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Research

Interactive effects of arrival date, territory quality and male polyterritorial behaviour on the mating system of the sedge warbler *Acrocephalus schoenobaenus*: a path analysis

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Classical models predict that male fitness is based on resources monopolized and invested in reproduction, and/or on individual quality providing offspring with sexually attractive traits or viable genes. However, these factors are frequently correlated, making their relative influence on male fitness difficult to describe and quantify. We analysed the relative influence of the main features of the sedge warbler's *Acrocephalus schoenobaenus* breeding system, i.e. age, arrival date, territory quality, male sexual activity (song and polyterritorial behaviour), on males' mating success, fledging success and local recruitment. Results show that this species' breeding system involves three main paths: 1) earlier-arriving males have higher mating success, regardless of territory quality, 2) the quality of territories pre-empted by earlier males directly influences recruitment and 3) mating success is influenced by male sexual activity (polyterritorial behaviour), but an additional territory also affects recruitment directly. As arrival date plays a significant role in all the paths, the whole system seems to depend on male quality; although the benefits accruing to male fitness are obtained not only through sexual selection but also through resource monopolization.

Keywords: arrival date, polyterritoriality, sexual selection, song repertoire, territory quality

Introduction

According to the classical theory of mating systems, resource-rich sites attract females. Hence, males monopolize such sites to secure sufficient resources for successful reproduction, and increase the likelihood of mating with one or more females (Emlen and Oring 1977). In migratory species, males settle in a suitable habitat every year, each time reopening the contest for territories. Early arriving males can outcompete rivals turning up later and benefit from occupying the best available territories (the 'pre-emption principle'; Pulliam and Danielson 1991). In this way, the order of settlement should determine their reproductive success (Sergio et al. 2007), promoting those males that will every year attempt to come earlier than their competitors.

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Individual variation in arrival time can be explained in a proximate way by condition-dependent features (Møller 1994, Ninni et al. 2004). However, if arrival time honestly reflects male quality, the marginal costs of early arrival must be greater for low-quality than high-quality individuals (Kokko 1999). This may lead to directional selection on early male arrival, which was shown to be more pronounced in strongly sexually selected species (Spottiswoode et al. 2006). Indeed, early males mate more successfully (Aebischer et al. 1996, Lozano et al. 1996, Smith and Moore 2005, Zając et al. 2006, Sergio et al. 2007), benefit from polygynous (Alatalo et al. 1984, Hasselquist 1998, Canal et al. 2021) and extrapair matings (Langefors et al. 1998, Møller et al. 2003, Cooper et al. 2011) or both (Reudink et al. 2009a, Canal et al. 2012). The time of male arrival is often related to the attractiveness of sexual signals, such as song (Arvidsson and Neergaard 1991, Lampe and Espmark 1994, Kipper et al. 2006) and plumage traits (Slagsvold and Lifjeld 1988, Møller 1994, Ninni et al. 2004, Jones et al. 2014).

A particular case of a behavioural trait influencing male reproductive success is polyterritorial behaviour: once paternity has been guaranteed on the original territory, early-arriving males have enough time during the season to seek an extra mate by displaying on an additional, mostly 'ritual' territory (Alatalo and Lundberg 1984, Zając et al. 2008a). Hence, the opportunity for adopting this strategy, aimed at polygyny, is constrained by the time of the male's arrival and of the initiation of the first brood (Zając et al. 2008a, Canal et al. 2020). Polyterritoriality, most thoroughly described in the pied flycatcher *Ficedula hypoleuca* (von Haartman 1969, Alatalo et al. 1981, Alatalo and Lundberg 1984), has been observed in a number of passerines, mainly long-distance migrants, with confirmed regular polygyny (Møller 1986, Ford 1996).

Among the various factors influencing male fitness in migratory species, arrival date seems to play a crucial role (Reudink et al. 2009a, Cooper et al. 2011). Also, earlier breeding, often closely related to early arrival, can positively influence reproductive success as it is often associated with a larger clutch (Verhulst et al. 1995, Smith and Moore 2005), the number of broods raised in a season (Møller et al. 2010), re-nesting opportunities after failure (Halupka et al. 2008, Cooper et al. 2011, Morrison et al. 2019), fledging success and survival (Naef-Daenzer et al. 2001) and ultimately with improved offspring recruitment (Hochachka 1990, Verboven and Visser 1998, Smith and Moore 2005). Mating success notwithstanding, early arrival and breeding might thus be advantageous per se, e.g. by giving juveniles sufficient time to mature. Furthermore, there are advantages accruing from territory/resource holding potential or other competitive asymmetries (Parker 1974, Kokko et al. 2006, Kelly 2008), which might be necessary for additional mating in polyterritorial males (Alatalo and Lundberg 1984, Zając et al. 2008a, Reudink et al. 2009b). Gauging the importance of each direct and indirect factor is difficult when analysed in isolation, in short-term studies.

The aim of this study is to determine male fitness consequences (in terms of mated females and the number of fledglings and recruited young) in relation to age, arrival date, territory quality and sexual characters (song and polyterritorial behaviour) in sedge warblers *Acrocephalus schoenobaenus*. Males compete intensively for territories in this species (Catchpole 1972, Zając et al. 2006, 2015), pre-empting them on the basis of vegetation cover, which influences recruitment success (Zając et al. 2006, 2008b). The same sites are preferred and repeatedly occupied over the years by the same or different males, and site occupancy rate is correlated with recruitment success (Zając et al. 2008b). Moreover, older males occupy higher quality territories (Zając et al. 2011), while additional territories are needed for polygynous mating (Zając et al. 2008a, 2015).

