

SEASONAL INDIVIDUAL AND POPULATION-ASSOCIATED PATTERNS OF MIGRATION OF GOLDFINCHES *CARDUELIS CARDUELIS* THROUGH THE WESTERN EDGE OF PYRENEES

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SUMMARY.—*Seasonal individual and population-associated patterns of migration of goldfinches *Carduelis carduelis* through the western edge of Pyrenees*

Aims: Contributing to know the migration strategies of goldfinches *Carduelis carduelis* passing over through the western edge of Pyrenees, focusing in time-associated variations in age and sex ratios and morphology.

Location: Txingudi and the surrounding mountain ranges, in NE Guipúzcoa (N Iberia).

Methods: Systematic sampling (ringing) sessions between Oct and Apr, from Mar 2004 to Apr 2008.

Results and discussion: Both sex and age ratios were similar among periods (autumn and spring migrations, and winter), with the same proportion of sexes and an age ratio biased to juveniles (80 % of captures). Concerning biometrics, spring migrants showed a shorter wing and tail, and were more fuel loaded than birds from autumn and winter. During autumn, adults tended to pass later than juveniles, as did long-distance like migrants (presumably from more northern breeding quarters) in relation to short-distance like ones. Both sex and age ratios did not vary across the spring, and long-distance like migrants tended to pass over earlier than short-distance like ones.

Key words: age, biometry, *Carduelis carduelis*, goldfinch, Iberia, migration, Pyrenees, sex, strategies.

RESUMEN.—*Patrones de migración individuales y poblacionales de jilgueros *Carduelis carduelis* a través del occidente del Pirineo.*

Objetivos: Profundizar en el conocimiento de la estrategia migratoria del jilguero *Carduelis carduelis* a su paso por el oeste de los Pirineos, principalmente en relación al patrón estacional de variación de las ratios de edad y sexo, así como los rasgos morfológicos.

Localidad: Txingudi y las montañas que rodean a esta zona, en el NE de Guipúzcoa (N de España).

Métodos: Sesiones de muestreo (anillamiento) entre los meses de octubre y abril, desde marzo de 2004 a abril de 2008.

Resultados y conclusiones: La ratio de sexo y edad no varió entre periodos, habiendo en conjunto un ratio de sexo 1:1 y más juveniles que adultos (80 %). Además, las aves que se capturaron en paso pre-nupcial tuvieron cola y alas más cortas que las que se capturaron en paso posnupcial e invierno, y las que se atraparon en invernada tendieron a alas y cola más largas que las del paso posnupcial. En otoño, el tiem-

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po de paso de los adultos fue más tardío que el de los juveniles, al igual que el de los individuos con una morfología típica de migrantes de distancias largas (presumiblemente de poblaciones que criarían más al norte). En primavera, la proporción de clases de edad y sexo se mantuvo constante. Por otro lado, las aves con alas más largas y apuntadas y una cola más corta tendieron a pasar antes que las de alas más cortas y redondeadas y una cola más larga.

Palabras clave: biometría, *Carduelis carduelis*, edad, España, estrategias, jilguero, migración, Pirineos, sexo.

INTRODUCTION

Timing of migration and its variation in relation to both individual and population viewpoints is one of the main chapters in the study of avian migration strategies (reviewed by Newton, 2008). Furthermore, the studies dealing with this kind of analyses have been called to play a relevant role in our understanding of the evolution of migration and its significance from a biological and ecological perspective.

At an intra-specific level, timing of migration is subjected to vary in relation to individual-associated features, such as age or sex. Differential migration is observed when timing, routes or distances of migration vary between age classes or/and sex (Gauthreaux, 1982). Focusing on timing of passage through given stopover sites or areas, adult birds often pass earlier than juveniles, both during the autumn and spring migrations (e.g. Cantos and Asensio, 1989; Basciutti *et al.*, 1997), but the opposite strategy is also documented (e.g. Grandío, 1997). This trend is found since adult birds normally show higher migratory speeds (Ellegren, 1991; Grandío, 1999), hence being able to arrive to their goal areas before less-experienced individuals. Between sexes, males often pass earlier than females, particularly in spring, giving rise to a phenomenon called *protandry* (Kokko, 1999; Rubolini *et al.*, 2004). This is because of earlier-arrival associated advantages, and by the fact that, normally, males are those having the responsibility of occupying a territory and finding a mate (Podulka *et al.*, 2004).

The timing of migration could also vary among populations (Newton, 2008). In Holarctic passerines, migration distances often increase with latitude in several species (e.g. Cramp, 1988, 1992; Cramp and Perrins, 1994). In parallel with this tendency, the migratory behaviour is known to shape birds' morphology, since migration promotes selection for adaptations for long-distance flight (reviewed in Berthold, 1996). Particularly, the longer the migration distances, the longer and more pointed the wings and shorter the tails (both at inter and intra-specific level; Winkler and Leisler, 1992; Mönkkönen, 1995; Copete *et al.*, 1999; Calmaestra and Moreno, 2001). Thus, populations which breed in further north regions and that must travel longer migration distances have commonly more marked long-distance-like morphologies than others breeding in further south regions (e.g. Fiedler, 2005). Even in populations with the same distances of migration, it can be found a high variation in wing shape that is caused by different wintering strategies, with resident birds showing shorter wings, whilst vagrants longer ones (Senar *et al.*, 1994). Thus, flight-associated morphology could be used to infer the relative migration distance (or geographic origin) or degree of vagrancy during winter of individuals passing over through a given stopover place or region (Chandler and Mulvihill, 1990; García-Peiró, 2003; Chernetsov, 2004).

