

# On the song resumption, polyterritorial behaviour and their population context in the Sedge Warbler *Acrocephalus schoenobaenus*

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**Abstract** Mating tactics in species with facultative polygyny seem to be very flexible and to depend on local environmental conditions. We analysed the habitat and population contexts of territorial behaviour, associated with polygyny, in a population of Sedge Warblers *Acrocephalus schoenobaenus* inhabiting natural wetlands. Nearly one-third of all breeding males (46 individuals) resumed song after completing their mating with the first female, in order to attract another one. Resuming males were usually the earliest arrivals. There was a continuity in the territorial behaviour between resuming song on first territory and polyterritorial behaviour. Fifty-nine percent of resuming males set up second territories, clearly separated from the first. The second territory was usually located close to the primary female activity area. The quality of the first and second territories were correlated, with second territories being significantly inferior. However, their quality was not significantly different from the territories of non-breeding males. The quality of the second territories was also negatively related to the distance from the first territories. Polyterritorialism was influenced by population numbers: the higher the number of territorial males, the lower the number of second territories settled and the lower their average quality. Although the polygyny frequency in the studied population was very low, polyterritorial males were significantly more likely to be polygynous. We concluded that polygyny frequency can be significantly influenced by population numbers, which might be one of the main

factors responsible for the variability in the mating system in this species.

**Keywords** Polyterritoriality · Polygyny · Territorial behaviour · Territory quality · Timing of breeding

## Introduction

Polygamous mating leads to enormous differences in the reproductive success of males. This diversification is particularly interesting in many monogamous species in which facultative polygyny occurs, owing to shifts from monogamy to polygyny within the species (Ligon 1999, p. 315). In many such species, the proximate mechanism of facultative polygyny consists of a male resuming song after completion of mating with the first female, in order to attract another one (Dyrz 1988). Irrespective of the extent to which the males resuming song are ultimately successful in attracting females, the study of ecological modalities of song resuming still throws light on both the ecological conditions favouring the occurrence of facultative polygyny and on its behavioural mechanism.

In studies on mating behaviour, little attention is paid to its population context, which can readily be expected to affect the nature of the behaviour displayed. For example, if the polyterritorial behaviour is conditional upon the availability of nest boxes, song posts or the event of whole territories required for resuming song, such an availability should be density dependent. In the case of numerous high-density populations which occupy most of the places available for nesting, the frequency of polyterritorialism should be low whereas in a small population it should be higher.

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Time is an essential variable. The male settles on the second territory only after the first female has begun incubation; as such, it happens fairly late in the season when most of the territories have already been occupied. As the best territories are occupied first (Pulliam and Danielson 1991), vacant territories should be of much poorer quality than average. In a small population, the quality of territories still available for settling should be higher than in a large high-density population. The variable quality of available territories is of key importance for the occurrence of polygyny, because the quality of the territory is one of the most important factors which determine the success of polygynous females (Ligon 1999).

The issue of the effect exerted by the spatial distribution of males may throw additional light on the validity of the “deception hypothesis” (von Haartman 1969; Alatalo et al. 1984), where the distance between subsequent territories occupied by a male is considered to be of key importance. The male, singing on a new territory, attracts the next female which, being unaware of the status of the displaying male, mates with him and bears the cost of caring for and feeding the offspring alone, as the male usually only feeds the young in the first nest (“deception”). The issue of “knowledge” of the female depends on the distance between her territory and that of the first female, which in turn depends upon the population number and spatial distribution of the population. If, in the case of small populations, the quality of the second territories matches those occupied first, the female should not be unduly affected by the excessive costs of polygyny.

The aim of this study is to examine the above spatial and population circumstances of the polyterritorial behaviour in a population of the Sedge Warbler *Acrocephalus schoenobaenus*, a species known to have a very variable mating system (Hasselquist and Langefors 1998; Borowiec 1999). Most of the earlier studies on polyterritoriality have been carried out in species occupying nest boxes, i.e. in situations where the distribution of breeding sites in a territory depends upon the decision of the researcher. These species occur in forested areas which limits the possibility for recording details of their behaviour. In contrast, our study was carried out in natural wetlands, where open landscape provides new opportunities to collect data on the effects of numbers and distribution of individuals and on their behaviour.

## Methods

The studies of the Sedge Warbler population were carried out in the period 1996–2005, in the area of natural wetlands occurring in the middle part of the Nida river valley (S Poland; 20°28′–20°32′E, 50°33′–50°35′N). The study

was carried out in a plot named HT (“heterogenous”, also named PPL in our previous publications) covering an area of ca. 26 ha of wetlands, divided by a network of old river beds extending concentrically around a large area of flood wetlands, overgrown by rushes, predominantly common cattail *Typha latifolia*, and somewhat drier areas covered by sedge communities (mainly *Carex gracilis*) or meadows, depending on the degree of moisture (Bielański et al. 2005 for details). Throughout the 10 years of study the plot was inhabited by 186 breeding males.

