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A COMPARISON OF STOPOVER BEHAVIOUR OF TWO SUBSPECIES OF THE BLUETHROAT *LUSCINIA SVECICA* IN NORTHERN IBERIA DURING THE AUTUMN MIGRATION PERIOD

COMPORTAMIENTO EN UN ÁREA DE DESCANSO DE DOS SUBESPECIES DE RUISEÑOR PECHIAZUL *LUSCINIA SVECICA* EN EL NORTE DE LA PENÍNSULA IBÉRICA DURANTE EL PERIODO DE PASO MIGRATORIO POSNUPCIAL

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Summary.—Iberia offers one of the last opportunities four migrants to refuel before crossing the Sahara. It is also a destination for populations that overwinter within the circum-Mediterranean region. Our aim was to analyse whether two bluethroat subspecies that stop over in northern Iberia and face different migration distances, show different stopover behaviour in terms of periods of passage, fuel management and stopover duration. The subspecies were *Luscinia svecica namnetum*, which overwinters within the circum-Mediterranean region; and *L. s. cyanecula,* some of which migrate to tropical Africa. Overall, we obtained 265 captures, involving 208 distinct bluethroats and 56 recaptures, at the Txingudi marshlands in northern Iberia, during the autumn migration periods of 2007 and 2008. Passage periods did not differ between both subspecies, nor did fuel load (body mass: 15.0 g; fat: 1.0), mass deposition rate (0.07 g/day) and stopover duration (15.3 days). However, late *L. s. cyanecula* showed higher fuel loads than early individuals, so these birds could potentially cover longer distances without needing to refuel. Mean fat score was low for both subspecies which, together with the very low rate of fuel accumulation, supports the hypothesis that Iberia is crossed in consecutive short steps. Long-distance *L. s. cyanecula* migrants could acquire the high fuel loads needed to migrate to tropical Africa in southern Iberia or north-western Africa.

Key words: Cormack-Jolly-Seber models, fuel deposition rate, fuel load, stopover duration, tidal marsh, Txingudi.

Resumen.—Para las aves, la península Ibérica ofrece gran cantidad de oportunidades para ganar reservas antes de cruzar el Sahara, a la vez que es una zona de invernada de gran relevancia. El objetivo de nuestro trabajo es analizar si las dos subespecies de pechiazul *Luscinia svecica* presentes en el norte de la Península y cuya distancia de migración es diferente (*L. s. namnetum*, invernante en la región

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mediterránea; *L. s. cyanecula*, con una fracción de individuos que migra hasta África tropical) tienen un comportamiento distinto en cuanto a tiempo de paso, cantidad de reservas y tiempo de estancia en un área de descanso. Se obtuvieron 265 capturas, de 208 ejemplares diferentes recapturados en 56 ocasiones en la marisma de Txingudi, en el norte de la Península, durante el periodo de paso posnucial en 2007 y 2008. La fecha de paso no varió entre ambas subespecies, ni la cantidad de reservas (medias: peso, 15,0 g; nivel de grasa, 1,0), su tasa de deposición (ca. 0,1 g/día) o el tiempo de estancia (15,3 días). No obstante, *L. s. cyanecula* mostró una cantidad de reservas mayor al final del paso. El bajo nivel medio de grasa, junto con una tasa de deposición de peso también baja, apoyan la idea de que el pechiazul atraviesa la Península en saltos cortos. Los ejemplares de *L. s. cyanecula* que van a invernar a África tropical podrían acumular en el sur de la península Ibérica o en el norte de África la gran cantidad de reservas teóricamente necesitada para alcanzar el sur del Sahara.

Palabras clave: cantidad de reservas, duración de la estancia en un área de descanso, marisma costera, modelos Cormack-Jolly-Seber models, tasa de deposición de reservas, Txingudi.

INTRODUCTION

With nearly 600,000 km^2 and a privileged geographic position on one of the main European migratory bird crossroads, Iberia offers good opportunities to analyse several aspects of bird migration strategies. It offers birds one of the last opportunities to refuel before crossing the Sahara Desert. It is also the destination for populations that overwinter within the circum-Mediterranean region (e.g. Cramp, 1988, 1992). There is still little information regarding whether populations with different migration distances show different stopover behaviour in Iberia (as observed elsewhere, e.g. Dierschke and Delingat, 2001). Migrants stopping over in northern Iberia that overwinter within the circum-Mediterranean region would not be expected to carry large fuel loads since they are near their destinations. Conversely, long-distance migrants that overwinter in tropical Africa need to accumulate large fuel loads since they have to cross a large, inhospitable desert (e.g. Schaub and Jenni, 2000). The latter could acquire such large fuel loads either in northern Iberia or in southern Iberia/northern Africa.

Alerstam and Lindström (1990) proposed that migrants optimise their migration by minimising travel time, energy-cost and/or predation risk. Such strategies predict different relationships between fuel deposition rate (amount of fuel gained per unit time) and fuel load (amount of fuel reserves) on departure. Time minimisers that experience a fuel deposition rate lower than expected will depart from a stopover site, so in this case departure fuel load and fuel deposition rate are correlated. In energy minimisers, however, the fuel deposition rate does not determine the departure fuel load, since birds would be expected to optimise their fuel loads to reach the next stopover site only. Predation risk, as well as fuel accumulation, is also likely to affect stopover duration although it has been less well studied.

