Ornis Fennica 103: 25–35. 2026. Special issue on Euro-African Flyways.

Morphological differentiation of breeding and migratory Linnets *Linaria cannabina* in eastern Spain

Juan Arizaga*, Salvador Escamilla, Joan Castany, Ana M. Barragan, Rafael Silvestre, Pascual Timor, Benjamín Pupla, Gerardo Arzo & Batiste Borrás

J. Arizaga, Department of Ornithology, Aranzadi Sciences Society, Zorroagagaina 11, 20014 Donostia, Spain
S. Escamilla, J. Castany, A.M. Barragan, R. Silvestre, P. Timor, B. Pupla, G. Arzo, B. Borrás, Grup Au d'Ornitologia, C/ Padre Ten 6, E12200 Honda (Castellón), Spain
** Corresponding author's email: jarizaga@aranzadi.eus*

Received 28 May 2025, accepted 27 November 2025

This paper aims to assess whether breeding and migratory populations of Linnets (*Linaria cannabina*) in eastern Spain show morphological differentiation and whether migration timing correlates with morphometric traits. For that, we collected biometric data from over 4,000 Linnets captured in breeding sites and at coastal migratory stopovers in Castellón, Spain. We used Principal Component Analyses and General Linear Models to test for differences across age, sex, breeding status and season. Morphological traits varied significantly between first- and second-calendar-year birds, especially feather and skeletal measurements. Migratory individuals showed a larger body size (compatible with a more northern origin according to Bergmann's Rule), proportionally higher and wider bills (which might reflect geographical trophic preferences), and a higher wing-tail ratio (compatible with a longer migration distance like morphology). Within each migration season, birds passing later tended to have traits associated with a more northern origin, suggesting population-level differences in migration phenology. Morphometric variation in Linnets reflected both migratory strategy and passage timing, highlighting the utility of biometric analyses for understanding migration dynamics and population structure in passerines.

1. Introduction

Morphological analyses are essential for understanding the adaptive response and evolutionary drivers shaping populations in varying ecological aspects (Mönkkönen 1995, Grant & Grant 1996, Tellería & Carbonell 1999, von Cramon-Taubadel 2019). By examining physical traits, it is possible to infer the roles of different environmental pressures, migratory behavior or genetic divergence, among many other stressors. This approach is of particular importance in studies on bird populations, where morphological differences often reflect adaptations to distinct life histories and environmental challenges.

Migrant species, or populations, show morphological traits adapted to improve flight efficacy, including a relatively longer, more

VERTAISARVIOITU
KOLLEGIALT GRANSKAD
PEER-REVIEWED
www.tsv.fi/tunnus

CC BY

pointed wings (Mönkkönen 1995) as well as a shorter tail (Tellería & Carbonell 1999). The examination of such traits has permitted the differentiation between migrant and resident bird populations (Pérez-Tris *et al*. 1999), or inferring differential migration patterns in terms of timing of passage for populations with presumably different origin (Arizaga *et al*. 2009, Arizaga & Barba 2011, Andueza *et al*. 2013).

The Linnet (*Linaria cannabina*), a small finch distributed across temperate Palaearctic latitudes (Collar *et al*. 2010), is a species showing a broad range of migratory strategies, with populations from higher latitudinal and altitudinal origin being strict migrants, whilst those from lower latitudes being partial migrants or resident (Newton 1972). The morphology of the species has been described mostly in northern Europe (Cramp & Perrins 1994), but very poorly across the south range of its distribution area, including Spain (but see Arizaga *et al*. 2017).

Eastern Spain is a region with an abundant Linnet population breeding at medium- to high-altitudes across the mountain chains parallel to the Mediterranean coastline (Molina *et al*. 2022). At the same time the region constitutes an important migratory corridor, being de facto one of the main flyways used by Linnets leaving (spring) or entering (autumn) Spain (Asensio 1987, Arizaga *et al*. 2022, Franks *et al*. 2022). The non-breeding distribution of Linnets in Spain is very extensive and dispersed, with higher concentrations through the western edge of the Pyrenees and the Ebro Valley, the Mediterranean façade, Madrid and the most thermic regions of southern Spain. The origin of these birds covers a broad geographic range, from western-central Europe (excluding the Atlantic area from France to Scotland) to Poland and southern Scandinavia (Franks *et al*. 2022).

Using data collected on both breeding and non-breeding (migratory) Linnets passing through several localities in eastern Spain, we aimed to:

1. Describe the morphology of the Linnet population breeding in this area. Apart from obtaining basic descriptive statistics, we tested for the effect of capture date on feather abrasion and other possible skeletal changes. Feather abrasion should hypothetically result in decreasing wing and tail length with the increasing age of the birds (Alonso & Arizaga 2006).
2. Evaluate the use of morphological traits to distinguish individuals of a breeding population from migrants passing through eastern Spain. It is here expected that, as compared to a breeding southern European population, migrants coming from northern Europe should exhibit larger body size as well as a higher wing-tail ratio, which is compatible with a longer-distance migration (Fiedler 2005).
3. Identify the existence of a possible gradient of passage of Linnets from potential different origin regions, with northernmost populations passing through eastern Spain later than southern ones. This should be detected by progressively increasing mean values associated with longer-distance migration-linked traits (such as increasing mean wing length, wing-tail ratio, *etc*.) (Arizaga *et al*. 2009, Förschler & Bairlein 2010, Arizaga & Barba 2011).