The sedge warbler is well known for the intensive sexual selection based on elaborate song displays, which influence male mating success (Catchpole 1980, Bell et al. 1997, Buchanan and Catchpole 1997). Populations differ in the level of polygyny (Zając and Solarz 2004). However, published data suggest that, apart from the effect of sheer territory size on the pairing date (Buchanan and Catchpole 1997), sexual selection operates in this species without reference to territory quality. Instead, it is founded on male sexual attractiveness (song complexity), indicative of male individual genetic diversity (Marshall et al. 2003), paternal effort (Buchanan and Catchpole 2000) and a parasite load (Buchanan et al. 1999), which affects the demography of the species (Bielański et al. 2017). Since song repertoire (Zając et al. 2015) and territory quality (Zając et al. 2006, 2008b) correlate with arrival date, male attractiveness and territory quality may also be correlated. Thus, assessing the role of these collinear traits in shaping male fitness requires a quantitative evaluation within a model integrating all the variables of the system. Here, we propose to use path models to disentangle the relative influences of age, arrival date, territory quality, male sexual activity (song and polyterritorial behaviour) on the mating, fledging and local recruitment success of males.

Material and methods

Study area and field procedures

Data were collected in 2002–2012 (excluding 2010, the year of catastrophic floods in the study area) in wetlands in the River Nida valley, southern Poland (50°33′–50°35′N, 20°28′–20°32′E). The study plot (36.5 ha) contained patches of common reed *Phragmites australis*, cattail *Typha latifolia* and sweetgrass *Glyceria maxima*, surrounded by extensive beds of sedge (*Carex* spp.) and meadows (Zając et al. 2008b, 2015). Before the start of each breeding season, the land cover of the study area was precisely mapped with GPS (submeter accuracy) and classified according to the main vegetation types. These mapped patches were then imported into ArcGIS ver. 10.1 software to create a fine-scale map, used for the fieldwork throughout the season. Male sedge warblers, usually turning up in late April to early May, were mist-netted and colour-ringed as soon as they were sighted in the study plot. Detailed surveys were carried out three times a week, during which the positions and behaviour of colour-ringed individuals were mapped. The frequency of our visits to the study plot ensured that the discrepancy between arrival and date of capture did not exceed two days. Just before capture, 10–15 min of continuous, spontaneous territorial song was recorded for each male between 06:00 and 09:00 h, using Denon FN-F20R and Marantz PMD660 digital recorders equipped with a Sennheiser ME 67 microphone. Recording was paused when a male's singing was interrupted by foraging, conflicts or other disturbances.

During each spring, we trapped an average of 40 males (range: 19–74), 26 of which (66%; range: 12–48) became mated. A male was considered mated when seen guarding a female, subsequently confirmed by observations of nests or of young being fed in his territory. Nests were found by observing the behaviour of the parents (mainly females carrying material for nest construction). The position of each nest was marked on the map, and the nests were monitored to record clutch size and hatching date. On the eighth day after hatching, nestlings were ringed, enabling identification of local next-season recruits. If there were no clear indications of subsequent failure, the nest was regarded as successful.

Data processing

Arrival date

Arrival date (i.e. first observation of each male in the study area) was made comparable between seasons by standardizing to the arrival date of the earliest male of the season (day 0). We excluded males that arrived later than 45 days after the earliest arriving male in a given year, owing to the possible influx of males that had lost their first broods in neighbouring areas earlier in the season.

Territory quality

Territory quality was measured as the percentage of the total cover of cattails and common reeds in circular spatial buffers 30 m in radius, delimited on a digital vegetation map in ArcGIS ver. 10.1 around all the songposts of males on the first day after their arrival (Zając et al. 2006). These tall wetland plants are preferred by males during settlement, and their proportion in the territory is correlated with recruitment success in the studied population (Zając et al. 2006, 2008b).

Song repertoire

We analysed the song recordings using Avisoft-SASLab Pro ver. 4.4. Visual inspection of the spectrogram made for the whole recording of each male enabled a ca 3 min. section with the most complex and variable songs to be selected. This was done by one person (WB) for the whole sample of males. Complete, uninterrupted songs in this section were then extracted (treating intervals longer than 1 s as separating individual songs) to give up to 60 s of songs (excluding the breaks between songs). We defined the male's repertoire as the number of distinct types of syllable extracted in this part of the spectrogram (see Catchpole and Slater 2008 for definitions of 'syllable' and 'repertoire'). To control for the effect of differences in song analyses between researchers analysing different seasons, we scored a male's repertoire as the percentage of the number of unique syllables of the male with the greatest repertoire for a given season.

Polyterritoriality

There were on average 4.1 polyterritorial males during the breeding season (range: 2–7) and polyterritorial males constituted 19% of breeding males. According to Zając et al. (2008a), polyterritorial behaviour is a prerequisite for polygyny in the sedge warbler, which is also confirmed by the current data ($\chi^2 = 16.96$, df = 1, $p < 0.0001$). We therefore included male polyterritoriality as a behavioural binary trait (1 – polyterritorial, 0 – not polyterritorial) in the analysis. Males were considered polyterritorial if they resumed singing and flight displays on a new, clearly separate territory while their mates were incubating on the primary one. Moreover, when displaying on the second territory, males were not active on the first one (Zając et al. 2008a). The quality of the second territory was not taken into consideration because 1) it was positively correlated with but always inferior to the first one of the same male, and 2) the qualities of secondary territories and the territories of non-breeding males did not differ significantly (Zając et al. 2008a). This suggests that the quality of the second territory reflected the quality of the first and was of little relevance to the success of polygynous matings.

Male age

Precise determination of age is not possible in adult sedge warblers (Svensson 1992, Jenni and Winkler 1994). However, since 82% of the 114 local recruits, recorded in our population between 1996 and 2012, were detected in their second year of life, we assumed on the basis of a previous paper (Bielański et al. 2017) that new settlers were dominated by second-year individuals. Thus, all first-time trapped, unringed birds and second-year local recruits (i.e. in their first breeding season) were pooled into the same artificial age class two (i.e. 'naïve birds'). Birds retrapped in subsequent years were then classified according to consecutive age classes: three, four and so on. The oldest birds recorded so far in our population were seven years old, but the maximum age of males in the database used here was five years.

Mating, fledging and recruitment success

The number of females mating with a male during the season was a measure of his mating success (0 – unmated, 1 – monogamous, 2 – polygynous). If the male was not polygamous and re-mated with another female after the first brood had been lost, he was still assigned the same mating success value as a monogamous male (i.e. one female). The total number of fledglings reared successfully in all nests of a male within a season was used as a measure of his fledging success (scores 0–11). The number of offspring raised by a male in a given season, recruited locally in subsequent seasons, was assigned to each male and used as a measure of recruitment success (scores 0–4).

