by halophytes with scattered tamarisks *Tamarix* spp., willows *Salix* spp. and ash trees *Fraxinus angustifolia*.

There is some evidence that some blackcaps stopping over at Loza in autumn continue southwest to reach Doñana: in 2004 a bird ringed at Loza on 1 October was recaptured at Doñana on 23 October and in 2006 a bird ringed at Loza on 5 October was recaptured at Doñana on 29 October.

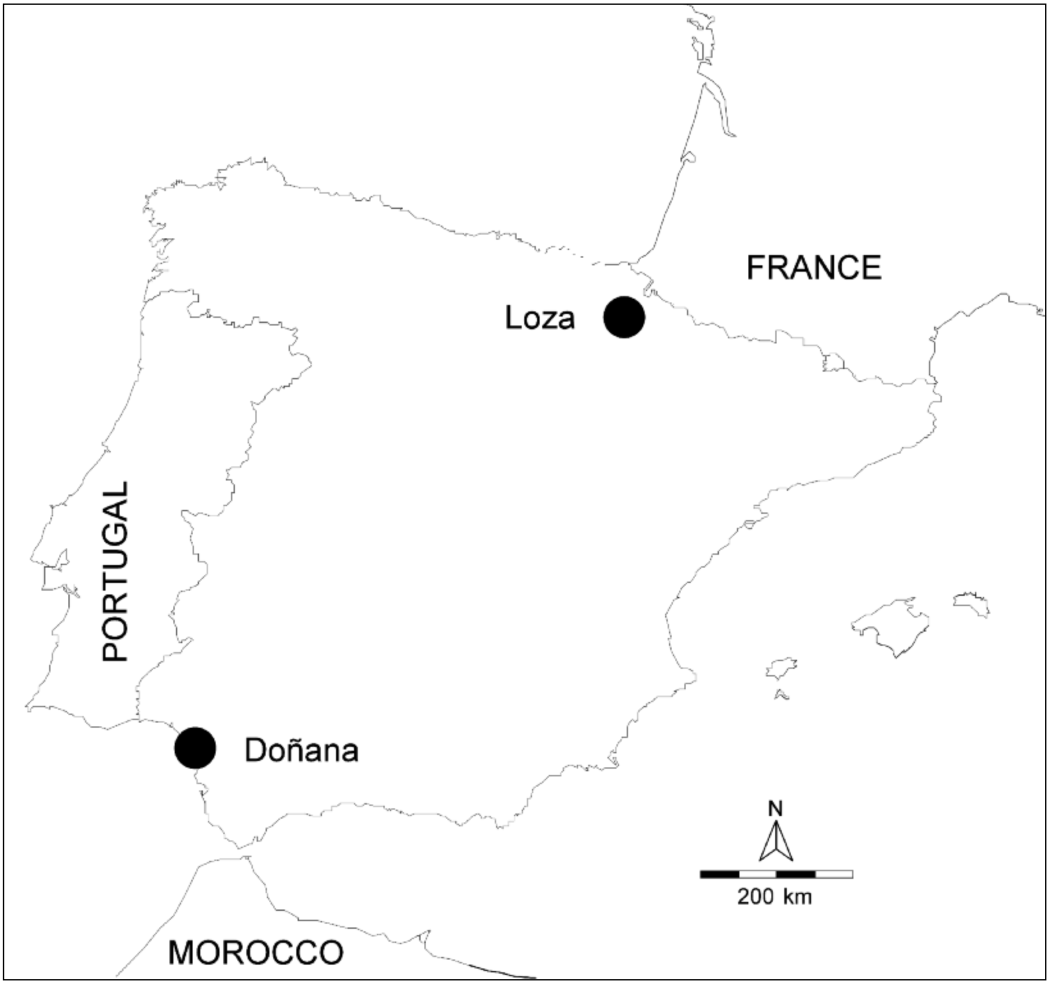

FIG. 2.—Locations of the sampling sites. Loza is located where many birds enter Iberia on the way to their wintering areas further south. Doñana is potentially a final stopover place before Africa.
[Puntos de muestreo en los cuales se realizó el estudio. La existencia de recapturas entre ambas zonas revela que las dos están en la misma ruta migratoria. Loza, en el N de España, se sitúa en un punto de entrada de aves en la Península. Doñana, en el SO de España, es potencialmente uno de los últimos lugares de descanso y ganancia de reservas antes de África.]

