

Protandry in a partially migrant population of the Stonechat (*Saxicola rubicola*): a field study in the central Apennines (Italy)

Steven Hueting

Abstract - Here I present the results of a 3-year field study on some aspects of spring migration in a partially sedentary population of the stonechat *Saxicola rubicola* in central Italy. By monitoring all suitable territories daily, including those occupied by resident pairs, I recorded the daily increase in the number of both sexes of stonechats in the study area.

As first-day sightings showed themselves to be insufficient to test protandry, the study demonstrates the existence of protandry in the stonechat in the field by calculating the daily male-to-female ratio of immigrant individuals, as typically done at ringing stations, and by analyzing the average arrival dates of males and females while correcting for a slightly male-biased detection.

Nevertheless, in apparent contradiction to the sex-biased arrival, about 40% of the stonechats arrived already paired in their breeding territories. For the first time, this fraction of stonechats arriving already paired on the breeding grounds, also reported by other authors, has been better analyzed and shown to be restricted to peak migration.

Additionally, the analysis of early male arrival and subsequent female mate acquisition suggested that any correlation was purely coincidental, in contrast with both the rank hypothesis and the mate opportunity hypothesis, proposed to explain the maintenance of protandry.

The discussion explores a hypothesis to reconcile these contradictory findings with the protandrous arrival of stonechats at the breeding grounds.

Key words: male-biased spring migration, pair arrival, male/female sex ratio, average arrival dates, first day sightings, breeding territories, mate choice, partially resident.

Riassunto - Protandria in una popolazione parzialmente migratrice del saltimpalo (*Saxicola rubicola*): uno studio sul campo nell'Appennino centrale (Italia).

Qui presento i risultati di uno studio sul campo della durata di tre anni su alcuni aspetti della migrazione primaverile in una popolazione parzialmente sedentaria di saltimpalo *Saxicola rubicola* nell'Italia centrale. Monitorando quotidianamente tutti i territori idonei, compresi quelli occupati da coppie residenti, ho registrato l'aumento giornaliero del numero di maschi e femmine di saltimpalo nell'area di studio.

Dato che le osservazioni del primo giorno di arrivo si sono rivelate insufficienti per testare la protandria, lo studio dimostra la protandria nel

saltimpalo sul campo calcolando il rapporto maschi-femmine giornaliero tra gli individui immigrati, come avviene tipicamente nelle stazioni di in-nellamento, e analizzando le date medie di arrivo di maschi e femmine, correggendo per una lieve maggiore rilevabilità dei maschi.

Tuttavia, circa il 40% dei saltimpali è arrivato già in coppia nei territori riproduttivi. Per la prima volta, questa frazione di saltimpali che giunge già accoppiata nei siti di riproduzione, segnalata anche da altri autori, è stata analizzata più approfonditamente e si è dimostrato che è limitata al picco della migrazione.

Inoltre, l'analisi delle date d'arrivo dei singoli maschi e le date dell'acquisizione di una compagna suggerisce che qualsiasi correlazione sia puramente casuale, in contrasto sia con la 'rank hypothesis' sia con la 'mate opportunity hypothesis', entrambe proposte per spiegare origine e mantenimento della protandria in specie migratorie.

La discussione esplora un'ipotesi per conciliare questi risultati contraddittori con la protandria del saltimpalo durante il suo ritorno nei siti di riproduzione.

Parole chiave: migrazione primaverile, protandria, arrivo in coppia, date medie di arrivo, date primi arrivi, 'mate choice', residenza parziale.

INTRODUCTION

Protandry, the phenomenon where males arrive at breeding grounds before females, is a well-documented aspect of migration in many animal species (Morbey & Ydenberg, 2001). In birds, particularly, protandry is widespread (Coppack & Pulido, 2009; Newton, 2023). Studies on bird migration, especially through ringing studies at stopover sites during spring migration, have consistently demonstrated the arrival of males of long-distance migrants before females (Rubolini *et al.*, 2004; Saino *et al.*, 2010; Newton, 2023). However, for short-distance migrants, the existence of differential spring arrival between sexes seems less evident. Their relatively short journey, early passage at stopover sites, and presence of resident conspecifics may distort ringing data at spring passage. More specifically, in the case of the Stonechat *Saxicola rubicola*, the few studies that consider protandry do not offer unequivocal results. Long-term ringing data from the Piedmont region in Italy between 1974 and 2016 suggest the existence of protandry with male stonechats arriving some 5 days earlier (Fasano *et al.*, 2018). In contrast, a 20-year ringing data survey (1983-2003) for the whole of Italy failed to provide evidence for protandry (Spina *et al.*, 1993). In this regard, it is worth noting that in central and southern Italy, stonechat populations are considered predominantly sedentary and elsewhere partially migratory

Tagliacozzo (AQ), Italy.

* Corresponding author: gshueting@gmail.com

© 2025 Steven Hueting

Received for publication: 28 November 2024

Accepted for publication: 13 June 2025

Online publication: 10 December 2025

(Brichetti & Fracasso, 2022), which may cause a bias in spring ringing data. An unknown proportion of the captured birds could be resident and not migratory, thus interfering with potential protandry. Moreover, as stonechats migrate very early, from the beginning of February onwards in central Italy, many ringing stations will not be active during the main passage of stonechats or with a frequency not sufficient to detect protandry as shown for another short-distance migrant, Blackcap *Sylvia atricapilla*, in northern Spain (Arizaga & Barba, 2009). For example, the ringing stations in four small islands along the Tyrrhenian coast started their activity on 16 March (Spina *et al.*, 1993), right at or after the peak of the spring migration of the stonechat (Spina & Volponi, 2008), when the earliest migrants have already passed over. Even with the recent anticipation of activity from these ringing stations up to 1 March, most of the adult male passages remain unintercepted (ANITA databank, Italian Bird Ringing Center, ISPRA). Consequently, their results failed to reveal potential protandry in the stonechat. Another factor masking protandry might be the provenience from different populations with different migration schedules (Newton, 2023), as suggested in ringing studies on the Wheatear *Oenanthe oenanthe* at a Mediterranean spring-stopover site (Maggini *et al.*, 2013). Therefore, to exclude the influence of different proveniences and migration schedules and obtain a clearer picture of protandry, only arrival times on the breeding grounds should be considered. For instance, in his field study on a breeding population near Minden, in central Germany, Ziegler (1966) found single male stonechats returning at their nesting site a few days before females, although 50% of the birds arrived already paired. Other observations of male-biased arrival at the breeding site in Germany were attributed to a major detectability of the male (Mildenberger, 1950), and were insignificant in Ukraine (Banik, 2019). In another 15-year study on a stonechat population near Cologne, in Germany, males appeared to arrive about five days earlier, though accuracy was low (Flinks *et al.*, 2008).