Statistical analysis

The full dataset for path analyses contained 180 records of 160 males (19 males appear multiple times in the database: 18 males in two seasons, 1 male in three seasons). In order to disentangle the significance of individual male quality from the effects of territory quality on male fitness we applied two models: A) one analysing the influence of male quality features (age, arrival date and song repertoire) on three measures of fitness, i.e. number of mated females, fledglings and local recruits (Fig. 1A), and B) the full path model, which analyses the effects of the same male quality features, polyterritorial behaviour and the quality of the main territory on the same measures of male fitness (Fig. 1B).

We performed path analysis using Mplus ver. 8.6 (Muthén and Muthén 2017). Path analysis is a powerful statistical technique to evaluate ecological and evolutionary hypotheses from observed associations among variables. Hypothesized relationships between variables are represented by a directional path diagram and evaluated statistically. Thus, one can include mediating variables (i.e. variables linking independent and dependent variables) and simultaneously examine

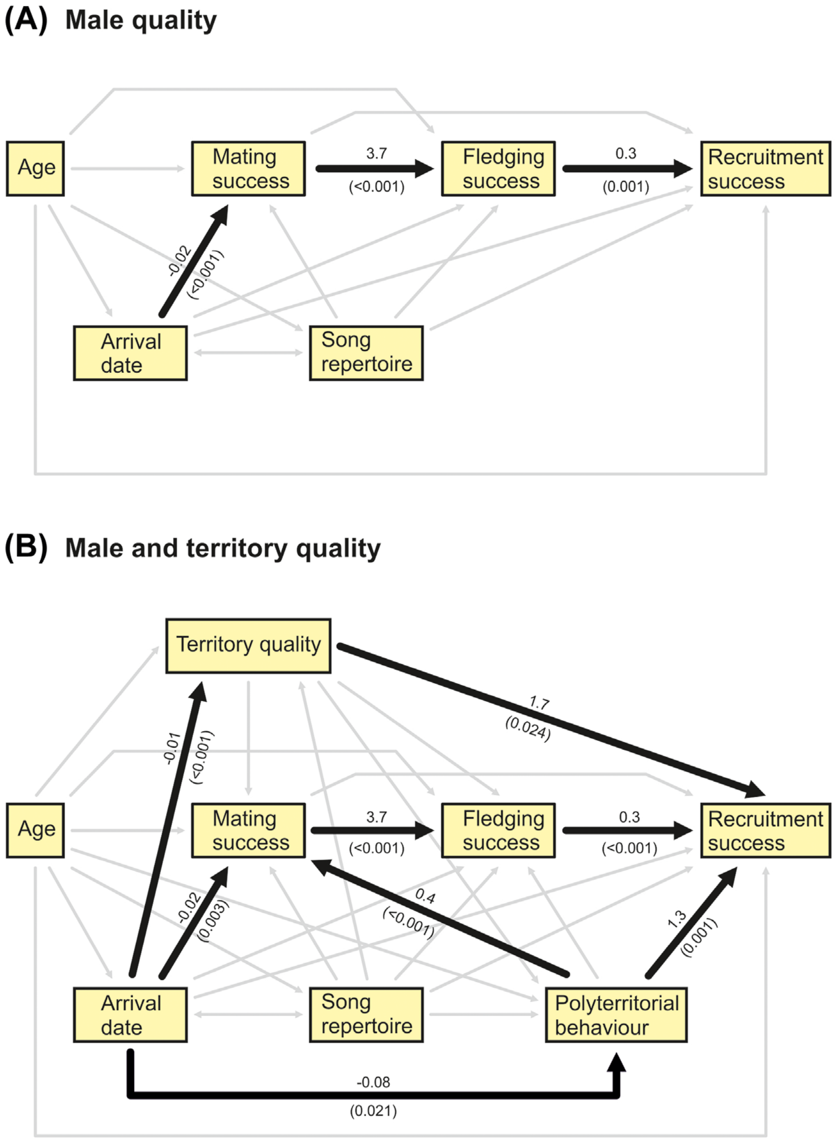

Figure 1. Path analysis of male sedge warblers' age, arrival date, territory quality, polyterritoriality and song repertoire size in relation to their mating, fledging and recruitment success, southern Poland, 2002–2012. (A) The model analysing the influence of male age, arrival date and song repertoire on the measures of their reproductive success: number of mated females, fledglings and local recruits; (B) the full model, which analyses the effects of both individual male features (age, arrival date, song repertoire) and factors related to his territorial activity (the quality of the main territory and the binary variable indicating his polyterritorial behaviour) on the same measures of male fitness. The sample size for both models is 180 records of 160 males (longitudinal data). Generated with Mplus ver. 8.6; a non-standardized path coefficient and statistical significance (in parentheses) are given for significant relationships; black arrows – significant relationships ($p < 0.05$); grey arrows – nonsignificant relationships.

both the direct and indirect effects of the model's variables (Shipley 2000). This is the main advantage of path analysis over other 'classical' multivariate approaches (e.g. GLM). We carried out longitudinal path analyses with a multilevel approach (two-level random). The nesting structure (clustering) was specified using the males' IDs. The count or binomial nature of the following variables, i.e. age (count), polyterritorial behaviour (binomial), mating success (count), fledging success (count) and recruitment success (count), was handled with the COUNT option. In addition, recruitment success was marked as a zero-inflated Poisson variable. Arrival date, territory quality and song repertoire were included in the analysis as continuous variables. All variables were set as user-observed (i.e. directly measured), within-subject (time-dependent) variables. In each model, the expectation maximization (EM) optimization algorithm was used, and the parameters were estimated using the maximum likelihood robust estimator (MLR), which is robust to non-normality and non-independence of observations. In Mplus, standardized path coefficients are not available for models with categorical, nominal, count or continuous-time survival mediating or predictor variables (Muthén and Muthén 2017), so our models present unstandardized coefficients (Pc). Since unstandardized coefficients cannot be directly compared, the dependence structure between the variables in the model is only shown by presenting and discussing significant paths ($p < 0.05$). Descriptive statistics and interrelationships between all the variables, as well as the full results of the path models are provided in the Supporting information.