Blackcaps were mist-netted (Loza: 60 linear m; Doñana: 252 linear m), during the autumn migration period in 2005. Netting was carried out at Loza from 12 September to 27 October and at Doñana from 23 September to 7 November. Mist-netting took place daily from dawn, for four hours at Loza and six hours at Doñana. Captured birds were ringed, sexed and aged as either first-year birds (retaining juvenile wing feathers; EURING code 3) or adults (two years old or older; EURING code 4) following Svensson (1996).

Wing length (± 0.5 mm), tarsus length (± 0.1 mm), body mass (± 0.1 g), and moult state (moulting/non-moulting) were also recorded.

Data selection

Some blackcaps breed at both localities but these are numerically negligible relative to migrants. To minimise the presence of these birds in our data set we excluded all individuals with a wing length < 72 mm (blackcaps breeding in Iberia have shorter wings than those coming from Northern Europe in winter; Tellería *et al.*, 1999). Wintering blackcaps have not been detected at Loza (Arizaga *et al.*, 2009) so all captures in this site were considered to be stopover migrants. A few winter in Doñana, however, but these mostly appear in November (Murillo and Sancho, 1969), so blackcaps caught before November are more likely to be migrants that only use this zone as a stopover site.

Only non-moulting birds for which age and sex were known, and for which all measurements had been recorded, were included in the analyses (Loza: $N = 730$; Doñana: $N = 502$; table 1). Moulting birds are known to show different stopover behaviour and are more likely to be local individuals (Schaub and Jenni, 2000b).

Fuel load, flight ranges and fuel deposition rate

Captures from ordinary trapping sessions at a stopover site are subject to certain constraints. In particular, the first and last captures of each individual are not always obtained at exact dates of arrival or departure (Schaub *et al.*, 2001). It is thus impossible to know daily fuel load variation for the entire stopover period of each individual. However, trapping sessions at ringing stations suffice to estimate fuel management

TABLE 1

Numbers of captures and recaptures of migrating blackcaps at Loza (Northern Iberia) and Doñana (Southern Iberia) during the 2005 autumn migration period. Individuals recaptured on more than one occasion are only included once. Only non-moulting birds of known age and sex and with other biometrics recorded are included.
[Número de capturas y recapturas (ejemplares para los que se obtuvieron una o más recapturas dentro de cada periodo) de currucas capirotadas migratorias en Loza (N de España) y Doñana (S de España) durante el periodo de paso migratorio posnupcial en 2005.]

		Loza		**Doñana**	
Age	**Sex**	**Captures**	**Recaptures**	**Captures**	**Recaptures**
Adults	Male	85	1	38	0
	Female	61	2	28	1
First-year	Male	327	18	259	3
	Female	257	15	177	3

of stopover migrants (Schaub and Jenni, 2000b, 2000a, 2001b).

To assess fuel load we calculated:

(i) An index of body mass corrected for body size (body mass/tarsus length), using tarsus length as a surrogate for body size (Senar and Pascual, 1997).
(ii) The fuel load/lean body mass ratio.