The goldfinch *Carduelis carduelis* is a widespread European songbird, breeding from Portugal to 96° E, and from the boreal margin to

the steppe and desert fringe in N Africa, as well as in the Canary Islands (Cramp and Perrins, 1994). A number of populations or individuals from northern and mid-Europe move to overwinter in the circum-Mediterranean region (reviewed by Cramp and Perrins, 1994). Noteworthy, Iberia is one of the chief wintering areas for many populations from W Europe, including France, The Low Countries, W Germany, Britain and Ireland (Asensio, 1986). The main phenological patterns of migration of goldfinches in Iberia are quite well known, with the autumn migration period occurring from Oct. to Nov. (Asensio, 1986) or mid-Dic. (García, 1975), with a peak by late-Oct., and the spring migration period from Mar. to mid-May, with a peak by mid-Apr. (Asensio, 1986; see also for a review Tellería *et al.*, 1999). Practically the only study which deals with the strategies of migrant goldfinches through Iberia is that by Asensio (1986). Using data from recaptures, Asensio (1986) observed that the timing of passage was similar between sexes (both in autumn and spring), and that the populations from further north breeding areas seemed to pass over Iberia later than those breeding in further south areas during autumn (data for the spring migration period were absent), though further studies supporting these results are lacking. Other issues, such as the possible differential migration between age classes, were not here analysed.

The Pyrenees are one of the most relevant geographic barriers shaping migration through Iberia (Galarza and Tellería, 2003). Thus, most birds tend to pass over them across the eastern or western corners, giving rise to two important migration corridors: one across the Mediterranean façade of Iberia (the eastern one), and another one passing over through central Iberia up to SW Iberia (the western one) (Asensio, 1986; Galarza and Tellería, 2003; Arizaga *et al.*, obs. per.). Accordingly, whatever of these two edges gives a good opportunity to analyse the pattern of migration and strategies of populations of migrants en-

tering in (autumn) or leaving Iberia (spring) in their route to or from their wintering areas, respectively.

Our aim here was to analyse the pattern of migration of the goldfinch through the western edge of Pyrenees, focusing on possible time-associated variations in age and sex ratios and morphological traits.

MATERIAL AND METHODS

Sampling places and ringing protocol

Data were obtained in NE Guipúzcoa (N Iberia, W edge of Pyrenees), at Txingudi and the surrounding mountain ranges (fig. 1). Goldfinches were caught weekly (when possible) with mist and pull nets (Bub, 1995), from Oct. to Apr. (Oct. to mid-Nov., autumn migration period; mid-Nov. to Feb., winter period; mid-Mar. to Apr., spring migration period), from Mar. 2004 to Apr. 2008, during 4 h from dawn per sampling day. Birds were encouraged to land or to move nearer mist nets with 2 to 4 living decoys (with permission of Diputación de Guipúzcoa) placed always (both during migration and wintering period) near the nets. Nets were placed in grasslands of rural areas, always in the same site for each sampling site. Sampling journeys were cancelled in days with strong wind or rain.

Once captured, each bird was ringed and its age and sex determined (Svensson, 1998). Moreover, the following variables were measured: wing length (method III by Svensson, 1998; ± 0.5 mm), tail length (± 0.5 mm), primary feathers lengths (P1 to P9, number from innermost to outermost; ± 0.5 mm), tarsus length (± 0.1 mm), head-and-bill length (± 0.1 mm), body mass (with a digital balance, ± 0.1 g). Only those birds with their age and sex known were here considered. Moreover, our own recaptures were excluded from the data set, so each individual was considered only once.

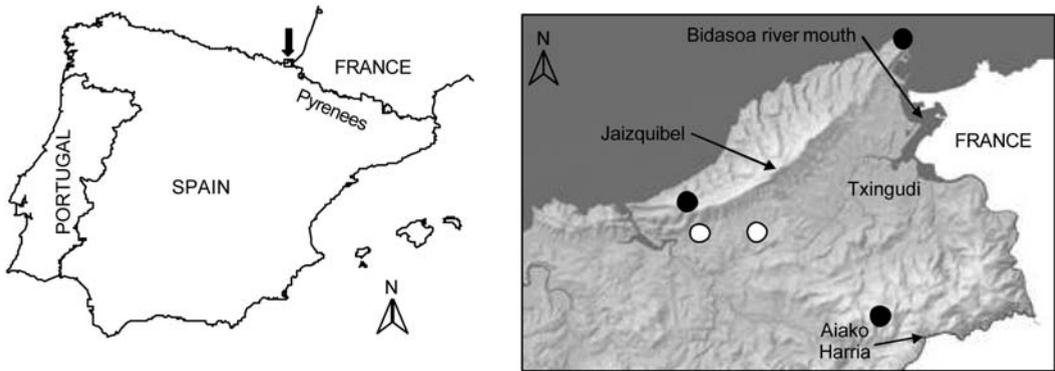


FIG. 1.—Location of Txingudi and the surrounding mountain ranges within Iberia (left) and the sampling sites where the study was done. Dark dots: places where birds were captured only during autumn or spring migrations. Open dots: places where birds were captured both during winter and migration. [Localización de Txingudi y montañas próximas en la Península (izda.) y puntos de muestreo en donde se realizó el estudio. Puntos negros: áreas donde sólo hubo capturas durante el periodo de paso, posnupcial y prenupcial. Puntos en blanco: áreas donde se capturaron aves en paso y en invernada.]

Analysis of age and sex ratios

Variations in proportion of age and sex categories were analysed (i) among the autumn, winter and spring migration period, and (ii) across the autumn and spring passages. In this second case, the time was divided into pentades (5-days time intervals). To test for the existence of different age or sex ratios between periods χ^2 -square contingency tables and CMH Stratified $R \times C$ χ^2 -square contingency tables were used. To test for the relationship between age/sex ratios and pentades within each period a Pearson's test of correlation was run. Data were pooled from different years owing to a sample size constraint.

