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Flock structure and phenology of migration of the Common Linnet *Linaria cannabina* through eastern Spain

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ABSTRACT

The main goal of this study was to describe in detail the structure and phenology of flocks of the Common Linnet (*Linaria cannabina*) passing through eastern Spain. Data were compiled during the spring and autumn migrations of 2019 to 2021 (excluding spring 2020), by counting and by capture for ringing. We counted 6151 flocks, comprising 17 732 birds, of which 7638 individuals were captured. The size of flocks ranged from 1 to 30 Linnets (mean ± 95% CI, 2.8 ± 0.1), with a higher proportion of solitary migrants in spring (46.8%) than in autumn (33.8%). Passage in spring peaked during the third hour after dawn, whilst in autumn this peak was just after dawn. There were more females than males (56%), probably as an indicator of latitudinal differential migration. Juveniles were significantly more abundant (c. 80%) than adults. The phenological pattern of the passage was more variable in spring than in autumn, and such variation could be useful to explore potential impacts of climate change on the migration ecology of the species.

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active migration; differential migration; finches; Iberia; phenology; ringing; sex and age ratios

In birds, sex and age classes can differ in the proportions of each that migrate, the timing of migration and distances travelled. Distances travelled give rise to spatial segregation between the sexes or age classes in winter, with one sex or age group overwintering closer to breeding quarters, in a phenomenon common to many taxa and known as differential migration (Kettersson & Nolan 1983). A good understanding of this phenomenon, including possible differential patterns in active migration, is crucial because the conservation status of migratory bird populations depends on circumstances experienced at both their breeding and non-breeding areas (Newton 2004).

The Mediterranean coastline of eastern Spain constitutes one of the main European migratory corridors, as it channels the flow of millions of birds of a broad range of taxa breeding in Europe, as they access the Iberian Peninsula through the eastern edge of the Pyrenees and follow a mainly northeast–southwest axis of migration (Bairlein 2001, Galarza & Tellería 2003, Newton 2008, Gargallo *et al* 2011, Andueza *et al* 2013, Arizaga *et al* 2015). Studies on bird migration along this corridor, therefore, can contribute to a better understanding of bird migration patterns in this part of Europe.

Finches are typically diurnal as migratory species, normally in flocks (Newton 1972, 2008), which often show differential migration distances, with females overwintering further south than males (Cristol *et al* 1999). Information from the non-breeding season generally derives from ring-recovery data (Asensio 1985a, 1985b, 1986, Wernham *et al* 2002, Bønløkke *et al* 2006, Bairlein *et al* 2014), or from flocks ringed at their wintering sites (Senar *et al* 1994, Arizaga *et al* 2009, 2012). The active migration ecology of finches still remains largely unknown in many parts of Europe, however; in contrast to other passerine birds that migrate at night and are caught at their stopover sites during the day (Chernetsov 2012), finches are captured insufficiently often by the standard approach based on constant-effort mist netting.

The Linnet (Common Linnet, *Linaria cannabina*) is a passerine species broadly distributed from western Europe and northwest Africa to the Middle East and central Asia north to Mongolia, avoiding the boreal region and the very arid zones of the Middle East and Kazakhstan (Collar *et al* 2010). European populations vary from resident to partially migrant or migratory, with migration mostly along a northeast–southwest axis; parallel migration patterns are evident, such that winter ranges indicate breeding ones (Spina *et al* 2022). Thus,

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birds from northwest and western Europe, including western Scandinavia, move southwestwards to southern France and Iberia, with some reaching Morocco (Röseler *et al* 2017). Birds from eastern Scandinavia and central and eastern Europe overwinter from eastern Iberia and southern France to Italy (Asensio 1987, Cramp & Perrins 1994). Huge numbers of Linnets enter Spain through the Mediterranean corridor (Tellería *et al* 1999), providing an excellent opportunity to investigate their passage while on active migration.

The main goal of this study was to describe in detail the flocking behaviour of Linnets passing through eastern Spain, in terms of flock structure and phenology, using data compiled over three consecutive pairs of autumn and spring passages. This is the first study of these characteristics in Spain and, to the best of our knowledge, in Europe as a whole.

Material and methods

Study area and data collection

This study was carried out at Sitjar Baix in the municipality of Onda, Castellón province, eastern Spain (39.98°N 1.95°W). The Common Linnet does not breed in this municipality or its surroundings (JC pers obs), and so all birds passing over the site are migrants.

