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STOPOVER OF BLUETHROATS *LUSCINA SVECICA CYANECULA* IN NORTHERN IBERIA DURING THE AUTUMN MIGRATION PERIOD

MIGRACIÓN DEL PECHIAZUL *LUSCINA SVECICA CYANECULA* EN EL NORTE DE ESPAÑA EN EL PASO POSNUPCIAL

Juan Arizaga* **[1], Emilio Barba***, Daniel Alonso** and Antonio Vilches** ****

Summary.—*Stopover of bluethroats* Luscina svecica cyanecula *in northern Iberia during the autumn migration period.*

Fuel management and stopover duration are parameters of great interest for the understanding of bird migration strategies. Our aim was to study the stopover of bluethroats *Luscinia svecica cyanecula* in northern Iberia. Data were collected at Badina de Escudera lagoon (reedbeds), Villafranca (42º 16' N 01º 42' W), Ebro Valley. Systematic mist-netting was performed during the autumn migration period between 2003 and 2006. The timing of passage did not vary between age and sex classes, with the bulk of migrants being captured in September. The stopover duration was very long (nearly 30 days) compared to that reported from other stopover sites. Main causes explaining these results could be: (i) an atypical September with unfavourable meteorological conditions, and (ii) the interference of apparently wintering specimens. Apart from a small fraction of birds with very large fuel loads, a mean fuel load of nearly 15 % over lean mass suggests that, if a fraction of migrants stopping-over in Badina overwinter in tropical Africa, they must refuel in areas further south to gain sufficient fuel before crossing the Sahara. Conversely, we cannot rule out that these less loaded birds overwintered within the circum-Mediterranean region. Adults were more fuel loaded than juveniles, but this was not due to a higher fuel deposition rate (mean 0.08 g/day). Bluethroats recaptured from 6 to 10 days after the first capture showed a higher mass deposition rate than those recaptured after 10 days or more. This suggests that birds with long stopovers were not true fuelling migrants, but more probably wintering specimens with balanced energy budgets. A long initial lost of mass (5 days) agrees with both the high competition and the interference of wintering specimens hypotheses. In conclusion, Badina de Escudera, in northern Iberia, is an area used by a true, stopping-over population, as well as by apparently wintering specimens.

Key words: age, bluethroat, fuel deposition rate, fuel load, *Luscinia svecica cyanecula*, migration, northern Iberia, stopover duration.

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RESUMEN.—*Migración del pechiazul* Luscina svecica cyanecula *en el norte de España en el paso posnupcial.*

La cantidad de reservas, su tasa de deposición y la duración de la estancia en un área de descanso son factores esenciales a la hora de analizar la estrategia migratoria en aves. El objetivo aquí ha sido estudiar el comportamiento de pechiazules migratorios *Luscinia svecica cyanecula* en el norte de España durante el periodo de paso postnupcial. El muestreo se desarrolló en el carrizal de la laguna de Badina de Escudera, Villafranca (42º 16' N, 01º 42' W), valle del Ebro, mediante anillamiento en estación de esfuerzo constante, durante el periodo de paso migratorio posnupcial, entre 2003 y 2006. El tiempo de paso no varió según la edad o sexo, siendo el pico en septiembre. La duración de la estancia (casi 30 días) en la laguna fue más alta que la registrada en estudios similares, posiblemente debido a: (i) un septiembre muy lluvioso con muchos días de viento poco favorable para la migración y (ii) la presencia de pechiazules invernantes cuya área de invernada se localizaría cerca del sitio de muestreo. Aunque hubo individuos con una cantidad de reservas muy alta, el promedio de 15 % sobre el peso libre de grasa apoyaría la idea de que si una fracción de los pechiazules que se detienen en Badina migra hasta África tropical, ésta ha de parar antes del Sahara para ganar la cantidad de reservas suficiente para cruzar el desierto. Alternativamente, es muy probable que parte de estas aves con poca cantidad de reservas pase el invierno en la cuenca mediterránea. La cantidad de reservas fue mayor entre los adultos, si bien su tasa de deposición de peso no difirió de la de los juveniles (promedio, 0.08 g/día). La tasa de ganancia de peso en las aves que se recapturaron entre 6 y 10 después de la primera captura fue mayor que la de aquellas recapturadas tras 10 o más días, sugiriendo que los individuos con periodos de estancia largos fueron posiblemente aves de carácter invernante, más que en paso. En las aves que se recapturaron entre 1 y 5 días después de la primera captura la tasa de deposición promedia fue negativa, sugiriendo la existencia de competencia así como de la interferencia de invernantes. En conclusión, la Badina de Escudera es empleada tanto por ejemplares en paso como por una población de aves aparentemente invernantes.

Palabras clave: cantidad de reservas, duración de la estancia en un área de descanso, edad, *Luscinia svecica cyanecula*, migración, norte de España, pechiazul, tasa de deposición de reservas.

INTRODUCCIÓN

During bird migration most time is consumed at stopover localities (e.g. Hedenstrom and Alerstam, 1997), so stopover features such as fuel deposition rate (i.e. amount of fuel stored per unit time), fuel load and stopover duration are key parameters determining strategies of bird migration (Alerstam and Lindström, 1990).

The bluethroat *Luscinia svecica* is a polytypic Palaearctic passerine (Cramp, 1988). Currently, two subspecies are accepted as being observed in Iberia: *L. s. namnetum*, that has its main breeding quarters in W France (Zucca and Jiguet, 2002), migrates along the coast of N Iberia (Arizaga *et al.*, 2006a) and spends the winter in SW Iberia and NW Africa (Zucca and Jiguet, 2002); *L. s. cyanecula*, that breeds in W Europe, also in Iberia, with this last population proposed as a separate subspecies, *L. s. azuricollis* (but see Zink *et al.*, 2003), that migrates across W Europe to overwinter in SW Europe and Africa, both N and S of the Sahara Desert (Cramp, 1988). Iberia, therefore, is used both as a goal wintering area and as a stopover region before resuming the migration to wintering areas further south. Apart from some succinct analyses in N Iberia (Grandío and Belzunce, 1987; González *et al.*, 2007), all previous analyses of bluethroat stopover ecology have been carried out in the southern half of Iberia (Peiró, 1997, Bermejo and De La Puente, 2004), where wintering birds are common and, therefore, mix with true, stopping-over migrants that overwinter in Africa (Hernández *et al.*, 2003). Compared with S Iberia, the bluethroat has no relevant wintering quarters in N Iberia (Hernández *et al.*, 2003), so this region is possibly acting as a last refuelling area before arriving at one of the chief wintering zones in S Iberia. Detailed data on bluethroat stopover features in N Iberia are lacking so investigation is needed to better understand the migration ecology of this species in Iberia.