Results

The first model (Fig. 1A), which analyses the influence of male quality features on male fitness, reveals a straightforward relationship, in which only arrival date governs mating success (Pc = −0.02), and which further influences the number of fledglings (Pc = 3.7) and local recruits (Pc = 0.3). In contrast, neither age nor song repertoire are significantly associated with the other male fitness components.

The second model, which combines factors related to male quality, behaviour and territory quality, shows a more complicated picture (Fig. 1B). Arrival date has a direct and very significant influence on the main territory quality (the earlier the male, the better the territory; Pc = −0.01), mating success (Pc = −0.02) and also on polyterritoriality (the earlier the male, the more frequently he has a second territory; Pc = −0.08). The 'fitness' path (mating → fledging → recruitment) remains very significant: mating success determines the number of fledglings (Pc = 3.7), which in turn significantly influences the number of recruits (Pc = 0.3). Mating success is significantly influenced by polyterritorial behaviour (Pc = 0.4), whereas territory quality does not directly influence mating success or fledging success. Recruitment is influenced by polyterritorial behaviour (Pc = 1.3) and territory quality (Pc = 1.7). Age is the least influential factor in the model as no significant relations were found.

Discussion

Using path analysis, we comprehensively analysed the direct and indirect associations among a set of variables, including male quality, behaviour and territory quality on a number of fitness components. The analysis revealed latent and complex relationships (Fig. 1B). The relationship between male displays, mating success and male fitness in sedge warblers was commonly understood to result from female preference for more complex sexual signals (Catchpole 1980, Bell et al. 1997, Buchanan and Catchpole 1997, Beynon et al. 2004). Our path analysis revealed that ultimate fitness could also stem directly from a sexually selected form of territorial behaviour, which seems to explain recruitment better than song complexity. Polyterritorial behaviour also indirectly affected recruitment through mediating variables like mating success and fledging success. Another non-obvious relation found in our study was that territory quality is not related to female preference as expected by classical models (Emlen and Oring 1977), but contributes directly to the post-fledging survival of the young.

Our path model, comprising both male features, territorial behaviour and habitat quality (Fig. 1B), clearly highlights three factors that significantly affect the 'fitness' path (mating → fledging → recruitment) of male sedge warblers: 1) arrival date, 2) territory quality and 3) polyterritorial behaviour.

Arrival date

The timing of male arrival impacts on crucial aspects of the sedge warbler's breeding system: pre-emption of territories, mating success and behaviour leading to polygyny. It is striking that no relationship between territory quality and mating success has been demonstrated, so in contrast to the classical polygyny threshold model (Verner and Wilson 1966, Orians 1969), it seems that females pay little attention to the quality of the main territory when taking mating decisions. The influence of arrival date on polyterritorial behaviour, and along this path on mating success, may explain how males acquire additional, polygynous matings, which gives them the opportunity to increase their reproductive success (cf. Canal et al. 2020, 2021). Last but not least, arrival date significantly governs territory pre-emption (based on territory quality), with its positive consequences for recruitment. This leads to the non-obvious conclusion that, in contrast to classical models, male's success is governed by resources (space and vegetation cover), whereas female decisions are driven by sexual selection.

Arrival date is assumed to reliably reflect a male's individual quality, as individuals endure rapid, long-distance spring migration and unpredictable, often harsh, early spring conditions upon arrival at the breeding grounds (Møller 1994, Møller et al. 2004, Ninni et al. 2004). Thus, the influence of arrival date on all three crucial factors explaining ultimate male fitness (territory quality, mating, second territory) should not be surprising. Early arrival gives a competitive advantage in territory pre-emption and mating opportunities, but many other factors not included in our models may provide additional, positive synergic effects (Reudink et al. 2009a, b, Cooper et al. 2011). Early arrival often determines an early breeding onset (Møller 1994, Ninni et al. 2004, Smith and Moore 2005, Cooper et al. 2011). In sedge warblers, earlier male arrival correlates not only with more matings (this study), but also with an earlier mating date (Zając et al. 2015). Arrival date has a strong influence on fledging and ultimately on recruitment success, which declines during the season in a number of temperate species (Verhulst and Nilsson 2008). The decline is attributed mainly to such proximate environmental factors as increasing predation pressure (Naef-Daenzer et al. 2001) and diminishing food availability later in the season (Verboven and Visser 1998, Grüebler and Naef-Daenzer 2008). Moreover, earlier fledging leaves more time for the young to mature, improve their condition and foraging experience (Tarof et al. 2011, Tomotani et al. 2016), moult (Helm and Gwinner 2001, Pulido and Coppack 2004) and prepare for a successful migration (Mitchell et al. 2012, Raja-aho et al. 2017). A longer post-fledging period can also benefit local recruitment in that suitable breeding habitats and nest sites can be prospected for prior to autumn migration (Reed et al. 1999, Davis and Stamp 2004, Mitchell et al. 2010). Arrival date may be subject to even stronger natural selection because of the time-constrained opportunity for raising second and replacement broods (Møller et al. 2010, Cooper et al. 2011, Zając et al. 2015, Morrison et al. 2019), which can significantly increase the production of recruits.

Territory quality

Sites with tall wetland vegetation are preferred and preempted by male sedge warblers. The earlier the males arrive, the greater the proportion of such vegetation within their territories, and the final path model suggests that territory quality directly influences the number of recruits. A larger area of tall wetland vegetation may secure food for the young (Bibby et al. 1976, Chernetsov 1998, Chernetsov and Manukyan 2000), but it can also ensure their survival as the dense cover of tall stems offers protection against predators (Ille and Hoi 1995, Aebischer et al. 1996, Graveland 1999). Our preliminary telemetry data of sedge warbler males showed that they roost overnight in dense reedbeds during the settlement period. It is well known that other birds, like wagtails, swallows and starlings, use reedbeds for communal roosting (Bibby and Lunn 1982, Kiviat 2019), demonstrating that this habitat is important in providing shelter and safety. In support of this statement, research by Nowak (2007) at the same study site showed that flightless sedge warbler fledglings remained at distances of up to 70 m from the nest for about two weeks. At this age, their wing feathers are almost fully grown and they then start to disperse significantly further afield. Fledglings mostly prefer patches of reed but also cattail and sweetgrass, actively moving to areas with larger proportions of such tall wetland vegetation even from remote territories, whereas the meadow and sedge communities that prevail in the study area appear to be avoided. Moreover, the share of distinct vegetation types in the male's territory is similar and highly correlated with their proportion in a 30 m buffer zone around the nest (Nowak 2007). Hence, males may acquire high-quality territories to secure future juvenile survival, which explains why the amount of tall wetland vegetation directly influences offspring recruitment rather than mating or fledging success.