Fieldwork was conducted on a daily basis during the spring and autumn passages, March–April and October–November (Tellería *et al* 1999), from 2019 to 2021. Due to the Covid19 pandemic, however, sampling during spring 2020 had to be curtailed in mid-March.

The sampling protocol was to count all the flocks seen passing over the sampling site, assigning each flock a code, and to capture the flocks whenever possible, using ground traps specifically designed for finches. We defined a flock as every group with a maximum separation of 10 m between individuals, including solitary birds that met this criterion.

The sampling team always held at least two people: one for counting, and another for catching, being a ringer with an official licence provided by the Aranzadi Ringing Scheme. Quite often, there were up to three additional helpers, either to relieve the counter or assist the ringer, especially on days when many captures were expected. Fieldwork sessions started at dawn, defined as the exact moment of sunrise, and lasted five hours. A longer sampling period was not logistically possible; overall, we estimate that with this effort we covered roughly 25–50% of the Linnets passing over the sampling site.

Counts were made by single skilled individuals with years of experience of observing the passage of Linnets within the region. Because flocks passing over the sampling site were attracted using lures, birds were counted by direct visual contact, without additional equipment like binoculars or a telescope. Overall, we estimate that the detection radius of such flocks was *c* 200 m around the observer.

Captures were made with a set of two symmetrical clap nets, covering a total area of 24 x 3.4 m (Bub *et al* 1996), together with a sound lure playing male song. Close to this trap we positioned three live, captive-bred decoys, under the appropriate permits for ringing and scientific permits issued by the Government of Valencia; each bird was confined in an individual cage. We have found that this method is the only effective technique for calling birds down from passing flocks during migration. Once captured, all the Linnets were kept in keeping bags, with the birds from each flock segregated until they could be processed, after which they were immediately released. Captured Linnets were ringed and their sex and age was determined (Svensson 1996): birds aged as juveniles, or found to be in their first year of life due to retained juvenile feathers in their wings and tail, were assigned EURING age codes of 3 in autumn and 5 in spring; older birds, with plumage showing a single generation of feathers after undergoing a complete moult and lacking contrast between old juvenile and newer adult feathers, were given EURING age codes 4 in autumn or 6 in spring. After ageing and sexing, we also took a number of morphological measurements which have not been used in this work.

Statistical analyses

Due to a Covid19 lockdown preventing fieldwork, and to avoid possible biases associated with a clearly truncated data set, the data from spring 2020 were removed from most analyses.

We analysed in detail the characteristics of the flocks and their passage over the sampling site. First, we conducted a chi-squared test to determine whether, overall, the proportion of single-bird flocks varied significantly between the two seasons (spring and autumn). Second, we constructed generalised linear models (GLMs) with flock size as a binary object variable (0 single, 1 two birds or more), year and period of passage as factors, and date or a quadratic effect of date as a covariate, with binomial distribution of the error and a logit-link function. The Akaike criterion (AIC) was used to decide whether a GLM considering a linear or a quadratic effect of the date fitted the data better (Burnham & Anderson 1998).

Models differing in less than 2 AIC values were considered to fit the data equally well (Akaike 2011).

There was a very strong and significant correlation between the number of flocks seen in a day and the number of individual Linnets counted, both in spring and autumn (spring r = 0.92, df 102, $P < 0.001$; autumn r = 0.90, df 142, $P < 0.001$). Thus, and because the phenology of the passage comprises individuals rather than flocks, analyses hereafter use every individual bird, and not the flock, as the object variable.

To analyse whether the numbers of Linnets passing over the sampling site through the morning varied between the autumn and spring periods, we used a chi-squared test on a contingency table on hour after sunrise, by period. Thereafter, we built GLMs on daily bird counts, with year and date or the quadratic effect of date as independent variables, for autumn and spring separately due to the lack of data in spring 2020. We tested alternative models considering either an additive effect or an interaction between year and date. Alternative approaches using non-linear, generalised additive models (GAMs) were also tested (Maggini *et al* 2020). Again, models were compared using their AIC values.

Finally, we analysed the structure of the flocks in relation to their age and sex proportions. For both age and sex, we conducted a chi-squared test to determine whether the proportion of ages or sexes varied significantly between spring and autumn, and built GLMs using age or sex category as a binary object variable (0 for juvenile or female; 1 for adult or male), year and period of passage as factors, and date or a quadratic effect of date as a covariate, with binomial distribution of the error and a logit-link function. Again, models were compared using their AIC values. Due to the lack of data in the spring of 2020, we conducted the GLMs for autumn and spring separately.