The timing of passage of age or sex classes is also of great importance in understanding the strategies of bird migration (Cristol *et al.*, 1999), because it is related either to age- or/and sex- associated variations in fuelling patterns and stopover duration during migration period or in departure time from wintering or breeding quarters, that normally is linked with other life processes such as moulting or breeding (Newton, 2008). In N Europe, Ellegren (1990) observed that adults of *L. s. svecica* migrated faster than juveniles during early autumn, but not during late autumn, suggesting that the timing of passage becomes more similar for both age classes when approaching their wintering areas. Previous studies carried out in the southern half of Iberia did not reveal any differential timing of passage between age or sex classes (Bermejo and De La Puente, 2004). In this scenario, additional analyses are required to know to what extent this lack of differential timing of migration also exists in N Iberia.

Fuel accumulation, mainly as fats, is one of the main features of migrants (Newton, 2008). In passerines that migrate from Europe to Africa, a fuel load higher than 35 % over lean body mass (i.e. mass without fats) is considered to be sufficient to arrive at tropical Africa crossing the Mediterranean and the Sahara Desert (Alerstam and Lindström, 1990). In contrast, the passerines that overwinter within the circum-Mediterranean region normally show lower fuel loads, around 15 % over lean body mass (Alerstam and Lindström, 1990). Nonetheless, exceptions are common for both Afro-tropical and circum-Mediterranean migrants. Thus, though fuel load by itself cannot be used to infer the location of the wintering areas, together with parameters such as fuel deposition rate and stopover duration, it can be used to deepen our knowledge of migration strategies (Schaub and Jenni, 2000).

During migration, a bluethroat is able to accumulate mass at a rate higher than 0.1 g/day with no food supplementation (Ellegren, 1991). However, a population studied in central Iberia showed a zero fuel deposition rate during the autumn migration period (Bermejo and De La Puente, 2004), indicating the interference of wintering specimens and/or the fact that the site did not provide good conditions to refuel satisfactorily. Indeed, this low fuel deposition rate was linked with a relatively short stopover (mean = 4.8 days), suggesting that birds which were unable to gain mass left the area (Weber *et al.*, 1999). If N Iberia is used more like a true stopping-over region, a positive fuel deposition rate, as well as a moderate to short stopover duration would be expected. In contrast, if this region is widely used by wintering specimens, a balanced energy budget, rather than a positive one, as well as a long stopover duration is expected.

Rate of fuel accumulation at a stopover site can vary among birds with similar food requirements competing for resources (e.g. Carpenter *et al.*, 1993a, Carpenter *et al.*, 1993b). Access to food in these cases is commonly mediated by social status, frequently determined by age, sex or body size (reviewed by Moore *et al.*, 2003). In *L. s. svecica*, adults and bigger birds were found to refuel more quickly, suggesting that, as being dominant or due to greater experience, they were able to priority access to food (Lindstrom *et al.*, 1990, Ellegren, 1991). Such differences associated with social status and, particularly, the age (body size-effect was not tested), has not been observed in Iberia (Bermejo and De La Puente, 2004). Complementary analyses are required to know whether this is due to a methodological constraint (Bermejo and De La Puente, 2004) or to the fact that fuel deposition rate in *L. s. cyanecula* is less influenced by social status.

Our aim here was to analyse the stopover features (timing, stopover duration, fuel load and fuel deposition rate) of bluethroats *L. s. cyanecula* in N Iberia, and the effect of age, sex and body size on them. Particularly, we examined to what extent this region is mainly used by true, stopping-over migrants or, in contrast, if it is used by a noticeable number of wintering specimens.

METHODS

Study area and sampling protocol

Data were collected in the reed bed *Phragmites australis* surrounding a 57 ha lagoon (Badina de Escudera) near Villafranca (42º 16’ N 01º 42’ W, Navarra, Ebro river basin, N Spain). The bluethroat occurs in Badina from August to April, but the number of resident wintering visitors is very marginal compared with the high number of captures during the autumn migration period (Arizaga *et al.*, 2009). In Badina de Escudera, a 5.8 % of bluethroats belong to the subspecies *L. s. namnetum* (Arizaga *et al.*, 2006a), whilst the rest are *L. s. cyanecula*.

Bluethroats were captured with mist nets from 2003 to 2006. Nets were placed across the reed bed, with a constant number of nets within each campaign (table 1), for 3 h per sampling day (from 2 h before to 1 h after dusk). The sampling period from 2003 to 2005 was carried out from 1 August to 15 November. In 2006, the sampling was concentrated around the period of maximum passage (table 1), and a tape lure (a male breeding song) was used with the aim of obtaining more recaptures by increasing the recapture likelihood of birds already controlled at Badina (Schaub *et al.*, 1999). The tape lure was put near the nets and only operated during the period of sampling.

Once captured, each bird was ringed and its sex and age determined. Birds were aged following Svensson (1996): adults (EURING code 4; 2-year or older birds, with no juvenile feathers), or juveniles (EURING code 3; birds with still some juvenile feathers in their wings). The following variables were measured from each bird: wing length (method III from Svensson, 1996; 0.5 mm accuracy), body mass (TANITA digital balance; 0.1 g accuracy) and fat score (scaled from 0 to 8, following Kaiser, 1993; 0.5 accuracy). We used wing length to assign each individual to a subspecies (*L. s. namnetum* or *L. s. cyanecula*), following Eybert *et al.* (1999). Subspecific-associated stopover variations cannot be excluded (e.g. Dierschke and Delingat, 2001). Thus, migrants assigned to *L. s. namnetum* were removed from the dataset due to the low number of captures (Arizaga *et al.*, 2006a).

