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**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**

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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. Banik, M. V. — Protandry, or the arrival of males prior to females to the breeding grounds is a widespread phenomenon in migratory birds though rarely examined in related species in which its manifestation can vary. European Stonechat and Whinchat are such a pair studied with use of individual marking in North-Eastern Ukraine in 1993–2008. An apparent protandry was found in Whinchat but not in European Stonechat. The difference between the arrival dates of male and female Whinchats (6 days) was significant. The mean time span between territory establishment by a male and subsequent pair formation was 10.6 days. By contrast, 38% of the first records of European Stonechats in spring were those of already paired birds and the difference between arrival dates of both sexes was non-significant. The proximate cause of protandry in Whinchat and its' absence in European Stonechat seems to be the differences (or the lack thereof) in the onset of spring migration. The time lapse between the start of migration of male and female Whinchats originates at African wintering grounds and is maintained en route. The absence of the protandry in European Stonechat is probably a relict behaviour from the residency. The protandry in migratory populations of this species is yet to be developed.

Key words: *Saxicola rubetra*, *Saxicola rubicola*, protandry, North-Eastern Ukraine.

Introduction

Males tend to arrive to the breeding grounds considerably earlier than females in many migratory bird species especially in passerines (Rubolini et al., 2004; Tøttrup, Thorup, 2008). This phenomenon is called protandry and parallels similar early emergence of males in insects and some other migratory animals (Wiklund, Fagerström, 1977; Morbey, Ydenberg, 2001). Protandry is usually considered as a result of evolutionary optimisation process that contributes to male fitness via occupying better territories or increasing chances of mating (Morbey, Ydenberg, 2001; Canal et al., 2012). The proximate causes of protandry receive less attention though firm evidences point out that it is a by-product of habitat and/or geographical segregation of sexes during a non-breeding period, sex differences in the onset of spring migration i. e. in photoperiodic responsiveness or sex differences in migration speed (Coppack, Pulido, 2009; Delgado, Coppack, 2010; Schmaljohann et al., 2015).

So far there were very few attempts to look at the level of protandry in closely related species or subspecies of birds (Borowske, 2015; Schmaljohann et al., 2015) though this can shed light on the origin of the phenomenon. One striking example of dramatic differences in manifestation of protandry in related species is a case of the Whinchat, *Saxicola rubetra* (Linnaeus, 1758), and the European Stonechat, *Saxicola rubicola* (Linnaeus, 1766)¹, (thereafter Stonechat) in Ukraine. Both are small flycatcher birds often sharing the same habitat but clearly distinct in the migration strategy. The Whinchat is a long-distance migrant to Africa south of Sahara while the Stonechat winters presumably in Mediterranean basin not very far from the breeding grounds.

Material and methods

The ecology of both species was studied in detail in 1993–2008 on a 350 ha plot in the Murom River flood-plain, Kharkiv Region, North-Eastern Ukraine (50°9′00″ N, 36°25′30″ E) where important observations were made on individually marked birds (50 adult Whinchats, 24 adult Stonechats). Here the bulk of the data on arrival and on the build-up of the local population in spring was gathered. This study is a part of a more comprehensive survey of the ecology of Whinchat and Stonechat in sympatry where more attention was paid to unveiling the events of the post-breeding period e. g. brood division or family groups' retention (Banik, 2006).

The first visits to the study plot have been made usually since late March just after intensive snowmelt in the Murom River flood-plain and before mass arrival of Stonechats. The plot was consistently inspected every 5–7 days throughout the breeding period but more often in some years to get a picture of the settlement of the birds of the local population i. e. territory acquisition by the males, the subsequent pair formation and so on. Additional data on the arrival of both species were collected in other parts of Kharkiv Region in 1989–2016 years.

The difference between the dates of the first record of males and females in spring was analysed for both species. The data on spring observations of the Stonechats between the first arrival date and 5–6 April (chosen as arbitrary dates for the termination of mass arrival) were used to get a complementary picture of the interrelation of the arrival dates for both sexes. The detailed data on the rate of acquisition of breeding territories and pair formation in both species at the study plot in the Murom River flood-plain were checked for 5 years (1994–1995 and 2002–2004) when the control was better. This was used to estimate the lapse between the arrival dates of males and females for the whole period of their settlement at breeding sites in spring. As the study plot was controlled on a daily basis only for small time intervals the actual value of the lapse should be somewhat lower than reported below. The difference between the dates of spring arrival of males and females was estimated for both species by t-test (for data sets with normal distribution after checking by Shapiro-Wilk W-test) or by Mann-Whitney U-test. Statistica 7.0 software package was used to perform the calculations.