The bluethroat *Luscinia svecica* is a widespread polytypic Holarctic passerine, that breeds from Iberia in Europe across the Palearctic and in Alaska and north-western Canada. Two of the ten recognised subspecies breed in west Europe (Collar, 2005): *L. s. namnetum* breeds in west France and migrates along the coast of northern Iberia (Arizaga *et al.,* 2006) to overwinter mainly in Portugal and north-western Africa (Zucca and Jiguet, 2002); *L. s. cyanecula* breeds in central Europe east to western Russia and in Iberia (although recent genetic studies (Johnsen *et al.,* 2006) suggest that the Iberian population is probably a different subspecies, *L. s. azuricollis*) and it migrates on a broad front to overwinter within the circum-Mediterranean region and in tropical Africa (Cramp, 1988). *L. s. namnetum* migrates no further than 2,000 km, and probably less than 1,000 km in most cases, over regions rich in food and wetlands. However, some *L. s. cyanecula* must cover more than 5,000 km and cross the Sahara Desert.

Thus, given that there are many potential stopovers in Europe, *L. s. namnetum* is expected to carry low fuel loads and make many short flights with short stopovers during the autumn migration period. In contrast, *L. s. cyanecula,* some of which are long-distance migrants, should be expected to accumulate more fuel and stop over for longer to obtain it, in order to cross the Mediterranean and the Sahara. However, such *cyanecula* individuals could still acquire just a low amount of fuel in northern Iberia provided that they stop over later in southern Iberia or northern Africa to refuel before the desert crossing. The latter strategy is supported by recent studies in the Ebro valley in northern Iberia (Arizaga *et al.,* 2009a). However, migrant bluethroats passing through the Ebro valley are intermixed with a population of wintering birds that may therefore, influence any observations made there. Observations in regions of northern Iberia where bluethroats only occur on passage are required to examine our hypotheses. If *L. s. cyanecula* is more time-stressed than *L. s. namnetum*, due to having to travel further to reach its wintering areas, then its fuel deposition rate should be correlated with departure fuel load, or correlated to a greater extent than in *L. s. namnetum* (Delingat *et al.,* 2006). The importance of understanding such subspecies-specific migration strategies is linked with the goal of studying the evolution of migratory strategies, for which the comparison of closely-related taxa is of particular interest.

We aimed to analyse whether the two bluethroat subspecies that stop over in northern Iberia, *L. s. namnetum* and *L. s. cyanecula*, show different stopover behaviour, during the autumn migration period. Data were obtained at Txingudi marshlands, at the point where the Atlantic flyway enters Iberia.

MATERIAL AND METHODS

Sampling area

Bluethroats were caught in a 25 ha reedbed *Phragmites australis* in Jaizubia stream, a site in the Txingudi marshlands, Hondarribi, Gipuzkoa, N Iberia; 43º 21' N 01º 49' W, 2 m above sea level. Txingudi is west of the Pyrenees and in the south-eastern corner of the Bay of Biscay. Its location produces a funnel effect for migrants (Galarza and Tellería, 2003). Most *namnetum* birds are likely to enter Iberia throughout Txingudi (Arizaga *et al.,* 2006) but bluethroats neither breed nor overwinter there.

Birds were captured with mist nets (204 linear m) at a constant-effort site during the autumn migrations of 2007 and 2008. Mist nets were open daily from 1 August to 30 October for 4 hours starting at dawn. Captured birds were ringed, aged and sexed (Svensson, 1998). They were aged as adults (EURING code 4; older than one year, with no juvenile wing feathers) or first-years (EURING code 3; same-year birds still with some juvenile wing feathers). The following biometric variables were also noted: wing length (± 0.5 mm, method III in Svensson, 1998), tarsus length (± 0.1 mm), body mass (± 0.1 g) and fat score (± 0.5; ranging from 0 to 8, Kaiser, 1993). Subspecies were determined by wing length, following Eybert *et al.* (1999). Individuals assigned to *L. s. namnetum* were those with the following wing lengths: first-year males, < 71 mm; adult males, < 72 mm; first-year females, < 67 mm; adult females, < 68 mm.

We captured 208 individual bluethroats, 57 of which were recaptured. Only birds for which we had a complete record of age and biometrics were included in the analyses. Sex was not included due to the small sample size (table 1) and because age, rather than sex, has been reported to be a variable that affects the fuel load of bluethroats (Ellegren, 1991).

Population structure, timing of passage

We used a stratified Cochran-Mantel-Haenzel chi-square test to analyse whether the proportion of age classes differed between the subspecies, with year as a control factor. General Linear Models (GLM) were used to analyse whether the timing of passage differed between subspecies, age class and year, since date fitted the normal distribution for each subspecies (Kolmogorov test: $P > 0.05$). Recaptures were excluded from all these analyses.

Corrected Akaike Information Criteria values (AICc) were used to rank the fit of GLMs to data (Burnham and Anderson, 1998). Models with an AICc difference less than 2 were considered to fit the data equally, and those for which the difference was higher than 2 were considered to differ.

Fuel load analyses

We examined whether fuel load varied between age classes and subspecies. Recaptures were excluded for this purpose, so only the data relating to the first capture event for each bird were considered. Date was used as a covariate since it could affect fuel manage-

TABLE 1

Number and ages of bluethroats captured only once or recaptured (captured twice or more per season) at Jaizubia, Txingudi marshlands, during the autumn migration period of 2007 and 2008. We only considered birds with a complete record of age, body mass, fat score, wing length and tarsus length. Subspecies were identified by wing length, following Eybert *et al.* (1999).