2. Materials and methods

2.1. Study area and data collection

This study was carried out at several sites located across the Castellón province, eastern Spain,

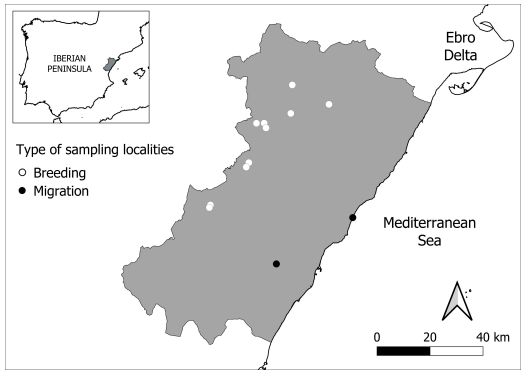

Fig. 1. Sampling localities in the Castellón province, Spain.

Table 1. Results from univariate GLM ANOVAs controlling for sex and age, conducted to determine the effect of 'abrasion', using age codes EURING 3 and 5 as a surrogate, on morphological traits of a Linnet breeding population in Castellón (Spain). P3: third primary feather.

	Age		Sex	
	F	*P*	*F*	*P*
Wing	18.0	<0.001	2309.0	<0.001
P3	13.3	<0.001	1374.1	<0.001
Tail	39.8	<0.001	360.4	<0.001
Tarsus	3.6	0.026	12.3	<0.001
Nalospi	5.4	0.020	5.8	0.016
Head+Bill	7.0	<0.001	159.1	<0.001
Head	1.0	0.374	38.2	<0.001
Bill length	7.1	<0.001	17.3	<0.001
Bill width	2.6	0.110	1.8	0.175
Bill depth	8.3	0.004	4.7	0.032

selected to take samples from both breeding and migratory Linnets (Fig. 1). Breeding localities were situated in a mountain area with ranges mainly following a northeast-southwest axis through the western border of the province. Landscapes in this zone comprises a Mediterranean mosaic of mountain dry pastures with scattered Mediterranean vegetation, olive and other Mediterranean groves, small cereal crops and woodlands of Holm Oak *Quercus ilex*, Black Pine *Pinus nigra* or Prickly Juniper *Juniperus oxycedrus*. The localities selected for capturing migratory Linnets were situated relatively close to the coast (Fig. 1) and the dominant vegetation here is comprised by a generally degraded landscape with orchards, some cereal fields or tree groves, together with scattered natural wetland patches, within an intensively urbanised matrix of towns and tourist complexes along the coast. The sites where migratory Linnets were captured are not used by local breeding birds, which avoid the coast, selecting the previously described mountain areas to breed.

Field work was done during the breeding period (mostly from July to September) and during the migration in the spring (March–April) and autumn (October–November). During migration seasons the fieldwork was conducted daily (Arizaga *et al*. 2022). Due to migratory phenology of Linnets arriving outside Spain (detected from October to March/April) (Asensio 1987) and the detailed knowledge of this species' Spanish breeding populations, it can be assured that Linnets captured during summer did not include migratory individuals.

Linnets were captured using clap nets (the system has 2 symmetric nets), covering a total surface of 24 × 3.4 m (Bub *et al*. 1996). To attract the Linnets to the net we used a sound lure playing male song, together with individually-caged live Canary decoys showing a colour pattern similar to a wild Linnet. This is the only feasible method to capture wild Linnets within the region in relatively sufficient numbers, particularly to attract and trap these birds on active migration (Arizaga *et al*. 2022). It is unknown to us whether these decoys might have an effect on the sex and age ratios of the captures but this effect should not have any impact on our study since the statistical models on biometrics controlled for the effect of these two factors (see below for details).

Once captured, Linnets were ringed with metal ring (Aranzadi ringing scheme) and their sex and age determined (Svensson 1996). Birds were aged as first-years (birds in their first year of life, assigned the EURING age code 3 in autumn, 5 in spring, and identified due to retained juvenile feathers in their wings and tail) or adult –birds- (EURING age codes 4 in autumn – hatched before current calendar year, 6 in spring/breeding – hatched before last calendar year; with plumage showing a single generation of feathers). After that, the following morphological variables were measured (Svensson 2023): wing length, P3 (3rd primary feather, numbered ascendently), tail length, tarsus length, nalospi (minimum distance between the nostril and bill tip), combined head and bill length, head length, and bill length, width and depth. Birds were measured by only two ringers who also passed a training regimes in

order to be standardized with each other, achieving an accuracy of 0.5 mm for wing and tail measurements (feather-related variables), and of 0.1 mm for the skeletal measurements (tarsus, head and bill variables).