Results

The mean date of first sightings of Whinchat in Kharkiv Region was 21st April (13th April–28th April; median was 21st April; n = 22 years). The males arrived prior to females and the mean time lapse between the first records of both sexes was 7 days (0 to 13 days; n = 16 years). At the study plot in the Murom River flood-plain where the observations were more regular the difference between the arrival of male and female Whinchats was 6 days (0 to 13 days; n = 13 years). The median time lapse between male and female arrival was 7 days for both samples. The difference between male and female arrival in the Whinchat was significant for both samples (two-tailed t-test; t =

¹ Two Western Palearctic subspecies of the former large polytypic species, the Common Stonechat *Saxicola torquatus* (Linnaeus, 1766), recently have been widely recognised as a separate species, *S. rubicola* (Urquhart, 2002; Zink et al., 2009; Christidis et al., 2018).

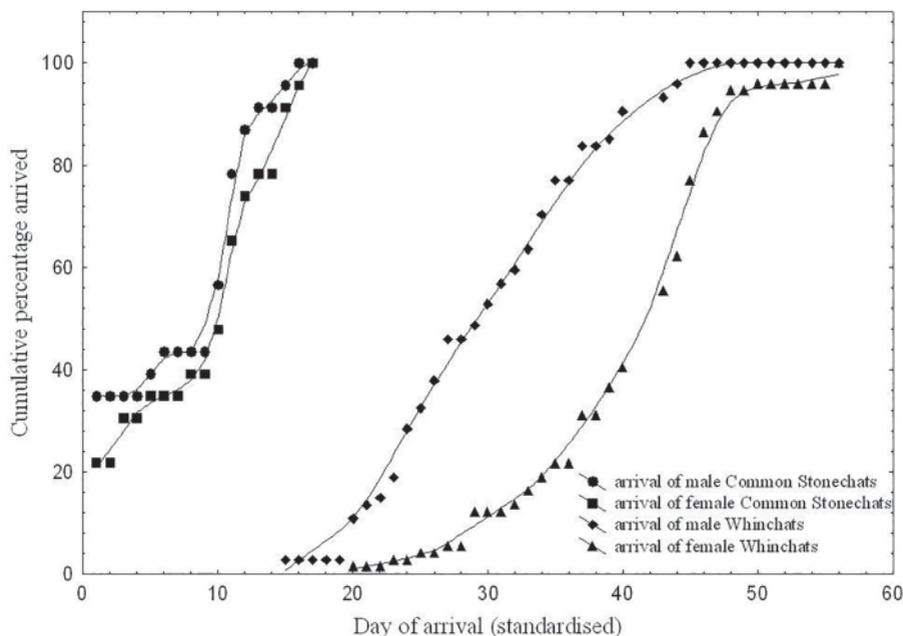


Fig. 1. Spring arrival schedules of male and female Common Stonechats (*Saxicola rubicola*) and male and female Whinchats (*S. rubetra*) at the study plot in the Murom River flood plain (Kharkiv Region, Ukraine). The dates were standardised by assigning 1 Day value for the arrival of first bird in a certain year (the data for years 1994–1995, 2002–2004 are presented).

–4.63; $p < 0.01$; $t = -3.92$; $p < 0.01$, for Kharkiv Region and the Murom River samples, accordingly). The mean interval between the occupation of a territory by a male and subsequent female arrival & pair formation at the study plot in the Murom River flood-plain was 10,6 days (0–23 days; median was 10 days; $n = 74$) for years 1994–1995, 2002–2004. Though some females may arrive very early and simultaneously with males (actually only 4 % in this sample) the majority appeared later and the difference between male and female arrival was highly significant (Mann-Whitney U-test; $p < 0.01$). Overall, there is an overlap of arrival schedules for male and female Whinchat at the study plot in the Murom River flood-plain (fig. 1). However, it's apparent that for the large portion of the period of settlement in spring the time span between initial male territory occupancy and pair formation is 10–12 days though it is fairly shorter earlier in spring (fig. 1).

The mean date of the arrival of the Stonechat in Kharkiv Region was 27th March (13th March–6th April; the median was 31st March; $n = 25$ years). Considerable proportion of the Stonechats first seen in spring were already paired (38 %; $n = 99$) though the majority of early spring records were of presumably lone males (60 %). The sightings of females apparently not accompanied by males were in vast minority (2 %). However, it shouldn't go unnoticed that the females often are fairly cryptic in this period and some evidently were missed in observations. Thus, actually the observations of pairs may constitute even higher proportion of the first spring records of the Stonechats.