From another point of view, research on migratory restlessness (Zugunruhe) in captive stonechats has shown that in males, spring migratory restlessness starts 4.6 days earlier than in females, suggesting that they may begin spring migration earlier than females (Van Doren *et al.*, 2017; Justen *et al.*, 2022), potentially accounting for protandry at the breeding site. It would be rather surprising if this innate sex-biased start of migratory restlessness were not expressed in the wild. However, observation in the field of the dates of departure from the wintering grounds does not offer clear indications of protandry as expected from this laboratory study. Rödl observed that male stonechats left their wintering territories in Israel earlier in 1989 but later than females in 1990. In his study, nonetheless, the breeding territories and life histories of these individuals were unknown (Rödl, 1995).

Here, in central Italy, during the first 2 years of a long-term study on the phenology of the stonechat in a partially migratory population, I observed, albeit superficially, that males appeared to return from their wintering quarters before females at the onset of spring. Therefore, considering the above-described uncertainties, I decided to investigate the potential existence of protandry in this population of

the stonechat during the next three years. The species is particularly suitable for a similar study, even without ringing procedures, because it is sexually dichromatic (Cramp, 1988), philopatric (Ziegler, 1966) and usually forms pairs both in winter, during the breeding season and even at the stopover sites during migration (Johnson, 1961; Urquhart, 2002) with high mate fidelity at least within the same season. Thus, in autumn, the resident part of the population remains wintering in its breeding territories while the migrant portion abandons its territories that remain vacant during the following winter (see the following section). Assuming habitat characteristics remain relatively stable, aside from normal seasonal changes, immigrant birds in spring are expected to re-occupy the breeding sites vacated the previous autumn, though not necessarily by the same individuals. This allows observation of stonechat arrival dynamics, with special attention to potentially transient individuals that may occupy suitable breeding sites only temporarily. In case of protandry, I would expect an initially male-biased sex ratio at the population level and males arriving earlier than females, at least in the first occupied territories. Furthermore, to explain how protandry can be maintained, according to the mate opportunity hypothesis (Kokko, 1999; Morbey & Ydenberg, 2001; Kokko *et al.*, 2006), the first incoming females should mate with those males that occupied the first, and presumably best, vacant territories. The present study aims to test these hypotheses in the wild using systematic field observations.

MATERIALS AND METHODS

Study area

The study area in the Central Apennines is located at the valley floor of the northwestern part of the Palentine Plain, 750 m above sea level, between the S. Nicola-Faito Mountain ranges to the northeast and the Arunzo-Difesa chain to the southwest, with its center at 42°03'26"N, 13°19'27"E. It consists of 264 ha of farmland with homogeneously structured habitat characteristics typical of a mosaic agricultural landscape with traditional crop rotation practices (Fig. 1). The successive lots of land rarely exceed 2 ha, separated by irrigation ditches or small hedgerows creating suitable ecotones for feeding and nesting of the stonechat.

The Imele River, running parallel to the main survey route, traverses a significant portion of the study area. The partitioning of the fields is finely structured by irrigation ditches, hedges, and fences, creating parcels that typically range from 0.5 to 2.0 ha each, with a maximum size of 4 ha. This creates numerous environmental ecotones within a sequence of ploughed fields, freshly sprouted winter wheat, dried-out alfalfa, maize stubble, and dried-out wildflower and grass fields. The vegetation, where present, measures less than 20 cm in height, except for parts of the fallow land where it can reach up to 120 cm.

Study period

I conducted regular censuses in the three years 2022, 2023, and 2024 from December 1 to January 31 to quantify the resident wintering population, identify the location of wintering territories in the study area, and observe possible

shifts in numbers and location through this period. Starting from 1 February, I initiated daily surveys to quantify the exact number and sex of individuals present in the wintering territories at the time of the first arrivals of migrants returning to their breeding grounds, although in previous years, the first individuals never arrived before February 10. From the same date onwards, I also surveyed all the potential breeding territories with daily censuses until March 15, at the start of the breeding season for stonechats in the study area.

Study population

Preliminary investigations into the population dynamics of the stonechat in the study area, which commenced in 2019, revealed that the stonechat population here is partially resident, with a resident fraction increasing significantly from 45% in 2022 to 80% in 2024. Population density has stabilized since 2021, when 37 breeding pairs accounted for a population density of 1.4 pairs/10 ha. The breeding of 37 pairs in 2022, 39 in 2023, and 44 in 2024, after 3 mild winters without prolonged snow cover, suggests that the maximum population density sustainable by the study habitat should be around 1.5 pairs/10 ha. Breeding typically initiates after March 10, with the earliest females commencing nest construction by March 15 (Huetting S., unpublished data). The first young fledge towards the end of April. Three breeding cycles are rather common with numbers of recently fledged birds peaking in the second decade of May, the first decade of July, and the second decade of August. The last migrant stonechats leave the study area in the first days of November. During autumn migration in the years 2019-2023, I have never noticed territories to be re-occupied that previously had been abandoned by the migratory fraction of the population.

Survey protocol

I started daily monitoring of all suitable breeding territories of the partially resident stonechat population in central Italy in the three years 2022, 2023, and 2024, from February 1, towards the end of the wintering period, until March 15, marking the beginning of the breeding season. This included both vacant territories and those occupied by resident pairs.