2.2. Statistical analyses

To describe the breeding population we used univariate General Linear Models (GLM)—ANOVA—on each morphological variable, with sex and age class as fixed, additive factors without interactions. Given the very low number of captures of birds older than two-years (aged as EURING 3 or 5: $n = 4034$; aged as EURING 4: $n = 35$), the analysis was limited to Linnets in their first year of life, caught before their first complete moult, which is undergone during the second summer of life (Jenni & Winkler 1994), *i.e.* individuals aged as EURING 3 and 5.

To compare the migrant (autumn and spring passages) and breeding Linnet populations, we conducted GLM on morphological traits obtained from Principal Component Analyses (PCA; see below for details on how the PCA were conducted), with sex and period (either breeding *vs*. autumn or breeding *vs*. spring) as factors, with interactions. These GLM were constrained to birds in their first calendar year, due to the extremely low number of captures of adults for the breeding population. To control for the effect of abrasion (see Results for further details), we selected data from birds aged as EURING 3 for the breeding-autumn comparison, and as EURING 5 for the breeding-spring comparison. To obtain components that summarised the main axes of variation of morphological traits, we conducted PCA. The PCA with the nine variables (head+bill length excluded as it does not add more information than head and bill length considered separately) showed that: (1) the component one (PC1) showed positive factor loadings for all variables (Appendix 1), making it a component linked to size; (2) PC2 showed high, positive loadings associated with bill length, and high but negative loadings for the rest of bill measures, so positive values of this component were associated with proportionally longer, slender bills, while negative values were associated with proportionally shorter but taller and wider bills, as well as a larger head; (3) PC3 also associated with bill size and structure related variables, but in the opposite direction to PC2. Even though this PC3 captured information somewhat different from that of PC2, it could be redundant to some extent, and thus we excluded it from the analysis. Moreover, we conducted a

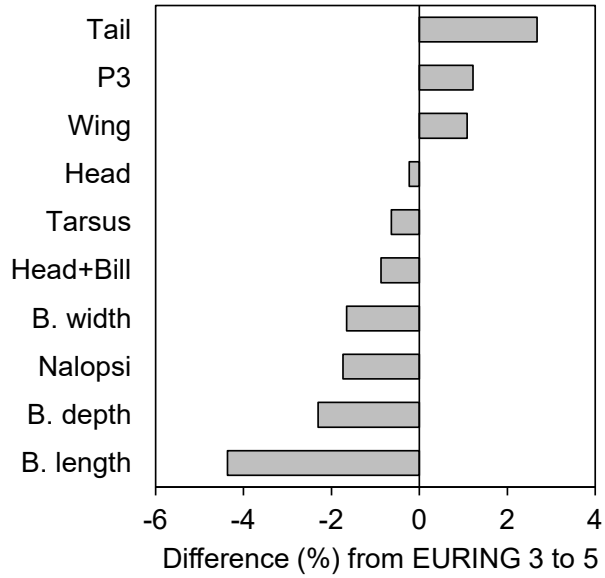

Fig. 2. Mean difference (in percentage) of each variable as recorded in first-calendar (EURING code 3) and second-calendar year (EURING code 5) of Linnets in their first year of life, caught before their first complete moult which is undergone during the summer of their second year of life. Sexes have been averaged for each age category. Positive values indicate that a variable is longer in first-years, whilst negative values indicate the contrary.

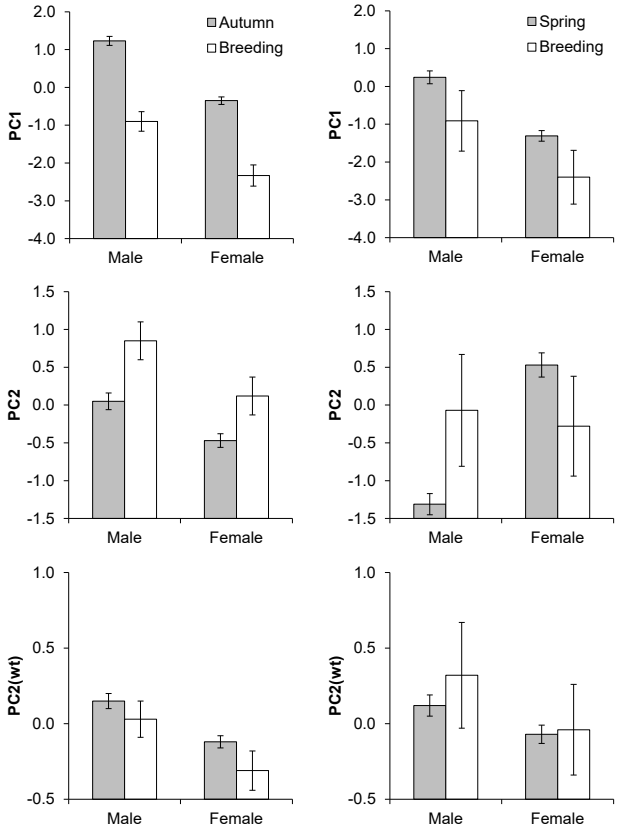

Fig. 3. Seasonal morphological differences (mean ± 95% confidence interval) of Principal Components (PC) used as proxies of body size (PC1), bill structure (PC2) or wing-tail ratio ($PC2_{wt}$) of Linnets during passage (autumn and spring) and during the breeding period in Castellón, eastern Spain.

