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LONG-TERM DYNAMICS OF STOPOVER USE BY THE BLUETHROAT *LUSCINIA SVECICA*

DINÁMICA A LARGO PLAZO DEL USO DE UN ÁREA DE PARADA MIGRATORIA EN EL RUISEÑOR PECHIAZUL *LUSCINIA SVECICA*

Juan Arizaga[1] * and Oscar Gordo[2]

Summary.—Understanding the dynamics of stopover site quality and the adaptive response of birds within these contexts is essential for comprehending migratory strategies and their impact on individual survival and fitness. To investigate these dynamics, we examined 16 years of Bluethroat *Luscinia svecica* monitoring at Txingudi, one of its key stopover sites in northern Iberia. Our aim was to examine annual variations and potential temporal trends in demographic structure (characterised by subspecies, age and sex ratios), population size, timing of passage, stopover duration, fuel load and fuel deposition rate. Such variations could signal a shift in the ecological value of this stopover site. The number of Bluethroats declined at an annual rate of 2.3%. Stopover probability and body mass varied annually, the latter showing a negative trend. However, population structure, passage timing and fuel deposition rate remained remarkably constant, with only minor deviations from the mean in specific years for certain parameters. The observed population decline mirrored that in the breeding population in France, suggesting changes in major stopover sites like Txingudi may reflect dynamics within breeding areas. Future research, including comparative studies across flyways, will be essential for comprehension of the long-term temporal dynamics of major stopover site usage.—Arizaga, J. & Gordo, O. (2024). Long-term dynamics of stopover use by the Bluethroat *Luscinia svecica*. *Ardeola,* 71: 291-306.

Key words: bird migration, coastal marshes, fuel deposition rate, fuel load, population dynamics, Spain, stopover ecology.

Resumen.—Entender la dinámica en la calidad en lugares de parada migratoria y la respuesta adaptativa de las aves a ella son dos aspectos fundamentales para comprender la estrategia migratoria de las especies así como su impacto en la supervivencia y eficacia biológica de los individuos. Para investigar esta dinámica, analizamos 16 años de seguimiento del ruiseñor pechiazul *Luscinia svecica* en Txingudi, una zona muy importante para la migración de la especie en el norte de España. Nuestro objetivo fue examinar las variaciones anuales y las posibles tendencias temporales en la estructura demográfica (proporción de subespecies, edad y sexo), el tamaño de la población, la fenología de paso, la duración de la parada migratoria, y la cantidad y tasa de ganancia de peso. Tales variaciones pueden

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indicar cambios en el valor ecológico de la zona como área de parada migratoria. El índice de abundancia mostró un descenso medio anual de 2,3 %. Asimismo, el tiempo de estancia (medido como la probabilidad de permanencia en la zona) y el peso variaron anualmente, mostrando este último una tendencia negativa. Sin embargo, la estructura de la población, el tiempo de paso y la tasa de deposición de reservas se mantuvieron constantes, con tan sólo pequeñas desviaciones respecto al valor medio anual en años concretos, para ciertos parámetros. El descenso registrado en la abundancia es comparable al observado en poblaciones reproductoras francesas, lo que sugiere que los cambios de abundancia en lugares de parada migratoria como Txingudi podrían reflejar la dinámica poblacional de las áreas de reproducción. En el futuro, la ampliación de este tipo de estudios, incluyendo comparativas entre rutas migratorias, serán esenciales para mejorar el conocimiento sobre la dinámica temporal a largo plazo en puntos de parada migratoria.—Arizaga, J. y Gordo, O. (2024). Dinámica a largo plazo del uso de un área de parada migratoria en el ruiseñor pechiazul *Luscinia svecica*. *Ardeola*, 71: 291-306.

Palabras clave: dinámica poblacional, ecología en puntos de parada migratoria, España, marismas costeras, migración de aves, reservas, tasa de deposición de reservas.

INTRODUCTION

During migration, most birds need to stop over primarily to rest and/or refuel before facing their next flight stage (Berthold, 1996; Newton, 2008). Stopovers can also be necessary to avoid adverse weather en route, reduce predation risk or make spatio-temporal adjustments during the course of migration (Mehlman *et al.,* 2005; Ferretti *et al.,* 2021; Schmaljohann *et al.,* 2022). The way in which stopover sites are used through migratory flyways is ecologically and evolutionarily determined by what is called 'migratory strategy', which results from a trade-off between the overall distance to be travelled and the availability of stopover sites offering adequate conditions to obtain the energy needed to successfully continue migration.

Bird populations have migratory strategies that prioritise stopover sites or areas where refuelling is maximised, or at the very least, where successful preparation for the next flight bout is ensured (Piersma, 1987; Biebach, 1990; Schmaljohann *et al.,* 2022). However, stopovers are dynamic environmental scenarios, and the quality and suitability of these sites can vary over time. Environmental changes may be slow and gradual, as in natural habitat ecological succession, or they can occur rapidly and drastically, as in anthropogenic landscape transformations. In both scenarios, migrants should have enough flexibility to modify their strategies to adjust to the environmental conditions found at each moment. Comprehending the dynamism of stopover site quality and how birds adapt to it is essential for understanding migratory strategies and their potential consequences on individual survival and fitness. However, this is one of the least studied aspects in stopover ecology research because it requires information collected over long periods of time.