Timing of migration and age and sex ratios

To analyse the patterns of passage between age classes only the data from 2003 to 2005 were used. Biases from a 1:1 distribution of age or sex ratios were tested with a Cochran-Maentel-Haenzen (CMH) test, controlling for sex when focusing on age ratios and for age when focusing on sexes. Secondly, we tested if the timing of passage through Badina varied (1) between age-sex classes (K-W test, four age-sex categories were considered: adult males, etc.) (2) in relation to body size (multiple linear function on body size in relation to date, year, age and sex). In those birds without any visible fat content (fat = 0; $N = 9$), body mass was better correlated with wing ($r = 0.877$, $P = 0.002$) than with tarsus length ($r = 0.789$, $P = 0.011$), suggesting that wing length was better to assess body size (Gosler *et al.*, 1998).

TABLE 1

Sampling effort and number of captures of *L. s. cyanecula* (each bird considered only once per year, with its age and sex determined) at Badina de Escudera, during the autumn migrations 2003-2006: birds with their body mass recorded (first capture event; $N = 395$); birds captured twice or more, for which the mass deposition rate was calculated ($N = 81$).

[Esfuerzo de muestreo y número de capturas de L. s. cyanecula *(cada ave sólo se ha considerado una vez por año, y sólo si su edad y sexo se pudo determinar) en la Badina de Escudera, durante el periodo de paso migratorio posnupcial de 2003 a 2006. En paréntesis: aves para las que se obtuvo el peso (primera captura, N = 395) y aves capturadas en dos o más ocasiones, utilizadas para calcular la tasa de ganancia de peso (N = 81).]*

				Juvenile		**Adult**	
Campaign	**Mist nets** (linear m)	**Sampling** days/week	**Period**	**Male**	**Female**	**Male**	**Female**
2003	96	One	1 Aug – 15 Nov	12 (10; 0)	10 (10; 0)	10 (10; 0)	11 (11; 1)
2004	120	Two	1 Aug – 15 Nov	69 (67; 15)	57 (57; 13)	26 (25; 6)	18 (18; 3)
2005	180	One	1 Aug – 15 Nov	18 (17; 2)	10 (9; 4)	17 (17; 2)	10 (10; 1)
2006	108	All	7 Sep – 9 Oct	52 (52; 15)	27 (27; 11)	38 (38; 3)	17 (17; 6)

Stopover duration

Accurate estimation of stopover duration requires daily sampling sessions (Schaub and Jenni, 2001), so in this case we used data from 2006. We calculated the stopover duration by means of (i) minimum stopover duration, as this has been done in other studies (e.g. Bermejo and De La Puente, 2004); (ii) Cormack-Jolly-Seber (CJS) models (Lebreton *et al.*, 1992), that estimate apparent survival (Φ; likelihood of a bird captured at time t to be still there at time $t+1$), seniority (γ; likelihood of a bird captured at time t to be there at time in $t-1$), and recapture likelihood (p) separately. Assuming that survival of migrants at a stopover site is nearly 1, Φ and γ can be used to assess the stopover duration (Schaub *et al.*, 2001).

We calculated the minimum stopover duration following Kaiser (1999): difference of time, in days, elapsed between the first and last captures +1 (because the species is a nocturnal migrant).

Models on Φ and γ were run in the software MARK 4.3 (White and Burnham, 1999). Before starting to select models we explored the fit of data to CJS assumptions. With this goal we used a goodness-of-fit (GOF) test. A GOF test on a CJS model where both Φ (or γ) and p varied with time [Φ(t) p(t)] was done with the U-CARE software (Choquet *et al.*, 2001), allowing us also to identify a basic starting model that fits the data from which to start model selection. GOF test for the data set was not significant ($\chi^2_{56} = 7.805$, $P = 0.999$), as it was not the Test 3SR specific for the occurrence of transients (migrants that depart from a stopover locality after arriving; i.e. birds in which $\Phi = 0$) ($\chi^2_{56} = 0.034$, $P = 0.973$). Thus, [Φ(t) p(t)] was the most complex model from which to start to select models. All other fitted models were nested within our starting one. Models considered in this analysis were those where Φ, γ and p were constant or affected by time. Minimum stopover duration did not vary between age and sex classes (see results for further details), so, due to the relatively low sample size, we did not include these factors into the CJS models. Corrected Akaike values (AICc) were used for ranking the fit of models to data (Burnham and Anderson, 1998). Models with a difference of AICc < 2 were considered to fit to data similarly, and those for which the difference was > 2 were considered to differ significantly.

Modelling fuel load and fuel deposition rate

To assess fuel load, we used (i) an index of body size-controlled body mass (body mass/wing length) (Schaub and Jenni, 2000), and (ii) fat scores (Kaiser, 1993). In contrast to this last variable, body mass/wing length reflects not only fat reserves, but also the amount of fuel that is stored as proteins (Klaassen *et al.*, 1997). Complementary, in order to compare our results with those from other studies and species, we also calculated fuel load over lean body mass: fuel load = [(actual body mass – lean body mass) / lean body mass] × 100. To assess lean mass (i.e. mass without fats) a regression of body mass on wing length was run in those birds where no fat deposits were detected (fat = 0): body mass = 0.391 × wing length – 12.672 ($r = 0.877$, $F_{1,8} = 23.366$, $P = 0.002$). Lean body mass varied with age and sex (age: $F_{1,394} = 11.855$, $P = 0.001$; sex: $F_{1,394} = 266.827$, $P < 0.001$; age×sex: $F_{1,394} = 0.058$, $P = 0.809$), being higher among males and adult birds.

The fraction of migrants captured more than once was used to estimate the mass deposition rate, calculated as difference of body mass between capture days.

Rate of mass accumulation fitted to normal distribution (Kolmogorov test, $P > 0.05$) and, though body mass/wing length showed a slight positive skew from this distribution (Kolmogorov test: $P < 0.05$), its SD was still low (SD/mean: 0.13). Thus, parametric Univariate Linear Models (that well support slight biases from normal distribution) were used to test for the effects of year, age and sex on body mass and mass deposition rate (Sokal and Rohlf, 1995). Concerning body mass, the sample size was sufficient to consider each year separately, but was insufficient for mass deposition rate (table 1). Here, data were lumped into years when the tape lure was (2006) and was not (2003-2005) used, as lures can create biases by attracting a higher proportion of birds with lower fuel (Borras and Senar, 1986).