In migrants, fat reserves are mostly stored in subcutaneous deposits (Kaiser, 1993), so body mass from birds with no subcutaneous fat can be used to assess lean body mass. Thus, by regressing body mass against tarsus length in a sample of blackcaps with no visible fat content ($N = 25$; data taken from Loza), we obtained a function used to assess lean body mass, m_0 [$r^2 = 0.319$, $F_{1,24} = 10.755$, $P = 0.003$; $m_0 = (0.810 \times \text{tarsus length}) + 0.347$]. Thereafter, the fuel load/lean body mass ratio was calculated as follows: $f = (m - m_0) / m_0$, where m = actual body mass. In all cases there was a slight positive skew from a normal distribution (Kolmogorov test: $P < 0.05$) but the coefficients of variation were < 15%. Thus, we used ANOVAs (that tolerate slight biases from normal distributions well) to test for the effects of site, age and sex on fuel load. Since the first and last captures of each individual are not always obtained on the exact dates of arrival or departure (Schaub *et al.*, 2001), it is likely that a sample of first- captures will include birds ranging from new arrivals to those just about to depart. Thus, we re-ran our analyses for the heaviest 25% fraction of blackcaps (Ellegren and Fransson, 1992).

In stopover migrants, mass gained per unit of time can be used to assess fuel deposition rate, as mass gain is mainly due to fat accumulation (Newton, 2008). Thus, we calculated fuel deposition rate on the basis of the difference in body mass between the last and first captures of an individual bird within the season. Although body mass can vary with capture time (Carlisle *et al.*, 2005), this variable was not measured systematically, except for a small data set from Loza. In this case, we did not detect any effect of time of day on body mass (Arizaga and Barba, 2009), so such an effect can be considered as negligible for our analyses. The number of recaptures at Doñana was very low in 2005 ($N = 7$, table 1), so recaptures from 2006-2008 were also included to obtain a larger sample size (Doñana: $N = 19$; Loza: $N = 36$; data not shown in table 1). The sampling protocol in 2006-2008 used the same methodology as in 2005.

Flight ranges were calculated by assuming that flying passerines lose mass at a constant rate of 1% per hour of flight (Hussel and Lambert, 1980; Kvist *et al.*, 1998). Using Delingat *et al.* (2008), potential flight ranges, Y [km], can be assessed as: $Y = 100 \times \mathrm{U} \times \ln(1 + f)$ (see Delingat *et al.*, 2008 for an explanation on how this equation is calculated), where U = groundspeed, (here considered to be 60 km/h; Salewski *et al.*, 2010). The standard error (SE) of this equation is:

$$\mathrm{SE}_Y = 100 \times \mathrm{U} \times [\mathrm{SE}_f / (1 - f)].$$

Stopover duration

To estimate stopover durations only first-year birds were considered, since adults were very scarce at both sampling localities (number of adults recaptured: $N = 3$ at Loza in 2005, $N = 2$ at Doñana during 2005-2008). The stopover duration was assessed:

(i) As the minimum stopover duration (Kaiser, 1999), which has been used so far in several studies and therefore has a comparative value.
(ii) Using Cormack-Jolly-Seber (CJS) models (Lebreton *et al.*, 1992), which enable estimation of survival (equiva-

lent to stay duration at a stopover site; Φ), seniority (γ; probability that a bird captured in t was at the site in $t-1$), and recapture probability (p; probability of capturing a bird given that it is present) separately (Schaub *et al.*, 2001).

The Doñana data from 2005 to 2008 were pooled into a single sample, due to the low number of recaptures per year. The timing of passage differs between Northern and Southern Iberia by about 15 days (Tellería *et al.*, 1999), so date 1 (day 1) was taken as 12 September at Loza and 23 September at Doñana, giving 46 sampling days per site and year. Overall, our matrices had a size of 588 blackcaps × 46 days (Loza), or 1095 blackcaps × 46 days (Doñana).

The CJS models were run using the MARK software (White and Burnham, 1999). Before starting to select models we used a goodness-of-fit (GOF) test to determine to what extent the data met the CJS assumptions. The GOF test on a CJS model where both Φ (or γ) and p were time-dependent [Φ(t) p(t)] was done with the U-CARE software (Choquet *et al.*, 2001). The overall GOF test was not significant for both the Loza and the Doñana datasets ($P > 0.05$), but for Doñana we detected the presence of transients ($P = 0.015$; test for transience for Loza, $P = 0.387$). Transience breaks CJS assumptions, since for these birds Φ after marking is zero (Pradel *et al.*, 1997). Thus, the most complex model from which to start modelling for Doñana was the one where Φ (or γ) and p were time-dependent and Φ (or γ) were also affected by transients [Φ (transients*t) p(t)] [for Loza, Φ(t) p(t)]. All other fitted models were nested within the starting one.