To assess the use of stopover sites, researchers have conventionally relied on variables such as stopover duration, fuel deposition rate (the amount of gained fuel per unit time), departure fuel load (fuel stored at the end of the stay), as well as demographic and body characteristics of the transient populations (Chernetsov, 2012). For example, a long stay accompanied by a high fuel deposition rate indicates that a site is used to refuel, i.e. it is a staging site *sensu* Warnock (2010). In addition, the occurrence of dominant individuals, such as adults or males is often hypothesised as evidence of an optimal site for a species, as subordinate birds, like first-years or females, are typically displaced and compelled to occupy suboptimal stopover sites (Carpenter *et al.,* 1993; Figuerola *et al.,* 2001). Therefore, alterations over time in these estimators might indicate shifts in the value of a stopover site and, consequently, changes in its importance within a flyway. Understanding these changes should be of the greatest interest to wildlife managers, as it would help to improve the conservation of migratory species and populations. For instance, a shortening of stopover duration, a decrease in the fuel deposition rate, a reduction in the proportion of dominant phenotypes, or a decline in migratory bird abundance could be, collectively or separately, warning signals that a stopover place is undergoing ecological degradation, rendering it suboptimal. In spite of the fact that stopovers may represent a tiny fraction of the distribution area used by individuals during their annual cycle, and are occupied for brief periods, stopovers play a pivotal role in connecting breeding and non-breeding areas and should attract maximum conservation efforts. However, due to their use just as passage areas, their importance for conservation compared to the breeding or wintering areas is usually neglected.

To understand the dynamics of stopover quality across migratory flyways, we used 16 years of monitoring data on Bluethroats *Luscinia svecica* during their passage through one of their key stopover sites in northern Iberia, Txingudi. The Bluethroat, a wetland-associated passerine, is included in Annex 1 of European Directive 2009/147/EC. In this context, it can be considered a species of concern, targeted from a conservation standpoint. Particularly in Txingudi, but also in other European wetlands, it functions as a ‘sentinel’ species indicating wetland quality. Our objective was to investigate the annual variations in population size, structure (in terms of age, sex and subspecies ratios), passage timing, stopover duration and fuel deposition rate. We aimed to know whether these annual fluctuations showed temporal trends indicative of a shift in the ecological value of the studied stopover site.

MATERIAL AND METHODS

Avian model

The Bluethroat is a widely distributed small passerine, breeding from Iberia to Alaska, with ten recognised subspecies (Shirihai & Svensson, 2018). Three of these subspecies breed in Western Europe (Johnsen *et al.,* 2006): *L. s. azuricollis*, which breeds in north-western Iberia (Arizaga *et al.,* 2011a) and overwinters in tropical Africa (Lomas-Vega *et al.,* 2019); *L. s. namnetum*, an endemic breeder from the French Atlantic coastal marshes, overwintering in southern Portugal and Morocco (Zucca & Jiguet, 2002); and *L. s. cyanecula,* the most abundant subspecies in western and central Europe, found in lowland wetlands, including the coastal marshes of the Wadden Sea shores stretching from northern France to Denmark and Germany (Keller *et al.,* 2020). It overwinters within a broad geographical range from southern Europe to tropical Africa (Arizaga & Tamayo, 2013). The species is not globally threatened (BirdLife International, 2023), but some subspecies, such as *L. s. namnetum*, have modest numbers and limited distribution ranges, making them deserving of special attention (Arizaga *et al.,* 2006). Although the species is assumed stable in Europe (BirdLife International, 2021), some particular populations have experienced declines attributed to factors such as drainage, degradation (e.g., reed-cutting and overgrazing) or natural succession in marshlands.

Study area and data collection

The Txingudi marshes are located at the south-eastern edge of the Bay of Biscay, at the Bidasoa estuary, which serves as the natural border between France and Spain. Txingudi is the first wetland found by migratory birds that reach the Iberian Peninsula when moving southwards along the French Atlantic coast (Figure 1; Etxaniz *et al.,* 1998; Arizaga *et al.,* 2011c). The research was specifically carried out at the Jaizubia stream (43º 21’ 00.00” N, 1º 48’ 44.52” W), a small tributary situated on the western side of the Bidasoa estuary. The sampling area encompassed an intertidal zone comprising a mosaic of mudflats, low halophytic vegetation and reedbeds (*Phragmites* spp.). These reedbeds are used by a large number of passerines that stopover in Txingudi during their post-nuptial migration towards their wintering areas either in southern Iberia or Africa (Arizaga *et al.,* 2011c). In particular, Txingudi is used as a stopover site by Bluethroats of the *L. s. namnetum* and, to a