To test for age or sex-associated variations in fat scores the CMH test was used. Specifically, we tested for age-variations controlling for sex and year, and for sex-variations controlling for age and year.

Programs SPSS v.15.0 for Windows and StatXact v.6.0 were used; means are given ± SE.

RESULTS

Timing of migration and age and sex ratios

Captures per year and age-sex categories are shown in table 1. Phenological analyses were run with the data from 2003 to 2005 ($N = 268$), and only the first capture event was considered for each bird.

The mean number of captures per campaign ranged from 2.9 captures/day/100 m in 2003 and 2005 to 6.3 captures/day/100 m in 2004, with a peak in Sep (fig. 1). Within each age class the sex ratio was constant ($\chi^2_1 = 0.045$, $P = 0.831$). Thus, with a 34.3 % of captures, adults tended to be less abundant ($\chi^2_1 = 28.328$, $P < 0.001$), although once controlled for sex, yearly-associated variations were registered (CMH test: $\chi^2_2 = 14.573$, $P < 0.001$; 2003: 48.8 %; 2004: 25.9 %; 2005: 49.1 %). Similarly, sex ratio was male-biased (56.7 %; $\chi^2_1 = 4.836$, $P = 0.028$), although once controlled for age no yearly-associated variations were detected (CMH test: $\chi^2_2 = 1.621$, $P = 0.445$).

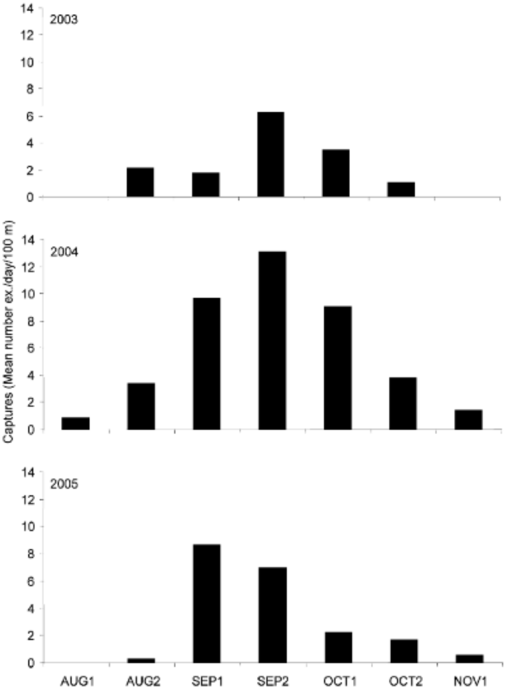

FIG. 1.—Mean number of captures of bluethroat (*L. s. cyanecula*) by fortnights from 2003 to 2005 at Badina de Escudera lagoon, in northern Iberia. *[Número promedio de capturas de pechiazul* (L. s. cyanecula) *de 2003 a 2005, en la laguna de Badina de Escudera, norte de España.]*

Median date of passage was similar for the four age-sex categories (K-W test: 2003: $P = 0.670$; 2004: $P = 0.075$; 2005: $P = 0.217$). Morever, mean effect size (difference between means divided by SD; i.e. proportion of variance due to the difference of means) was relatively low for age (0.288) and sex categories (0.270). Wing length remained constant with the date ($r = 0.668$, $P < 0.001$; B-parameters: date, $P = 0.995$; year, $P = 0.228$; age, $P = 0.002$; sex, $P < 0.001$).

Stopover duration

Data from 2006 (134 captures) were used to assess stopover duration. Minimum stopover duration did not vary between age-sex classes (age: $U = 596.5$, $P = 0.505$; sex: $U = 809.0$, $P = 0.784$) and it was 10.2 ± 1.2 days (fig. 2).

Best models that fitted to data were those with constant Φ, γ and p (table 2). Overall, p was relatively low in both Φ and γ models (Φ models: $p = 0.04 \pm 0.03$; γ models: $p = 0.05 \pm 0.03$). Mean stopover duration was 33.2 ± 0.5 days (26.9 ± 0.5 days if removing from the dataset two birds recaptured after 25 days; fig. 2).

Fuel load and fuel deposition rate

ULM on body mass/wing length showed an effect of age (fig. 3) and year but, in this last case, only among males (fig. 4) (age: $F_{1,394} = 18.260$, $P < 0.001$; sex: $F_{1,394} = 3.060$, $P = 0.081$; year: $F_{3,394} = 3.709$, $P = 0.012$; interactions with P-values < 0.05: year × sex: $F_{3,394} = 2.884$, $P = 0.036$). No interactions between age-sex classes were detected, supporting the hypothesis that age-associated variations were consistent for all sexes. Moreover, body mass/wing length was positively correlated with the date, supporting that late migrants were relatively more fuel loaded ($r = 0.356$, $P < 0.001$; standardised B-para-