The mean interval between the first sightings of male and female Stonechats was circa 2 days (1.58 ± 1.41 days; $n = 19$ years) but the median was zero for 1989–2016 years' period. The difference between male and female arrival dates was non-significant (Mann-Whitney U-test; $p = 0.67$). The dynamics of the arrival, territory occupancy and pair formation within the study plot in the Murom River flood-plain for 1994–1995, 2002–2004 was used to estimate the time lapse between male and female arrival additionally and to complement the similar data on the Whinchat (fig. 1). The

mean interval between the arrival of male and female Stonechats for this data set was 1.44 ± 0.67 days ($n = 23$) and the median was zero. The difference between the arrival of males and females wasn't significant (two-tailed t-test; $t = -0.82$; $p = 0.42$). In 4 cases it was possible to estimate the interval between the occupation of a territory by a male and subsequent female arrival and pair formation more precisely. These comprise 1 case in 1995 and 3 cases in 2002 including two observations on marked birds (one male and one female in 2002). The maximum time lapse between these events was 5 days in 3 cases and 3 days in 1 case, while the minimum was only 1 day in 3 cases and 2 days in 1 case. That corresponds fairly well with the mentioned time span between the first observations of males and females in spring.

Discussion

The proximate causes for the evident protandry in the Whinchat observed in this study seem to be linked to the aspects of migration strategy (long-distance migrant) and namely to sex differences in the onset of spring migration. Male and female Whinchats are known to occupy separate individual territories at wintering sites (Leisler, 1990; Blackburn, Creswell, 2015; Lerche-Jørgensen, 2017) and to start spring migration at different times. The time lapse between the onset of northward migration in male and female Whinchats in Nigeria is 8 days and the sex is also the only significant factor influencing departure date (Risely et al., 2015).

The time gap between the passage schedules of males and females persists throughout the migration period. For example, the time lapse between the median dates of spring passage of male and female Whinchats in Western and Central Mediterranean is 6 days (Spina et al., 1994). Closer to the breeding grounds e. g. on Christiansø island in Baltic Sea migrating males precede females for 3–4 days (Tøttrup, Thorup, 2008). In Salisbury, England male Whinchats arrive to the breeding grounds earlier than adult females (on 6 days) and significantly earlier than first-year females (on 18 days; Taylor, 2015). This corresponds fairly well with the data of this study in which the growing time lapse between male and female arrival in the course of the spring season probably indicates the same differences in the schedules of adult and first-year birds (see Results). Thus, the pattern of male and female Whinchat arrival at the Murom River study plot may reflect the prevalence of first-year birds in this population. Overall, all mentioned data points to the apparent protandry in the Whinchat across Europe.

The similar level of protandry was found recently in the Northern Wheatear (*Oenanthe oenanthe*), also a long-distance chat species. Like in the Whinchat, no latitudinal sex segregation was evidenced in the Northern Wheatear (Schmaljohann et al., 2015) that is known for many other Palearctic-African long-distance passerine migrants as well (Berthold, 2001). Female Northern Wheatears initiated spring migration significantly later than males (Schmaljohann et al., 2015). Moreover, it was shown that in the northern subspecies of Northern Wheatear (*Oe. oe. leucorhoa*) breeding in Iceland and Greenland the arrival date of males significantly advances with age that contributes to the higher degree of protandry in these northernmost populations as compared to the nominate form *Oe. oe. oenanthe* (Schmaljohann et al. 2015).

In general, the differences in the departure time from wintering sites seem to be the most powerful source of the differences in arrival time at breeding grounds (Schmaljohann et al., 2015). These differences are innate (endogenously controlled) and not related to photoperiod or environmental conditions as was shown in 'common garden' experiments (Maggini, Bairlein, 2012).

The ultimate causes of protandry in birds most probably are linked to reproduction strategy that is demonstrated by the well-known phenomenon of earlier arrival of females as compared to males in species with reversed sex roles e. g. in some waders

(Newton, 2008). In species with ordinary sex roles the origin of sex differences in the onset of migration is presumably related to the benefits for males which occupy breeding territories earlier in the season. There are many indications that in migrant species the rank and productivity of males depends on the arrival date i. e. the males who arrive earlier are more successful (Currie et al., 2000; Pärt, 2001). In the Whinchat no significant correlation was found between breeding success and territory settlement date but failed breeders occupied their territories on average 3 days later than successful birds (Taylor, 2015).

That the differences in the time of onset of northward migration are indeed linked to breeding challenges is indirectly proved by the comparison of the start of spring versus autumn nocturnal restlessness in hand-raised birds in 'common garden' experiments in the Northern Wheatear. No sex differences were observed for autumn start of restlessness (Maggini, Bairlein, 2012). This corresponds fairly well to the absence of sex differences in the time of departure and autumn migration in several species of Palearctic passerine migrants (Newton, 2008). For example, recently no differences were found between the autumn migration dates of adult males and females in 3 long-distance migrant passerine species in Finland (Lehikoinen et al., 2017).