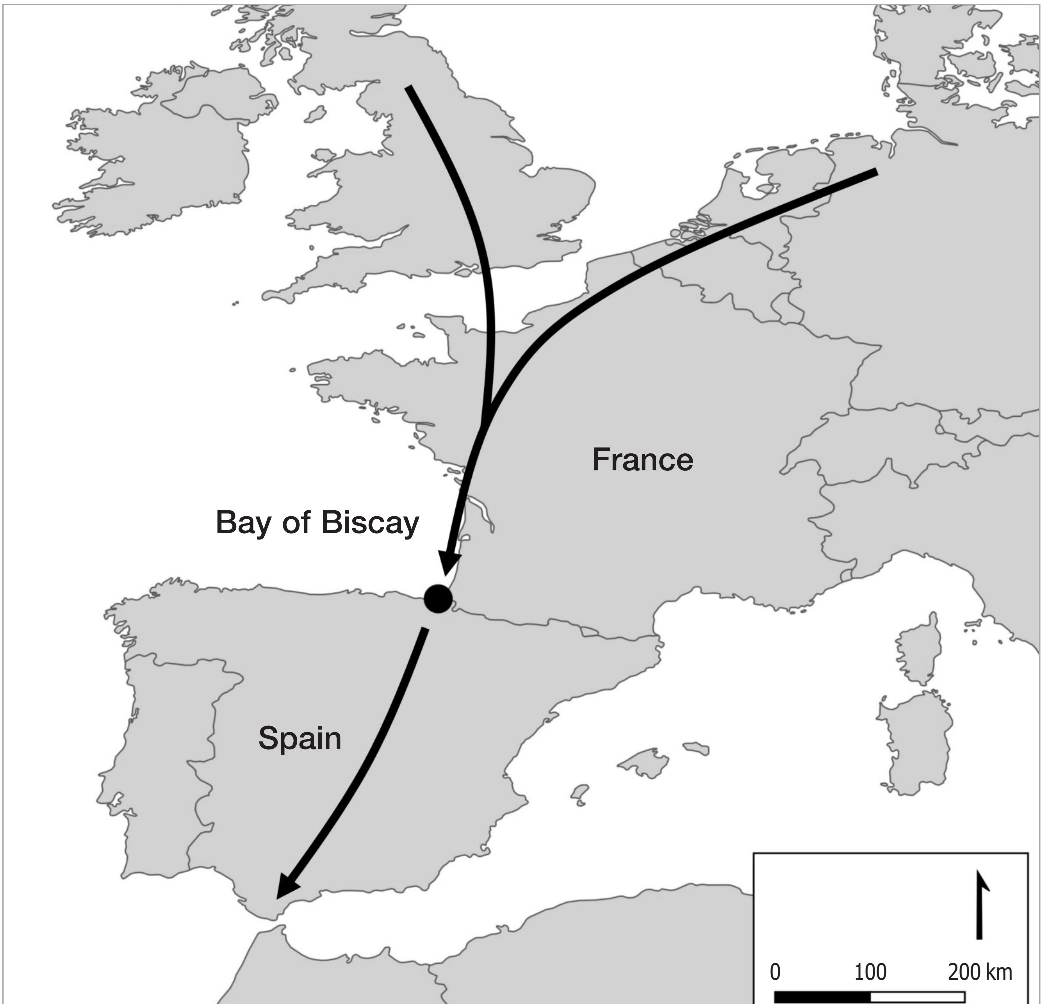

FIG. 1.—Location of Txingudi (dot) within the East-Atlantic migratory flyway (arrows).
[Localización de Txingudi (punto) en el contexto de la ruta migratoria del Atlántico oriental (flechas).]

lesser extent, the *L. s. cyanecula* subspecies (Arizaga *et al.,* 2006; Arizaga *et al.,* 2011b).

A constant-effort ringing site operated on a daily basis from 1 August to 30 September between 2007 and 2022 (16 years). This sampling period was designed to capture the passage of many migratory passerines, including Bluethroats, which were of special interest in this monitoring scheme (Mendiburu *et al.,* 2009; Arizaga *et al.,* 2011b). Sampling was conducted during continuous four-hour intervals starting at dawn, using 204m of mist nets that were 2.5m high, with a mesh size of 16mm, placed always in the same site within the reedbed. From 2007 to 2012, a tape-lure featuring the song of a male Aquatic Warbler *Acrocephalus paludicola* was employed to boost captures of that species (Julliard *et al.,* 2006). While the tape lure might affect the capturability of other bird species (de la Hera *et al.,* 2017; Sebastianelli *et al.,* 2020), we assumed its effect was negligible in the case of Bluethroats (Arizaga *et al.,* 2015). Once captured, each bird was marked with a metallic ring, aged and sexed, and its wing length (maximum wing chord; ±0.5mm accuracy) and body mass (with a digital balance, ±0.1g accuracy) measured. Age was determined by identifying moult limits in the wing: first-year birds show a moult limit in their great coverts and/or tertials, whilst adults do not show any moult limit as they undergo a complete moult after breeding (Svensson, 1996). Sex was determined by examining the colour patterns of the throat and breast (Svensson, 1996).

Statistical analyses: population structure and trends

Birds were classified as *L. s. namnetum* or *L. s. cyanecula* by applying the equation of Neto & Correia (2012), which is based on wing length measurements taken from birds of known age and sex. This equation, based on freshly moulted individuals, is more suitable for our birds caught in autumn than the one originally provided by Eybert *et al.* (1999). The latter was based on birds with worn plumages captured at their breeding sites.