Model selection employed information theory (Burnham and Anderson, 1998). Akaike's Information Criterion (AIC) was used for ranking the fit of the models to the data (Burnham and Anderson, 1998), the best-fitting model being that with the lowest AIC value. Models that differed in AIC by less than two units ($\Delta AIC < 2$) were taken as similar to each other (Burnham and Anderson, 1998). We calculated stopover duration as a function of Φ and γ (Schaub *et al.*, 2001): stopover duration = $-(1/ln\ \gamma) - (1/ln\ \Phi)$.

RESULTS

Fuel load, flight ranges and fuel deposition rate

Blackcaps captured at Loza were heavier than at Doñana (Loza: 0.927 ± 0.003 g/mm, 12.2 ± 0.4% over lean body mass, $N = 730$; Doñana: 0.857 ± 0.004 g/mm, 3.7 ± 0.5% over lean body mass, $N = 502$), both for all birds and for the heaviest 25% fraction (table 2, fig. 3). Fuel load differed between age classes, but only for Loza and when the entire population was considered, with adults having higher fuel loads than first-year-birds (fig. 3).

Estimated flight ranges were always longer in Loza than in Doñana (table 3). First-year birds tended to have longer flight ranges than adults at Doñana, but not at Loza, although in all cases the differences were small (table 3).

Recaptures were proportionally more abundant at Loza than in Doñana (table 1; Loza, 4.9%; Doñana, 1.4%), and most of them were first-year birds (table 1). Blackcaps tended to gain mass at Loza (0.14 ± 0.09 g/day, $N = 33$), but not at Doñana (-0.11 ± 0.13 g/day, $N = 17$; means given for first-year birds). In adults (sampling places pooled), fuel deposition rate was 0.18 ± 0.05 g/day ($N = 5$). In first-year birds, fuel deposition rate was positively correlated with the minimum stopover duration at Loza (Loza: $r = 0.397$, $P = 0.022$, $N = 33$), but not at Doñana: $r = 0.432$, $P = 0.083$, $N = 17$). The fuel deposition rate was correlated with body mass at final capture in Loza, but not in Doñana (fig. 4).

TABLE 2

ANOVAs used to test for the effects of site, age and sex on two different variables assessing fuel load for all birds and the heaviest 25% fraction of migrating blackcaps.
[ANOVAs utilizados para comprobar el efecto de la zona, edad y sexo en dos variables que se emplearon como estima de la cantidad de reservas de toda y el 25% de la fracción de la población de currucas capirotadas migratorias.]

	Body mass/Tarsus length		**Fuel load over lean mass**	
100% population	$F_{1,1231}$	P	$F_{1,1231}$	P
Site	119.067	**< 0.001**	118.876	**< 0.001**
Age	0.122	0.727	0.123	0.726
Sex	0.716	0.398	0.675	0.411
Site×Age	7.129	**0.008**	7.075	**0.008**
Site×Sex	0.613	0.434	0.624	0.430
Age×Sex	3.405	0.065	3.385	0.066
Site×Age×Sex	3.185	0.075	3.187	0.074
25% heaviest fraction	$F_{1,307}$	P	$F_{1,307}$	P
Site	38.241	**< 0.001**	35.876	**< 0.001**
Age	1.661	0.198	1.439	0.231
Sex	0.252	0.616	0.076	0.783
Site×Age	0.001	0.978	0.115	0.735
Site×Sex	0.301	0.584	0.487	0.486
Age×Sex	0.699	0.404	1.122	0.290
Site×Age×Sex	1.436	0.232	1.508	0.220

TABLE 3

Flight ranges (km ± SE) of blackcaps captured in Northern Iberia (Loza) and Southern Iberia (Doñana) during the autumn migration period.
[Rangos de vuelo (en km, SE) de currucas capirotadas capturadas en el norte (Loza) y sur de España (Doñana) durante el periodo de paso migratorio posnupcial.]