[Pechiazules capturados (cada ejemplar se ha tenido en cuenta una vez por año) o recapturados (número de aves capturadas dos o más veces por año; cada ejemplar se ha considerado sólo una vez por año) en Jaizubia, marismas de Txingudi, durante el periodo de paso posnupcial 2007 y 2008. Sólo se han considerado las aves de edad conocida y para las que se ha medido la masa corporal, nivel de grasa, longitud alar y tarso. Las subespecies se han identificado por la longitud alar, siguiendo a Eybert et al. *(1999).]*

		L. s. namnetum		***L. s. cyanecula***	
		First-year	**Adults**	**First-year**	**Adults**
2007	Captured	73	14	31	5
	Recaptured	20	4	9	2
2008	Captured	38	4	37	6
	Recaptured	11	1	8	1

ment at stopovers (Bayly, 2006). We used body mass (controlled for body size, for which the tarsus length was used a surrogate of body size; Senar and Pascual, 1997) and fat scores to estimate fuel load. Body mass fitted the normal distribution (Kolmogorov test: $P = 0.080$), so parametric procedures (GLM) were used to compare whether body mass controlled for body size differed between subspecies. Conversely, fat scores did not fit a normal distribution ($P < 0.001$) so therefore non-parametric procedures (U-tests) were used to compare fat scores between subspecies and age classes.

The rate of fuel deposition, hereafter the 'mass deposition rate', was calculated as the difference between body mass at the last and first capture events of each bird, divided by the interval between such events. This variable was normally distributed, so GLMs were used to test for the effect of subspecies and age on mass deposition rate.

In both body mass and mass deposition rate analyses, we considered the AICc values to rank the fit of models to the data and thus to select those models that best fitted the data. Such an approach was not used for fat score since this variable was not normally distributed.

Stopover duration analyses

Migrants at a stopover site are very likely to be present before they are first captured, as well as to remain for some time after they are last captured (Schaub *et al.*, 2001). Cormack-Jolly-Seber (CJS) models estimate survival (Φ; the likelihood that an individual caught at time t will be present at time $t+1$), seniority (γ; the likelihood that an individual caught at time t was present at time $t-1$) and recapture likelihood separately. As a bird's survival at a stopover site from one day to the next is nearly 1 (Schaub *et al.*, 2001), Φ here is the stay likelihood. We calculated stopover duration as a function of Φ and γ (Schaub *et al.*, 2001): stopover duration $= -(1/ln\ \gamma) - (1/ln\ \Phi)$. In other words, stopover duration was calculated as the sum of the time a bird spent at a site before/after it was captured. The time spent on site after a bird was captured is a measure of survival (estimation of Φ and p) and the time before the bird was captured is a measure of recruitment (estimation of γ and p).

Before model selection, we explored the fit of the data to CJS assumptions, using a goodness-of-fit (GOF) test. A GOF test on a CJS model where both Φ (or γ) and p varied with time [$\Phi(\mathrm{t})\ p(\mathrm{t})$] was carried out using U-CARE software (Choquet *et al.*, 2001), allowing us to identify a basic starting model that fitted the data. The global GOF test for the data set was not significant ($\chi^2_{66} = 13.622$, $P = 0.999$), neither were the specific GOFs used to test for the presence of trap-dependence and transients ($P > 0.05$), so our data set conformed with the CJS assumptions (Pradel *et al.*, 1997; Belda *et al.*, 2007). $\Phi(\mathrm{t})\ p(\mathrm{t})$ was the most complex model from which we began model selection. All other fitted models were nested within this initial model. The models considered in this analysis were those where Φ and γ were constant or affected by subspecies. The AICc values were used to rank the fit of models to data.

We also calculated the minimum stopover duration for each subspecies (the difference in days between the last and first capture event +1). The 1 is added since the bluethroat is a nocturnal migrant (Cramp, 1988), a procedure used in other studies on bluethroat migration (Ellegren, 1991, Bermejo and De la Puente, 2004).

Software

We used MARK 4.3 software (White and Burnham, 1999) for CJS models and SPSS 18.0 for the other analyses. All means are given ± SE.

RESULTS

Population structure, timing of passage

Most of the captured bluethroats (62.0%) were *L. s. namnetum* although they comprised a higher proportion in 2007 (70.7%) than in 2008 (49.4%), a significant difference ($\chi^2_1 = 9.699$, $P = 0.002$). Controlling for year, the proportion of different age classes did not vary between the two subspecies (CMH test: $\chi^2_1 = 0.003$, $P = 0.960$) but first-year birds (86.1%) were more abundant than adults.