In all analyses, we examined whether the variable of interest exhibited annual variation either stochastically (with year as a categorical factor) or following linear temporal trends (with year as a continuous variable). To achieve this goal, we controlled for several confounding factors (such as age, sex, subspecies, etc.) and considered two alternative models for each variable, with the year included either as a factor or a continuous variable. Both models, together with the null one, were compared using their Akaike Information Criterion values corrected for small sample sizes (AICc; Burnham & Anderson, 1998) and the best one was selected. Models differing in fewer than two AICc units were deemed to have similar support.

To assess the annual variation in the proportion of age classes (first-years vs adults), sexes (males vs females) and subspecies (*namnetum* vs *cyanecula*), generalized linear models (GLM) with a binomial distribution were applied to each of these response variables, with year as predictor (considered either as a factor or as a continuous variable). GLMs were run in R software (R Core Team 2023).

The annual abundance and phenology (dates of passage) of Bluethroats at Txingudi cannot be estimated from raw capture data from each year due to imperfect sampling. This was due to unforeseen causes such as spring tide episodes, adverse weather (such as heavy rains) or logistical constraints. These factors led to incomplete sampling on certain days every year. To calculate unbiased estimates of abundance and phenology for each year, we fitted General Additive Models (GAM) with negative binomial distribution errors and a log-link function using the daily captures of each year as response variable and the day of the year as predictor. We used function gam in the mgcv library (version 1.8-22) from R with penalised thin plate regression splines as smoothing basis and REML method for parameter estimation (Wood, 2017).

For each year, we simulated 10,000 datasets of virtual captures spanning the 61 consecutive days of the sampling period. These virtual captures followed a negative binomial distribution with the parameters obtained from the previous GAM. For each simulated dataset we fitted another GAM with a negative binomial distribution and a log-link function, producing predictions for the whole sampling period (for details, see Supplementary Electronic Material, Appendix 1). Adding up the daily predicted values yielded the total predicted captures for the entire season in each simulated dataset. The annual abundance was estimated as the median of these 10,000 values (±95% confidence intervals).

The estimated annual captures were further transformed into an abundance index, calculated as the ratio of captures in year *i* relative to 2007. Therefore, an abundance index of 1 corresponded to the year 2007, with subsequent years reflecting the proportion of increase or decrease compared to the initial year. This data processing from raw data to the abundance index was repeated for two subsets of captures: first-year birds (with the two subspecies *L. s. namnetum* and *L. s. cyanecula* pooled) and first-year individuals *L. s. namnetum* only. These subsets aimed to represent more homogeneous samples of individuals. We ran simple linear regression models with the year as predictor to ascertain the temporal trend of these indexes.

Migratory phenology was quantified in each one of the previously simulated datasets as the day with the 50% of accumulated captures. Then, the annual passage date of each year was estimated as the median of these 10,000 values (±95% confidence intervals).

Statistical analyses: stopover probability and fuel deposition rate

In small passerine birds settled in a stopover site, the actual survival from one day to the next can be assumed to be 1. This assumption allows apparent daily survival to be interpreted as the probability of remaining within that stopover site (Schaub *et al.*, 2001). Estimating this apparent daily survival improves the accuracy of calculating stopover duration compared to direct computation of the time between the first and last capture of a bird (Schaub *et al.*, 2001). We employed Cormack-Jolly-Seber (CJS) models, fitted using the MARK Program (White & Burnham, 1999), to estimate apparent survival (ϕ) and recapture probability (p) separately. Our dataset consisted of a matrix with 1,146 rows (individuals), categorised by year, and 61 columns (days from 1 August to 30 September). A goodness-of-fit test, conducted in the U-CARE Program (Choquet *et al.*, 2009), indicated the absence of transient-related (test for the presence of transients, statistic = 1.22, $P = 0.222$) or trap-dependence issues (statistic = −1.10, $P = 0.268$) in our dataset. We explored alternative models considering constant (ϕ), year-specific (ϕ_{year}) or linear trend-based ($\phi_{year.linear}$) survival probabilities. We also evaluated models with both constant and year-specific recaptures probabilities, factoring potential date-dependence on p.

Finally, we used GLMs to analyse body mass or fuel deposition rate. The models incorporated age, sex, subspecies and recaptured status (only for body mass models) as categorical factors, with wing length as a covariate, and a linear or categorical effect of year. Fuel deposition rate was calculated on an individual basis, as the difference in body mass between the last and first capture divided by the number of days between these dates. Same-day recaptures could not be included in this calculation since these birds were immediately released upon recapture without weighing. Therefore, the percentage of recaptures and fuel deposition rate refers to birds recaptured after one or more days from the first capture event. Furthermore, in the fuel deposition rate models, birds recaptured one day after the first capture ($n = 28$) were also excluded to avoid potential effects of handling on bird behaviour.

RESULTS

Population structure

A total of 851 individuals were captured, 312 (36.6%) of which were recaptured at least once within the same sampling season (range: 1-6 recaptures per individual). The average time elapsed between the first capture and the last recapture was 6.8 days. When considering each bird only once per day, there were 1,566 captures.