	100% population		**25% heaviest fraction**	
	Loza	**Doñana**	**Loza**	**Doñana**
First-year birds	659 ± 32	229 ± 33	1509 ± 63	1028 ± 59
Adults	805 ± 62	137 ± 75	1388 ± 68	1018 ± 179

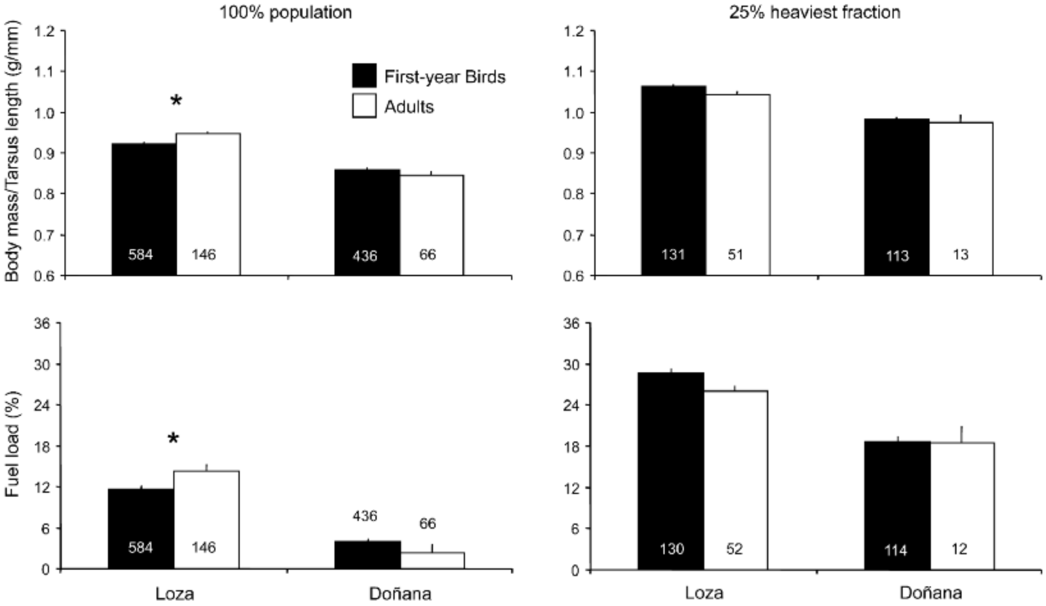

FIG. 3.—Fuel loads of blackcaps during the autumn migration period in relation to age and site, for the entire sample and the heaviest 25% fraction. Significant differences between age classes are asterisked (*). There were significant differences between sampling points in all cases (see text).

[Cantidad de reservas durante el periodo de paso postnupcial en relación a la edad y la zona, para toda y la fracción (25%) de aves con más peso relativo/reservas.]