Adults were always scarce ($N < 10$ for *L. s. cyanecula* in 2007 and 2008 and for *L. s. namnetum* in 2008; table 1), so we did not

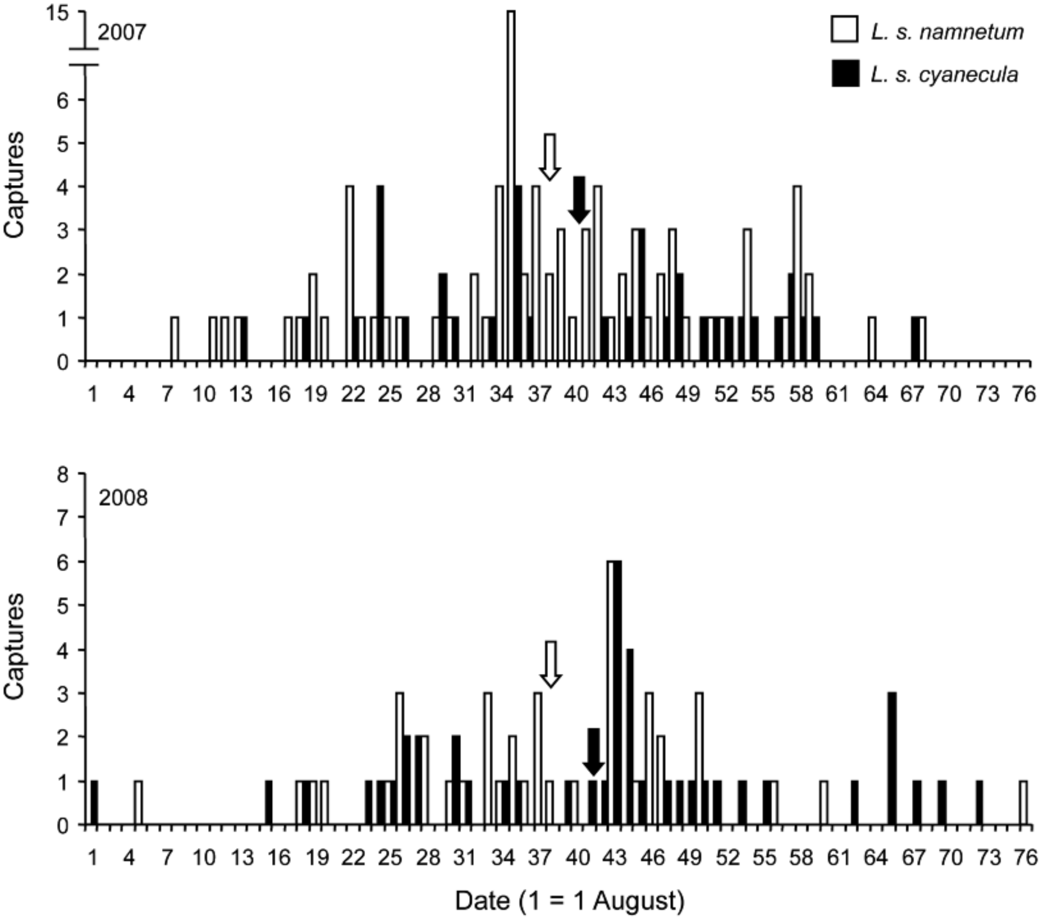

FIG. 1.—Numbers of captures (each bird considered only once) of the two bluethroat susbspecies stopping-over at Txingudi marshlands (northern Iberia) during the autumn migration period. Arrows show mean passage dates.

[Número de capturas (cada ejemplar sólo se ha considerado una vez) de las dos subespecies de pechiazul presentes en Txingudi (N de España) durante el periodo de paso migratorio posnupcial. Las flechas señalan la fecha media de paso.]

include age classes as an additional factor in the ULM that was used to test for the effect of subspecies and year on the timing of passage. The best model that fitted the data included only an effect of the subspecies, but not year nor the interaction between these factors on date (AICc values for all possible models: subspecies, 1673.502; subspecies + year, 1675.487; year, 1675.919; subspecies × year, 1677.472). Although *L. s. cyanecula* tended to pass later than *L. s. namnetum* (fig. 1; the proportion of variation explained by differential timing of passage between subspecies: 2007 = 0.19; 2008 = 0.28), we did not detect significant differences (subspecies: Wald statistics = 2.876, *P* = 0.090; complete GLM: subspecies: Wald = 2.606, *P* = 0.106; year: Wald = 0.133, *P* = 0.716; subspecies × year: Wald = 0.114, *P* = 0.735), with the peak being the first ten days of September (fig. 1). For *L. s. namnetum* in 2007, timing of passage did not differ between age classes (t_{85} = 0.232, *P* = 0.817; effect size: 0.08).

Fuel load

For body mass, models 2 and 4 had the lowest AICc values without significant differences between them (table 2). After controlling for tarsus length (used here as a proxy of body size) we observed that body mass differed between age classes and covaried with date subspecies-specifically (sub., Wald = 0.628, *P* = 0.428; age, Wald = 5.179, *P* = 0.023; tarsus length, Wald = 17.048,

TABLE 2

Model selection of GLM on parametric data (body mass, mass deposition rate) associated with fuel load and fuel deposition rate. Models included control factors (S, subspecies; A, age) and covariates (T, tarsus length; D, date); (×), interactions. AICc, corrected Akaike values, ΔAICc, difference of AICc values for each model and the model with the lowest AICc.

[Selección de Modelos Lineales Generales (GLM) utilizado con las variables paramétricas (peso y tasa de deposición de peso) asociadas a la cantidad de reservas y su tasa de deposición. Los modelos incluyen factores control (S, subespecie; A, edad) y covariables (T, tarso; D, fecha); (×), interacción. AICc, valor Akaike corregido, ΔAICc, diferencia entre el valor Akaike de cada modelo con el del modelo con el valor AICc menor.]