As the stonechat is territorial on both breeding and wintering grounds, I performed data sampling according to the territory mapping procedure (Bibby *et al.*, 2000). To register the very date of arrival in the study area of each migrant individual of stonechat, I designed a 12 km-long non-continuous survey route along sparsely frequented paved and unpaved roads, enabling meticulous and efficient observation of all sections of the study area with suitable habitat characteristics. Riding slowly by car along the road, I made observation stops at 40 lookout posts along the survey route, indicated by yellow dots in Fig. 1. The observation points remained consistent throughout the entire study period.

The selection of each observation point was based on preliminary surveys of the area in the preceding years 2020 and 2021, conducted in both summer and winter. These revealed the population structure of the stonechat in the study area and the distribution of all existing and potential stonechat territories in winter and summer. Although the birds were unmarked, I presumed that the daily and continuous presence of the resident wintering pairs confined to their territories allowed for the identification of newly arriving birds in unoccupied territories as migratory individuals.

All 40 observation points provided excellent visibility in all directions with binoculars and a spotting scope, allowing for the simultaneous observation, where necessary, of two or more neighboring territories, including potential ones. Except for the rare bad weather conditions, the spotting scope allowed for adequate determination of both sexes from distances up to 300 m.

Based on years of experience with stonechat surveys, I did not rigidly standardize the observation time at each stop. Stonechats, especially freshly arrived individuals compared with wintering ones, are morphologically and behaviorally conspicuous and very mobile, moving with short and straight flights from one perch to another, where they manifest themselves by vigorous tail and wing flickering. These characteristics, combined with the low vegetation on flat land, allowed for the identification of all individuals present in the area investigated from each lookout within a short time, typically between 1 and 10 minutes. Thus, for example, the immediate identification of



Fig. 1 – Screenshot of satellite winter view of the study area with overlays, courtesy of Google Earth. Yellow dots indicate observation points. The white line indicates the study area circumference. / Screenshot della vista satellitare invernale dell'area di studio con sovrapposizioni, cortesia di Google Earth. I punti gialli indicano i punti di osservazione. La linea bianca delimita il perimetro dell'area di studio.

a known pair of resident winterers in their territory allowed more time to be spent detecting the potential presence of immigrants in vacant territories. Only in case of opportunities, such as windy conditions, or when individuals of neighboring territories had to be seen simultaneously, observation times were longer. The medium distance between the lookouts was 330 m. A typical day of surveying lasted from 9.00 to 14.00.

In the field, I recorded geolocalized positions of all detected individuals using the 'Naturalist' mobile phone application (Biolovision.net). I estimated distances between the GPS position of the lookout and the observed individuals by utilizing easily recognizable landmarks. After controlling and making any necessary corrections to all positions using Google Earth imaging on the desktop, the data have been stored on both the Ornitho.it platform (Biolovision.net) and an Excel worksheet.

I assigned freshly arrived birds to a territory empirically. In my experience, stonechat breeding territories in the study area have remained stable over the years. When a newly arrived individual settled in one of these territories and remained there throughout the successive parts of the study period, I designated that territory as occupied by that bird. Although not ringed, I assumed that the bird(s) that settled in the territory remained the same throughout the study period. Successive records of the birds' positions in the territory indicated its approximate extension and boundaries, which were then visualized on the Google Earth satellite map of the study area. After detecting the presence in one territory, I verified the simultaneous presence of the occupants of neighboring territories to avoid any bias in territory assignment. I identified new territories, not used as breeding territory in previous years, applying the same procedure.

To correct for male-biased detection, I estimated the average detectability difference between males and females by utilizing a large dataset of male and female sightings that should be obtained following the same survey protocol outlined in this study, focusing specifically on resident wintering pairs to ensure the concurrent presence of both sexes. I collected such data for another study during the winters of 2022-2023 and 2023-2024, from December 1 to February 10, and reported them in *Supplementary Tab. 1*. The observed average female/male (F/M) detectability ratio is 0.94.

I excluded from the database concerning protandry at the territory level those individuals observed in areas never occupied for breeding or wintering in previous years, and/or present only for one or two days. These transient birds, at the population level instead, presumably directed to nearby areas with similar migration schedules, do not introduce bias to potential protandry and will be included in the database for analyzing population-level protandry. Here, it is noteworthy that the combined effect of an increase in the resident population during the study period, saturation of suitable breeding sites, and philopatry of returning migrants born in the study area might result in an increase in transient bird numbers.

Survey weather conditions

All three winters were mild without prolonged snow cover (never more than one day), and day temperatures

never fell below 0°C. The days of the study period with appreciable rainfall were one in 2022, six in 2023 and eight in 2024 (data collected from www.3BMeteo.it). Weather conditions did not permit accurate surveys on just 3 days during the entire study period. I did not detect any exceptional 'fallout' of birds from any species due to weather conditions throughout the entire study period.

Data analysis

I compiled the daily increase of arrivals in a table, both raw and corrected for relative female detectability. I then tested for χ^2 using Excel's statistical analysis toolset (CHISQ.TEST function) in MS Office 15. Under the null hypothesis, the expected increase in the number of males and females was assumed to be equal; therefore, the total number of individuals arriving each day was divided equally between the two sexes. In the 2-table dataset, I corrected the number of observed females for female detectability, $F_{\text{corrected}} = F_{\text{observed}} * 1,06$ for each day and consequently for the expected individuals, $M_{\text{expected}} = F_{\text{expected}} = (M_{\text{observed}} + 1,06 F_{\text{observed}}) / 2$.

In the dataset that includes the transient birds in the whole study area, I further corrected the null hypothesis with the overall male/female (M/F) ratio = 1.31, calculated at the end of the study period by dividing all male immigrants observed by all female immigrants observed. The ratio might be overestimated because transient males cannot be excluded from being floating and might have been counted twice at different places. Therefore, I did chi-square tests for the dataset, both corrected and uncorrected for the M/F ratio. I used Julian days (with January 1 as 1) to represent arrival dates, calculating average arrival dates (period from Julian day 37 (February 6) until Julian day 72 (March 13)) by $(\sum_{J=37 \text{ to } 72} N_{Mj} * J) / N_{Mt}$ where N_{Mj} is number of males arrived on each Julian day, J the Julian day and N_{Mt} the total number of all males arrived in the study area during the study period. The analog formula for all females, single males, single females, and pairs. I did all calculations, both separately for the three study years and for the cumulative study period. Besides the assessment of protandry in the entire study population, I also recorded the difference in arrival time of both sexes in their breeding territories. Although I surveyed the study area daily, to improve clarity and ensure a statistically relevant sample size, Tab. 1 and Fig. 2 in the results section present the cumulative increase of males and females in consecutive five-day periods (pentads) rather than the daily pattern of increase.