second PCA with the aim of obtaining a variable that may summarise the flight apparatus (in terms of a wing-tail ratio). This second PCA with wing and tail length showed a PC1 indicating size, and a PC2 indicating a proportionally longer wing as compared to tail length (Appendix 2). Accordingly, we used this PC2 ($PC2_{wt}$) as a wing-tail ratio index. Once the two PCAs were conducted, we used the PC1 and PC2 from the main PCA, and the PC2 from the wing-tail PCA ($PC2_{wt}$) as object variables within the GLM.

Finally, in order to analyse the morphological variation through each passage period (*i.e.*, how morphology varied though migratory seasons), we built GLM with age, sex and an additive effect of date on the PC1, PC2 and the $PC2_{wt}$ as object variables. Note that in this case we also included adults aged as EURING 4 in autumn, or EURING 6 in spring within the analysis.

All statistical analyses were done in R (R Core Team 2023), using the basic statistical tools (packages) together with the additional package 'MASS' (Venables & Ripley 2002).

3. Results

3.1. Breeding population

All morphological traits except head length and bill width varied significantly between age classes (Table 1; for statistics see Table 2), highlighting that caution must be paid when individuals aged as EURING 3 and 5 lump

Table 2. Morphological traits (mean ± 95% confidence interval, range; all measures are in mm) of a Linnet breeding population in Castellón (Spain). Sample sizes are shown in parenthesis (*n*) below sexes for each age category.

	First-year (EURING code: 3)		Second-year (EURING code: 5)	
	Male (*n* = 1997)	Female (*n* = 1861)	Male (*n* = 108)	Female (*n* = 68)
Wing	80.1 ± 0.1 (73.5-86.0)	77.8 ± 0.1 (72.5-84.5)	79.0 ± 0.3 (74.5-83.5)	77.1 ± 0.5 (73.0-82.5)
P3	61.7 ± 0.1 (51.5-68.0)	59.9 ± 0.1 (52.5-66.5)	60.8 ± 0.4 (56.0-67.0)	59.3 ± 0.5 (56.0-64.0)
Tail	54.4 ± 0.0 (47.5-64.5)	53.2 ± 0.1 (47.0-64.0)	52.9 ± 0.3 (47.5-58.0)	51.8 ± 0.6 (47.0-58.0)
Tarsus	15.7 ± 0.0 (12.7-18.0)	15.7 ± 0.1 (13.3-17.5)	15.8 ± 0.1 (14.5-17.1)	15.8 ± 0.1 (14.6-17.0)
Nalospi	8.0 ± 0.0 (7.0-9.5)	8.0 ± 0.0 (7.0-8.9)	8.2 ± 0.1 (7.1-8.7)	8.1 ± 0.1 (7.2-8.8)
Head+Bill	26.3 ± 0.0 (23.1-28.8)	26.0 ± 0.1 (21.0-27.7)	26.5 ± 0.1 (25.4-27.4)	26.3 ± 0.2 (24.8-27.4)
Head	12.6 ± 0.0 (10.5-17.7)	12.5 ± 0.1 (10.2-15.6)	12.7 ± 0.2 (10.1-14.8)	12.5 ± 0.2 (10.1-13.6)
Bill length	13.6 ± 0.1 (9.6-16.5)	13.3 ± 0.0 (9.0-16.0)	14.1 ± 0.1 (12.8-15.9)	13.9 ± 0.1 (13.1-15.9)
Bill width	6.0 ± 0.0 (5.3-6.8)	5.9 ± 0.0 (5.3-6.9)	6.2 ± 0.1 (5.8-6.6)	6.0 ± 0.1 (5.5-6.4)
Bill depth	6.7 ± 0.0 (5.9-7.2)	6.6 ± 0.0 (6.0-7.1)	6.9 ± 0.1 (5.9-7.4)	6.7 ± 0.0 (6.5-7.1)

together for comparative morphological analyses. Compared to second-calendar-year (EURING 5), first calendar-year birds (EURING 3) showed longer feather-related measurements (varying from +2.6% in tail length to 1.0% in wing length), but shorter skeletal-related measurements (varying from -0.2% in head length to -4.4% in bill length; for details see also Fig. 2).