The population was mostly composed of first-year birds (mean: 83.0%, 95%CI: ±2.4%; range: 74.4%-90.8%). There was also a slightly higher proportion of males compared to females (mean: 60.2%, 95%CI: ±4.2%; range: 47.4%-80.6%). The majority of captured Bluethroats belonged to the *L. s. namnetum* subspecies (mean: 79.5%, 95%CI: ±3.4%; range: 64.7%-92.4%).

The AICc values of the models assessing age, sex and subspecies ratios indicated that a continuous linear effect of the year was better than its effect as a factor (see Supplementary Electronic Material, Appendix 2). However, the linear model never outperformed the null model, with AICc values either higher or just within the two units range. This suggests the absence of a linear trend. Indeed, this linear effect was not statistically significant in any of these response variables (age: $\beta = 0.028$, SE = 0.018, $P = 0.113$; sex: $\beta = 0.002$, SE = 0.014, $P = 0.837$; subspecies: $\beta = 0.028$, SE = 0.016, $P = 0.091$), when a hypothesis testing approach was applied.

Population trend

The abundance index declined significantly over the study period, with an annual rate of 2.30% ($R^2 = 0.346$, $F_{1,14} = 7.398$, $P = 0.017$; Figure 2a). Consequently, it is estimated that the annual captures of Bluethroats in Txingudi decreased by 34.5% from 2007 to 2022. When considering only the subset of first-year birds, the annual decline rate was slightly higher (slope = −2.58%, $R^2 = 0.360$, $F_{1,14} = 7.893$, $P = 0.014$). Such similarity was expected, considering the high correlation between the estimated annual numbers obtained from the simulated datasets total captures and first-years ($r = 0.988$, $P < 0.001$), as a result of the over-dominance of first-years in the population (see previous section). Nevertheless, when considering only the subset of first-year birds belonging to the subspecies *L. s. namnetum,* the annual decline was even steeper (slope = −3.40%, $R^2 = 0.386$, $F_{1,14} = 10.447$, $P = 0.006$). Once again, the estimated annual values for *namnetum* first-years were strongly correlated with the total captures of Bluethroats ($r = 0.939$, $P < 0.001$), due to the dominance of this subspecies in Txingudi.

Passage period

The estimated mean passage date was 5 September (range: 1-10 September). Migratory phenology did not show any significant linear trend during the study period ($R^2 = 0.024$, $F_{1,14} = 0.346$, $P = 0.566$; Figure 2b).

Stopover probability and fuel deposition rate

The average proportion of recaptured Bluethroats within each year was 26.6% (95% CI: ±4.0%; range: 11.0%-44.4%). The best model indicated annual variations in this proportion, but without a consistent tendency (AICc values 1156.8 vs 1161.5 for