RESULTS

The days of first sightings suggest the absence of protandry in 2022 and 2024, like reported by Banik (2019), but the numbers of males and females arrived on the day of first sighting impose further analysis (Tab. 2).

Like M/F ratios reported from ringing stations during spring passage of migratory birds, used to estimate protandry, Tab. 1 presents the average M/F ratios calculated for all the stonechat individuals that arrived in each of six consecutive 5-day periods in the whole study area. These values presumably were the same at the last stopover sites, preceding arrival in the study area, and clearly indicate protandry to exist.

Tab. 1 – Average proportion of male and female stonechats (male/female ratio) during successive periods of 5 days (pentads) of spring arrival in the study area in 2022, 2023, and 2024. / Proporzione media di maschi e femmine di saltimpalo (rapporto maschi/femmine) durante periodi successivi di 5 giorni (pentadi) di arrivo primaverile nell’area di studio negli anni 2022, 2023 e 2024.

Last Julian day of each pentad	2022			2023			2024		
	M	F	M/F	M	F	M/F	M	F	M/F
40	0	0	nd	0	0	nd	7	2	3.50
45	8	2	4.00	2	0	nd	3	1	3.00
50	12	6	2.00	1	0	nd	10	7	1.43
55	7	11	0.64	18	11	1.64	11	5	2.20
60	7	6	1.17	10	9	1.11	7	4	1.75
65	3	3	1.00	2	7	0.29	0	3	0.00
70	1	2	0.50	7	4	1.75	0	2	0.00
75	0	0	nd	0	3	0.00	0	0	nd

M, males; F, female; M/F, male/female ratio; nd not determined.

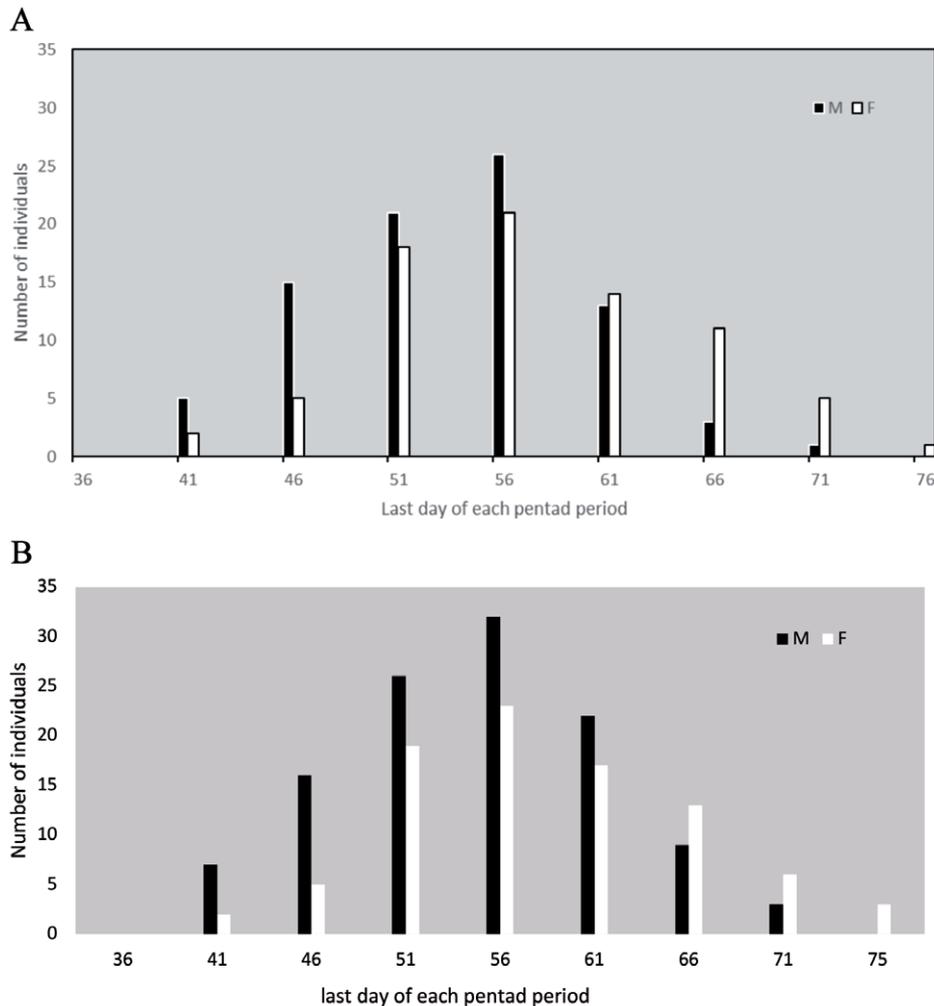


Fig. 2 – A) Cumulative arrivals (2022–2024) of male (M) and female (F) stonechats in their territories during successive 5-day fractions (pentads) of the immigration period in spring (test $\chi^2=0.03$). The number of individuals arriving during each pentad was recorded on the last Julian day of the pentad; B) cumulative arrivals (2022–2024) of M and F stonechats in the study area during successive 5-day fractions (pentads) of the immigration period in spring (test $\chi^2=0.06$). The number of individuals arriving during each pentad was recorded on the last Julian day of the pentad. / A) Arrivi cumulativi (2022–2024) di maschi (M) e femmine (F) di saltimpalo nei rispettivi territori durante frazioni successive di 5 giorni (pentadi) del periodo di immigrazione primaverile (test $\chi^2 = 0,03$). Il numero di individui arrivati in ciascuna pentade è stato registrato nell’ultimo giorno giuliano della pentade; B) arrivi cumulativi (2022–2024) di M e F di saltimpalo nell’area di studio durante frazioni successive di 5 giorni (pentadi) del periodo di immigrazione primaverile (test $\chi^2 = 0,06$). Il numero di individui arrivati in ciascuna pentade è stato registrato nell’ultimo giorno giuliano della pentade.