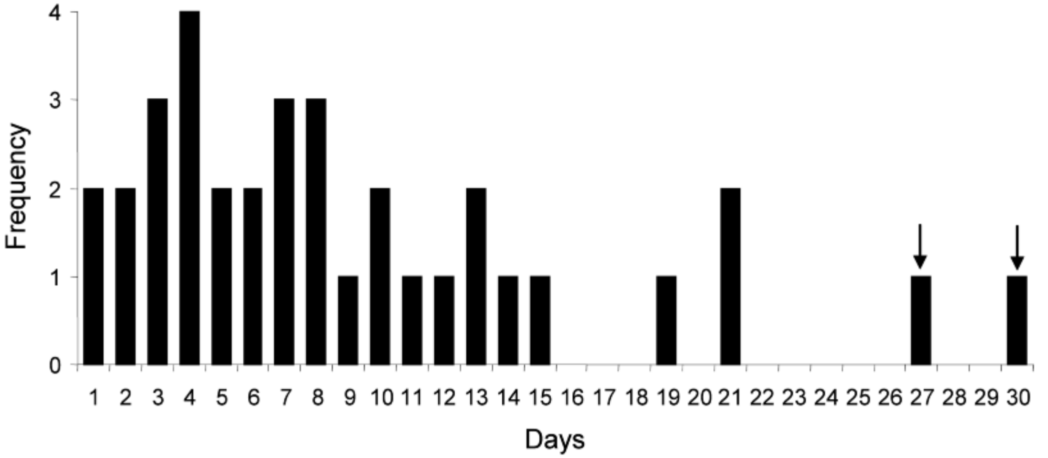

FIG. 2.—Distribution of recaptures ($N = 35$) from 2006 in relation to days elapsed between the first and last captures. Minimum stopover duration: 10.2 ± 1.2 days (range: 2 - 31 days). After removing two outliers with a very long stopover (arrows), the stopover duration was 9.1 ± 1.0 days (range: 2 - 22). *[Distribución de las recapturas que se obtuvieron en 2006 (N = 35) en relación al número de días entre la primera y última captura. Duración mínima de la estancia: 10.2 ± 1.2 días (rango: 2 - 31 días). Tras eliminar dos* outliers *con una estancia muy prolongada (flechas), se obtuvo una nueva media de 9.1 ± 1.0 días (rango: 2 - 22).]*

TABLE 2

Cormack-Jolly-Seber models used to estimate the stopover duration. AICc = corrected Akaike values (Burnham and Anderson, 1998); ΔAICc = difference of models' AICc values in relation to the model one; *np* = number of parameters; Φ = survival; γ = seniority.
[Modelos de Cormack-Jolly-Seber utilizados para la estimación de la duración de la estancia en la Badina de Escudera. AICc = criterio de Información de Akaike, corregido (Burnham and Anderson, 1998); ΔAICc = diferencia entre el valor AICc de un modelo respecto al primer modelo; np = número de parámetros; Φ = supervivencia; γ = reclutamiento.]

Models	**AICc**	**ΔAICc**	**AICc Weight**	***np***	**Deviance**
1. Φ(.) *p*(.)	480.379	0.00	1.00	2	300.259
2. Φ(.) *p*(t)	526.652	46.27	0.00	32	272.794
3. Φ(t) *p*(.)	540.742	60.36	0.00	32	286.883
4. Φ(t) *p*(t)	623.680	143.30	0.00	61	286.883
1. γ(.) *p*(.)	449.308	0.00	0.99	2	–
2. γ(.) *p*(t)	458.914	9.61	0.01	32	–
3. γ(t) *p*(.)	498.55	49.24	0.00	32	–
4. γ(t) *p*(t)	541.184	91.88	0.00	60	–

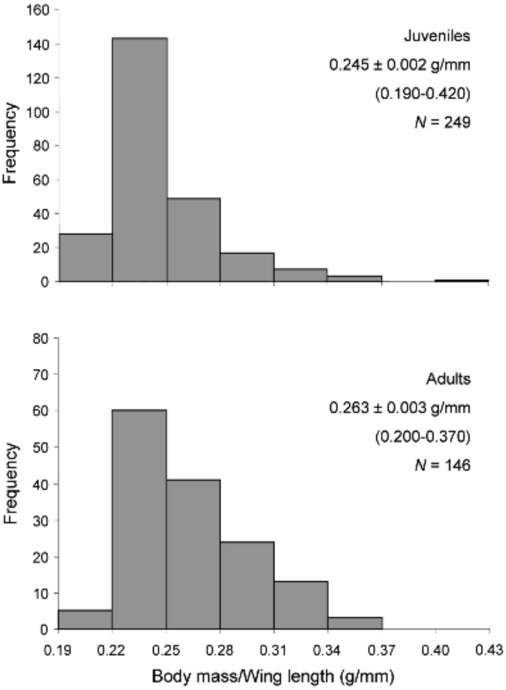

FIG. 3.—Distribution of body size-controlled body mass (together with mean ± SE, ranges and sample size) between age classes. Body mass for adults was 19.6 ± 0.2 g (14.5 - 28.2 g), and for juveniles, 18.1 ± 0.2 g (14.2 - 31.2 g). Equivalent fuel load over lean body mass for adults was 18.5 ± 1.2 %, and for juveniles, 11.7 ± 0.9 %. *[Distribución de la masa corporal relativa al tamaño corporal (se muestran, además, las medias ± SE, rangos y tamaño muestral) para cada edad. La masa corporal en los adultos fue 19.6 ± 0.2 g (14.5 - 28.2 g); para los juveniles fue 18.1 ± 0.2 g (14.2 - 31.2 g). La cantidad de reservas, o* fuel, *respecto a la masa corporal libre de grasa en los adultos fue 18.5 ± 1.2 %, mientras que en los juveniles, 11.7 ± 0.9 %.]*

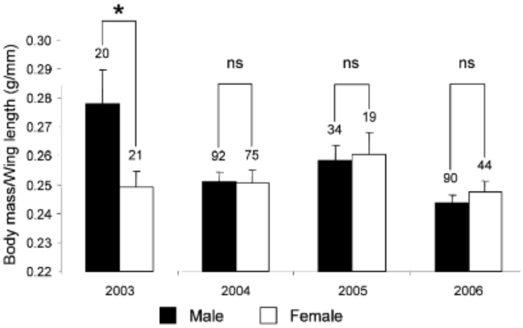

FIG. 4.—Yearly variations of relative body mass (mean ± SE; sample size) between sex classes. *A posteriori* analyses revealed that relative body mass did not vary among years, except in 2003, when males were observed to be proportionally more fuel loaded: $P < 0.05$ (*); $P > 0.05$ (ns). *[Masa corporal (relativa al tamaño corporal) según sexos y años (media ± SE, tamaño muestral). Análisis a posteriori muestran que las únicas diferencias fueron causadas por una mayor masa entre los machos de 2003. P < 0.05 (*); P > 0.05 (ns).]*

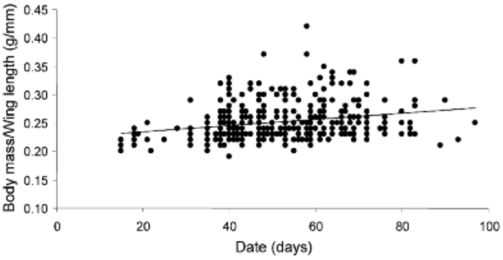

FIG. 5.—Biplot of relative body mass (body mass/ wing length) *versus* date ($N = 395$). *[Representación gráfica de la masa corporal relativa (masa/longitud del ala) frente a la fecha (N = 395).]*

meters: age, 0.254, $P < 0.001$; sex, –0.004, $P = 0.934$; year: –0.129, $P = 0.008$; date: 0.185, $P < 0.001$; fig. 5).