Results

During three consecutive campaigns in the springs and autumns of 2019–21, omitting spring 2020, we counted 6151 flocks, comprising 17 732 birds, of which we were able to capture 7638 individuals (43.1%; Table 1).

Flock behaviour and structure

The size of the flocks ranged between one and 30 Linnets (mean ± 95% CI, 2.8 ± 0.1 Linnets). The proportion of single-bird 'flocks' was very high in spring (46.8%), and slightly but significantly lower in autumn (33.8%, $\chi^2 = 72.7$, df 1, $P < 0.001$). A more detailed analysis revealed that single-bird 'flocks' were statistically more likely in spring, in 2021, and also at the beginning and the end of the passage within each season (Table 2, Figures 1 & 2).

In spring, the number of flocks that passed over the sampling site in a single day ranged from one to 51 (mean ± 95% CI, 15.4 ± 2.6 flocks), and in autumn between one and 95 (33.8 ± 3.2 flocks).

Phenology

The number of Linnets passing over the sampling site tended to decrease through the morning, though hourly patterns varied significantly between the two seasons ($\chi^2 = 1347.0$, df 4, $P < 0.001$; Figure 3). In spring the passage peaked during the third hour after dawn, whilst in autumn this peak was during the first hour after dawn.

Both migrations were characterised by subsequent waves of passage that gave rise to several relative peaks within each season (Appendix 1). Overall, it can be seen that the main peak of passage appeared to differ by year, both in spring and autumn. However, the median date of passage did not vary significantly between 2019 and 2021 for spring (unpaired Wilcoxon W = 917.5, df 1, $P = 0.4892$) or for autumn (Kruskal–Wallis $\chi^2 = 4.30$, df 2, $P = 0.116$). More elaborate statistical models showed that, in spring, the passage had a better fit to a linear model using a quadratic effect of date (Table 3), with this model predicting that the mean number of birds counted per day varied annually (lower in 2021 than 2019; beta parameter ± SE -2.49 ± 0.99, $P = 0.015$), almost marginally with the date (date: +0.07 ± 0.06, $P = 0.288$; date^2 = 0.00 ± 0.00, P = 0.074), and without interaction between the year and the quadratic effect of date (all P values

Table 1. Initial and final sampling dates, grand totals and daily means ± 95% confidence interval for numbers of flocks and of Linnets counted, and numbers of captures, with their percentage of the grand total of the Linnets counted. per season and year.

	First date	Last date	Flocks	Birds counted	Captures
Spring					
2019	10 March	24 April	529, 16.0 ± 4.3	1286, 39.0 ± 11.2	402, 31.3%
2020	1 March	20 March	298, 17.5 ± 4.6	546, 32.1 ± 10.2	264, 48.4%
2021	3 March	23 April	759, 14.9 ± 3.3	1844, 36.2 ± 9.5	845, 45.8%
Autumn					
2019	7 October	24 November	1659, 36.9 ± 6.1	5180, 115.1 ± 27.5	2172, 41.9%
2020	1 October	24 November	1750, 33.7 ± 5.4	5374, 103.3 ± 22.4	2351, 43.8%
2021	3 October	22 November	1454, 30.9 ± 4.9	4048, 86.1 ± 17.2	1868, 46.2%

Table 2. Beta-parameter estimates from a binomial model predicting flock size (0 = 1 bird; 1 = >1 bird) of Linnets passing over the sampling site in eastern Spain. Overdispersion: 1.00.

	beta	SE (*beta*)	*P*
Year: 2020*	-0.11	0.07	0.115
Year: 2021	-0.30	0.06	<0.001
Period: spring*	-0.46	0.06	<0.001
Date	+0.06	0.01	<0.001
Date^2	-0.00	0.00	<0.001

*Reference *beta* values (*beta* = 0): autumn 2019.

>0.05) (Figure 4). In autumn, however, the passage had a better fit to non-linear additive models rather than to linear models (Table 3). GAMs showed a significant effect of year (with fewer birds counted in 2021 than in 2019 or 2020; effect of 2020 referred to 2019, -0.03 ± 0.10, $P = 0.776$; effect of 2021, -0.36 ± 0.10, $P < 0.001$) and date (smooth term 6.95, $P < 0.001$) (Figure 4).

Age and sex ratios

Overall, the proportion of each sex did not differ between the spring and autumn periods ($\chi^2 = 0.06$, df 1, $P = 0.825$: females 56.2% in autumn and 55.8% in spring). By contrast, the proportion of each age category did differ between the two periods ($\chi^2 = 7.14$, df 1, $P = 0.008$; first-year birds 85.0% in spring and 81.8% in autumn).