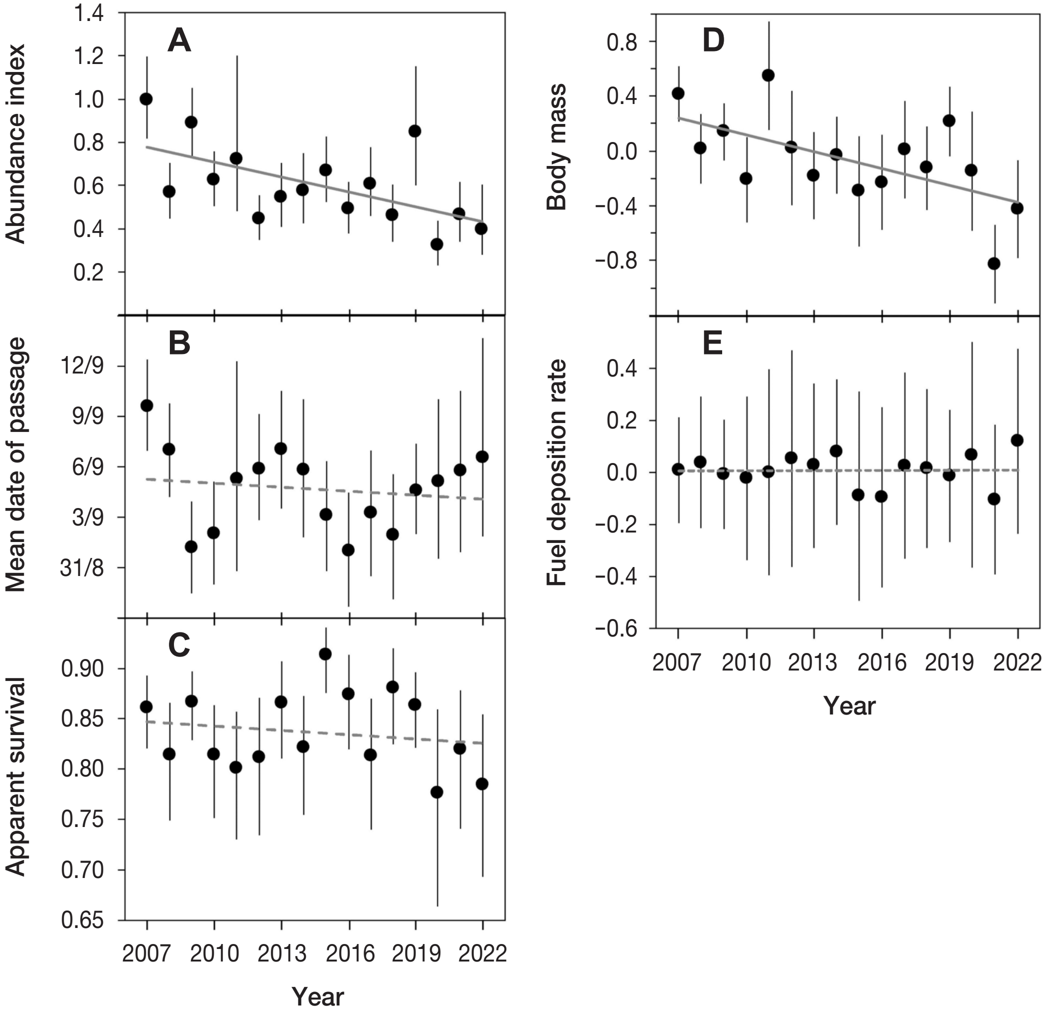

FIG. 2.—Annual values of the population traits of Bluethroats *Luscinia svecica* stopping over in Txingudi marshlands during 2007-2022. Error bars denote the 95% confidence interval. Grey lines are the fitted linear temporal trend (dotted lines are not significant). A and B, annual median values estimated from 10,000 simulated datasets of captures; C, annual mean daily apparent survival (equivalent to an average staying probability from one day to the next) obtained from Cormack-Jolly-Seber models; D and E, annual mean of residual values from a GLM including wing length, sex, age and subspecies as predictors (also whether or not a bird was recaptured in the case of body mass).

[Valores anuales obtenidos para la población de ruiseñores pechiazules Luscinia svecica *que utiliza las marismas de Txingudi como área de parada migratoria, durante el periodo 2007-2022. Las barras representan el intervalo de confianza al 95 %. Las líneas grises representan la tendencia temporal lineal (líneas de puntos, cuando las tendencia son no significativas). A y B, valores medianos anuales estimados a partir de 10.000 simulaciones; C, supervivencia aparente diaria media anual (equivalente a la probabilidad de permanencia diaria en Txingudi) obtenida a partir de un modelo de Cormack-Jolly-Seber; D y E, media anual de los residuos de un GLM incluyendo longitud del ala, sexo, edad y subespecie como predictores (también si un ave fue recapturada o no en el caso de la masa corporal).]*

the categorical vs continuous linear models, respectively). Differences among years were driven by the years 2011 and 2022, when the probability of recapturing a Bluethroat within the season was significantly smaller (Table 1).

Cormack-Jolly-Seber models revealed an average daily staying probability of 0.850 (95% CI: 0.834-0.864) for the study period. However, in concordance with the previous result for recapture probability, the staying probability varied annually, but without a significant linear trend between 2007 and 2022 (Figure 1c; AICc values 3941.3 vs 3945.5 for the categorical vs continuous linear model, respectively).

Although there was evidence for a significant reduction of body mass at their first capture in Txingudi (Figure 2d), AICc values indicated that the model including year as factor fitted better to data (3219.9 vs 3235.4; Table 2). As expected, body mass also differed in relation to subspecies, age and sex (with *L. s. cyanecula*, adults and males being heavier than *L. s. namnetum*, first-years and females), while controlling for the confounding effect of wing length (Table 2). Those birds recaptured later were lighter at their first capture than those never recaptured again within the same migratory season (Table 2).

For the fuel deposition rate, the model considering a linear effect of year fitted the data better than the one considering the year as a factor (AICc values 53.0 vs 70.9, respectively), but such a linear effect was not significant (Table 3; Figure 2e). None of the other tested variables (age, sex and subspecies) showed a significant effect on fuel deposition rate (Table 3).

TABLE 1

Parameter estimates obtained from the GLM used to estimate the probability of recapturing a Bluethroat *Luscinia svecica* ringed within the season in Txingudi in relation to year as factor. *[Parámetros del GLM aplicado para determinar si la probabilidad de recapturar dentro del mismo otoño un ruiseñor pechiazul* Luscinia svecica *anillado en Txingudi varía interanualmente.]*

Year	β	SE	*P*
2008	−0.32	0.32	0.331
2009	−0.17	0.29	0.564
2010	−0.34	0.34	0.317
2011	−1.08	0.39	0.005
2012	−0.66	0.39	0.085
2013	−0.03	0.35	0.930
2014	−0.66	0.36	0.063
2015	+0.36	0.37	0.325
2016	+0.13	0.42	0.765
2017	−0.77	0.39	0.050
2018	+0.23	0.40	0.566
2019	−0.45	0.33	0.171
2020	−0.71	0.47	0.130
2021	−0.44	0.38	0.253
2022	−1.83	0.56	0.001

DISCUSSION

We investigated annual variations in the population structure, abundance, date of passage, stopover duration and fuel deposition rate of Bluethroats stopping over in a tidal marsh in northern Iberia. We found an annual decline in the captures of Bluethroats. In addition, stopover probability and body mass showed statistically significant fluctuations year to year. The population structure, date of passage and fuel deposition rate

TABLE 2

Parameter estimates obtained from the GLM used to estimate the effect of year (as a factor), age, sex, subspecies, recapture and wing length on the body mass measured at the first capture.
[Parámetros del GLM aplicado para estimar el efecto del año (como factor), edad, sexo, subespecie, recaptura y longitud alar en el peso medido en la primera captura.]