Fat scores also varied between age classes, both when controlling for sex (CMH test: $\chi^2_6 = 41.129$, $P < 0.001$) and for year ($\chi^2_6 = 38.039$, $P < 0.001$), being higher in adults (fig. 6). Sex-associated variations were also observed when controlling for age ($\chi^2_6 = 13.042$, $P < 0.042$), but not for year ($\chi^2_6 = 12.199$, $P < 0.058$), supporting the hypothesis that these variations were due to yearly variations of fat.

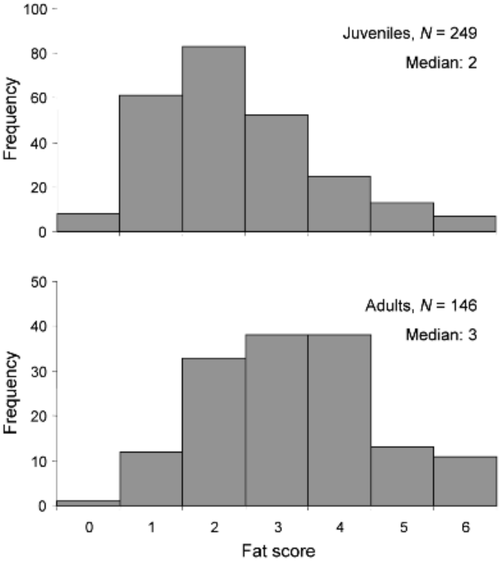

FIG. 6.—Distribution of fat scores (together with median values and sample size) between age classes. Fat scores scaled following Kaiser (1993). *[Distribución del nivel de grasa subcutánea (Kaiser, 1993) para cada edad. Se indica, además, la mediana y el tamaño muestral.]*

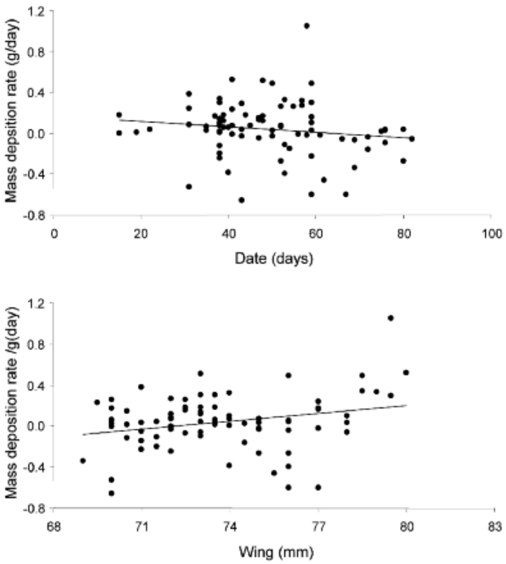

FIG. 7.—Biplots of mass deposition rate *versus* date and wing length ($N = 82$). *[Representación gráfica de la tasa de deposición de peso frente a la fecha y la longitud del ala (N = 82).]*

ULM on mass deposition rate showed that this did not vary with age, sex or the use of a tape lure, but it was positively correlated with wing length (fig. 7) (age: $F_{1,81} = 0.429$, $P = 515$; sex: $F_{1,81} = 2.478$, $P = 0.120$; tape lure: $F_{1,81} = 2.208$, $P = 0.142$; wing: $F_{1,81} = 10.241$, $P = 0.002$; interactions of age, sex and tape lure: $P > 0.05$). This supports that long-winged birds stored fuel at higher rates than short-winged birds. In contrast to body mass/wing length, mass deposition rate was not unmistakably correlated with the date ($r = 0.340$, $P = 0.008$; standardised B-parameters: date, –0.219, $P = 0.046$; wing, 0.311, $P = 0.005$). Mean rate of mass deposition was 0.04 ± 0.03 g/day ($N = 82$, range: –0.66 to 1.05 g/day). Data on recaptures show that migrants stopping-over at Badina gained mass (17.8 ± 0.2 g *versus* 18.7 ± 0.3 g, $N = 82$; paired sample t test: $t_{81} = 2.805$, $P = 0.006$).

More migrants gained mass than lost it (52 *versus* 30; $\chi^2_1 = 5.902$, $P = 0.015$), and this was observed to be constant for all age-sex categories ($\chi^2_3 = 0.464$, $P = 0.927$). As revealed by fig. 8, change in body mass in relation to stopover duration revealed that: up to 5 days, migrants lost mass (but the mean did not differ from zero) and the variance was very high; up to 10 days, the mean was positive, tended to differ from zero, and the variance was moderate or high; from 11 days, the mean was positive but it did not differ from zero; the variance was very low. Wing length tended to be longer in migrants with a stopover duration of 6 to 10 days (74.8 ± 0.6 mm, $N = 26$) than in migrants apparently stopping-over for shorter and longer (1 - 5 days: 73.2 ± 0.7 mm, $N = 15$; >10 days: 73.2 ± 0.4 mm, $N = 41$; ULM: age, $F_{1,81} = 7.913$, $P = 0.006$; sex: $F_{1,81} = 53.811$, $P < 0.001$; period: $F_{2,81} = 6.913$,

P = 0.002; interactions: $P > 0.05$). Age (χ^2_2 = 0.510, P = 0.775) and sex ratios did not differ among the three periods shown in fig. 8 (χ^2_2 = 0.430, P = 0.806). Focusing in the period one from fig. 8 (when mass was lost), wing length was not correlated with mass deposition rate (r = 0.041, P = 0.886), and age and sex ratios did not vary from the days 1 - 2 to days 3 - 4 after the first capture (age: χ^2_1 = 0.188, P = 0.999; sex: χ^2_1 = 0.689, P = 0.576), supporting that all birds had a similar pattern of fuel accumulation during this period. However, this result must be very considered cautiously because of the low sample size (e.g. only 4 birds for the first two days; fig. 8).