Aphids are important for the condition of sedge warblers during migration (Bibby et al. 1976, Bibby and Green 1981), and appear in reedbeds later in the season, after the development of fresh stems. Their availability, related to the area of reeds within the territory, is expected to have only a slight influence on female fecundity and nestling feeding efficiency, but a significant influence on the condition of juveniles, their pre-migratory fuelling and subsequent survival (Chernetsov 1998, Chernetsov and Manukyan 2000). Hence, this could further explain why territory quality directly influences recruitment.

Polyterritorial behaviour

Our analysis confirms that polyterritorial behaviour significantly affects male reproductive success. Figure 1B shows that mating success depends on a binary factor determining whether a male does or does not hold an additional territory on which he displays. It has been demonstrated that this behaviour is a necessary prerequisite for polygyny, not only in the sedge warbler (Zając et al. 2008a) but also in other species (Alatalo and Lundberg 1984, Secunda and Sherry 1991), and allows a male to enhance his mating success. Polyterritorial behaviour also influences recruitment directly, a possible result of the superior quality of early males: the male's ability to defend another territory indicates that he can prolong the display period with long display flights and has sufficient competitive abilities to control both territories (cf. Reudink et al. 2009b).

Our path model revealed no significant effect of song repertoire on either mating success or sexual behaviour, although we had reported its relation to arrival date in a previous study (Zając et al. 2015). Thus, the outcomes of this path analysis do not conform directly to Catchpole's results regarding female preference for song complexity (Catchpole 1980, Catchpole et al. 1984), although this could have resulted from too small a sample size (or the insufficient characterization of repertoire sizes). In our spatially fluctuating and dispersed population (Zając et al. 2008b), the 'display arena' function of males' second territories could greatly facilitate matings in terms of 'passive attraction' (Parker 1982, 1983).

An intriguing property of the breeding systems of many migratory birds is that the males' mating success is related to their arrival date (review in the Introduction). Although sedge warbler females arrive on average 1–2 weeks after the males (Borowiec 1999, Zając et al. 2015), the distributions of male and female arrival dates in the studied population largely overlap (Fig. 1 in Zając et al. 2015). Assuming that male arrival date is a condition-dependent trait, honestly reflecting male quality (Møller 1994, Kokko 1999), females can apply certain cues reflecting the time since the establishment of the male in his territory (Saino et al. 2010, Spottiswoode and Saino 2010). However, the issue of male quality is very relevant to females that mate late with males displaying on secondary territories, when unmated males are still available. These late females cannot usually directly perceive the exact arrival of the earliest males. In fact, polygynous females in the studied population mated later than others (monogamous and double-brooded) but with earlier-arriving males (Zając et al. 2015). Thus, females must have perceived a male's quality indirectly, probably from his courtship behaviour, reinforced by his singing and flight displays on a separate polyterritory (cf. Lifjeld and Slagsvold 1988).

The results of our models are consistent with the 'good genes' hypothesis regarding female choice of male quality, reflected by arrival date and resource holding potential as regards polyterritoriality. However, they stand in contrast to classical models (the 'age indicator' mechanism; Trivers 1972, Kokko 1998, Jennions et al. 2001), because the age of male sedge warblers did not influence mating success, nesting success or recruitment. This might stem from methodological limitations, as it was not possible to precisely specify the age of sedge warblers. Previous suggestions that age influences both territory (Zając et al. 2011) and individual quality (Bielanski et al. 2017) were not confirmed by our model.

Concluding remarks

Mating systems should not be analysed solely in simple predictor-response designs, because interactions found in the wild are usually impossible to account for using simple comparisons. Our path model suggests that a male's reproductive success depends above all on his individual quality as reflected in arrival date, the feature that mediates almost all components of the system. The mating success of a male was based on territorial activity, which was linked to sexual selection rather than to securing food for the young. The model implies that males, when pre-empting territories, influence the local recruitment of their offspring most likely by ensuring safety for the fledged young. Research priorities for future studies should take into account our results' suggestion that the factors crucial to reproductive success in sedge warbler males occur before and after the nesting period.

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Permits – The research reported here complied with all the legal ethical requirements and legislation of Poland. Field procedures were carried out under the permits from the Local Ethical Committee in Krakow (no. 37/OP/2004 and 24/2010).

Author contributions

Wojciech Bielański: Conceptualization (supporting); Data curation (lead); Formal analysis (equal); Funding acquisition (supporting); Investigation (equal); Methodology (equal); Project administration (equal); Resources (equal); Visualization (lead); Writing – original draft (equal); Writing – review and editing (lead). **Adam M. Ćmiel**: Conceptualization (supporting); Data curation (supporting); Formal analysis (equal); Investigation (supporting); Methodology (equal); Resources (supporting); Writing – review and editing (supporting). **Tadeusz A. Zając**: Conceptualization (lead); Formal analysis (supporting); Funding acquisition (lead); Investigation (equal); Methodology (equal); Project administration (equal); Resources (equal); Writing – original draft (equal); Writing – review and editing (supporting).

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Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.ffbg79czb> (Bielański et al. 2022).

Supporting information

The Supporting information associated with this article is available with the online version.

References

Aebischer, A., Perrin, N., Krieg, M., Studer, J. and Meyer, D. R. 1996. The role of territory choice, mate choice and arrival date on breeding success in the Savi's warbler *Locustella luscinioides*. – J. Avian Biol. 27: 143–152.