A more detailed analysis revealed that the sexes had equal catching probabilities, with no effect in relation to period, year and date (Table 4; Appendix 2a). The probability of being an adult was always low, ranging from <0.1 to *c* 0.3 (Figure 5). This probability, in addition, varied significantly in relation to period, year and date. It tended to be higher in autumn than in spring, and higher in 2021 than in 2019 and 2020, also increasing with date within each period (Figure 5; but see details in Appendix 2b).

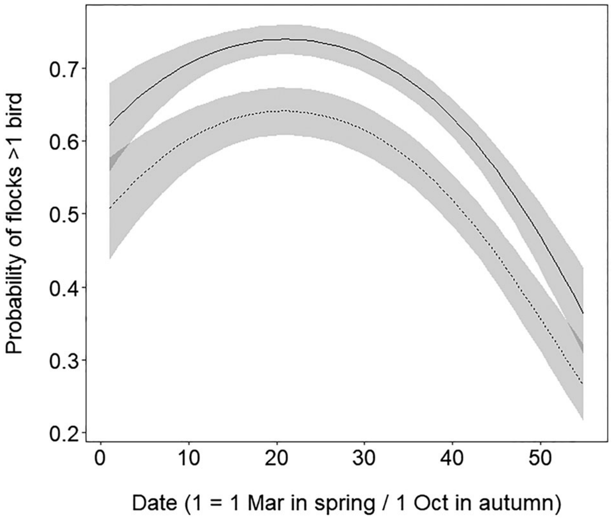

Figure 1. Predicted probability and its 95% CI (shaded) of flocks of more than one bird passing over the sampling site, in relation to a quadratic effect of date: dotted line, spring; solid line, autumn.

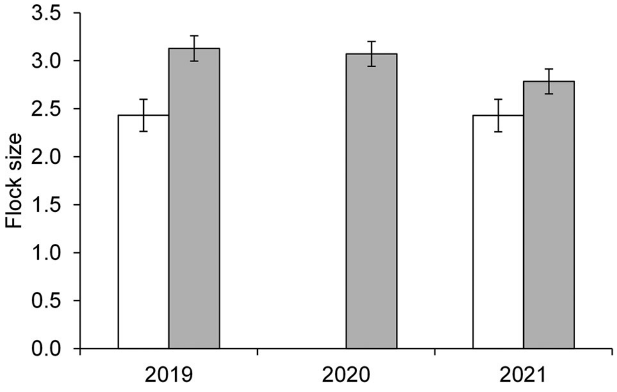

Figure 2. Flock size (mean ± 95% CI) of Linnets passing over a sampling site in eastern Spain during the spring and autumn migrations of 2019–21: spring, open bars; autumn, shaded bars. Observations in spring 2020 were curtailed by the Covid19 pandemic and are not shown.

The proportion of adults in single-bird flocks was higher in autumn than spring, and the proportion of males was higher in spring than autumn, though in neither season were the proportions of the sexes significantly different (Table 5).

Discussion

This is, to our knowledge, one of the few papers analysing the structure and phenological patterns of a small passerine bird during active migration through mainland Europe (Newton 1972, Schekkerman 1999, Arizaga *et al* 2009, Scebba *et al* 2015).

Even though finches typically migrate in flocks, we observed that solitary birds were very common,

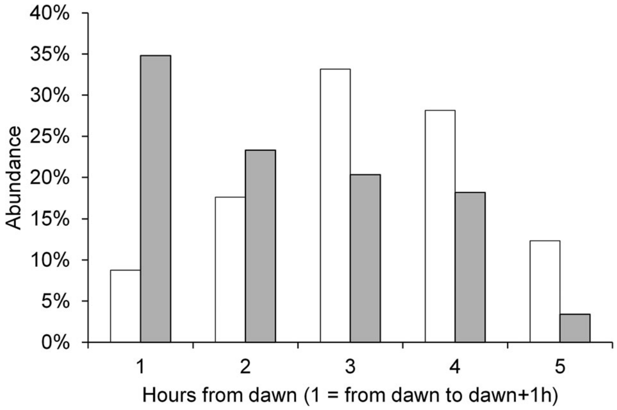

Figure 3. Percentages of Linnets passing over the sampling site in each of the first five hours after dawn, in spring (open bars) and in autumn (shaded bars).