Interestingly, in each of the 3 years, the decline in the M/F ratio, following the arrival of the first females, is temporarily interrupted by a slight increase before male arrivals come to a complete halt. Although birds were not marked, and age is impossible to determine through plumage characteristics in the field, the pattern aligns with the widespread phenomenon of age differential arrival timing (from 3 to 6 days) observed in many bird species (Stewart *et al.*, 2002). Second-year, inexperienced birds tend to arrive later, when most breeding territories are already occupied by adult pairs (Newton, 2023). Accordingly, second-year males outnumber the last arriving adult females, causing an increase in the M/F ratio.

To quantify the amount of protandry, I calculated the average arrival dates of males and females in their respective territories and the corresponding statistical significance. As shown in Tab. 3, male-biased arrival amounts to about 4 days. Note that in 2022 and 2024, immigrant in-

dividuals were more than accounted for by the increase in territory numbers (pairs), due to resident territories occupied by a single individual at the start of immigration and subsequently joined by an immigrant mate. Similarly, including transient individuals, I calculated average protandry for all individuals arriving in the study area as reported in Tab. 4.

As expected, the pattern of average arrival dates remained unchanged but consistently shifted forward by 2 days. Significantly, the increasing difference in the number of immigrants (N) during the 3 study years is shown in Tabs. 3 and 4 (6, 14, 22, respectively), representing the transient birds, may reflect the earlier suggested combined effect of increasing residency, limited number of suitable breeding sites, and philopatry.

Further analysis of the average arrival dates revealed paired stonechats to arrive some 4 days later than single males but 2 days before single females (Tab. 5). The fraction

Tab. 2 – Day of first sightings of males and females and corresponding number of individuals in the study area in spring 2022, 2023, and 2024. / *Giorno delle prime osservazioni di maschi e femmine e corrispondente numero di individui presenti nell'area di studio nelle primavere 2022, 2023 e 2024.*

2022		2023		2024		Average day of first sighting		
Julian day	N	Julian day	N	Julian day	N	Julian day	Date	Sex
44	5	43	1	37	4	41,33	10-feb	M
44	1	52	4	37	1	44,33	13-feb	F

Julian day 1, 1 January; N, number of individuals.

Tab. 3 – Average arrival date of male and female immigrant stonechats in their territories, days of protandry, days of immigration, total number of immigrant individuals, and increase in the number of occupied breeding territories in springs 2022, 2023, 2024, and in the entire study period. Test χ^2 corrected for female visibility. / *Data media di arrivo di maschi e femmine di saltimpalo immigrati nei rispettivi territori, giorni di protandria, giorni di immigrazione, numero totale di individui immigrati e incremento del numero di territori riproduttivi occupati nelle primavere 2022, 2023, 2024 e nell'intero periodo di studio. Test χ^2 corretto per la visibilità delle femmine.*

Period	Julian days		Gregorian days		P	I	N	dT	Test χ^2
	M	F	M	F					
SP	51.21	55.36	20-feb	24-feb	4.15		161		0.03
2022	50.78	54.13	19-feb	23-feb	3.35	26	62	30	
2023	54.55	58.71	23-feb	27-feb	4.17	29	60	30	
2024	47.52	51.79	16-feb	20-feb	4.27	33	39	18	

M, male; F, female; P, days of protandry; I, days of immigration; N, total number of immigrant individuals; dT, increase in the number of occupied breeding territories; SP, study period.

Tab. 4 – Average arrival date of male and female immigrant stonechats in the study area, days of protandry, days of immigration, and total number of immigrant individuals in springs 2022, 2023, 2024, and in the entire study period. Test χ^2 corrected for only female visibility and test χ^2 C, corrected for female visibility, and overall male/female ratio. / *Data media di arrivo di maschi e femmine di saltimpalo immigrati nell'area di studio, giorni di protandria, giorni di immigrazione e numero totale di individui immigrati nelle primavere 2022, 2023, 2024 e nell'intero periodo di studio. Test χ^2 corretto solo per la visibilità delle femmine e test χ^2 C corretto per la visibilità delle femmine e per il rapporto complessivo maschi/femmine.*

Period	Julian days		Gregorian days		P	I	N	Test χ^2	Test χ^2 C
	M	F	M	F					
SP	52.64	56.16	21-feb	25-feb	3.52		204	0.03	0.06
2022	51.84	54.13	20-feb	23-feb	2.29	27	68		
2023	56.56	60.00	25-feb	29-feb	3.44	32	74		
2024	49.00	53.25	18-feb	22-feb	4.25	34	62		

M, male; F, female; P, days of protandry; I, days of immigration; N, total number of immigrant individuals; SP, study period.

Tab. 5 – Average arrival date of single males, single females, and paired male and female in their breeding territories in springs 2022, 2023, and 2024. / Data media di arrivo di maschi singoli, femmine singole e coppie (maschio e femmina) nei rispettivi territori riproduttivi nelle primavere 2022, 2023 e 2024.

	2022		Average arrival day 2023		2024	
	Julian	Gregorian	Julian	Gregorian	Julian	Gregorian
Single M	49.30	18-feb	54.24	23-feb	48.68	17-feb
Paired MF	53.25	22-feb	55.20	24-feb	50.77	19-feb
Single F	54.72	24-feb	60.67	29-feb	56.18	25-feb

M, male; F, female.

of pair arrivals in the breeding territories in the years 2022, 2023, and 2024 was 38%, 36%, and 43%, respectively.

Fig. 2 illustrates the progression of male and female arrivals during spring migration. To enhance clarity and ensure adequate sample sizes for the chi-square test in statistical analysis, I grouped all arriving individuals of both sexes into consecutive five-day periods (pentads) across the three study years. The 161 individuals that settled in breeding territories (Fig. 2A) and the 203 birds arriving in the study area, including transients (Fig. 2B), clearly demonstrate the pattern of protandry in the stonechat and closely resemble that documented by ringing data from Piedmont, Italy, by Fasano *et al.* (2010).