Alatalo, R. V. and Lundberg, A. 1984. Polyterritorial polygyny in the pied fycatcher *Ficedula hypoleuca*: evidence for the deception hypothesis. – Ann. Zool. Fenn. 21: 217–228.

Alatalo, R. V., Carlson, A., Lundberg, A. and Ulfstrand, S. 1981. The conflict between male polygamy and female monogamy: the case of the pied flycatcher. – Am. Nat. 117: 738–753.

Alatalo, R. V., Lundberg, A. and Ståhlbrandt, K. 1984. Female mate choice in the pied flycatcher *Ficedula hypoleuca*. – Behav. Ecol. Sociobiol. 14: 253–261.

Arvidsson, B. L. and Neergaard, R. 1991. Mate choice in the willow warbler – a field experiment. – Behav. Ecol. Sociobiol. 29: 225–229.

Bell, B. D., Borowiec, M., McConkey, K. R. and Ranoszek, E. 1997. Settlement, breeding success and song repertoires of monogamous and polygynous sedge warblers *Acrocephalus schoenobaenus*. – Vogelwarte 39: 87–94.

Beynon, M. J., Buchanan, K. L. and Tang, Y. C., 2004. The application of a fuzzy-rule-based system in an exposition of the antecedents of sedge warbler song flight. – Expert Syst. 21: 1–10.

Bibby, C. J. and Green, R. E. 1981. Autumn migration strategies of reed and sedge warblers. – Ornis Scand. 12: 1–12.

Bibby, C. J. and Lunn, J. 1982. Conservation of reed beds and their avifauna in England and Wales. – Biol. Conserv. 23: 167–186.

Bibby, C. J., Green, R. E., Pepler, G. R. M. and Pepler, P. A. 1976. Sedge warbler migration and reed aphids. – Brit. Birds 69: 384–399.

Bielański, W., Biedrzycka, A., Zając, T., Ćmiel, A. and Solarz, W. 2017. Age-related parasite load and longevity patterns in the sedge warbler *Acrocephalus schoenobaenus*. – J. Avian Biol. 48: 997–1004.

Bielański, W., Ćmiel, A. M. and Zając, T. A. 2022. Data from: Interactive effects of arrival date, territory quality and male polyterritorial behaviour on the mating system of the sedge warbler *Acrocephalus schoenobaenus*: a path analysis. – Dryad Digital Repository, <https://doi.org/10.5061/dryad.ffbg79czb>.

Borowiec, M. 1999. Biology and breeding ecology of a population of sedge warbler *Acrocephalus schoenobaenus* in the vicinity of Wrocław. Breeding behaviour and evolutionary strategies of males and females. – Proc. Zool. Univ. Wratislav. 33: 1–92.

Buchanan, K. L. and Catchpole, C. K. 1997. Female choice in the sedge warbler *Acrocephalus schoenobaenus*: multiple cues from song and territory quality. – Proc. R. Soc. B 264: 521–526.

Buchanan, K. L. and Catchpole, C. K. 2000. Song as an indicator of male parental effort in the sedge warbler. – Proc. R. Soc. B 267: 321–326.

Buchanan, K. L., Catchpole, C. K., Lewis, J. W. and Lodge, A. 1999. Song as an indicator of parasitism in the sedge warbler. – Anim. Behav. 57: 307–314.

Canal, D., Jovani, R. and Potti, J. 2012. Multiple mating opportunities boost protandry in a pied flycatcher population. – Behav. Ecol. Sociobiol. 66: 67–76.

Canal, D., Schlicht, L., Manzano, J., Camacho, C. and Potti, J. 2020. Socio-ecological factors shape the opportunity for polygyny in a migratory songbird. – Behav. Ecol. 31: 598–609.

Canal, D., Schlicht, L., Santoro, S., Camacho, C., Martínez-Padilla, J. and Potti, J. 2021. Phenology-mediated effects of phenotype on the probability of social polygyny and its fitness consequences in a migratory passerine. – BMC Ecol. Evol. 21: 1–12.

Catchpole, C. K. 1972. A comparative study of territory in the reed warbler *Acrocephalus scirpaceus* and sedge warbler *A. schoenobaenus*. – J. Zool. 166: 213–231.

Catchpole, C. K. 1980. Sexual selection and the evolution of complex songs among European warblers of the genus *Acrocephalus*. – Behaviour 74: 149–166.

Catchpole, C. K. and Slater, P. J. B. 2008. Bird song: biological themes and variations, 2nd ed. – Cambridge Univ. Press, Cambridge.

Catchpole, C. K., Dittami, J. and Leisler, B. 1984. Differential responses to male song repertoires in female songbirds implanted with oestrodiol. – Nature 312: 563–564.

Chernetsov, N. 1998. Habitat distribution during the post-breeding and post-fledging period in the reed warbler *Acrocephalus scirpaceus* and sedge warbler *A. schoenobaenus* depends on food abundance. – Ornis Svec. 8: 77–82.

Chernetsov, N. and Manukyan, A. 2000. Foraging strategy of the sedge warbler *Acrocephalus schoenobaenus* on migration. – Vogelwarte 40: 189–197.

Cooper, N. W., Murphy, M. T., Redmond, L. J. and Dolan, A. C. 2011. Reproductive correlates of spring arrival date in the eastern kingbird *Tyrannus tyrannus*. – J. Ornithol. 152: 143–152.

Davis, J. M. and Stamps, J. A. 2004. The effect of natal experience on habitat preferences. – Trends Ecol. Evol. 19: 411–416.

Emlen, S. T. and Oring, L. W. 1977. Ecology, sexual selection and the evolution of mating systems. – Science 197: 215–223.

Ford, N. L. 1996. Polyterritorial polygyny in North American passerines. – J. Field Ornithol. 67: 10–16.

Graveland, J. 1999. Effect of reed cutting on density and breeding success of reed warbler *Acrocephalus scirpacaeus* and sedge warbler *A. schoenobaenus*. – J. Avian Biol. 30: 469–482.

Grüebler, M. U. and Naef-Daenzer, B. 2008. Fitness consequences of pre- and post-fledging timing decisions in a double-brooded passerine. – Ecology 89: 2736–2745.