	Body mass		**Mass deposition rate**	
Models	**AICc**	**ΔAICc**	**AICc**	**ΔAICc**
1. S, A, S×A, T, D, D×S, D×A	716.526	2.099	18.898	9.805
2. S, A, T, D, D×S, D×A	715.964	1.537	16.101	7.008
3. S, T, D, D×S, D×A	718.916	4.489	13.643	4.550
4. A, T, D, D×S, D×A	714.427	0.000	13.475	4.382
5. S, A, S×A, T, D	719.949	5.522	13.665	4.572
6. S, A, T, D	720.237	5.810	11.175	2.082
7. S, T, D	723.054	8.627	9.093	0.000
8. A, T, D	728.651	14.224	12.797	3.704

$P < 0.001$; date, Wald = 0.006, $P = 0.940$; date × sub., Wald = 4.286, $P = 0.038$; date × age, Wald = 2.974, $P = 0.085$). Similarly, fat scores did not differ between subspecies, but differed significantly between age classes (U-tests: sub., $U = 4803.5$, $P = 0.456$; age, $U = 1391.5$, $P < 0.001$) (fig. 2). Fuel load was significantly higher in adults (body mass: 15.6 ± 0.3 g; fat: 1.5 ± 0.1, $N = 29$) than among first-year birds (body mass: 15.0 ± 0.1 g; fat: 0.9 ± 0.1, $N = 179$). Moreover, fuel load increased with date in *L. s. cyanecula* (body mass: $r = 0.323$, $P = 0.004$; fat: $r_S = 0.238$, $P = 0.035$) but not in *L. s. namnetum* (mass: $r = 0.093$, $P = 0.292$; fat: $r_S = 0.050$, $P = 0.571$).

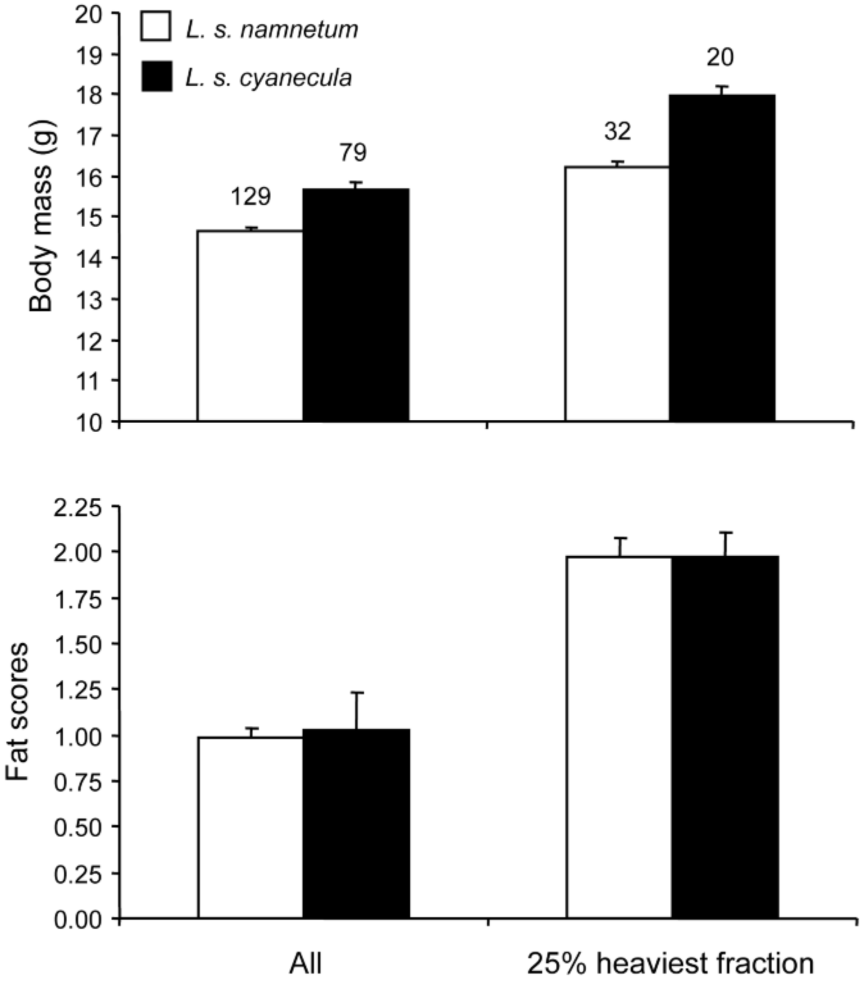

FIG. 2.—Fuel load (± SE) for all sample and the heaviest 25% in bluethroats stopping-over at Txingudi marshlands, in northern Iberia.

[Cantidad de reservas (± SE) para el conjunto y la fracción (25%) de aves con más peso capturados en Txingudi.]

We recalculated fuel load for the heaviest 25% of migrants for each subspecies since these were more likely to include birds that were about to depart (Ellegren and Fransson, 1992). Again, body mass controlled for body size was similar for the two subspecies (body mass: sub., Wald = 0.449, $P = 0.503$; tarsus length, Wald = 2.693, $P = 0.101$; date, Wald = 8.803, $P = 0.003$; date × sub., Wald = 6.337, $P = 0.012$), as was fat ($U = 318.0$, $P = 0.968$). The tendency of *L. s. cyanecula* to carry more fuel was due to the presence of the more fuel-loaded late *L. s. cyanecula* migrants.