To examine the potential correlation between early male arrival and subsequent early mate acquisition, potentially leading to earlier breeding, I compared each male's arrival date with that of his female mate within his territory. Clearly, single males arrive in their territories before their female mates. However, the pattern observed across all three years excludes any correlation and suggests that pair formation in breeding territories occurs largely by chance (Fig. 3).

DISCUSSION

As to the methodology applied in this study, although birds were not marked, careful daily counts of stonechat numbers across the entire study population can reliably indicate trends in protandry, as individual identity does not affect the number of immigrants. However, caution is needed regarding the time lag between the arrival of a single male in its territory and the subsequent arrival of a female mate. Since the birds are unmarked, I cannot rule out the possibility that the fittest immigrant males may displace resident males from their territories and mate with the resident females.

In such cases, the displaced resident males, shown to be less fit, must occupy vacant territories and wait for immigrant female mates. However, the steadily increasing proportion of resident birds during the study period (see M & M) suggests that residency provided a survival advantage to wintering birds. Consequently, resident individuals are expected to be fitter than migratory ones, with resident males being more competitive in retaining their female mates.

Therefore, I assume that the first arriving single males occupy only vacant territories, and remain there awaiting a female mate, even if they had temporarily intruded into occupied ones. Furthermore, the observed casual pattern

of mating between immigrant single stonechats remains unchanged throughout the study period, suggesting that increased residency and the resulting decline in vacant suitable breeding territories did not influence this pattern.

Despite good evidence for protandry in the study population of the stonechat, particularly during the first 10 days of immigration, two key questions remain. How can protandry persist if the first arriving males do not seem to gain any advantage, such as earlier mate acquisition and consequent earlier breeding? In addition, why is protandry almost absent during the peak migration period, when most individuals arrive already paired? And why do these arrive already paired just in the central period of migration?

To my knowledge, the observed pattern of spring arrival of stonechats on the breeding grounds is unique among migratory bird species with sex biased spring arrival, in that no other species reach their breeding sites with part of the individuals already paired. Significantly, Banik (2001; 2019) reported 56% and 38% of pair arrivals in Ukraine, and Ziegler (1966) reported 50% in Germany. Thus, it appears that a fraction of already paired immigrant birds, between 40 and 60%, is consistent between years and populations. This pattern might be explained by the marked tendency of stonechats to form pairs and defend territories wherever possible, on the breeding and wintering grounds, but also on the stopover sites (Johnson, 1961), despite being assumed to migrate as single individuals (Rödl, 1995; Urquhart, 2002).

Therefore, a possible explanation for the correlation between pair arrival at the breeding grounds and both protandry and the mate choice hypothesis, proposed as a mechanism for maintaining protandry (Saino *et al.*, 2010; Newton, 2023), can be outlined as follows.

Limiting reasoning to my study population, it is a representative part of a much larger, rather isolated, population which inhabits the Palentine and Fucino plains at 600-700 m above sea level, surrounded in all directions by mountains with altitudes consistently above 1600 m above sea level. In February, snow cover makes these mountain chains highly unsuitable as migration routes that, instead, are likely to have evolved and stabilized along one or more valley floors gradually ascending to the breeding areas of the population. These valleys canalize and concentrate the return movements of all the migrant stonechats belonging to the isolated population that inhabits 350 km² of suitable habitat, facilitating encounters between individuals of both sexes at stopover sites during the central period of spring return when male and female arrival times overlap.