Biometric analysis

We analysed here (i) the biometric variation among the autumn, winter and spring migration period, and (ii) the biometric variation across the timing of passage within each period (autumn and spring migration period). Four

biometric variables were used: wing and tail length (WL and TL, respectively; this last in relation to body size), wing morphology (pointedness, WP), body mass (BM, in relation to body size). Body size was assessed with tarsus length (TL), since other approaches, such as the use of the component one from a Principal Component Analysis (PCA) on variables including both feathers and skeletal measurements uses to give biased data, due to the high variance of measurements on feathers (Pascual and Senar, 1996, 1997; Senar and Pascual, 1997). WP was assessed with the C_2 index, which is used to assess wing pointedness (Lockwood *et al.*, 1998). This index is based on a modified PCA, the Size-Constrained Component Analysis (SCCA), controlling for the effect of body size. Positive values of the index are associated with a relatively more rounded wing, whilst negative values correspond to a more pointed wing.

To test for variations between periods Univariate Linear Models (ULM) on WL, WP, TL and BM, with period, age and sex as factor and the TL as a covariate (for TL and BM) were

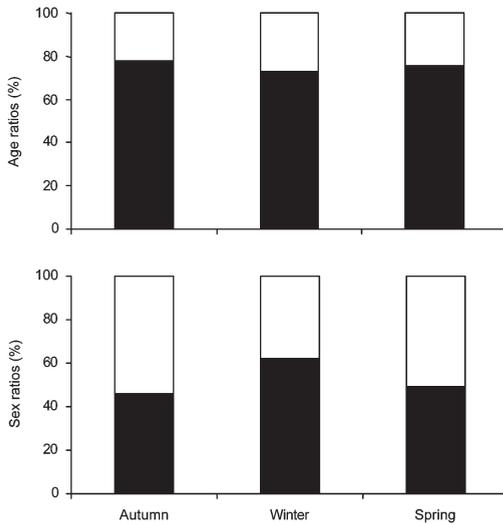


FIG. 2.—Seasonal-associated variations on age and sex ratios at Txingudi. Age ratios: black bars, juveniles; white bars, adults. Sex ratios: black bars, males; white bars, females.

[Variabilidad estacional de la proporción de clases de edad y sexo en Txingudi. Ratios de edad: barras negras, juveniles; barras en blanco, adultos. Ratios de sexo: barras negras, machos; barras en blanco, hembras.]

used. To test for date-associated variations in flight-associated morphology and fuel load ULM with the age and sex as factor were used. Time may not be included as a factor (months were too big time-intervals to detect differential timing of migration, and the use of fortnights lowers within-cell sample size too much). Thus, the date was included as a covariate.

Statistics were done with StatXact v.7.0 and SPSS v.15.0 for Windows, and means are given \pm SE.

RESULTS

Overall, 301 goldfinches were caught during the autumn migration period (ranges: 36 in 2007, 130 in 2006), 74 during winter (ranges:

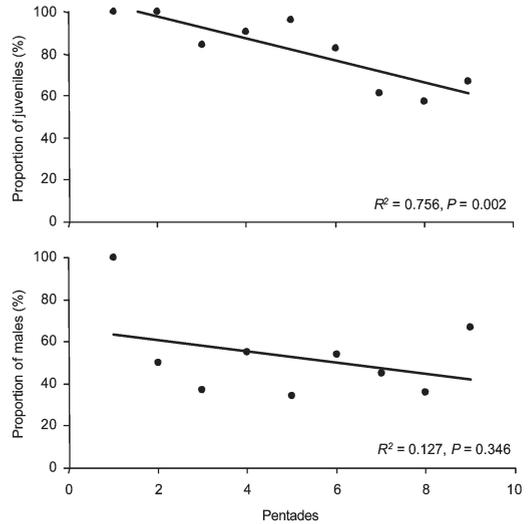


FIG. 3.—Proportion of age and sex categories across the autumn migration period. Time, in pentades: 1 = 01-05 Oct., 9 = 11-15 Nov.

[Proporción de clases de edad y sexo durante el periodo de paso posnupcial. Tiempo, en pentadas: 1 = 01-05 de Oct., 9 = 11-15 de Nov.]

3 in 2008, 28 in 2007), and 308 during the spring one (22 in 2005, 124 in 2006).

Time-associated variations of age and sex ratios

Overall, most captures were juveniles (almost 80%), and this age ratio did not vary from autumn to spring ($\chi_2^2 = 0.946$; $P = 0.623$; fig. 2), even when it was controlled for sex ($\chi_2^2 = 0.372$; $P = 0.830$). Nonetheless, this percentage varied across the autumn, decreasing from higher than 80% to around 60% by mid-Nov. (fig. 3). Conversely, the age ratio did not vary across the spring migration period (fig. 4).

Sex ratios varied between periods ($\chi_2^2 = 6.070$; $P = 0.048$; fig. 2), being 1:1 both during autumn ($\chi_1^2 = 1.757$; $P = 0.185$) and during spring ($\chi_1^2 = 0.052$; $P = 0.820$), though slightly biased to males (c.a. 60%) during win-

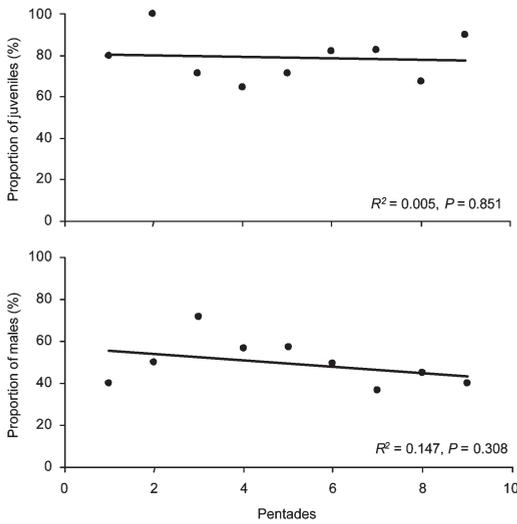


FIG. 4.—Proportion of age and sex categories across the spring migration period. Time, in pentades: 1 = 16 - 20 Mar., 9 = 26 - 30 Apr.