Model 7 best fitted the data for mass deposition rate (table 2; sub., Wald = 4.138, $P = 0.042$; tarsus length, Wald = 0.734, $P = 0.391$; date, Wald = 1.069, $P = 0.301$). According to this model, the mass deposition rate tended to be slightly higher for *L. s. namnetum* (*L. s. namnetum*, 0.1 ± 0.1 g/day, $N = 37$, *L. s. cyanecula*, 0.0 ± 0.1 g/day, $N = 20$). More migrants gained fuel ($N = 36$) than lost fuel (mass deposition rate ≤ 0.0 g/day; $N = 21$; $\chi^2_1 = 3.947$, $P = 0.047$), and body mass loss tended to be found in birds that were recaptured after one or two days (fig. 3). Body mass when last captured was positively correlated

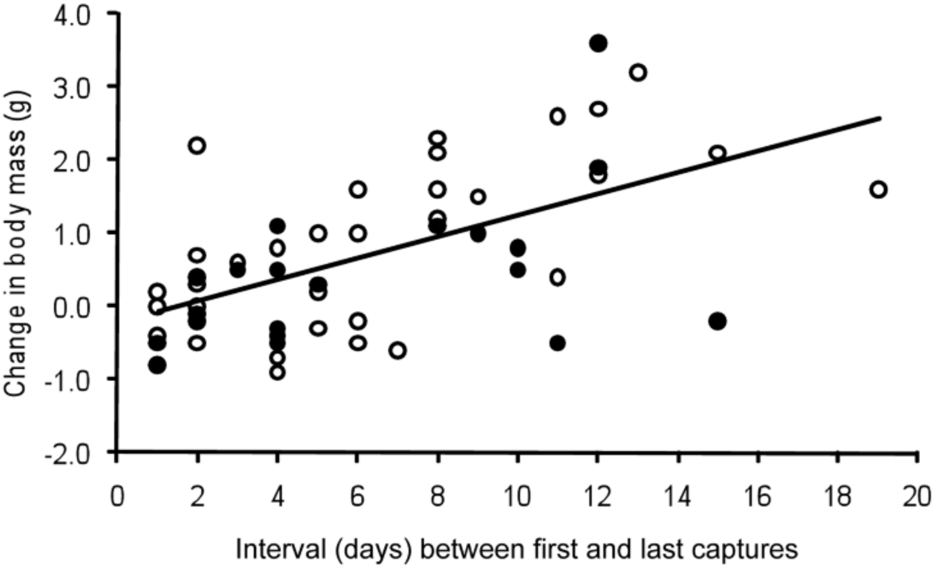

FIG. 3.—Body mass gain in relation to number of days elapsed between the first and last captures (*L. s. namnetum*, white dots; *L. s. cyanecula*, black dots). This correlation was significant ($r = 0.571$, $P < 0.001$), and the function was (with the two subspecies pooled): Δbody mass = 0.146 (days) – 0.247. Consequently, fuel accumulation is expected to be positive when Δdays ≥ 2 days. For each subspecies: *L. s. namnetum*, $r = 0.622$, $P < 0.001$, Δbody mass = 0.161 (days) – 0.210; *L. s. cyanecula*, $r = 0.494$, $P = 0.027$, Δbody mass = 0.118 (days) – 0.316.

*[Ganancia de peso en relación al número de días transcurridos entre la primera y la última captura (*L. s. namnetum*, puntos en blanco;* L. s. cyanecula*, puntos negros). La correlación fue significativa (r = 0,571, P < 0,001), y la ecuación: Δpeso = 0,146(días) – 0,247. Así, la ganancia de peso se espera positiva cuando Δdías ≥ 2 días. Para cada subespecie:* L. s. namnetum*, r = 0,622, P < 0,001, Δpeso = 0,161 (días) – 0,210;* L. s. cyanecula*, r = 0,494, P = 0,027, Δpeso = 0,118 (días) – 0,316.]*

with mass deposition rate in *L. s. namnetum* ($r = 0.443$, $P = 0.006$, $N = 37$) but not in *L. s. cyanecula* ($r = 0.049$, $P = 0.838$, $N = 20$). However, a *cyanecula* individual was observed to have an atypically high body mass (18.0 g) for its very low mass deposition rate (–0.8 g/day) and a *namnetum* individual had a very high mass deposition rate (+1.1 g/day). After removing these outliers, the mass deposition rate and body mass at last capture were positively correlated in both subspecies [*L. s. namnetum*: $r = 0.482$, $P = 0.003$, $N = 36$, body mass = 15.0 + 3.8 (mass deposition rate); *L. s. cyanecula*: $r = 0.498$, $P = 0.030$, $N = 19$, body mass = 15.4 + 3.8 (mass deposition rate)].

Stopover duration

Most recaptures (94.7%) occurred less than 15 days after the first capture event (fig. 4). CJS models showed that the best models for survival (Φ) and recruitment likelihoods (γ) were those with no differences between subspecies (table 3). Focusing on Φ models, we observed that the second model (Φ(subspecies), p) showed a difference in AICc of nearly 2, suggesting a null difference from the model one. Thus, mean (± SE) Φ as assessed by the first model was 0.88 ± 0.02, and p was 0.04 ± 0.01. Concerning γ models, the first model [γ (t), p] fitted data as well as the second one (γ, p), arguing for a constant γ (0.88 ± 0.02). Therefore, mean stopover duration was 15.3 ± 0.5 (SE) days. Minimum stopover duration did not vary between both subspecies (mean: 7.2 ± 0.6 days; $t_{55} = 0.010$, $P = 0.992$). Although it tended to be longer among first-year birds (7.3 ± 0.6 days) than in adults (6.4 ± 0.9 days), the difference was not significant ($t_{55} = 0.562$, $P = 0.576$).