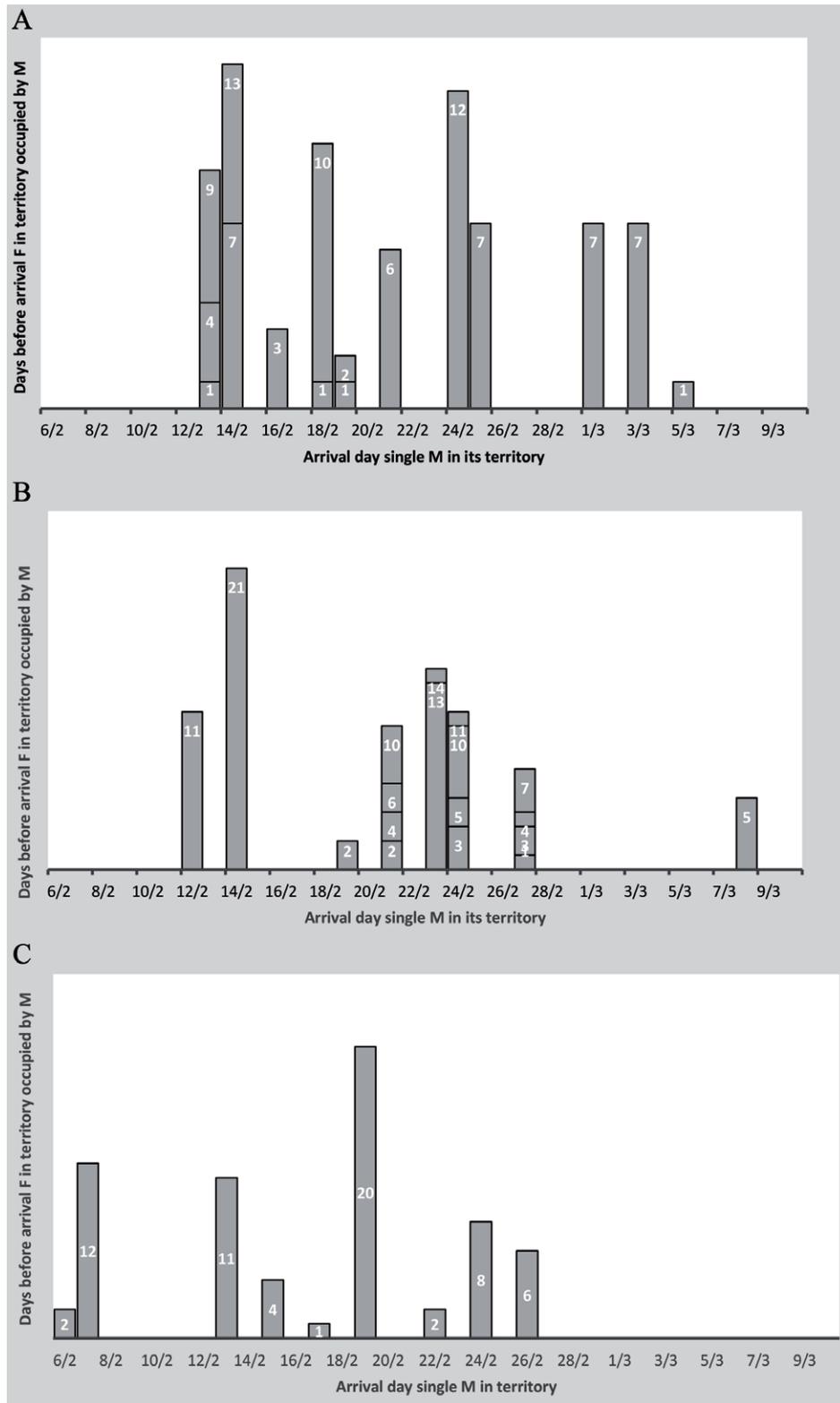


Fig. 3 – A) Time lag (days) between the arrival date of the single male stonechat in its territory and the subsequent single female mate arrival in spring 2022; B) time lag (days) between the arrival date of the single male stonechat in its territory and the subsequent single female mate arrival in spring 2023; C) time lag (days) between the arrival date of the single male stonechat in its territory and the subsequent single female mate arrival in spring 2024. / A) Intervallo temporale (giorni) tra la data di arrivo del singolo maschio di saltimpalo nel proprio territorio e la successiva data di arrivo della singola femmina in primavera 2022; B) intervallo temporale (giorni) tra la data di arrivo del singolo maschio di saltimpalo nel proprio territorio e la successiva data di arrivo della singola femmina in primavera 2023; C) intervallo temporale (giorni) tra la data di arrivo del singolo maschio di saltimpalo nel proprio territorio e la successiva data di arrivo della singola femmina in primavera 2024.

In case of protandry, initially, the sex ratio will be male-biased, offering the first arriving females optimal mate choice occasions. There, only the very first arriving males will not encounter females and proceed alone to their breeding sites, while a few days later, the first females will meet there the main cohort of early-arrived males. Consequently, males and females may mate according to the mate choice hypothesis, with the fittest females pairing with the fittest males (Rubolini *et al.*, 2004; Saino *et al.*, 2010). These newly formed pairs will reach the nearby breeding areas together, thus presumably accounting for the 50% fraction of birds arriving already mated. This rather stable fraction derives from the arrival time distribution of both sexes at the stopover sites near the breeding grounds that overlap to a degree determined by the days of protandry and the rate of stonechat migration (percentage of total number of migrants per day of migration).

Therefore, if an advantage in the choice of partner by the female drives protandry (Saino *et al.*, 2010), this, even if not found at the breeding site, has nevertheless achieved its beneficial effect on sexual selection. In this hypothesis, males compete for scarce females at the last stopover sites. Outcompeted males will proceed alone to the breeding grounds, where they must wait for the arrival of a mate, contributing to the observed positive M/F ratio. Thus, paradoxically, the fittest males from the female's perspective may not be the first arriving single males on the breeding grounds; the fittest males will arrive already paired.

Furthermore, the proposed explanation for the observed pair arrival in the breeding territories implies an inherent sacrifice for the first males, which do not encounter females, proceed without mating, and have to wait in their early-occupied territories for the arrival of single females not mated before on the stopover sites.

For the described sequence of events to occur, several conditions must be met. Migratory routes must be stable in time and pass through one or more bottlenecks, like valleys that separate high mountain areas, islands during sea crossing, or narrow sea crossing points, which would favor both migration route and stopover site fidelity. Additionally, one or more suitable stopover sites for resting and feeding must be present at or near the last bottlenecks approaching the breeding grounds. These conditions would guarantee a sufficient concentration of birds of both sexes to allow for suitable mate choice opportunities.

Analyzing ringing recoveries of four migrant warblers in Spain, Cantos and Telleria (1994) in fact revealed the existence of stopover site fidelity in small migrant passerines. Payevsky (2024) used long-term ringing data at the Curonian Spit (Lithuania) to demonstrate that a significant part of the migratory populations of chaffinch and willow warbler (34-41%, respectively, of recaptured birds) retains the same migration path and approximately the same migration timing in other years after ringing. Similarly, Vogt *et al.* (2012) demonstrated stopover site fidelity in the Tennessee warbler in North America. However, Catry *et al.* (2004) report very low stopover site fidelity of long-distance migratory passerines in Portugal, although they found stopover site fidelity to increase significantly when near the breeding or wintering grounds.

Although only future studies at stopover sites near the breeding areas during spring return can reveal whether the

proposed explanation is correct or not, some data on stonechat concentrations at specific sites along the autumn migration routes are available. Along the coast near Circeo (central Italy), more than 40 individuals fed and rested for a few days at the end of October 2023 in a wasteland area (di Lieto, pers. comm.). Additionally, during fall migration, hundreds of individuals stopped at the island of Linosa, halfway between Sicily and Tunisia (Ornitho.it).

Other research is necessary into the breeding success of stonechats arriving in pairs. According to the above-proposed hypothesis, I would expect these pairs to be more successful than pairs formed by early arrived single males and their later-arriving female mates.

ACKNOWLEDGEMENTS

I sincerely thank Giovanni Boano for his useful comments on the first draft and the anonymous referees for their helpful and constructive comments.