3.2. Comparison between migrant and local breeding populations

Once controlled for a sex effect, the Linnet population breeding in Castellón differed morphologically from Linnets passing through this region both in autumn and spring (Table 3). In autumn, passing Linnets showed a significantly larger body size, proportionally higher and wider bills and higher wing-tail ratios than their counterparts caught during breeding period (Fig. 3). In spring, such differences were detected to be significant only for body size (Fig. 3).

3.3. Seasonal variation during migration

Once controlled for age and sex effects, linear models showed that, in autumn, Linnets with a longer and higher wing-tail ratio and a larger body size tended to pass later than those showing shorter wings, lower wing-tail ratios and a smaller body size (Table 4). In spring, we obtained a similar pattern for the wing-tail ratio, but the opposite for body size. In addition, models also revealed that Linnets with slender, more pointed bills passed later within spring (Table 4).

4. Discussion

This research paper provides new insights into the morphological traits of Linnet populations breeding and passing through eastern Spain (Castellón province), a key flyway for this species, during the autumn and spring migration (Asensio 1984, 1987, Franks *et al*. 2022). The examination of different biometric measurements

Table 3. Results from GLM used to test for the effect of sex and periods (used here as population surrogates) on morphological traits summarised with components (PC1, PC2 and $PC2_{wt}$ from a wing-tail PCA) from Principal Component Analyses (Appendix 1). Sex-period interactions were non-significant for all models so they have been removed from the table.

	Sex		Period	
	F	*P*	*F*	*P*
Breeding - Autumn (EURING 3)				
PC1	394.7	<0.001	381.4	<0.001
PC2	76.8	<0.001	52.3	<0.001
$PC2_{wt}$	66.9	<0.001	10.2	0.001
Breeding - Spring (EURING 5)				
PC1	190.8	<0.001	16.3	<0.001
PC2	21.0	<0.001	2.8	0.092
$PC2_{wt}$	16.6	<0.001	0.7	0.392

across different life stages and seasons revealed consistent patterns of morphological differentiation linked to age, sex, and migratory status.

Firstly, morphological analysis of a breeding Linnet population revealed differences in first calendar-year birds captured at the beginning and end of their first year of life (*i.e.*, aged as EURING 3 and 5, respectively). In particular, as expected, we observed a shortening of feather length related variables, attributable to wear (Alonso & Arizaga 2006, Neto & Correia 2012). But, additionally, changes in skeletal measures were observed. All such skeletal variables were, to a greater or lesser extent, shorter in younger birds. These changes, therefore, suggest that the skeletal structures of Linnets, particularly in head and bill, grow during this first year of life. The underlying causes of such changes are unknown to us: these could simply be associated with a developmental process, but they might also represent an ontogenic adaptation beyond the embryonic stage that could confer advantages associated with the species trophic ecology. These findings entail that the capture date can be a relevant factor to consider when detailed morphological comparisons are conducted.

Moreover, we also detected clear, significant morphological differences between the Linnets captured at their breeding sites in Castellón and those captured in active migration, both in autumn and spring. Migratory individuals, presumably originating from northern Europe (Asensio 1987), showed longer wings, a higher wing-tail ratio, as well as a larger body size than breeding ones. Whereas a larger body size is linked with higher latitudes following Bergmann's Rule, a longer wing and higher wing-tail ratio would be classically be associated with longer-distance migration (Mönkkönen 1995, Fiedler 2005), and support the hypothesis that selection pressures linked to flight efficiency have shaped distinct morphotypes between populations showing different migration distances (Förschler & Bairlein 2010).

These differences between Linnets with presumably different migration distances also emerged when we analysed morphological traits through each migratory period. It must be highlighted here, however, that we had no additional data to unequivocally link the observed morphology with migratory distances, which would demand correlating biometrics with recoveries of birds of known origin, stable isotopes (Hobson *et al*. 2004) or geolocation (Röseler *et al*. 2017). In this regard, it is true that the scientific evidence accumulated from studies with mainly other passerine birds is consistent with the fact that, within a species, a higher wing-tail ratio is correlated with individuals with longer migration distances (Tellería & Carbonell 1999, Fiedler 2005, Förschler & Bairlein 2010). Strictly speaking, we should refer to terms like longer-distance-like *vs*. shorter-distance-like morphotypes. According to ring-recovery data analyses (Franks *et al*. 2022), more longer-distance-like migrants passing through eastern Spain could originate from areas such as Scandinavia and the northern part of Germany or Poland, whereas shorter-distance-like migrants could originate from areas located further south across a NE-SW axis connecting Scandinavia with eastern Spain.

In autumn, birds captured later within the season were larger and had on average longer,

Table 4. Results (Beta-parameter estimates ± SE, *P*-values in parenthesis) from GLM used to test for the effect of sex, age and date on morphological traits of Linnets passing through eastern Spain during the autumn and spring migration. PCA meanings: PC1 correlates positively with body size, PC2 with a proportionally more pointed bill, $PC2_{wt}$ with wing pointedness.