Rate of mass deposition was not correlated with the time elapsed between the first and last captures when all the data were considered (r = 0.097; P = 0.387), but it was positively correlate with time when only the data up to 10 days were considered (r = 0.423; P = 0.006; mass deposition rate = 0.057 × difference of days – 0.328). Thus, a bird would need 5-6 days to gain mass (fig. 8).

DISCUSSION

Timing of migration and age and sex ratios

Autumn migration lasted three months, from mid-August to mid-November, with a peak in September, agreeing with the data reported for all Iberia (Tellería *et al.*, 1999). However, first bluethroats reach N Iberia 15 days before (Grandío and Belzunce, 1987; this work) S Iberia (Peiró, 1997; Bermejo and De La Puente, 2004).

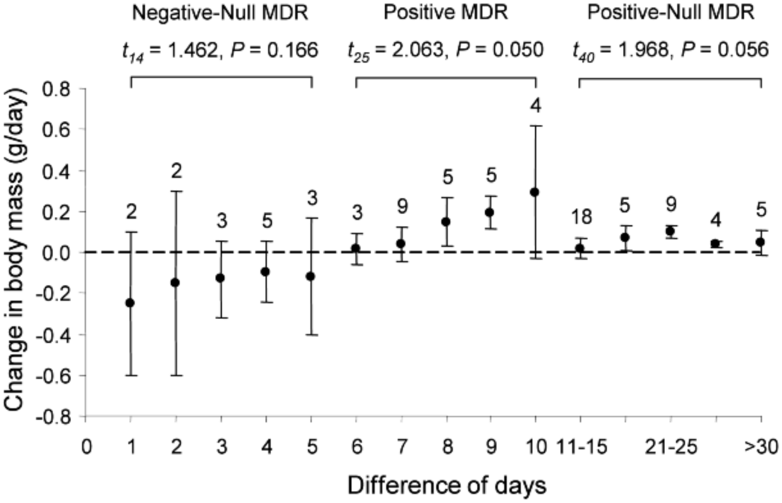

FIG. 8.—Patterns of mass deposition rate (MDR) in relation to time elapsed between the first and last captures. Mean ± SE and sample size are shown. To have a higher sample size, data were lumped into 5-days groups from the 11th day onwards. A t-test was used to test whether mean deposition rate differed from zero for each of the three periods shown above.

[Patrones de deposición de peso (MDR) in relación al número de días entre la primera y última captura. Se indica la media ± SE y el tamaño muestral. Para aumentar el tamaño muestra, los datos del día 11 en adelante se agruparon en periodos de 5 días. Se empleó un test de t para comprobar si la tasa de deposición de peso de cada uno de los periodos marcados en la zona superior de la figura difirieron de cero.]

Overall, the proportion of adults ranged from 35 % to 50 % (with noticeable yearly variations), whilst sex ratios, slightly male-biased, were constant across the years. This result does not vary from those found in other areas from Iberia, both for *L. s. cyanecula* and *L. s. namnetum* (Peiró, 1997, Bermejo and De La Puente, 2004, González *et al.*, 2007). Concerning recaptures from abroad within Iberia, Hernández *et al.* (2003) obtained a higher proportion of adults, though these data might be biased, since adults often outnumber juveniles in a marked population. Variations in age ratios are attributable to yearly-variations in productivity at breeding quarters (Bermejo and De la Puente, 2002), whilst a nearly 1:1 and constant sex ratio may show the sex ratio at the breeding quarters.

Differential timing of migration is frequently attributed to the fact that one age, or sex is able to maintain higher migration speeds (Cristol *et al.*, 1999), normally by stopping-over for less time. This was not the case for Badina, also agreeing with the data obtained with *L. s. cyanecula* migrants in S Iberia (Bermejo and De La Puente, 2004), supporting that the timing of passage is similar for all age-sex categories in Iberia. However, our sample of adults was not sufficiently high to consider this conclusion definitely. In N Europe, adults from *L. s. svecica* were observed to stopover for shorter and to maintain higher migration speeds than juveniles (Ellegren, 1990 and 1991), and if the timing of passage was similar between age classes it was due to the fact that adults left their breeding quarters later (Ellegren, 1991), a question that remains totally unknown for *L. s. cyanecula* populations.

Stopover duration

We registered a mean stopover duration of 26.9 days (minimum stopover duration: 10.2 days). Though data used to estimate this variable were obtained over 32 sampling days, it is unlikely that it was underestimated due to the fact that 75 % of last individual recaptures were obtained in less than 10 days. Such a long stopover had not been reported previously for passerines (ranges: 7.7 to 9.6 days (ranges: 7.7 to 9.6 days; Schaub and Jenni, 2001; Arizaga *et al.*, 2008), suggesting (i) methodological biases of CJS models (Schaub *et al.*, 2004), (ii) peculiar conditions that lengthened the stopover and/or (iii) interference of wintering specimens. Although an overestimation of the stopover duration cannot be rejected because of the low sample size (Schaub *et al.*, 2004), we have enough data supporting the hypothesis of interference of wintering specimens and, to a lesser extent, some likely impact of peculiar conditions. Thus, in 2006, the autumn was featured by very unfavourable meteorological conditions. Indeed, during the period of sampling the rainfall was 111.2 mm, with the mean for this same period in the previous ten years being 43.0 mm (range: 7.1 mm in 2004 to 90.8 mm in 1998). Moreover, head winds were dominant for 60 % of days. Both rain and head winds are known to lengthen the stopover duration (Akesson and Hedenstrom, 2000; Akesson *et al.*, 2002; Schaub *et al.*, 2004). However, when migrants are not crossing large inhospitable areas, they are able to depart even with a moderate head wind (Dierschke and Delingat, 2001). Thus, such a long stopover at Badina can not be caused only by unfavourable meteorological conditions, thus supporting the "interference hypothesis". Also supporting this hypothesis, we observed that migrants stopping over for long periods showed balanced energy budget (Keller *et al.*, 1989), rather than a true positive fuel deposition rate.