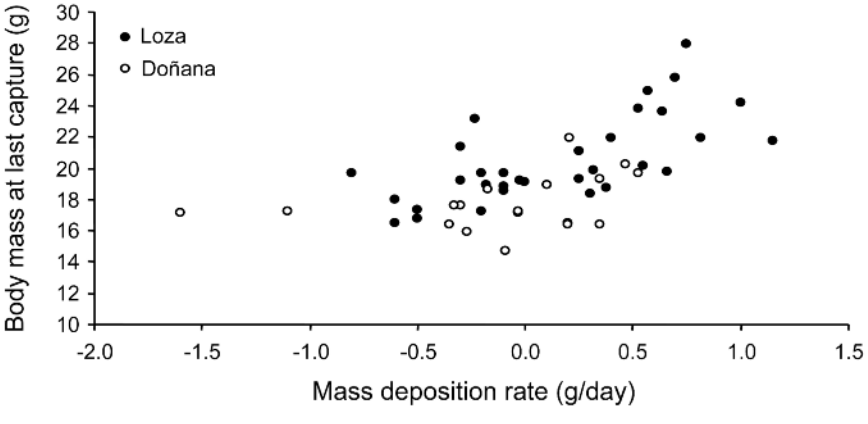

FIG. 4.—Body mass at final recapture related to rate of accumulation (adults excluded) for Loza and Doñana. The correlation coefficients are: Loza, $r = 0.667$, $P < 0.001$ ($N = 33$); Doñana, $r = 0.347$, $P = 0.173$ ($N = 17$).

[Relación entre el peso en la última captura y la tasa de ganancia de peso (adultos excluidos), para Loza y Doñana. Los coeficientes de correlación son: Loza, r = 0,667, P < 0,001 (N = 33); Doñana, r = 0,347, P = 0,173 (N = 17).]

Stopover duration

Most recaptures were obtained within an interval of < 15 days although one blackcap from Doñana was recaptured after 25 days (fig. 5). After excluding this untypical bird, we did not observe differences between sites (Loza: 5.6 ± 0.7 days, $N = 33$; Doñana: 5.9 ± 1.0 days, $N = 16$; $t_{47} = 0.279$, $P = 0.781$).

CJS models detected the presence of transients, i.e. blackcaps that tended to depart from the area the day after arrival, at Doñana but not at Loza. For Loza, the best models that fitted the data were those where Φ, γ and p were constant (table 4). Recapture likelihood, p, was 0.02 ± 0.00 and stopover duration, 8.9 ± 0.6 days. For Doñana, the best models were those that considered the occurrence of transients (table 4). The proportion of transients was 6.6%. Φ for the fraction of non-transients was 0.86 ± 0.04, and the stopover duration was 11.3 ± 0.6 days.

DISCUSSION

Northern Iberia

Blackcaps passing through Northern Iberia carried higher fuel loads than in Southern Iberia, but lower fuel loads than in Southern England and Holland (Langslow, 1976). Such a result supports the hypothesis that fuel load decreases along a north-to-south axis (Grandío, 1997). This hypothesis states that blackcaps accumulate relatively large fuel loads in or close to their breeding areas, so as to arrive in Southern Europe by several consecutive flights interrupted by relatively short stopovers (Ellegren and Fransson, 1992).

With a mean fuel load of nearly 15% over lean body mass, blackcaps stopping over in Northern Iberia had sufficient fuel to reach Southern Iberia or Northern Africa. Moreover, the heaviest blackcaps, those just about to depart (Ellegren and Fransson, 1992),