Dependent variable	Date	Sex[1]	Age[2]	Sex-Age interaction
Autumn				
Wing length	+0.04 ± 0.01 (<0.001)	-2.44 ± 0.10 (<0.001)	+1.10 ± 0.16 (<0.001)	-0.33 ± 0.23 (0.150)
PC1	+0.02 ± 0.01 (<0.001)	-1.60 ± 0.08 (<0.001)	+0.75 ± 0.12 (<0.001)	-0.22 ± 0.17 (0.192)
PC2	+0.01 ± 0.01 (0.055)	-0.44 ± 0.08 (<0.001)	+0.18 ± 0.12 (0.104)	+0.05 ± 0.16 (0.730)
$PC2_{wt}$	+0.01± 0.00 (<0.001)	-0.26 ± 0.04 (<0.001)	-0.01 ± 0.06 (0.885)	+0.04 ± 0.08 (0.613)
Spring				
Wing length	+0.00 ± 0.01 (0.668)	-3.32 ± 0.30 (<0.001)	-1.56 ± 0.25 (<0.001)	+0.98 ± 0.34 (0.004)
PC1	-0.02 ± 0.01 (<0.001)	-2.16 ± 0.24 (<0.001)	-1.05 ± 0.20 (<0.001)	+0.56 ± 0.26 (0.031)
PC2	+0.02 ± 0.01 (0.001)	-0.72 ± 0.24 (0.002)	-0.32 ± 0.19 (0.098)	+0.30 ± 0.26 (0.254)
$PC2_{wt}$	+0.01 ± 0.00 (0.028)	-0.20 ± 0.10 (0.064)	-0.06 ± 0.08 (0.443)	+0.00 ± 0.11 (0.980)

Reference values for sex and age (Beta = 0): [1]Sex: male; [2]Age: first-year birds.

more pointed wings, traits compatible with a more northern origin. Our results suggest, therefore, that northern Linnets pass through the western Mediterranean region later than their southern counterparts also entering to Iberia in autumn. This result reveals a pattern that, due to sample size constraints, remained unsolved in a classical ring-recovery data analyses (Asensio 1987). The passage of more northern migrants as the autumn migration season advances has been also reported in other passerine birds (Arizaga & Barba 2011), including other close-relatives, like the goldfinch *Carduelis carduelis* (Arizaga *et al*. 2009). Causes explaining this presumably population- or origin-associated differential passage might include that, (1) due to warmer climatic conditions, southern populations have an advanced breeding period, and therefore they can leave their breeding areas and start the autumn migration before their northern counterparts; (2) in addition, they also travel a shorter distance to arrive in Spain, so even leaving their breeding sites at similar periods, they would pass over the Mediterranean coast before their northern counterparts.

In spring, the same relationship was found for wing pointedness, suggesting a recurring pattern of morphological sorting across the season. However, the patterns was not so clear for other traits, including wing length or body size (which indeed showed a reversed trend with birds captured later in the season having on average a smaller body size). It remains unclear, therefore, that in spring presumably northern migrants would pass also later within the season.

Overall, our results confirm that morphological analyses are a powerful tool to explore population structure and migration dynamics in small passerine birds that can be captured in large numbers during migration period. The presence of distinct morphotypes across the season, independently of variation between age and sex classes, reveals both ecological and evolutionary underlying processes that shape variation among Linnet populations. Moreover, the observed morphological gradients in migration timing provide further support for population- or origin-associated differential

migration patterns. Future studies combining genetic or tracking data with morphology could validate these inferences and deepen our understanding of the mechanisms underlying these observed patterns.

Morfologinen erilaisuus pesivien ja muuttavien hemppojen (*Linaria cannabina*) välillä itäisessä Espanjassa

Tämän tutkimuksen tavoitteena on selvittää, esiintyykö pesivien ja muuttavien hemppopopulaatioiden (*Linaria cannabina*) välillä itäisessä Espanjassa morfologista erilaisuutta ja korreloiko muuton ajoittuminen morfometrisiin piirteisiin. Tätä varten keräsimme yli 4000 hempon biometriset tiedot pesimäalueilta ja rannikon muuton levähdysalueilta Castellónissa, Espanjassa. Käytimme pääkomponenttianalyysejä ja yleisiä lineaarisia malleja testataksemme eroja iän, sukupuolen, pesinnän vaiheen ja vuodenajan mukaan. Morfologiset piirteet vaihtelivat merkittävästi ensimmäisen ja toisen kalenterivuoden lintujen välillä, erityisesti höyhen- ja luustomitoissa. Muuttavat yksilöt olivat kooltaan suurempia (yhteensopivaa pohjoisemman alkuperän kanssa Bergmannin säännön mukaan), niillä oli suhteellisesti korkeammat ja leveämmät nokat (mikä saattaa heijastaa maantieteellisiä trofiatason ravintoeroja) sekä suurempi siipi–pyrstömittasuhde (yhteensopivaa pidemmän muuttomatkan morfologian kanssa). Kunkin muuttojakson sisällä myöhemmin muuttavat linnut olivat taipuvaisia omaamaan piirteitä, jotka liittyvät pohjoisempaan alkuperään, mikä viittaa populaatiotason eroihin muuton fenologiassa. Hemppojen morfometrinen vaihtelu heijasti sekä muuttostrategiaa että muuttoajankohtaa, mikä korostaa biometrisen analyysin hyödyllisyyttä muuttodynamiikan ja populaatiorakenteen ymmärtämisessä varpuslinnuilla.