Variable	**β**	**SE**	***P***
Year (2008)	−0.400	0.184	0.030
Year (2009)	−0.268	0.168	0.113
Year (2010)	−0.618	0.193	0.001
Year (2011)	+0.136	0.190	0.473
Year (2012)	−0.388	0.204	0.058
Year (2013)	−0.597	0.204	0.003
Year (2014)	−0.443	0.190	0.020
Year (2015)	−0.705	0.223	0.002
Year (2016)	−0.648	0.248	0.009
Year (2017)	−0.409	0.204	0.045
Year (2018)	−0.542	0.240	0.024
Year (2019)	−0.190	0.183	0.298
Year (2020)	−0.565	0.245	0.021
Year (2021)	−0.241	0.211	<0.001
Year (2022)	−0.847	0.213	<0.001
Age (adult)	+0.758	0.108	<0.001
Sex (male)	+0.416	0.095	<0.001
Subspecies (*namnetum*)	−0.991	0.168	<0.001
Recaptured (yes)	−0.296	0.091	0.001
Wing length	0.138	0.021	<0.001

TABLE 3

Parameter estimates obtained from the GLM used to estimate the effect of year (as a continuous variable), age, sex, subspecies and wing length on fuel deposition rate.
[Parámetros del modelo lineal aplicado para estimar el efecto del año (como variable continua), edad, sexo, subespecie y longitud alar en la ganancia de peso.]

Variable	**β**	**SE**	***P***
Year	−0.002	0.004	0.504
Age (adults)	−0.090	0.055	0.100
Sex (male)	+0.020	0.041	0.622
Subspecies (*namnetum*)	−0.030	0.081	0.711
Wing length	−0.015	0.009	0.088

remained stable across the study period, with only minor deviations from the mean in specific years for certain parameters.

Structurally, the population was predominantly composed by individuals born in that year's breeding season (i.e., first-years) of the *L. s. namnetum* subspecies, and these proportions appeared to remain relatively stable across years, without showing discernible temporal trends in any of the parameters. These findings suggest consistent and largely unaltered utilisation of the area over the past 16 years by the two subspecies known to stop over in Txingudi, *L. s. namnetum* and *L. s. cyanecula* (Arizaga *et al.*, 2006; Arizaga *et al.*, 2011b). These observations might reflect a certain degree of consistency in migratory flyways, at least within this temporal window of 16 years. However, ongoing continuous monitoring is still necessary, as migratory routes can rapidly change (Berthold *et al.*, 1992), particularly given the current climate change scenario (Sonnleitner *et al*., 2022; Madsen *et al*., 2023).

One of the main findings of this study was the notable decline in the population, with an estimated average annual decrease of 2.3% and a cumulative loss of 34.5% from 2007 to 2022. Bluethroats captured in Txingudi primarily originate from the western French marshes (*L. s. namnetum* breeding area; Dupuy & Sallé, 2022), as well as to a lesser extent from other parts of France and neighbouring western European countries that host *L. s. cyanecula* populations, including the Benelux countries and the western part of Germany (Arizaga & Tamayo, 2013). Available data on breeding Bluethroats in France show contradictory temporal tendencies of their populations: (1) The national breeding bird survey reports a 3.5% decline for all France between 2001 and 2019, although the associated error is large enough to include population stability also as a possibility (Fontaine *et al.,* 2020); (2) The migratory atlas of birds of France reports a stable population trend for the period 2001-2021, though the estimate is uncertain for 2012-2021 (Dupuy & Sallé, 2022); (3) In Arcachon bay, SW France, a breeding site for the *L. s. namnetum* subspecies situated on the Atlantic coast flyway, the trend was characterised by fluctuations followed by long-term stability from 2001 to 2011 (Leconte *et al.,* 2012). Nevertheless, it is worth noting that much of the Txingudi data collection period (2007-2022) falls outside the monitoring timeframe of Arcachon's population. In other western European regions where the *L. s. cyanecula* subspecies breeds, population increases have been recorded, with an annual growth rate of 5% in The Netherlands between 2011 and 2022 (source: www.stats.sovon.nl), and more than a 100% increase during the 1985-2009 in Germany (Gedeon *et al.,* 2015). Therefore, there is no obvious link between the observed trend in Txingudi and that recorded in the breeding areas of the species. While there is some uncertainty regarding the *L. s. namnetum* subspecies, it is remarkable that the 3.5% decrease observed for all France (Fontaine *et al.,* 2020) is compatible with the trend found in Txingudi. This suggests that the captures from Txingudi may reflect the decline of the main population source of Bluethroats passing through this stopover site. An updated assessment of the size and productivity of the *L. s. namnetum* subspecies in France could provide further insights into the underlying causes of the observed Bluethroat decline in Txingudi. It is important to highlight that a significant fraction of the Bluethroats (*L. s. namnetum*) recaptured in Txingudi were ringed along the French coast (Arizaga, 2019). While lower numbers in autumn may indicate low productivity, they may not be directly related to breeding population size estimates, which also need to consider survival of first-year birds during their first winter.