[Proporción de clases de edad y sexo durante el periodo de paso prenupcial. Tiempo, en pentadas: 1 = 16 - 20 de Mar., 9 = 26 - 30 de Abr.]

ter ($\chi_1^2 = 4.378$; $P = 0.036$). However, this difference was not significant when it was controlled for age ($\chi_2^2 = 5.497$; $P = 0.064$), supporting a masked effect of age on sex ratios. Conversely to autumn migration period, the sex ratios did not vary across the timing of migrations (fig. 3 and 4).

Time-associated biometric variations

Overall, most age/sex-associated biometric variations were due to sex, with the main tendency being that males showed a longer wing and tail, higher body mass, and a more pointed wing. Moreover, WL also varied between age classes, with adults having a mean longer wing than juveniles (table 1).

Practically all the biometric variables (except WP) varied between periods (table 1; fig. 5). Overall, captures from both autumn and

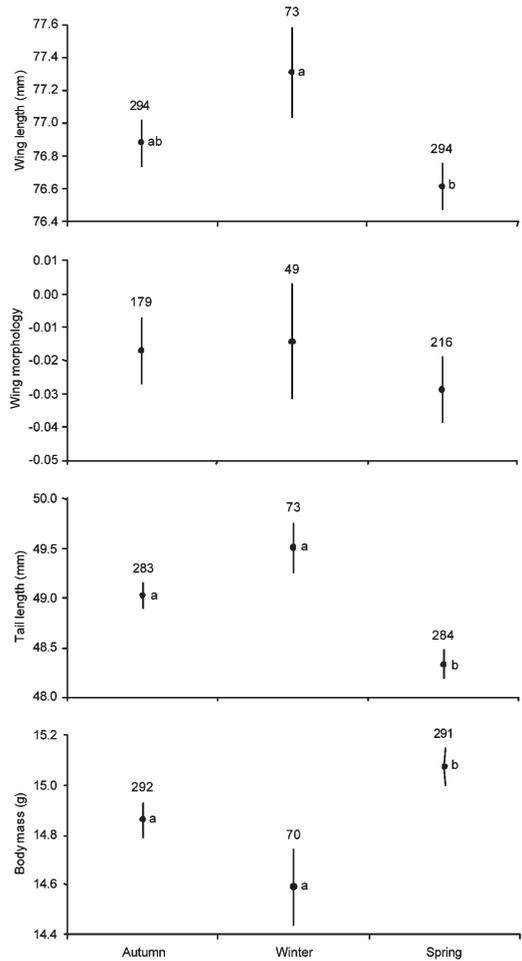


FIG. 5.—Seasonal-associated biometric variations in goldfinches at Txingudi. When significant differences were observed ($P < 0.05$), *a posteriori* tests were done. In these cases, mean values with the same letter are those between which no significant differences were observed.

[Variabilidad estacional de la biometría de jilgueros en Txingudi. En caso de encontrarse diferencias significativas ($P < 0,05$), se consideraron tests *a posteriori*. En estos casos, las medias con una misma letra son aquellas para las que no se encontraron diferencias significativas.]

winter showed a longer wing and tail and lower fuel loads than those from spring. Moreover, captures from winter tended to have a longer

TABLE 1

Univariate Linear Models used to test for between-periods (autumn, winter and spring) biometric variation. [*Modelos Lineales Univariados utilizados para analizar la variabilidad de la biometría entre periodos (paso posnupcial, invierno y paso prenupcial).*]

Factor	WL	WP	TL	BM
Period	$F_{2,660} = 6.569$ $P = 0.001$	$F_{2,443} = 0.696$ $P = 0.499$	$F_{2,594} = 11.626$ $P < 0.001$	$F_{2,594} = 4.958$ $P = 0.007$
Age	$F_{1,660} = 8.249$ $P = 0.004$	$F_{1,443} = 0.245$ $P = 0.621$	$F_{1,594} = 11.980$ $P = 0.001$	$F_{1,594} = 2.357$ $P = 0.125$
Sex	$F_{1,660} = 213.659$ $P < 0.001$	$F_{1,443} = 4.356$ $P = 0.037$	$F_{1,594} = 57.549$ $P < 0.001$	$F_{1,594} = 58.003$ $P < 0.001$
Period x Age	$F_{2,660} = 2.454$ $P = 0.087$	$F_{2,443} = 0.876$ $P = 0.417$	$F_{2,594} = 0.226$ $P = 0.798$	$F_{2,594} = 1.140$ $P = 0.320$
Period x Sex	$F_{2,660} = 1.033$ $P = 0.357$	$F_{2,443} = 0.586$ $P = 0.557$	$F_{2,594} = 0.567$ $P = 0.567$	$F_{2,594} = 1.185$ $P = 0.306$
Age x Sex	$F_{1,660} = 0.773$ $P = 0.380$	$F_{1,443} = 1.034$ $P = 0.357$	$F_{1,594} = 0.070$ $P = 0.792$	$F_{1,594} = 0.006$ $P = 0.938$
Co-variate: tarsus length	-	-	$F_{1,594} = 2.445$ $P = 0.118$	$F_{1,594} = 8.112$ $P = 0.005$

wing and tail and lower fuel loads than those from autumn, though this difference was not significant.