Acknowledgements. We are grateful for the one-time financial contributions received from the town councils of Vilafranca and Vistabella del Maestrat for maintaining the feeding stations. Likewise, during the breeding season, the support of non-ringing group members who took charge of supplying these stations with turnip rape was very important. Jaume Gil Saura, Jorge Colomer Marín, and Víctor Jiménez Naranjo at the Vistabella del Maestrat station, and Ximo Fabregat Fortanet, Héctor Prades Andrés, and Albert Prades Monfort at the Vilafranca station. We also extend special thanks to the large group of fellow ringers from the Grup Au and colleagues who joined us in several field sessions. Thanks as well to the SEPRONA and the environmental agents from the zones where the field work was carried out. Two anonymous referees, the Associate Editor and the Editor-in-Chief provided very valuable comments that helped us to improve an earlier version of this work.

Conflict of interest. The authors report no conflicts of interest.

Author contributions. J. Arizaga: Conceptualization, Data analysis, Writing, Review & Editing, Supervision. S. Escamilla: Conceptualization, Field work, Review & Editing. J. Castany: Conceptualization, Field work, Writing, Review & Editing, Supervision. A.M. Barragan: Field work, Review & Editing. R. Silvestre: Field work, Review & Editing. P. Timor: Field work, Review & Editing. B. Pupla: Field work, Review & Editing. G. Arzo: Field work, Review & Editing. B. Borrás: Field work, Review & Editing.

References

Alonso D. & Arizaga J. 2006: Biometrics of Citril Finch *Serinus citrinella* in the West Pyrennes and the influence of feather abrasion on biometric data. — Ringing & Migration 23: 116–124. https://doi.org/10.1080/03078698.2006.9674354

Andueza M., Barba E., Arroyo J.L., Feliu J., Greño J.L., Jubete F., Lozano L., Monrós J.S., Moreno-Opo R., Neto J.M., Onrubia A., Tenreiro P., Valkenburg T., Zumalacárregui C., González C., Herrero A. & Arizaga J. 2013: Connectivity in Reed Warblers *Acrocephalus scirpaceus* between breeding grounds in Europe and autumn stopover sites in Iberia. — Ardea 101: 133–140. https://doi.org/10.5253/078.101.0208

Arizaga J., Andueza M. & Fernández B. 2017: Morfología de aves paseriformes nidificantes en Navarra y regiones limítrofes. — Sociedad de Ciencias Aranzadi, Donostia. (In Spanish)

Arizaga J. & Barba E. 2011: Differential timing of passage of populations of migratory Blackcaps (*Sylvia atricapilla*) in Spain: evidence from flight-associated morphology and recoveries. — Ornis Fennica 88: 104–109. https://doi.org/10.51812/of.133768

Arizaga J., Cuadrado J.F. & Romero L. 2009: Seasonal individual and population-associated patterns of migration of goldfinches *Carduelis carduelis* through the western edge of Pyrenees. — Ardeola 56: 57–69.

Arizaga J., Escamilla S., Castany J., Barragán A.M., Timor P., Silvestre R., Rebollo A., Adelantado J., Pupla B. & Cantos A. 2022: Flock structure and phenology of migration of the Common Linnet *Linaria cannabina* through eastern Spain. — Ringing & Migration 37: 63–72. https://doi.org/10.1080/03078698.2023.2242051

Asensio B. 1984: Migración de aves fringílidas (Fringillidae) a base de resultados de anillamiento. — Ediciones de la Universidad Complutense, Madrid. (In Spanish)

Asensio B. 1987: Migración en España del Pardillo Común (*Carduelis cannabina*, L.). — Miscelania Zoologica 11: 347–352. (In Spanish with English summary)

Bub H., Hamerstrom F. & Wuertz-Schaefer K. 1996: Bird Trapping & Bird Banding. — Cornell University Press, USA.

Collar N.J., Newton I. & Clement P. 2010: Family Fringillidae (Finches). — In: Del Hoyo J., Elliot A. & Christie D.A. (eds). Family Fringillidae (Finches). Lynx, Barcelona, pp. 440–617.

von Cramon-Taubadel N. 2019: Multivariate morphometrics, quantitative genetics, and neutral theory: Developing a "modern synthesis" for primate evolutionary morphology. — Evolutionary Anthropology 28: 21–33. https://doi.org/10.1002/evan.21761

Cramp S. & Perrins C. M. 1994: Handbook of the Birds of Europe, the Middle East and North Africa. Vol. 8. — Oxford University Press, Oxford.