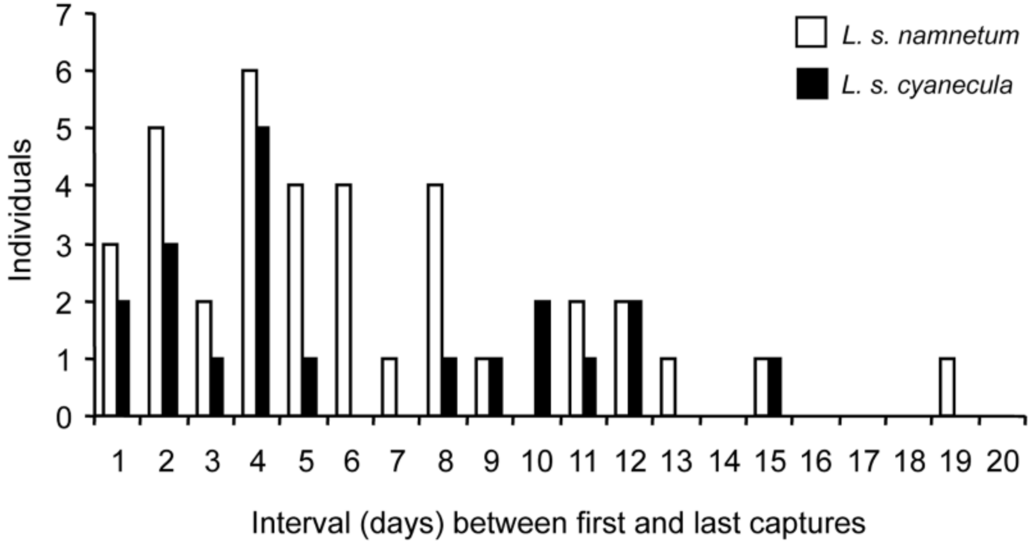

FIG. 4.—Intervals (days) between first and last captures of the two bluethroat subspecies of passing through Txingudi marshlands, northern Iberia, during the autumn migration period.
[Número de días transcurridos entre la primera y última captura para las dos subespecies de pechiazul presentes en el norte de la península Ibérica, durante el periodo de paso migratorio posnupcial.]

DISCUSSION

Population structure, timing of passage

As expected, *L. s. namnetum* was the commonest subspecies (Arizaga *et al.*, 2006) but its abundance varied from 70% in 2007 to 50% in 2008. Our sampling area did not show relevant habitat changes between these two years, so we attribute this fact to possible variations in relative survival and/or productivity of the two subspecies within their breeding areas. Such data are not available.

Adults were much less abundant than first-year birds, representing fewer than 15% of captures. A reasonable cause could be the so called 'coastal' effect, due to the over-representation of first-year birds along coast lines relative to adult birds (Payesvsky, 1998). This result may also be a consequence of differences in the age ratios on the breeding quarters (Bermejo and De la Puente, 2002), or perhaps a larger fraction of adult birds can travel faster (Ellegren, 1990), thus stopping-over at fewer sites and/or for less time at each site. In support of this latter idea, adults at Txingudi tended to stop over for less time (25% of variance in timing of passage was due to the age classes), although no significant differences were detected, in part due to the low sample size.

Peak migration occurred during the first 10 days of September and, although *L. s. cyanecula* tended to pass later than *L. s. nam-*

TABLE 3

Cormack-Jolly-Seber models used to estimate the stopover duration. Abbreviations: Φ, *p* and γ are survival, recapture and recruitment likelihoods, respectively; "t" is a time effect in Φ, *p* or γ; for AICc, and ΔAICc see table 2. Stopover duration was calculated as a function of Φ and γ (see methods for details).
[Modelos de Cormack-Jolly-Seber utilizados para determinar la duración de la estancia. Abreviaciones: Φ, p y γ son, respectivamente, la probabilidad de supervivencia, recaptura y reclutamiento; "t" indica un efecto del tiempo (fecha) en Φ, p o γ; Para AICc y ΔAICc, véase la tabla 2. La duración de la estancia se calculó en función de Φ y γ (ver para más detalles la sección de métodos).]

Models	AICc	ΔAICc	AICc weight	No. Parameters	Deviance
Φ, *p*	582.10	0.00	0.73	2	578.06
Φ(subspp), *p*	584.14	2.04	0.27	3	578.05
Φ(t), *p*	599.69	17.59	0.00	22	551.47
Φ, *p*(t)	607.50	25.40	0.00	38	518.27
Φ(t), *p*(t)	615.91	33.80	0.00	49	494.90
γ(t), *p*	580.77	0.00	0.66	21	534.95
γ, *p*	582.72	1.95	0.25	2	578.67
γ(subspp), *p*	584.64	3.87	0.09	3	578.55
γ(t), *p*(t)	592.72	11.95	0.00	49	471.82
γ, *p*(t)	604.93	24.16	0.00	39	513.00

netum (effect size: 0.25), no significant differences were detected. A higher capture effort per day might have allowed us to detect these differences as significant (Arizaga *et al.*, 2009b). However, the relative low effect size (< 0.5) obtained here suggests that such a difference was not relevant. Future research could focus on the extent to which any such difference is biologically relevant, e.g. in terms of avoiding inter-subspecies competition at stopovers. Since populations of *L. s. cyanecula* breed further north and east than *L. s. namnetum* (Cramp, 1988), our results suggest that west European *L. s. cyanecula* populations could abandon their breeding areas before *L. s. namnetum*. Although stopover duration did not differ between both subspecies at Txingudi, assuming that they both travel at the same speed of migration in northern Iberia, we cannot exclude the possibility that they could maintain different migration speeds when crossing France.