During autumn, migrants with a long-distance-like morphology (with a longer, more pointed wing) and more fuel loaded were more abundant at the end of the period (table 2, fig. 6). In spring, in contrast, long-distance-like and more fuel loaded migrants tended to be more abundant in mar (fig. 7), though in this case no significant differences were detected (table 2).

DISCUSSION

Differences between periods

Overall, more juveniles than adults were caught (around 80 %). This is a frequent rule observed in several bird species (reviewed by Podulka *et al.*, 2004), particularly in r-selective ones, such as many passerines, that are able

to rear many fledglings per pair and broods per year. Moreover, due to the higher over-winter survival of adults (Holmes *et al.*, 1989; Stutchbury, 1994), proportion of adults uses to increase from autumn to spring (Podulka *et al.*, 2004). Contrasting with this rule, however, the age ratios did not vary between periods at Txingudi. Decoys have been reported to attract certain age or sex categories better than others (Borrás and Senar, 1986; Figuerola and Gustamante, 1995; Lecoq and Catry, 2003). Though living decoys may favour the capture of similar age ratios, we were able to detect differential timing of passage between age classes in autumn (see below for further details), with only a difference from c.a. 80 % of juveniles during early autumn to 60 % during late autumn. Thus, methodological-associated biases should have a slight effect (bias) on age ratio and, if they had such an effect, seasonal-associated variations on age ratio were small. Spatio-temporal variations in distribu-

TABLE 2

ULM used to test for biometric variation within each period of migration.

[*Modelos Lineales Univariados utilizados para analizar la variabilidad de la biometría dentro de cada uno de los periodos de paso migratorio.*]

Period	Factor	WL	WP	TL	BM
Autumn	Age	$F_{1,293} = 12.686$ $P < 0.001$	$F_{1,178} = 0.152$ $P = 0.697$	$F_{1,259} = 6.788$ $P = 0.010$	$F_{1,258} = 1.907$ $P = 0.168$
	Sex	$F_{1,293} = 174.833$ $P < 0.001$	$F_{1,178} = 9.010$ $P = 0.003$	$F_{1,259} = 35.585$ $P < 0.001$	$F_{1,258} = 60.232$ $P < 0.001$
	Age x Sex	$F_{1,293} = 2.379$ $P = 0.124$	$F_{1,178} = 0.031$ $P = 0.861$	$F_{1,259} = 0.085$ $P = 0.770$	$F_{1,258} = 0.738$ $P = 0.391$
	Co-variate: date	$F_{1,293} = 8.204$ $P = 0.004$	$F_{1,178} = 4.421$ $P = 0.037$	$F_{1,259} = 3.675$ $P = 0.056$	$F_{1,258} = 17.337$ $P < 0.001$
	Co-variate: tarsus length	-	-	$F_{1,259} = 1.537$ $P = 0.216$	$F_{1,258} = 2.904$ $P = 0.090$
Spring	Age	$F_{1,293} = 1.825$ $P = 0.178$	$F_{1,215} = 0.008$ $P = 0.928$	$F_{1,264} = 3.270$ $P = 0.072$	$F_{1,268} = 0.028$ $P = 0.868$
	Sex	$F_{1,293} = 149.478$ $P < 0.001$	$F_{1,215} = 4.537$ $P = 0.034$	$F_{1,264} = 35.671$ $P < 0.001$	$F_{1,268} = 50.181$ $P < 0.001$
	Age x Sex	$F_{1,293} = 4.094$ $P = 0.044$	$F_{1,215} = 3.147$ $P = 0.077$	$F_{1,264} = 3.964$ $P = 0.048$	$F_{1,268} = 0.978$ $P = 0.323$
	Co-variate: date	$F_{1,293} = 1.250$ $P = 0.264$	$F_{1,215} = 1.699$ $P = 0.194$	$F_{1,264} = 0.001$ $P = 0.972$	$F_{1,268} = 1.331$ $P = 0.250$
	Co-variate: tarsus length	-	-	$F_{1,264} = 0.722$ $P = 0.396$	$F_{1,268} = 3.260$ $P = 0.072$

tion of different age classes may also explain these results, though this is very hard to be confirmed, mainly due to the lack of accurate data on age ratios for different periods and regions of Iberia.

Sex ratios did not differ from 1:1, and they were constant from autumn to spring, once omitted the age effects. In Iberia, Asensio (1986) observed a decreasing proportion of males towards south, agreeing with the fact the goldfinch performs differential distance of migration, with males over-wintering in further north regions than females (Newton, 1972), as reported in several other species (reviewed by Cristol *et al.*, 1999). Thus, N Iberia seemed to be intermediate between regions of S Iberia,

with a female-biased winter population, and N and mid-Europe, with a male-biased winter population (Cramp and Perrins, 1994).