It seems that 'mate opportunity' hypothesis (Petersen, 1947; Wiklund, Fagerström, 1977; Morbey, Ydenberg, 2001; Kokko et al., 2006) may be the most suitable for explaining evolutionary significance of protandry in the Whinchat. As applied to birds the hypothesis postulates that early arriving males have more chances to pair with more fecund females and increase opportunities of extra-pair copulations with receptive females as well (Coppack et al., 2006; Kokko et al., 2006). This is the case of the Whinchat as the early arriving males became founders in the clusters of breeding pairs and having leeway in the course of reproduction apparently take an advantage of extra-pair copulations with females on neighbouring sites (own observations). 'Mate opportunity' hypothesis was corroborated recently because the relations between the manifestation of protandry and the level of extra-pair paternity were found in five species of European passerine birds (Coppack et al., 2006). This study indicated that the more is the level of extra-pair paternity, the more advanced are the dates of arrival of males as compared to females. Moreover, 'mate opportunity' hypothesis was considered as the most plausible explanation for the origin of protandry in the Northern Wheatear (Schmaljohann et al., 2015).

The degree of protandry clearly is an evolutionary changing trait that was evidenced by the differences in its manifestation in two distinct subspecies of the Northern Wheatear which face different constraints both on migration routes and at breeding sites (Maggini, Bairlein, 2012; Schmaljohann et al., 2015). The exceptionally rapid change of the degree of protandry has been recently demonstrated also for the populations of Pied Flycatcher (*Ficedula hypoleuca*) which migrate across Hungary (Harnos et al., 2015).

The migratory behaviour of the Stonechat in Europe, unlike that of Whinchat's, is extremely flexible ranging from sedentary in the westernmost and southern parts of the continent to partially migratory (e. g. in Great Britain) to fully migratory in the northern and eastern portions of the range. No differential migration is known for this species i. e. there are no differences in the migration distance and winter distribution between sexes (Helm et al., 2006). Moreover, Stonechats are known to form pairs on wintering grounds and even at migration stopovers (Moreau, Moreau, 1928; Johnson, 1961, 1971; Kostin, 1983; Gwinner et al., 1994; Rödl, 1994). Detailed studies in Israel showed that 70 % to 80 % of birds stay at wintering sites in pairs (Rödl, 1994). Such pairs are unstable and may disintegrate and associate again readily. Notably, the territorial behaviour and pair formation at wintering sites isn't under the control of steroid hormones e.g. testosterone opposite to the situation at breeding grounds (Gwinner et al., 1994).

In spring the partners in winter pairs in Israel usually start migration separately (17 of 22 cases) and males depart earlier than females (12 of 17 cases; Rödl, 1994). These data clearly demonstrate as well that in more than one-fifth of the cases both partners in a Stonechat pair depart from a wintering site almost simultaneously and that in nearly 30 % of the cases the onset of northward migration was earlier in females than in males. By no means is this indicative of the retention of a pair bond en route and of possibility that some Stonechats arrive to the breeding grounds being already paired. Rather, this is an indication that sex differences in timing of migration in Stonechat are negligible that is confirmed also in the present study.

Similar behaviour is known in the White Wagtail (*Motacilla alba*) which is also represented by sedentary, partially migratory and fully migratory populations throughout its vast range. The tendency to form temporary winter pairs is pronounced in different parts of the White Wagtail range (Zahavi, 1971; Davies, 1976; Higuchi, Hirano 1983). In this species just as in the Stonechat the pairs often stay together for only a part of a wintering period, so some birds change partners and move to neighbouring territories. Males and females start northward migration at different dates and apparently do not breed together (Zahavi, 1971). The winter pair territoriality was also found in partially migratory Wheatear species (Matthysen, 1993).

Apparent pair territoriality both at stopover sites and at wintering grounds is quite an unusual social organization in a non-breeding period in migrants, thus the Stonechat represents one of a very few examples (Matthysen, 1993). It's safe to suggest that this trait is a relict behaviour from the residency since it's very likely that migratory populations of the Stonechat in Europe originated from resident ones. Indeed, there are resident birds whose social organization in a non-breeding period most often manifests in pair territoriality (Matthysen, 1993). This conclusion is corroborated by the data from Western Europe where resident and migratory populations of the Stonechat live in sympatry and exhibit similar behaviour (Phillips, Greig-Smith, 1980).

Our data showed that despite the Stonechats from migratory populations in Ukraine face with the same problems as migratory Whinchats i. e. with a need to occupy or re-occupy the most suitable sites for breeding every spring they have not yet developed a similar rate of protandry as the latter species. Generally, the differences in male and female arrival to the breeding grounds represent a fundamental distinction between ecologically similar Whinchat and European Stonechat. The latter species has a suite of traits which possibly are linked to its recent residency while the former demonstrates well-developed and evolutionarily long-enduring migratory habits.

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