Fuel load

Fuel load was rather similar between the two subspecies, although migrants captured late in the season had more fuel than those that passed earlier, a trend also found by Grandío and Belzunce (1987) for the same area. This higher fuel load late in the season was observed in *L. s. cyanecula* but not in *L. s. namnetum*. This supports the hypothesis that, in contrast to *L. s. namnetum*, late *L. s. cyanecula* could undertake longer flights without needing to stop over to refuel. Moreover, this also suggests that late *L. s. cyanecula* migrants were probably more time-stressed than late *L. s. namnetum*, something that may be due to the fact that a fraction of *L. s. cyanecula* are likely to be long-distance migrants that overwinter in tropical Africa (Cramp, 1988).

Nevertheless most *L. s. cyanecula* showed low fat scores (mean < 2 in a scale from 0 to 8), suggesting that most birds of this subspecies overwinter in Iberia or need to stop over further south to acquire sufficient fuel to migrate to tropical Africa. Because fuel deposition rates and fuel loads are still low when bluethroats pass through central Iberia (Bermejo and De la Puente, 2004), most refuelling probably occurs in southern Iberia or northern Africa. This result also suggests that Iberia is likely to be crossed in several steps interrupted by relatively short stopovers. The occurrence of suitable stopover areas further south could allow *L. s. cyanecula* overwintering in tropical Africa to carry small fuel reserves whilst crossing Europe, which could be advantageous to avoid extra energy costs during flight (Newton, 2008) and/or the elevated risk of predation that comes with carrying larger fuel loads (Kullberg *et al.,* 1996, 2000; Lind *et al.,* 1999).

The mean mass deposition rate (*c.* 0.1 g/day) was slightly higher than that observed at other Iberian localities further south (Ebro Valley, 0.04 g/day; Arizaga *et al.,* 2009a; Central Iberia: zero mass deposition; Bermejo and De la Puente, 2004), and it differed slightly between the two subspecies. In particular, *L. s. cyanecula* tended to have a zero energy budget whilst *L. s. namnetum* showed a positive mass gain rate (0.1 g/day). The difference, however, was quite small and, probably, biologically insignificant. Explaining this result *a posteriori* is difficult, especially due to the lack of data on possible subspecies-specific variations in foraging behaviour and/or the effect of exogenous parameters on the mass deposition rate of each subspecies. We must also note that the sample was smaller for *L. s. cyanecula*. In *L. s. svecica* bluethroats stopping-over in northern Europe, the mass deposition rate differed little from that observed at Txingudi (0.09 g/day; Ellegren, 1991). This indicates that, overall, bluethroats seem to have low fuel deposition rates when crossing Europe. However, subspecies-specific data from *L. s. cyanecula* are lacking for other areas north of

Iberia, and therefore we cannot totally reject the hypothesis that some bluethroats could have high rates of fuel accumulation before reaching or passing through Iberia.

The mass deposition rate was positively correlated with body mass at last capture, supporting the hypothesis that both subspecies were time-minimisers. However, such a result must be considered as preliminary, since the final capture is commonly not on the day of departure, so that there is uncertainty in the accuracy of such a correlation. Future research using more exact methodological approaches (e.g. Bayly, 2006) will be important to compare and evaluate the validity of the methodology used here.

Stopover duration

Stopover duration did not differ between subspecies or age classes, and it was relatively long (estimation with CJS models: 15.3 days; minimum stopover duration: 7.2 days). This duration (assessed by CJS models) is even longer than that observed in other long-distance European migrants (e.g. 9.5 days in reed warblers *Acrocephalus scirpaceus*, 7.7 days in garden warblers *Sylvia borin*; Schaub and Jenni, 2001). A possible explanation for such a low rate may be the very low fuel deposition rate observed in bluethroats, which could force them to stop over for longer. The minimum stopover duration of bluethroats passing through central Iberia was lower than found at Txingudi (4.8 days, Bermejo and De la Puente, 2004). In contrast to those sites, the study reedbed at Txingudi is in tidal marshlands, so the ground was inundated for more than 6 hours per day. Since bluethroats feed on the ground (Cramp, 1988), the tides could be a relevant factor constraining feeding opportunities, forcing bluethroats to rest when the tide was high or to move out of the reedbeds, exposing themselves to predators and spending more time looking for food. Data on stopovers of bluethroats in other tidal marshes from northern Iberia or west France are lacking and so we cannot evaluate to what extent tides might constrain refuelling.

CONCLUSION

In conclusion, both *L. s. namnetum* and *L. s. cyanecula* pass through northern Iberia at similar times of year, they show the same stopover durations, they carry similar fuel loads and have similar rates of fuel accumulation. However, late *L. s. cyanecula* migrants carry higher fuel loads than earlier individuals, so these birds could be able to cover longer distances without needing to stop over to refuel. The mean fat score was low for both subspecies which, together with the very low rates of fuel accumulation, supports the hypothesis that Iberia is crossed in short consecutive steps. Long-distance *L. s. cyanecula* migrants may acquire the high fuel loads needed to migrate to tropical Africa in southern Iberia or north-western Africa.

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