From a biometric viewpoint, goldfinches caught during spring differed from those from autumn and winter by having a shorter wing and tail, as well as higher fuel load (wing morphology did not differ statistically between periods). It is reasonable to consider that such shortening of wing and tail during spring may have been due to abrasion of feathers: in late summer or autumn flight-feathers are new, but over the course of winter months abrasion will reduce the length of feathers (Martin, 1996; Alonso and Arizaga, 2005). However, winter captures tended to have a longer wing and tail

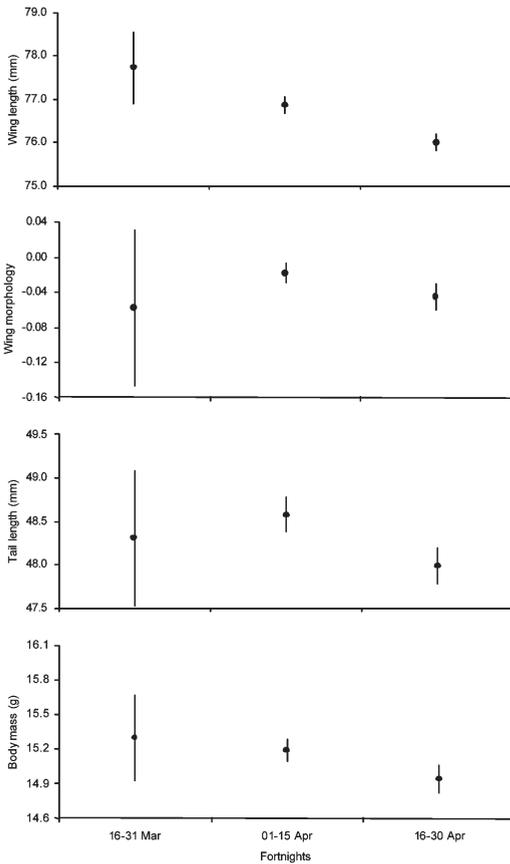


FIG. 6.—Within seasonal-associated biometric variations of goldfinches passing over through Txingudi during autumn migration period (for further details see table 2). To make the figures clearer the data have been pulled in fortnights.

[Variabilidad estacional de la biometría de jilgueros en Txingudi durante el periodo de paso posnupcial (para más detalles ver la tabla 2). Para que los gráficos fueran más claros los resultados se agruparon en quincenas.]

than those from autumn (if no significant differences were detected, it may be possibly due to the high over-dispersion of data during winter, likely linked with lower sample sizes then). This prevents us to consider the abrasion hypothesis cautiously, suggesting that the bio-

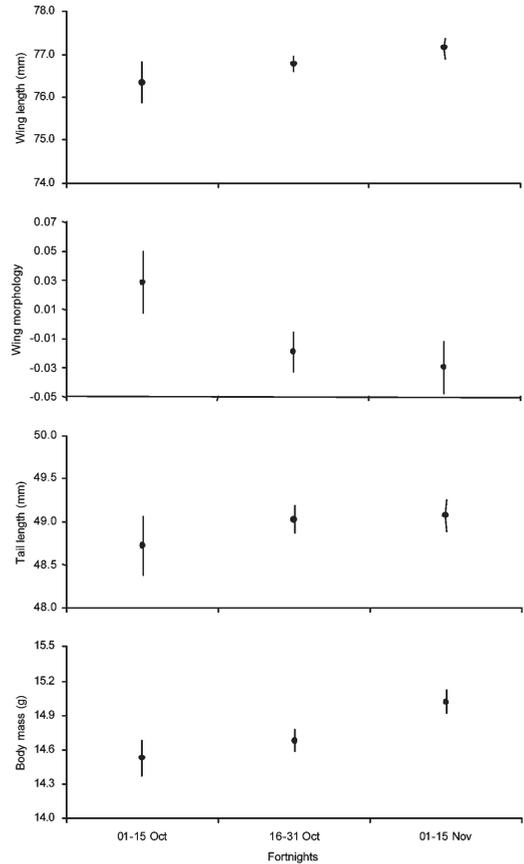


FIG. 7.—Within seasonal-associated biometric variations of goldfinches passing over through Txingudi during spring migration period (for further details see table 2). To make the figures clearer the data have been pulled in fortnights.

[Variabilidad estacional de la biometría de jilgueros en Txingudi durante el periodo de paso prenupcial (para más detalles ver la tabla 2). Para que los gráficos fueran más claros los resultados se agruparon en quincenas.]

metric variations may be also (or complementary) due to the occurrence of populations/individuals with a different migratory or wintering behaviour, or from distinct origin places.

Assuming an increasing long-distance-like morphology with latitude for the goldfinch

(Asensio, 1984; Cramp and Perrins, 1994), it can be stated that these wintering birds came from more northern breeding quarters than many passing over through Txingudi in their route to (autumn) or from (spring) other wintering areas in further south regions, though the origin places of these wintering birds are still unknown to us. To what extent native birds depart from or remain within our region during winter whilst other winter visitors arrive to this area is still an issue to be investigated. Data on recaptures and biometrics show that a relevant fraction of breeders from Iberia move southwards to over-winter even in northern Africa (Asensio, 1984, 1986). Occurrence of longer-winged and tailed birds during winter in Txingudi is in agreement with the fact that northern migrants occupy Iberia during winter, while local birds could be forced to depart from their breeding areas (Domínguez *et al.*, 2007), though this is just a hypothesis that requires to be tested specifically.

Winter population showed lower fuel loads than birds caught during both autumn and spring migrations (remarkable variations were especially registered between winter and spring periods), supporting that these last birds were true migrants (Berthold, 1996). Moreover, spring migrants were also observed to show a higher fuel load than autumn ones. This is a widespread phenomenon in several migrant species (reviewed by Newton, 2008), and it has been reported to be advantageous from selective viewpoint. Indeed, a higher fuel load allows migrants to keep higher migratory speeds, mainly since fewer stopovers to refuel must be made. Thus, during spring, those birds arriving early would be able to find a mate or a good territory with a higher likelihood than those arriving later (Francis and Cooke, 1986; Kokko, 1999).

Autumn

During autumn, adults tended to pass over the study area later than juveniles, supporting

differential timing of migration between age classes. This had not been reported in Iberia (Asensio, 1986), and points out that, whilst distances of migration vary between sex classes (Newton, 1972), timing of migration, at least in autumn, varies between age classes. Two main hypotheses would explain these results: (i) adults could leave their breeding areas later (as suggested for other European birds; Ellegren, 1991; Arizaga, 2008), or (ii) if both age classes would abandon their breeding quarters at a same time, adults could maintain lower migration speed. However, we lack data on both issues, so this is a question to be considered in future analyses.