Fiedler W. 2005: Ecomorphology of the external flight apparatus of Blackcaps (*Sylvia atricapilla*) with different migration behavior. — Annals of the New York Academy of Sciences 1046: 253–263. https://doi.org/10.1196/annals.1343.022

Förschler M. I. & Bairlein F. 2010: Morphological shifts of the external flight apparatus across the range of a passerine (Northern Wheatear) with diverging migratory behaviour. — Plos One 6: e18732. https://doi.org/10.1371/journal.pone.0018732

Franks S., Fiedler W., Arizaga J., Jiguet F., Nikolov B., van der Jeugd H., Ambrosini R., Aizpurua O., Bairlein F., Clark J., Fattorini N., Hammond M., Higgins D., Levering H., Skellorn W., Spina F., Thorup K., Walker J., Woodward I. & Baillie S.R. 2022: Online Atlas of the movements of Eurasian-African bird populations. — EURING/CMS. https://migrationatlas.org/

Grant B. S. & Grant P. R. 1996: High survival of Darwin's Finch Hybrids: effects of beak morphology and diets. — Ecology 77: 500–509. DOI: 10.2307/2265625

Hobson K., Bowen G., Wassenaar L., Ferrand Y. & Lormee H. 2004: Using stable hydrogen and oxygen isotope measurements of feathers to infer geographical origins of migrating European birds. — Oecologia 141: 477–488. https://doi.org/10.2307/2265625

Jenni L. & Winkler R. 1994: Moult and ageing of European passerines. — Academic Press, London.

Molina B., Nebreda A., Muñoz A. R., Seoane J., Real R., Bustamante J. & Del Moral J.C. 2022: III Atlas de aves en época de reproducción en España. — SEO/BirdLife, Madrid. https://atlasaves.seo.org/ (In Spanish)

Mönkkönen M. 1995: Do migrant birds have more pointed wings?: a comparative study. — Evolutionary Ecology 9: 520–528. https://doi.org/10.1007/BF01237833

Neto J. M. & Correia E. 2012: Biometrics and sub-specific identification of white-spoted bluethroats *Luscinia svecica cyanecula* and *L. s. namnetum* during autumn. — Ardeola 59: 309–315. http://dx.doi.org/10.13157/arla.59.2.2012.309

Newton I. 1972: Finches. — Collins, London.

Pérez-Tris J., Carbonell R. & Tellería J.L. 1999: A method for differentiating between sedentary and migratory Blackcaps *Sylvia atricapilla* in wintering areas of southern Iberia. — Bird Study 46: 299–304. https://doi.org/10.1080/00063659909461142

R Core Team. 2023: R: A language and environment for statistical computing. — R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Röseler D., Schmaljohann H. & Bairlein F. 2017: Timing of migration, routes and wintering grounds of a short-distance diurnal migrant revealed by geolocation: a case study of Linnets *Carduelis cannabina*. — Journal of Ornithology 158: 875–880. https://doi.org/10.1007/s10336-017-1450-y

Svensson L. 1996: Guía para la identificación de los paseriformes europeos. — Sociedad Española de Ornitología, Madrid. (In Spanish)

Svensson L. 2023: Identification Guide of European Passerines. — Lullula Förlag, Stockholm.

Tellería J. L. & Carbonell R. 1999: Morphometric variation of five Iberian Blackcap *Sylvia atricapilla* populations. — Journal of Avian Biology 30: 63–71. https://doi.org/10.2307/3677244

Venables W.N. & Ripley B.D. 2002: Modern Applied Statistics with S (4th edition). — Springer, New York. https://doi.org/10.1007/978-0-387-21706-2

Appendix 1

Factor loadings of the Principal Components (PC) obtained from a Principal Component Analysis on nine morphological measures of both breeding and non-breeding (migratory) Linnets.

	PC1	PC2	PC3
Wing	+0.492	+0.246	+0.129
P3	+0.458	+0.272	+0.175
Tail	+0.413	+0.284	+0.195
Tarsus	+0.295	-0.014	-0.153
Nalospi	+0.270	-0.233	+0.003
Head	+0.222	-0.473	+0.460
Bill length	+0.062	+0.462	-0.544
Bill width	+0.267	-0.370	-0.471
Bill depth	+0.305	-0.394	-0.403
Eigenvalue	2.946	1.654	1.366
Variance (%)	32.7	18.4	15.2

Appendix 2

Factor loadings of the Principal Components (PC) obtained from a Principal Component Analysis on wing and tail length of both breeding and non-breeding (migratory) Linnets.

	PC1	PC2
Wing	+0.707	+0.707
Tail	+0.707	-0.707
Eigenvalue	1.630	0.371
Variance (%)	81.5	18.5