Alternatively, it could be hypothesised that Bluethroats may simply be using stopover sites less frequently, resulting in fewer captures. However, our results would not support this hypothesis, as the proportion of subordinate individuals did not increase, and parameters such as stopover duration, fuel deposition rate, and the proportion of recaptures did not show consistent decreases along the study period. In contrast, body mass was observed to decrease along the study period, a phenomenon compatible with deteriorating habitat quality. However, variations in mean body mass, which can serve as an indicator of fuel load (Salewski *et al.,* 2009), may also be influenced by factors operating on broader spatial scales. For instance, an increase in the quantity and quality of stopover sites along a migratory flyway could potentially reduce the necessity for birds to store large amounts of fuel. This reduction in fuel load is known to offer benefits by reducing flight costs and predation risk (Kullberg *et al.,* 1996;

Hedenström & Alerstam, 1997; Lind *et al.,* 1999). Alternatively, the lower body mass recorded in Bluethroats arriving at our study site in recent years could be a result of the opposite situation in the Atlantic flyway: poor environmental conditions in the French stopovers prior to Txingudi would deny the individuals a proper refuelling.

Overall, our findings suggest that Txingudi is probably as suitable as it was in 2007. In addition, a notable fraction of Bluethroats stayed in Txingudi for some days. These birds were lighter on arrival at Txingudi than those that were never recaptured within the same season. This evidence further supports the notion that Txingudi is used to refuel, *sensu* a true 'staging' stopover (Warnock, 2010), as observed in other stopover sites considered to be optimal for the species (Chenaval *et al*., 2011). This seemingly favourable conservation status of Txingudi does not preclude the possibility that (1) other stopover sites within the flyway may have recently improved or could improve, due, for example, to projects aimed at creating or restoring coastal marshes in northern Iberia and along the Atlantic coast of France (Arizaga *et al*., 2014; Fontanilles *et al*., 2020), and/or (2) the prevailing wind regimes and the main migration route has shifted east-west, leaving Txingudi outside the main migratory flow used by *L. s. namnetum* Bluethroats heading towards Portugal (Zucca & Jiguet, 2002; Dupuy & Sallé, 2022).

One of the main effects of climate change are the phenological shifts in many migratory birds, resulting in either advancement or delay of their migration timing (Gordo & Sanz, 2006; Tomotani *et al.,* 2018; Haest *et al.,* 2019; Maggini *et al.,* 2020; Horton *et al.,* 2023). However, for Bluethroats in Txingudi, we did not detect any significant linear trend in the mean date of passage over a 16-year period. The pressure on migration timing is particularly evident in spring, as birds need to match their breeding season with the peak of food availability that follows the vegetal blooming after the winter as much as possible (Visser *et al.,* 2006). In contrast, this pressure is less pronounced in autumn, leading to more heterogeneous phenological shifts among species. The lengthening of summer and increased vegetation productivity in autumn (Gordo & Sanz, 2009; Gallinat *et al.,* 2015) appear to be major drivers causing delayed autumn migration in several species (Jenni & Kéry, 2003; Mills, 2005; Lehikoinen & Jaatinen, 2012, but see Briedis *et al.,* 2020). Bluethroats, however, do not behave in such a way, but the reasons for this behaviour remain unknown. One plausible explanation is that the species may simply disregard environmental cues due to its habitat preferences: primarily intertidal coastal upper marshes for the *L. s. namnetum* (Zucca & Jiguet, 2002; Arizaga *et al.,* 2013, but see Fontanilles *et al.,* 2020), with its main prey potentially influenced by other ecological processes different from the typical autumnal senescence of forest habitats. Moreover, it should be noted that Bluethroats have 1-2 broods, and also need to moult prior to migration (Cramp, 1988), so there may be little scope/purpose in extending the breeding season.

In conclusion, whilst nearly all the parameters associated with the stopover behaviour of Bluethroats in a coastal wetland in northern Spain remained relatively stable over a 16-year period, the population, mostly composed of the *L. s. namnetum* subspecies, exhibited a tendency to decline at an annual rate of 2.3%. This decline is similar to the one reported for the breeding population in France, suggesting that changes in major stopover sites such as Txingudi may mirror the dynamics occurring at breeding grounds. Future research, including comparative studies across different flyways, will be necessary for deeper comprehension of the long-term temporal dynamics in the utilisation of what are currently considered major stopover sites.

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Appendix 1. Predicted daily total captures of Bluethroats *Luscinia svecica* for each year with their 95% confidence intervals. *[Capturas totales diarias previstas de ruiseñor pechiazul* Luscinia svecica *para cada año, con su intervalo de confianza al 95%.]*

Appendix 2. GLM used to test for the effect of year as a factor or as a continuous linear predictor on the age, sex and subspecies ratios. *[GLM utilizados para testar el efecto del año como factor o como variable continua sobre el ratio de edad, sexo y subespecie.]*

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