Long-distance-like migrants tended to pass over Txingudi during late autumn, suggesting that northern breeders (so a higher proportion of *C. c. carduelis*) passed over later than southern ones (among which we could find still some *C. c. parva*) with, presumably, a more rounded and shorter wing. Alternatively, it could be also possible that rather than a higher proportion of northern breeders by the end of autumn, a higher proportion of transients was captured (Senar *et al.*, 1994). Though this hypothesis can not be rejected, data on recaptures show that northern breeders pass over later than southern ones (Asensio, 1986). Differential timing of passage in autumn in populations with (presumably) different migration distances is reported in several species of both Europe (Lövei, 1983; García-Peiró, 2003; Chernetsov, 2004; Arizaga, 2008) and the Nearctic (Chandler and Mulvihill, 1990).

In parallel with the fact that northern European breeders seemed to pass over Txingudi during late-autumn, we observed these northern, long-distance like migrants were more fuel loaded than those birds passing over earlier. Thus, this suggests that northern-like migrants would be able to cover a longer distance without stopping-over to refuel. Though a fraction of northern-like migrants seem to over-winter in more northern quarters than southern ones (as shown above), it can not be rejected

that some northern-like migrants could also cover longer distances of migration, being under these circumstances advantageous to be more fuel loaded. Conversely (or complementary), late migrants have been suggested to be benefited of carrying more fuel during autumn, due to the decreasing food supply and higher likelihood of adverse bad weather (Newton, 2008). Future data on geographic distribution of populations during winter will be definitive to face this question.

Spring

In contrast to autumn, timing of passage was similar for both sex and age categories. To some extent this lack of significant differences could have been promoted by having pulled the study years (increasing hence the noise from a statistical viewpoint), the relatively low sampling effort during the passages (Leal *et al.*, 2004; Arizaga, 2008) and the low sample size per year. Future studies dealing with daily-based trapping sessions are called to be crucial to clarify this question.

As observed during autumn, migrants with distinct flight-associated morphology tended to pass over Txingudi differentially (with a higher number of long-distance like migrants during early spring), though in this case no significant differences were detected. To some extent this may have been due to the high overdispersion of data during early spring (particularly in Mar.), promoted in part by lower sample sizes during this period.

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BIBLIOGRAPHY

- ALONSO, D. and ARIZAGA, J. 2005. Biometrics of Citril Finch *Serinus citrinella* in the west Pyrenees and the influence of feather abrasion on biometric data. *Ringing and Migration*, 23: 116-124.
- ARIZAGA, J. 2008. *Patrones de migración de Sylvia atricapilla, Linnaeus, 1758 (Aves) en España y comportamiento en un área de descanso*. PhD Thesis. Universidad de Navarra.
- ASENSIO, B. 1984. Sobre los orígenes de los fringílicos migrantes en el extremo sur de España. *Ardeola*, 32: 49-56.
- ASENSIO, B. 1986. La migración en España del Jilguero (*Carduelis carduelis*, L.) según los resultados de anillamiento. *Ardeola*, 33: 176-183.
- BASCIUTTI, P., NEGRA, O. and SPINA, F. 1997. Autumn migration strategies of the Sedge Warbler *Acrocephalus schoenobaenus* in northern Italy. *Ringing & Migration*, 18: 59-67.
- BERTHOLD, P. 1996. *Control of bird migration*. Academic Press. London.
- BORRÁS, A. and SENAR, J. C. 1986. Sex, age and condition bias of decoy trapped Citril Finches (*Serinus citrinella*). *Miscelanea Zoologica*, 10: 403-406.
- BUB, H. 1995. *Bird Trapping & Bird Banding*. Cornell University Press. New York.
- CALMAESTRA, R. G. and MORENO, E. 2001. A phylogenetically-based analysis on the relationship between wing morphology and migratory behaviour in passeriformes. *Ardea*, 89: 407-416.
- CANTOS, F. J. and ASENSIO, B. 1989. La migración postnupcial de la Lavandera Boyera (*Motacilla flava*) a lo largo de las costas mediterráneas españolas. *Ardeola*, 36: 139-147.
- CHANDLER, C. R. and MULVIHILL, R. S. 1990. Wing-shape variation and differential timing of migration in Dark-eyed Juncos. *Condor*, 92: 54-61.
- CHERNETSOV, N. 2004. Intraspecific variation in wing pointedness index in juvenile *Acrocephalus* warblers in the southeastern Baltic. *Journal of Ornithology*, 145: 105-108.