Halupka, L., Dyrcz, A. and Borowiec, M. 2008. Climate change affects breeding of reed warblers *Acrocephalus scirpaceus*. – J. Avian Biol. 39: 95–100.

Hasselquist, D. 1998. Polygyny in great reed warblers: a long-term study of factors contributing to male fitness. – Ecology 79: 2376–2390.

Helm, B. and Gwinner, E. 2001. Nestling growth and post-juvenile moult under a tight seasonal schedule in stonechats *Saxicola torquata maura* from Kazakhstan. – Avian Sci. 1: 31–42.

Hochachka, W. 1990. Seasonal decline in reproductive performance of song sparrows. – Ecology 71: 1279–1288.

Ille, R. and Hoi, H. 1995. Factors influencing fledgling survival in the marsh warbler *Acrocephalus palustris*: food and vegetation density. – Ibis 137: 586–589.

Jenni, L. and Winkler, R. 1994. Moult and ageing of European passerines. – Academic Press.

Jennions, M. D., Møller, A. P. and Petrie, M. 2001. Sexually selected traits and adult survival: a meta-analysis. – Q. Rev. Biol. 76: 3–36.

Jones, T. B., Drake, A. and Green, D. J. 2014. Individual quality explains association between plumage colouration, arrival dates and mate acquisition in yellow warblers *Setophaga petechia*. – BMC Ecol. 14: 13.

Kelly, C. D. 2008. The interrelationships between resource-holding potential, resource-value and reproductive success in territorial males: how much variation can we explain? – Behav. Ecol. Sociobiol. 62: 855–871.

Kipper, S., Mundry, R., Sommer, C., Hultsch, H. and Todt, D. 2006. Song repertoire size is correlated with body measures and arrival date in common nightingales, *Luscinia megarhynchos*. – Anim. Behav. 71: 211–217.

Kiviat, E. 2019. Organisms using *Phragmites australis* are diverse and similar on three continents. – J. Nat. Hist. 53: 1975–2010.

Kokko, H. 1998. Good genes, old age and life-history trade-offs. – Evol. Ecol. 17: 739–750.

Kokko, H. 1999. Competition for early arrival in migratory birds. – J. Anim. Ecol. 68: 940–950.

Kokko, H., López-Sepulcre, A. and Morrell, L. J. 2006. From hawks and doves to self-consistent games of territorial behavior. – Am. Nat. 167: 901.

Lampe, H. M. and Espmark, Y. O. 1994. Song structure reflects male quality in pied flycatchers, *Ficedula hypoleuca*. – Anim. Behav. 47: 869–876.

Langefors, Å., Hasselquist, D. and von Schantz, T. 1998. Extra-pair fertilizations in the sedge warbler. – J. Avian Biol. 29: 134–144.

Lifjeld, J. T. and Slagsvold, T. 1988. Female pied flycatchers *Ficedula hypoleuca* choose male characteristics in homogeneous habitats. – Behav. Ecol. Sociobiol. 22: 27–36.

Lozano, G. A., Perreault, S. and Lemon, R. E. 1996. Age, arrival date and reproductive success of male American redstarts *Setophaga ruticilla*. – J. Avian Biol. 27: 164–170.

Marshall, R. C., Buchanan, K. L. and Catchpole, C. K. 2003. Sexual selection and individual genetic diversity in a songbird. – Proc. R. Soc. B 270: S248–S250.

Mitchell, G. W., Newman, A. E. M., Wikelski, M. and Norris, D. R. 2012. Timing of breeding carries over to influence migratory departure in a songbird: an automated radiotracking study. – J. Anim. Ecol. 81: 1024–1033.

Mitchell, G. W., Taylor, P. D. and Warkentin, I. G. 2010. Assessing the function of broad-scale movements made by juvenile songbirds prior to migration. – Condor 112: 644–654.

Møller, A. P. 1986. Mating systems among European passerines: a review. – Ibis 128: 234–250.

Møller, A. P. 1994. Phenotype-dependent arrival time and its consequences in a migratory bird. – Behav. Ecol. Sociobiol. 35: 115–122.

Møller, A. P., Brohede, J., Cuervo, J. J., de Lope, F. and Primmer, C. 2003. Extrapair paternity in relation to sexual ornamentation, arrival date and condition in a migratory bird. – Behav. Ecol. 14: 707–712.

Møller, A. P., de Lope, F. and Saino, N. 2004. Parasitism, immunity and arrival date in migratory bird, the barn swallow. – Ecology 85: 206–219.

Møller, A. P., Flensted-Jensen, E., Klarborg, K., Mardal, W. and Nielsen, J. T. 2010. Climate change affects the duration of the reproductive seasons in birds. – J. Anim. Ecol. 79: 777–784.

Morrison, C. A., Alves, J. A., Gunnarsson, T. G., Þórisson, B. and Gill, J. A. 2019. Why do earlier-arriving migratory birds have better breeding success? – Ecol. Evol. 9: 8856–8864.

Muthén, L. K. and Muthén, B. O. 2017. Mplus user's guide, 8th edn. – Muthén and Muthén.

Naef-Daenzer, B., Widmer, F. and Nuber, M. 2001. Differential post-fledging survival of great and coal tits in relation to their condition and fledging date. – J. Anim. Ecol. 70: 730–738.

Ninni, P., de Lope, F., Saino, N., Haussy, C. and Møller, A. P. 2004. Antioxidants and condition-dependence of arrival date in a migratory bird. – Oikos 105: 55–64.

Nowak, K. 2007. Post-fledging dispersal of sedge warblers *Acrocephalus schoenobaenus* in relation to the vegetation structure in the middle Nida wetlands. – MSc thesis, Jagiellonian Univ., Poland, in Polish.

Orians, G. H. 1969. On the evolution of mating systems in birds and mammals. – Am. Nat. 103: 589–603.

Parker, G. A. 1974. Assessment strategy and the evolution of fighting behaviour. – J. Theor. Biol. 47: 223–243.

Parker, G. A. 1982. Phenotype limited evolutionary stable strategy. – In: King's College Sociobiology Group (ed.), Current problems in sociobiology. Cambridge Univ. Press, pp. 173–201.