Contrary to expectations, in a stopover site from S Iberia with a population of wintering bluethroats, the minimum stopover duration was reported to be only 4.8 days during the autumn migration period (Bermejo and De La

Puente, 2004). Such difference with Badina may be due to the fact that the wintering specimens from S Iberia were removed from the autumn migration period data set (Bermejo and De La Puente, 2004).

Fuel management

Bluethroats that stopped over at Badina de Escudera showed a mean fuel load of nearly 15 % over lean body mass. Fuel accumulation over lean mass is due to both fats and proteins (up to 18 % of proteins; Klaassen *et al.*, 1997). Thus, as proteins have a lower calorific value than fats (Jenni and Jenni-Eiermann, 1998), flight ranges would be lower than expected if all fuel was pure fat. Moreover, note that birds were caught before dusk, when the crop should be expected to be full and the bird to weigh more. Part of this mass, however, can be not stored as fuel, so the mean fuel load was likely to be lower than here shown.

A bird like a bluethroat, that must stopover to refuel, requires a fuel load of more than 30 % to arrive directly to tropical Africa from southern Europe (Newton, 2008). Although some birds were very heavy (weighing even more than 30 g, equivalent to a fuel load of some more than 90 % over lean body mass), having then enough fuel to go directly to tropical Africa, a mean fuel load of around 15 % suggests that, if a fraction of migrants stopping-over in Badina overwinter in tropical Africa (Cramp, 1988), they must refuel in areas further south to gain enough fuel before the Sahara. Conversely, it is reasonable that these less loaded birds overwinter within the circum-Mediterranean region (Hernández *et al.*, 2003).

Adults showed a higher body size-relative body mass and fat reserves, indicating that they were more fuel loaded. Such a difference is very frequent in migrants (e.g. Veiga, 1986; Grandío, 1999), and it has also been reported for the bluethroat (Lindström and Hasselquist, 1989; Ellegren, 1991). This is attributed to the fact that adults are faster at accumulating fuel or able to start to store fuel in less time (i.e. they experience lower settlement costs after arriving at a stopover site) (Ellegren, 1991; Grandío, 1999). Adults from Badina did not gain mass at a faster rate than juvenile birds and there was no evidence to support that they had lower settlement costs. Nonetheless, this last result must be considered with caution because of the low number of adults recaptured during the first days after their first capture at Badina. Variations of fuel load between age classes at Badina were likely to have originated in more northerly regions.

The mean rate of mass accumulation at Badina (0.04 g/day; equivalent to 0.2 % over lean body mass/day) was above the zero rate reported from areas further south (Bermejo and De La Puente, 2004), and below the 0.09 g/day (0.65 %) observed in *L. s. svecica* in N Europe (Ellegren, 1991). Such a difference of *L. s. cyanecula* compared with *L. s. svecica* is probably due to the interference of wintering specimens in Iberia, a fact that becomes more evident with decreasing latitude (Bermejo and De La Puente, 2004). Indeed, birds recaptured after 6 - 10 days showed a higher mass deposition rate than those recaptured after more than 10 days, that showed a balanced energy budget. This suggests that migrants stopping-over for long were not true fuelling migrants but, probably, birds that were close to their wintering area (Hernández *et al.*, 2003), that simply did not refuel.

Migrants lost mass for 5 days after being first captured, suggesting a settlement-associated cost of energy. This cost is very common in migrants (Alerstam and Lindström, 1990), although it used to be no longer than 1 - 2 days, even for the bluethroat (Ellegren, 1991). This suggests a peculiar scenario at Badina, hypothetically featured by (i) food shortage, (ii) competition, or (iii) interference of wintering specimens that did not refuel. Probably, food availability at Badina was not low during the autumn migration period, since some birds were able to gain up to 1 g/day. This is equivalent to a fuelling rate of more than 5 % over lean body mass/day, which is above the 1 % observed in food supplemented bluethroats (Lindstrom *et al.*, 1990). In contrast, both the competition and interference hypotheses are very likely to happen at Badina. As bluethroats are territorial in autumn (Cramp, 1988), contests for available resources are expected to happen. Thus, it can be stated that given high competition the settlement-associated cost should be also higher. However, such a long period of 5 days was still too long compared with other zones where, presumably, the competition was also high (Ellegren, 1991). Moreover, in such a scenario, patterns of the fuel deposition rate should differ between dominants and subordinates. Although long-winged birds were among the birds with higher mass deposition rates, suggesting that they were dominant (Lindstrom *et al.*, 1990), we have no evidence of them to refuelling more efficiently than short-winged birds, especially when dealing with migrants captured some few days after being first caught, a period in which dominant birds should be able to start to gain mass faster than subordinates. However, our sample was too low for this period, so this conclusion must be considered very cautiously. The interference of wintering specimens, that simply did not refuel, together with the fact that they may also suffer a settlement cost syndrome, is also a very likely hypothesis for Badina. This, indeed, supports a very high variance of mean mass deposition rate during this period. In conclusion, a long period of settlement-associated cost of energy in Badina was likely due to the combined effect of high competition and the interference of wintering specimens that did not refuel.

A settlement-associated cost of energy is also attributed to the fact that the migrants need some time to make their digestive track functional after a flight period. This phenomenon, that has been reported in migrants after crossing large barriers (i.e. those that must fly for long periods and do not feed for a long time) (Hume and Biebach, 1996; Gannes, 2002), is likely to be irrelevant over areas where such long flights or periods without feeding are very unlikely (Delingat *et al.*, 2006).

In conclusion, Badina de Escudera, in northern Iberia, is an area used by a true, stopping-over population, as well as by specimens that are apparently wintering. This last population is the one that most possibly caused a low mean fuel deposition rate and very long stopover duration. In contrast, migrants stopping-over for less than 10 days (a stopover duration comparable with that observed in similar species) showed a higher, positive rate of mass accumulation, supporting the hypothesis that they behaved as expected in fuelling migrants. Moreover, this fraction of migrants was featured by having a longer wing, suggesting that "true" migrants were bigger, or had a more marked long-distance type morphology: a longer wing in this case could be associated with longer distances of migration (Arizaga *et al.*, 2006b).

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