REFERENCES

- Arizaga J. & Barba E., 2009 – Importance of sampling frequency to detect differential timing of migration: a case study with Blackcaps *Sylvia atricapilla*. *Ardea*, 97: 297-304.
- Banik M., 2001 – Distinctive behavioural traits of early stages of reproductive cycle in migratory populations of the Common Stonechat (*Saxicola torquata* (L.)) in Kharkiv region, Ukraine. Programme and abstract book 3rd EOU Conference, 21-25 August 2001, Haren/Groningen, The Netherlands.
- Banik M., 2019 – Sharp differences in the timing of male and female spring arrival in the European Stonechat, *Saxicola rubicola*, and the Whinchat, *S. rubetra* (Passeriformes, Muscicapidae), in north-eastern Ukraine. *Vestnik Zoologii*, 53: 483-490.
- Bibby C. J., Burgess N. D., Hill D. A. & Mustoe S. H., 2000 – Bird census techniques. London: *Academic Press*.
- Brichetti P. & Fracasso G., 2022 – The birds of Italy. Vol.3. Cisticolidae-Icteridae. Latina: *Edizioni Belvedere*.
- Cantos F. J. & Telleria J. L., 1994 – Stopover site fidelity of four migrant Warblers in the Iberian Peninsula. *Journal of Avian Biology*, 25: 131-134.
- Catry P., Encarnacao V., Araujo A., Fearon P., Fearon A., Armelin M. & Delaloye P., 2004 – Are long-distance migrant passerines faithful to their stopover sites? *Journal of Avian Biology*, 35: 170-181.
- Coppack T. & Pulido F., 2009 – Proximate control and adaptive potential of protandrous migration in birds. *Integrative and Comparative Biology*, 49: 493-506.
- Cramp S., 1988 – Handbook of the birds of Europe the Middle East and North Africa. The birds of the western palearctic. Vol. V: Tyrant Flycatchers to Thrushes. Oxford: *Oxford University Press*.
- Fasano S. G., Tamiotti A., Ferro G., Bandini M., Tibaldi B. & Gruppo inanellatori piemontesi e valdostani, 2018 – L'attività di inanellamento a scopo scientifico in Piemonte e Valle d'Aosta: anni 1974-2016. Parte II. Passeriformi e Ricatture. *Tichodroma*, 9. <https://www.gpso.it/wp-content/uploads/2018/09/Tichodroma_n9-2018_INNpII.pdf>
- Flinks H., Helm B. & Rothery P., 2008 – Plasticity of moult and breeding schedules in migratory European Stonechats *Saxicola rubicola*. *Ibis*, 150: 687-697.
- Johnson E.D.H., 1961 – The pair relationship and polygyny in the Stonechat. *British Birds*, 54: 213-225.
- Justen H., Hasselmann T., Illera J. C., Delmore K., Serrano D., Flinks H., Senzaki M., Kawamura K., Helm B. & Liedvogel M., 2022 – Population-specific association of Clock gene polymorphism with annual cycle timing in stonechats. *Scientific Reports*, 12: 7947.

- Kokko H., 1999 – Competition for early arrival in migratory birds. *Journal of Animal Ecology*, 68: 940-950.
- Kokko H., Gunnarsson T. G., Morrell L. J. & Gill J. A., 2006 – Why do female migratory birds arrive later than males? *Journal of Animal Ecology*, 75: 1293-1303.
- Maggini I., Spina F., Voigt C. C., Ferri A. & Bairlein F., 2013 – Differential migration and body condition in northern wheatears (*Oenanthe oenanthe*) at a Mediterranean spring stopover site. *Journal of Ornithology*, 154: 321-328.
- Mildenberger H., 1950 – Beiträge zur Ökologie und Brutbiologie des Schwarzkehlchens (*Saxicola torquata rubicola*). *Bonner Zoologische Beiträge*, 1: 11-20.
- Morbey Y. E. & Ydenberg R.C., 2001 – Protandrous arrival timing to breeding areas: a review. *Ecology Letters*, 4: 663-673.
- Newton I., 2023 – The migration ecology of birds. 2nd ed. London: *Academic Press*.
- Payevsky V. A., 2024 – Are migrant passerines faithful to their individual paths and migration timing throughout their lives? *Proceedings of the Zoological Institute RAS*, 328: 197-203.
- Rödl T., 1995 – The wintering of territorial Stonechat pairs *Saxicola torquata* in Israel. *Journal of Ornithology*, 136: 423-433.
- Rubolini D., Spina F. & Saino N., 2004 – Protandry and sexual dimorphism in trans-Saharan migratory birds. *Behavioral Ecology*, 15: 592-601.
- Saino N., Rubolini D., Serra L., Caprioli M., Morganti M., Ambrosini R. & Spina F., 2010 – Sex-related variation in migration phenology in relation to sexual dimorphism: a test of competing hypotheses for the evolution of protandry. *Journal of Evolutionary Biology*, 2010: 2054-2065.
- Spina F., Massi A., Montemaggiori A. & Baccetti N., 1993 – Spring migration across the mediterranean. *Vogelwarte*, 37: 1-94.
- Spina F. & Volponi S., 2008 – Atlante della migrazione degli uccelli in Italia. 2. Passeriformi. Ministero dell'Ambiente e della Tutela del Territorio e del Mare, Istituto Superiore per la Protezione e la Ricerca Ambientale (ISPRA). Roma: *Tipografia SCR*.
- Stewart R. L. M., Francis C. M. & Massey C., 2002 – Age-related differential timing of spring migration within sexes in passerines. *The Wilson Bulletin*, 114: 264-271.
- Urquhart E., 2002 – Stonechats: a guide to the genus *Saxicola*. London: *Christopher Helm*.
- Van Doren B. M., Liedvogel M. & Helm B., 2017 – Programmed and flexible: long-term Zugunruhe data highlight the many axes of variation in avian migratory behaviour. *Journal of Avian Biology*, 48: 155-172.
- Vogt D. F., Hopey M. E., Mayfield G. R., Soehren E. C., Lewis L. M., Trent J. A. & Rush S. A., 2012 – Stopover site fidelity by Tennessee Warblers at a southern Appalachian high-elevation site. *Wilson Journal of Ornithology*, 124: 366-370.
- Ziegler G., 1966 – Beobachtungen an Schwarzkehlchen, *Saxicola torquata rubicola*, im nördlichen Teil des Kreises Minden/Westf. *Journal für Ornithologie*, 107, 187-200.