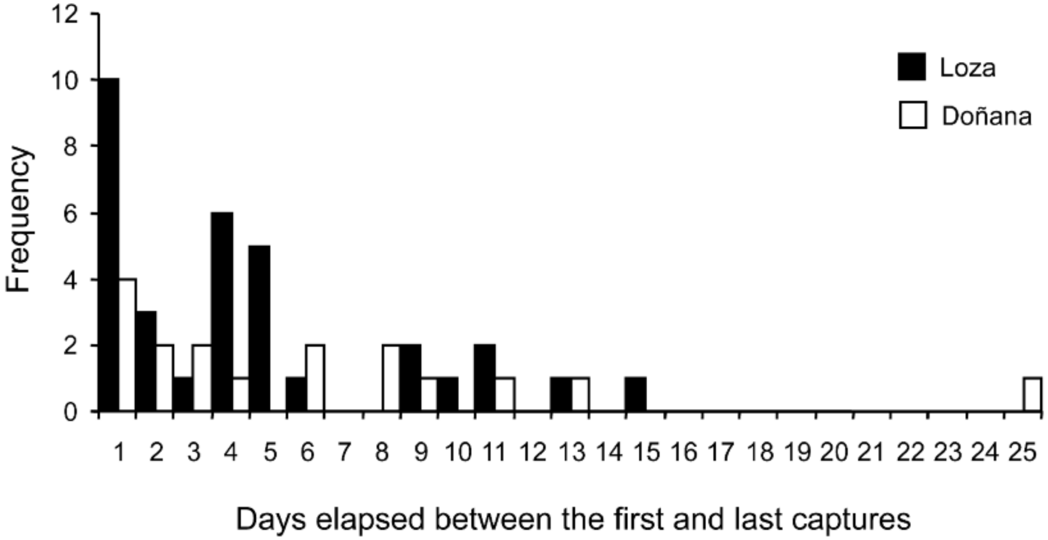

FIG. 5.—Distribution of recaptures in relation to the period between the first and last captures.
[Distribución de recapturas en relación al número de días transcurridos entre la primera y última captura.]

would be able to reach the northern edge of the Sahara. This suggests that if some blackcaps that stop over in Northern Iberia overwinter in tropical Africa, they would need to refuel before crossing the Sahara (Arizaga and Barba, 2009).

Adults carried greater fuel loads than did first-year birds. However, this was not due to a higher fuel deposition rate but because adults already carry high fuel loads when arriving in Loza (Arizaga *et al.*, 2008). However, such a difference in fuel load did not appear when

TABLE 4

Cormack-Jolly-Seber models used to estimate stopover durations. AICc = corrected Akaike values; ΔAICc = difference of models' AICc values in relation to the model one; np = number of parameters; Φ = survival; γ = seniority; p = recapture probability.

[Modelos Cormack-Jolly-Seber empleados para estimar el tiempo de estancia. AICc = valores Akaike corregidos; ΔAICc = diferencia de valores AICc de cada modelo respecto del primer modelo; np = número de parámetros; Φ = supervivencia; γ = reclutamiento; p = probabilidad de recaptura.]

Models	**AICc**	**ΔAICc**	**AICc weight**	***np***	**Deviance**
Loza, N Iberia					
1. Φ, p	435.264	0.00	1.00	2	191.828
2. Φ, p(t)	475.454	40.19	0.00	46	136.517
3. Φ(t), p	490.348	55.08	0.00	46	151.411
4. Φ(t), p(t)	517.585	82.32	0.00	74	109.875
1. γ, p	433.307	0.00	1.00	2	
2. γ, p(t)	471.957	38.65	0.00	46	
3. γ(t), p	480.406	47.10	0.00	46	
4. γ(t), p(t)	518.473	85.17	0.00	74	
Doñana, S Iberia					
1. Φ(transients), p	319.380	0.00	1.00	3	162.991
2. Φ, p	335.257	15.88	0.00	2	180.878
3. Φ(transients), p(t)	365.310	45.93	0.00	47	116.666
4. Φ, p(t)	379.203	59.82	0.00	46	132.741
5. Φ(t), p	402.204	82.82	0.00	45	157.920
6. Φ(t), p(t)	426.012	106.63	0.00	75	114.544
1. γ, p	336.470	0.00	0.66	2	
2. γ(transients), p	337.814	1.34	0.34	3	
3. γ, p(t)	379.395	42.92	0.00	46	
4. γ(transients), p(t)	379.395	42.92	0.00	46	
5. γ(t), p	400.513	64.04	0.00	46	
6. γ(t), p(t)	421.733	85.26	0.00	75	

only the heaviest 25% fraction of the population was considered. Indeed, first-year birds tended to be slightly more fuel loaded than adults in this subsample, which would support the suggestion that first-year birds may migrate to regions further south than adult birds (Shirihai *et al.*, 2001).

A moderate fuel deposition rate of 0.14 g/day, together with a mean stopover duration of 8.9 days, suggests that blackcaps did not gain more than 1.5 g at Loza. This suggests that high fuel deposition rates are not usual in Northern Iberia, probably due to the vicinity of a major wintering area in Southern Iberia, and the fact that opportunities to refuel across Iberia are available along the whole route.