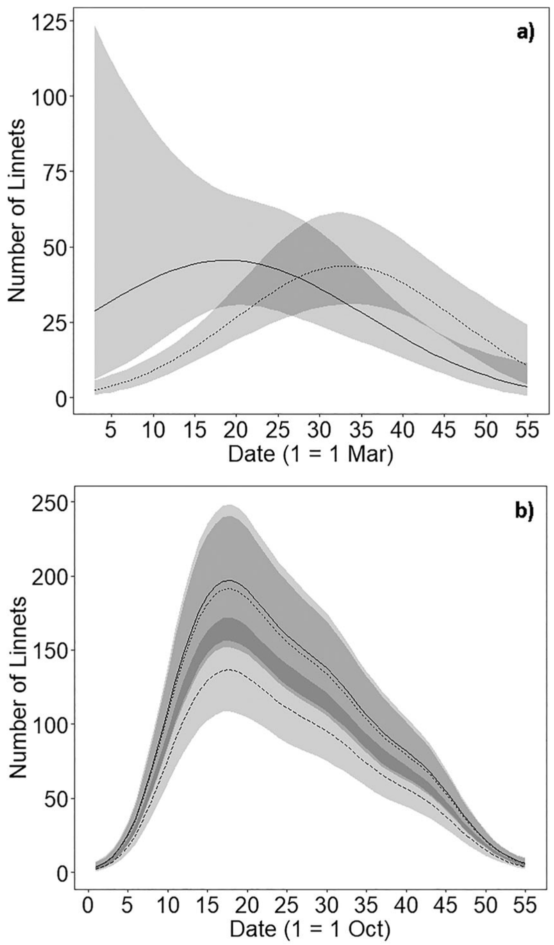

Figure 4. Predicted distributions, with 95% CI, of the number of Linnets passing over the sampling site in relation to date and year in (a) spring, as obtained from a linear model using a quadratic effect of date, and (b) autumn, from a generalised additive model using a smoothed term for date. (a) 2019, solid line; 2021, dotted line. (b) 2019, solid line; 2020, dotted line; 2021, broken line.

especially in spring and at the beginning and the end of the passage within each season. Furthermore, we must acknowledge that the detection probability decreases with distance to observer, and this decrease is likely to be more pronounced for solitary birds than flocks, so the proportion of single-bird 'flocks' could have been underrepresented. Yearly differences also emerged, with a higher proportion of single-bird flocks during spring 2021 than spring 2019. In part, this difference might be because we missed the start of migration in 2019 (Appendix 1). We also found that large flocks of Linnets were uncommon, given that a mean of up to 46.8% of flocks were single birds in spring and that the mean overall flock size was 2.8 birds. During days of intense passage, however, these small flocks were passing one after the other, and it is possible that, through calling behaviour, they might have been maintaining some degree of cohesion. The methodological approach in this work ignores the possibility of any nocturnal migration.

Table 3. General performance and fit to the data of Generalised Linear or Additive Models (GLM, GAM,) used to assess the effect of year and date (spring, autumn) on the number of Linnets passing over the sampling site per day. GLMs consider a quadratic effect of date on bird counts. In GLM, we also determined whether the effects of year and date were additive (year+date) or interactive (year×date).

	AIC	r^2	Overdispersion
Spring			
GLM year+date	227.90	0.29	0.82
GLM year×date	216.52	0.41	0.70
GAM year+date	218.16	0.38	0.69
Autumn			
GLM year+date	258.35	0.70	0.34
GLM year×date	262.78	0.71	0.34
GAM year+date	211.14	0.79	0.23

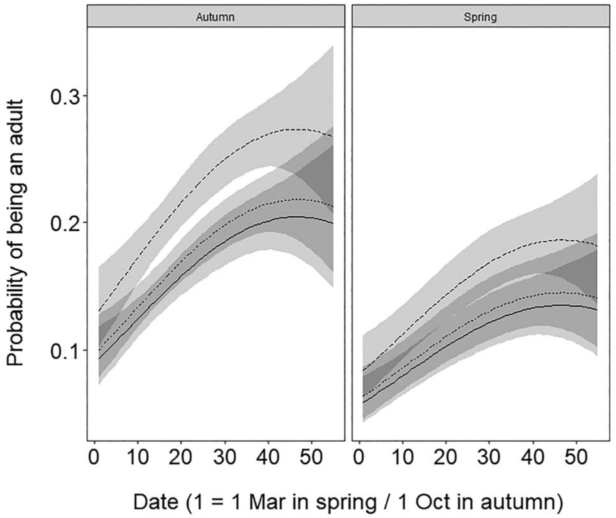

Figure 5. Predicted probability, with 95% CI, of being an adult Linnet passing over the sampling site in relation to date and year in spring and autumn, according to the model described in Table 4: 2019, solid line; 2020, dotted line; 2021, broken line. Note that results for spring 2020 are an artefact, because this passage was removed from the data set.