Parker, G. A. 1983. Mate quality and mating decisions. – In: Bateson, P. (ed.), Mate choice. Cambridge Univ. Press, pp. 141–166.

Pulido, F. and Coppack, T. 2004. Correlation between timing of juvenile moult and timing of migration in the blackcap, *Sylvia atricapilla*. – Anim. Behav. 68: 167–173.

Pulliam, R. H. and Danielson, B. J. 1991. Sources, sinks and habitat selection: a landscape perspective on population dynamics. – Am. Nat. 142: 42–58.

Raja-aho, S., Eeva, T., Suorsa, P., Valkama, J. and Lehikoinen, E. 2017. Juvenile barn swallows *Hirundo rustica* L. from late broods start autumn migration younger, fuel less effectively and show lower return rates than juveniles from early broods. – Ibis 159: 892–901.

Reed, J. M., Boulinier, T., Danchin, E. and Oring, L. W. 1999. Informed dispersal: prospecting by birds for breeding sites. – Curr. Ornithol. 15: 189–259.

Reudink, M. W., Marra, P. P., Boag, P. T. and Ratcliffe, L. M. 2009b. Plumage coloration predicts paternity and polygyny in the American redstart. – Anim. Behav. 77: 495–501.

Reudink, M. W., Marra, P. P., Kyser, T. K., Boag, P. T., Langin, K. M. and Ratcliffe, L. M. 2009a. Non-breeding season events influence sexual selection in a long-distance migratory bird. – Proc. R. Soc. B 276: 1619–1626.

Saino, N., Rubolini, D., Serra, L., Caprioli, M., Morganti, M., Ambrosini, R. and Spina, F. 2010. Sex-related variation in migration phenology in relation to sexual dimorphism: a test of competing hypotheses for the evolution of protandry. – J. Evol. Biol. 23: 2054–2065.

Secunda, R. C. and Sherry, T. W. 1991. Polyterritorial polygyny in the American redstart. – Wilson Bull. 103: 190–203.

Sergio, F., Blas, J., Forero, M. G., Donázar, J. A. and Hiraldo, F. 2007. Sequential settlement and site dependence in a migratory raptor. – Behav. Ecol. 18: 811–821.

Shipley, B. 2000. Cause and correlation in biology. A user's guide to path analysis, structural equations and causal inference. – Cambridge Univ. Press.

Slagsvold, T. and Lifjeld, J. T. 1988. Plumage colour and sexual selection in the pied flycatcher *Ficedula hypoleuca*. – Anim. Behav. 36: 395–407.

Smith, R. J. and Moore, F. R. 2005. Arrival timing and seasonal reproductive performance in a long-distance migratory landbird. – Behav. Ecol. Sociobiol. 57: 231–239.

Spottiswoode, C. and Saino, N. 2010. Sexual selection and climate change. – In: Møller, A. P., Fiedler, W. and Berthold, P. (eds), Effects of climate change in birds. Oxford Univ. Press, pp. 169–190.

Spottiswoode, C. N., Tøttrup, A. P. and Coppack, T. 2006. Sexual selection predicts advancement of avian spring migration in response to climate change. – Proc. R. Soc. B 273: 3023–3029.

Svensson, L. 1992. Identification guide to European passerines, 4th edn. – L. Svensson, BTO, Thetford.

Tarof, S. A., Kramer, P. M., Hill III, J. R., Tautin, J. and Stutchbury, B. J. M. 2011. Brood size and late breeding are negatively related to juvenile survival in a Neotropical migratory songbird. – Auk 128: 716–725.

Tomotani, B. M., Gienapp, P., Beersma, D. G. M. and Visser, M. E. 2016. Climate change relaxes the time constraints for late-born offspring in a long-distance migrant. – Proc. R. Soc. B 283: 20161366.

Trivers, R. 1972. Parental investment and sexual selection. – In: Campbell, B. (ed.), Sexual selection and the descent of man: 1871–1971. Aldine Press, pp. 136–79.

Verboven, N. and Visser, M. E. 1998. Seasonal variation in local recruitment of great tits: the importance of being early. – Oikos 81: 511–524.

Verhulst, S. and Nilsson, J. A. 2008. The timing of birds' breeding seasons: a review of experiments that manipulated timing of breeding. – Phil. Trans. R. Soc. B 363: 399–410.

Verhulst, S., Van Balen, J. H. and Tinbergen, J. M. 1995. Seasonal decline in reproductive success of the great tit: variation in time or quality? – Ecology 76: 2392–2403.

Verner, J. and Wilson, M. F. 1966. The influence of habitat on mating systems of North American passerine birds. – Ecology 47: 143–147.

von Haartman, L. 1969. Nest-site and evolution of polygamy in European passerine birds. – Ornis Fenn. 46: 1–12.

Zając, T. and Solarz, W. 2004. Low incidence of polygyny in a long term study of the sedge warbler *Acrocephalus schoenobaenus* in natural wetlands (the Nida River Valley, S-Poland). – Acta Ornithol. 39: 47–50.

Zając, T., Bielański, W. and Solarz, W. 2008a. On the song resumption, polyterritorial behaviour and their population context in sedge warbler *Acrocephalus schoenobaenus*. – J. Ornithol. 149: 49–57.

Zając, T., Bielański, W. and Solarz, W. 2011. Territory choice during the breeding tenure of male sedge warblers. – Behav. Ecol. Sociobiol. 65: 2305–2317.

Zając, T., Bielański, W., Ćmiel, A. and Solarz, W. 2015. The influence of phenology on double-brooding and polygyny incidence in the sedge warbler *Acrocephalus schoenobaenus*. – J. Ornithol. 156: 725–735.

Zając, T., Solarz, W. and Bielański, W. 2006. Adaptive settlement in sedge warblers *Acrocephalus schoenobaenus* – focus on the scale of individuals. – Acta Oecol. 29: 123–134.

Zając, T., Solarz, W. and Bielański, W. 2008b. Site-dependent population dynamics: the influence of spatial habitat heterogeneity on individual fitness in the sedge warbler *Acrocephalus schoenobaenus*. – J. Avian Biol. 39: 206–214.