- COPETE, J. L., MARINÉ, R., BIGAS, D. and MARTÍNEZ-VILALTA, A. 1999. Differences in wing shape between sedentary and migratory Reed Buntings (*Emberiza schoeniclus*). *Bird Study*, 46: 100-103.
- CRAMP, S. 1988. *Handbook of the birds of Europe, the Middle East and North Africa. Vol. V*. Oxford University Press. New York.
- CRAMP, S. 1992. *Handbook of the birds of Europe, the Middle East and North Africa. Vol. VI*. Oxford University Press. New York.
- CRAMP, S. and PERRINS, C. M. 1994. *Handbook of the birds of Europe, the Middle East and North Africa. Vol. IX*. Oxford University Press. New York.
- CRISTOL, D. A., BAKER, M. B. and CARBONE, C. 1999. Differential migration revisited. Latitudinal segregation by age and sex class. In, V. Nolan, E. D. Ketterson & C. F. Thompson (Eds.): *Current Ornithology 15*, pp. 33-88. Plenum Publishers. New York.
- DOMÍNGUEZ, M., BARBA, E., CANTÓ, J. L., LÓPEZ, G. M. and MONRÓS, J. S. 2007. Seasonal interchange of the European Robin *Erithacus rubecula* populations in an evergreen holm oak forest. *Acta Ornithologica*, 42: 15-21.
- ELLEGREN, H. 1991. Stopover ecology of autumn migrating Bluethroats *Luscinia s. svecica* in relation to age and sex. *Ornis Scandinavica*, 22: 340-348.
- FIEDLER, W. 2005. Ecomorphology of the external flight apparatus of Blackcaps (*Sylvia atricapilla*) with different migration behaviour. *Annals of the New York Academic of Sciences*, 1046: 253-263.
- FIGUEROLA, J. and GUSTAMANTE, L. 1995. Does the use of tape lure bias samples of Curlew Sandpipers captured with mist nets? *Journal of Field Ornithology*, 66: 497-500.
- FRANCIS, C. M. and COOKE, F. 1986. Differential timing of spring migration in wood warblers. *Auk*, 103: 548-556.
- GALARZA, A. and TELLERÍA, J. L. 2003. Linking processes: effects of migratory routes on the distribution of abundance of wintering passerines. *Animal Biodiversity and Conservation*, 26: 19-27.
- GARCÍA, A. 1975. Migrantes y migración visible en la zona de Gibraltar, años 1972-1974. *Ardeola*, 21: 627-655.
- GARCÍA-PEIRÓ, I. 2003. Intraspecific variation in the wing shape of the long-distance migrant Reed Warbler *Acrocephalus scirpaceus*: effects of age and distance of migration. *Ardeola*, 50: 31-37.
- GAUTHREAU, S. A. 1982. Age-dependent orientation in migratory birds. In, F. Papi & H. G. Wallraff (Eds.): *Avian navigation*, pp. 68-74. Springer-Verlag. Berlin.
- GRANDÍO, J. M. 1997. Sedimentación y fenología otoñal de tres especies de currucas (*Sylvia spp.*) en el extremo occidental del Pirineo. *Ardeola*, 44: 163-171.
- GRANDÍO, J. M. 1999. Migración postnupcial diferencial del Carricerín Común (*Acrocephalus schoenobaenus*) en la marisma de Txingudi (N de España). *Ardeola*, 46: 171-178.
- HOLMES, R. T., SHERRY, T. W. and REITSMA, L. 1989. Population structure, territoriality and overwinter survival of two migrant warbler species in Jamaica. *Condor*, 91: 545-561.
- KOKKO, H. 1999. Competition for early arrival in migratory birds. *Journal of Animal Ecology*, 68: 940-950.
- LEAL, A., MONRÓS, J. S. and BARBA, E. 2004. Migration and wintering Blackcaps *Sylvia atricapilla* in Eastern Spain. *Ardeola*, 51: 345-364.
- LECOQ, M. and CATRY, P. 2003. Diurnal tape-luring of wintering Chiffchaffs results in samples with biased sex ratios. *Journal of Field Ornithology*, 74: 230-232.
- LOCKWOOD, R., SWADDLE, J. P. and RAYNER, M. V. 1998. Avian wingtip shape reconsidered: wingtip shape indices and morphological adaptations to migration. *Journal of Avian Biology*, 29: 273-292.
- LÖVEI, G. L. 1983. Wing shape variations of Chiffchaffs on autumn migration in Hungary. *Ringing & Migration*, 4: 231-236.
- MARTIN, A. 1996. The use of primary abrasion on ageing Siskins *Carduelis spinus*. *Ringing and Migration*, 17: 33-35.
- MÖNKKÖNEN, M. 1995. Do migrant birds have more pointed wings?: a comparative study. *Evolutionary Ecology*, 9: 520-528.
- NEWTON, I. 1972. *Finches*. Collins. London.
- NEWTON, I. 2008. *The migration ecology of birds*. Academic Press. London.
- PASCUAL, J. and SENAR, J. C. 1996. What are different biometric measures of avian body size measuring? *Bulletí GCA*, 13: 1-8.

- PASCUAL, J. and SENAR, J. C. 1997. La medición del tamaño corporal en aves. *EtoloGuía*, 15: 9-16.
- PODULKA, S., ROHRBAUGH, R. W. and BONNEY, R. 2004. *Handbook of bird biology*. Cornell Lab. of Ornithology. New Jersey.
- RUBOLINI, D., SPINA, F. and SAINO, N. 2004. Protandry and sexual dimorphism in trans-Saharan migratory birds. *Behavioural Ecology*, 15: 592-601.
- SENAR, J. C., LLEONART, J. and METCALFE, N. B. 1994. Wing-shape variation between resident and transient wintering Siskins *Carduelis spinus*. *Journal of Avian Biology*, 25: 50-54.
- SENAR, J. C. and PASCUAL, J. 1997. Keel and tarsus length may provide a good predictor of avian body size. *Ardea*, 85: 269-274.
- STUTCHBURY, B. J. 1994. Competition for winter territories in a Neotropical migrant: the role of age, sex and color. *Auk*, 111: 63-69.
- SVENSSON, L. 1998. *Guía para la identificación de los Passeriformes europeos*. SEO/BirdLife. Madrid.
- TELLERÍA, J. L., ASENSIO, B. and DÍAZ, M. 1999. *Aves Ibéricas. II. Paseriformes*. J. M. Reyero (Ed.). Madrid.
- WINKLER, H. and LEISLER, B. 1992. On the ecomorphology of migrants. *Ibis*, 134: 21-28.

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