Blackcaps stopping over at Loza seem to minimise duration of migration, since the rate of mass accumulation was correlated with the mass at last capture (fuel accumulation fitted a linear function, so body mass at last capture is used here as a surrogate of departure body mass; Arizaga *et al.*, 2008), and because birds with lower fuel deposition rates stopped over for shorter periods (Alerstam and Lindström, 1990). Arriving early to their wintering areas may allow blackcaps to increase the likelihood of finding a good winter territory. The existence of age-related segregation between high- and low-quality habitats during winter suggests that competition for better territories exists (Pérez-Tris and Tellería, 2002).

Southern Iberia

Blackcaps at Doñana carried lower fuel loads than those in Northern Iberia, even when just the heaviest 25% fractions are compared, and the former had a balanced energy budget (i.e. null fuel accumulation). This suggests that blackcaps that overwintered in Southern Iberia, and thus were not stopover migrants, were present at Doñana. Such a circumstance, which probably applies to the entire Mediterranean region (Shirihai *et al.*, 2001), compels us to consider the data from Doñana very cautiously. However, the stopover duration at Doñana was brief (*c.* 10 days), suggesting that most blackcaps, if not all, left the area before the winter. It is noteworthy that Doñana in general, and our sampling site in particular, lacks a significant wintering blackcap population (Murillo and Sancho, 1969). It is thus likely that a considerable number of the blackcaps present in Doñana in October migrate further to Northern Africa or other zones of Southern Iberia.

If the Doñana sample included trans-Saharan birds, their low loads of fuel would not allow them to fly directly to tropical Africa. They would hence need to refuel somewhere before crossing the Sahara. Since even the heaviest blackcaps captured in Northern Iberia could not reach tropical Africa without refuelling, we can reject the idea that long-distance migrants gain large loads of fuel in zones further north than Southern Iberia. A more likely strategy is that these birds refuel at stopovers either elsewhere in Southern Iberia or in Northern Africa. The mean body mass of blackcaps at Doñana (17.8 g) was nearly one gram lower than at Gibraltar in Autumn (Finlayson, 1981). This suggests that Doñana might not offer such good opportunities to refuel as other nearby sites, although there might be high year-to-year variability both within and between sites. The fact that 6.6% of blackcaps arriving in Doñana left the area the next day is compatible with this hypothesis, although the body condition in which these birds left the area is also relevant. Unfortunately, the very low number of recaptures in Doñana (only 7 blackcaps in 2005) did not allow us to test whether fuel load differed between blackcaps captured only once or more than once. A fraction of the Doñana blackcaps may also resume their migration as far as Northern Africa. This last behaviour is probably very widespread among *Sylvia* warblers that normally feed on fruits during the autumn migration period, which often acquire high fuel loads just before reaching the northern edge of the Sahara (Izhaki and Maitav, 1998; Fransson *et al.*, 2008). It is also possible that the fraction of blackcap populations that Winter in tropical Africa is small, in which case it would be very difficult to identify the trans-Saharan migrants among the huge number of blackcaps that winter around the Mediterranean.

Although some blackcaps departed from Doñana immediately, most remained there for some time. It is interesting that, in contrast to Loza, blackcaps with negative or very low fuel deposition rates did not leave Doñana sooner than others with higher rates. Together with the lack of correlation between fuel deposition rate and fuel load at departure, this suggests that blackcaps from Doñana, if they were still migrating, did not behave as time-minimisers. Alternatively, we cannot rule out the possibility that most blackcaps captured at Doñana were staying to winter there.

Conclusions

Our results support the observation that blackcaps lose fuel along a north-south axis that connects their breeding and final wintering areas. Even when only the heaviest 25% fraction is considered, blackcaps from Doñana showed lower fuel loads than in Northern Iberia, and so would be unable to reach tropical Africa from there without refuelling. They would need to refuel somewhere before crossing the Sahara, either at other stopover sites in Southern Iberia or in Northern Africa.

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