Table 4. Beta-parameter estimates from binomial models predicting the probability of a Linnet passing over the sampling site in eastern Spain being an adult or a male. Overdispersion: 1.00.

	beta	SE (*beta*)	*P*
Sex models			
Year: 2020*	-0.12	0.06	0.050
Year: 2021	-0.46	0.06	0.422
Period: spring*	-0.08	0.07	0.324
Date	+0.01	0.00	0.262
Date^2	-0.00	0.00	0.752
Age models			
Year: 2020*	+0.08	0.08	0.304
Year: 2021	+0.38	0.08	<0.001
Period: spring*	-0.50	0.09	<0.001
Date	+0.04	0.01	0.001
Date^2	-0.00	0.00	0.050

*Reference *beta* values (*beta* = 0): autumn 2019.

Table 5. Percentages of age and sex classes in relation to flock class of Linnets passing through eastern Spain during the autumn and spring migrations. Samples come from birds captured for ringing and assigned individually to the flocks from which they were lured.

	Flock class	Number of birds		Percentage	χ^2	*P*
Age classes		*Juvenile*	*Adult*	*% adults*		
Autumn	Single	676	237	26.0%	43.67	<0.001
	>1 bird	4493	910	16.8%		
Spring	Single	288	61	17.5%	2.38	0.128
	>1 bird	756	123	14.0%		
Sex classes		*Female*	*Male*	*% males*		
Autumn	Single	501	412	45.1%	0.80	0.390
	>1 bird	3049	2351	43.5%		
Spring	Single	182	168	48.0%	2.95	0.094
	>1 bird	505	375	42.6%		

That Linnets tended to aggregate into flocks more frequently in autumn could relate to several factors, for which we can advance some plausible hypotheses. Bird populations reach their maximum sizes after breeding (Newton 2013), and this may increase the chance for single birds to join a flock along the route. Alternatively, or additionally, flocks may have already formed in their breeding areas, being at least partly composed of family units, where offspring could remain cohesive with one or both parents (e.g. Alonso & Arizaga 2004). Through the winter, these flocks might disaggregate progressively. Furthermore, sexual selection in spring could stimulate males in particular to return to their breeding areas more rapidly (Kokko 1999), which would prioritise solitary strategies. It is also possible that Linnet populations passing through eastern Spain in autumn could have stopped over in large numbers in zones before reaching our sampling point, which could give rise to increasing flock sizes during autumn at our locality.

Overall, we captured more females (56%) than males, with no significant seasonal differences. We have no evidence to conclude that females were more likely to be attracted to lures than males, so the sex ratios of the captures may in principle be representative of the structure of the flocks passing over the area. Indeed, it has been found that males tend to be more attracted by lures (Schekkerman 1999), so that in such a case an underrepresentation of females would be expected. In theory, breeding populations show a balanced sex ratio and, therefore, a female-biased ratio should be interpreted as proof of latitudinal differential migration (Cristol *et al* 1999), with female Linnets migrating longer distances than males, so that in places more distant from the breeding areas the non-breeding population is female-biased (Asensio 1987). This result reinforces the importance of Iberia in southern Europe for the conservation of a significant part of female Linnets from the European population. The fact that the sex ratio was similar between the two periods of passage may suggest that there was no differential mortality between the two sexes in winter.

Juveniles (>80%) were much more abundant than adults, which might also suggest there is some latitudinal differential migration between the two age classes (Cristol *et al* 1999). Interestingly, the age ratio was even more biased towards juveniles in spring; this might be because adults departed from their wintering sites earlier than juveniles (Schwarzova *et al* 2010), and some had already passed through before our spring sampling started in March. Alternatively, or additionally, it is possible that some adult Linnets might take a different route in spring.

Our study also shows some variability between seasons and years, allowing the investigation of potential impacts on the migration ecology of the study species of factors like climatic warming. In this context, our findings indicate that the spring passage is more variable than that in autumn and, therefore, that it would be in this period where any impact might be more visible.

Another interesting aspect of our results is the difference in the daily pattern of captures between autumn and spring: in spring the peak was reached around mid-morning, not around dawn as in autumn. Since birds are under more pressure to return as soon as possible to their breeding areas in spring than to reach their wintering areas in autumn (Newton 2008), a possibility could be that in spring the urgency for them to return also leads to more hours a day being spent in flight. In addition, we cannot reject the idea that the main roosting area of Linnets heading north in spring is closer than the roosting area of those passing south in autumn.

In conclusion, Linnets migrating through eastern Spain tended to pass in rather small flocks or solitarily, especially in spring and at the beginning and the end of the passage within each season. Overall, we captured more females than males, probably as a consequence of latitudinal differential migration. Juveniles were significantly more abundant than adults. The phenological pattern of the passage was more variable in spring than in autumn, and such variation could be useful to explore the potential impacts of climate change on the migration ecology of this study species.

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Disclosure statement

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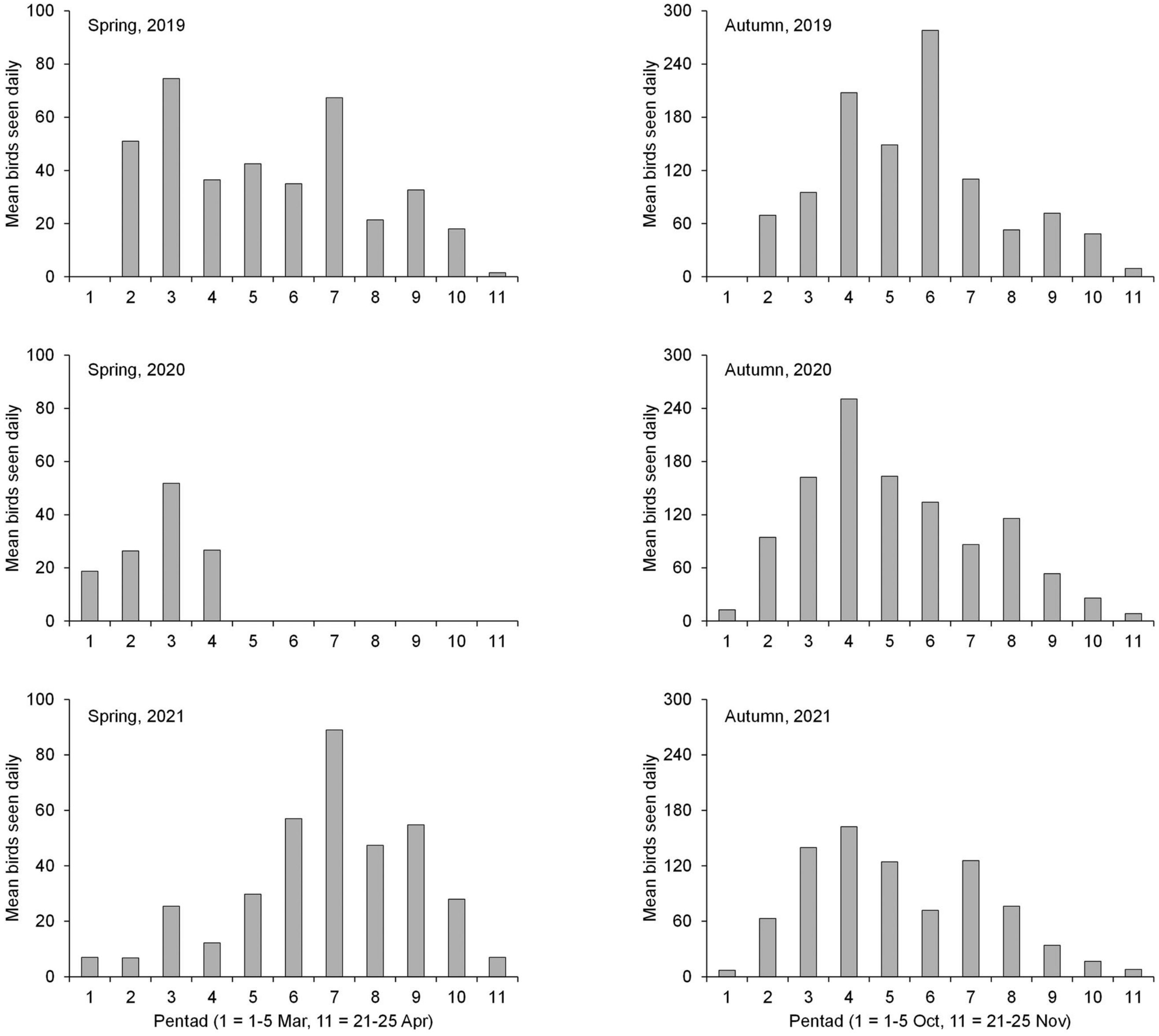
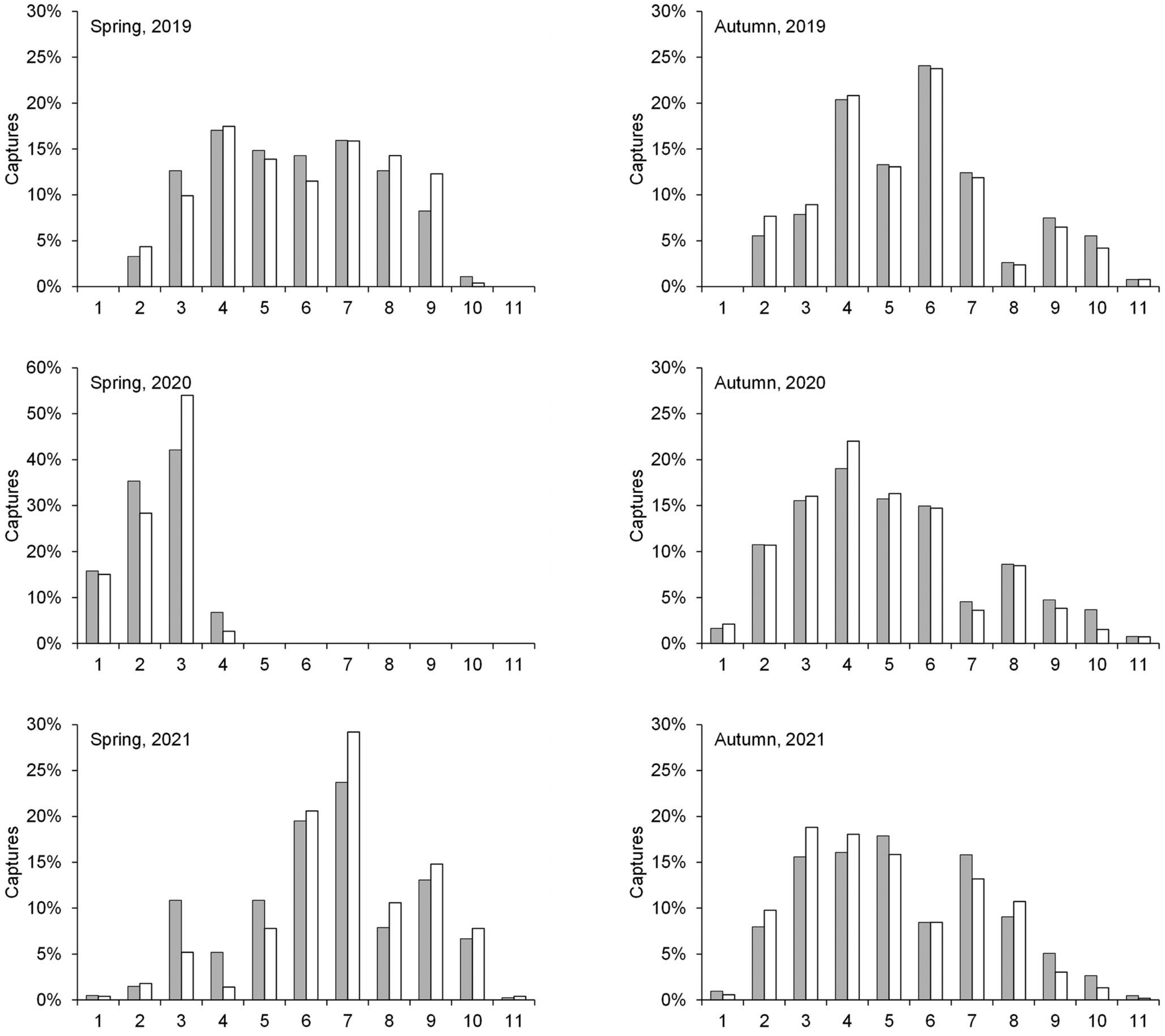
Appendix 1. Mean number of Linnets seen by period (pentad), season and year.



Appendix 2a. Percentage of captures in relation to sex: open bars, females; shaded bars, males. Pentads as in Appendix 1.



Appendix 2b. Percentage of captures in relation to age: open bars, adults; shaded bars, juveniles. Pentads as in Appendix 1.