Before the beginning of each study season, all patches of vegetation throughout the whole area as well as areas covered by open water tables were charted in detail (1-m accuracy) with the use of a GPS (Geoplotter II). The collected data was imported into a GIS system (ArcInfo) where a detailed digital map of the study area was created.

Throughout the study season, the study plot was visited three times a week. All newly arriving males were identified, promptly caught and marked with an aluminium ring with a unique number as well as a unique code of three colour rings. The birds caught were sexed on the basis of cloaca protuberance (Svensson 1992) and released in the same spots. In almost all cases, the territorial males stayed at those places without displaying any alteration in behaviour. Apart from catching the newly arriving individuals, during each further visit to the plot, the place of occurrence and the type of behaviour of each of the previously marked birds was identified and marked on the contour vegetation map (at the scale of 1:2,000).

The following categories of behaviour were distinguished and noted: singing, display flights, mate guarding, territorial conflicts, and nest building.

The date of arrival was used as a measure of the individual quality of a male. As reliable morphological traits enabling age identification of Sedge Warblers are not available, we took into consideration only individuals which were observed in the study area for the first time (likely to be in their second calendar year of life), thus reducing the variability resulting from age to the minimum (Zajac et al. 2006). The analyses included only the mated males, because the occurrence of atypical behaviour of non-mated males is irrelevant to the topic of song resuming and polygyny.

The extent of the territory of a male was determined after the study season in ArcView as a minimum convex polygon (ArcView, Animal Movement Analysis extended function), circumscribed on the observations of its singing and displaying. For each male, the extent of his territory was determined firstly from his arrival until mating with the first female, then secondly after the female started to incubate and the male resumed his display flights and singing. We regarded a male as polyterritorial if (1) his territorial behaviour was unequivocally switched to a new

area of activity, i.e. his second territory was clearly separated in terms of distance from the previous site (there was a clear area without male records in between), and (2) when he was displaying exclusively on the second territory (no displays on the first territory).

In order to determine the quality of habitat occupied by males, the vegetation cover was quantitatively described as a unit of space, being the same for all males. On the first day that singing resumed, circles with a radius of ca. 30 m (i.e. representing roughly the size of the average territory; Król et al. 2002) were drawn on the vegetation map around all observations of a singing male. Then the data concerning proportions of individual types of vegetation in each circle were converted into averages in order to obtain the quantitative characteristics of an average unit occupied by the given male which we later called “site” (Zajac et al. 2006 for details). In the studied population of Sedge Warblers, the positions of territories are directly correlated with the proportion of tall wetland vegetation, namely common reed *Phragmites australis* and common cattail, within the territory, thus this proportion may used as an indicator of the territory quality (Zajac et al. 2006).

The size of the breeding population was determined based on the number of males which had territories and mated females (those for which mate guarding was observed or that had a nest built, or whenever a nest with eggs or nestlings was found). It is only such males that maintain and fiercely defend territories throughout the season, and thus occupy the space within the study area.

The female Sedge Warblers are much harder to observe. In order to minimise breeding losses, the majority of females were not caught at the beginning of the season and hence the number of females with colour rings was usually low at that time. For this reason, the size of the area penetrated by a female was determined based on a sample of

17 individually-marked females, for each of which at least ten observations were made. Out of all the observations for a given female, the two most distant points were chosen and the distance between them measured. Half this distance was then assumed as a maximum radius of a female’s activity around the centre of the territory. The same method was used to determine the radius of the areas of activity for males. The calculations did not include evident extra-territorial forays, but only the observations occurring as a distinct grouping.

**Results**

Territorial behaviour

The average number of breeding pairs in the study area was 18.6 (Table 1). The number of breeding males varied within the range 11–29. Of the 46 instances of song resumption, the males in 19 cases resumed singing on their own territories (Fig. 1a). Fairly often there were characteristic alterations of the territory borders to accompany a new period of displaying (Fig. 1b). In 27 cases, we regarded the behaviour as typical polyterritorialism (Fig. 1c). The average (arithmetic mean) distance between the centre of the second territory and the first one was 98.3 m (SD = 77.73, *n* = 27; Fig. 1e). There were also cases where the second territories had been established at a great distance from the first territory, or cases of multiple secondary territories, although often singing on the latter lasted only a short time. There are no clear criteria by which to decide whether the activity in some places should be regarded as unambiguously territorial (Fig. 1d).

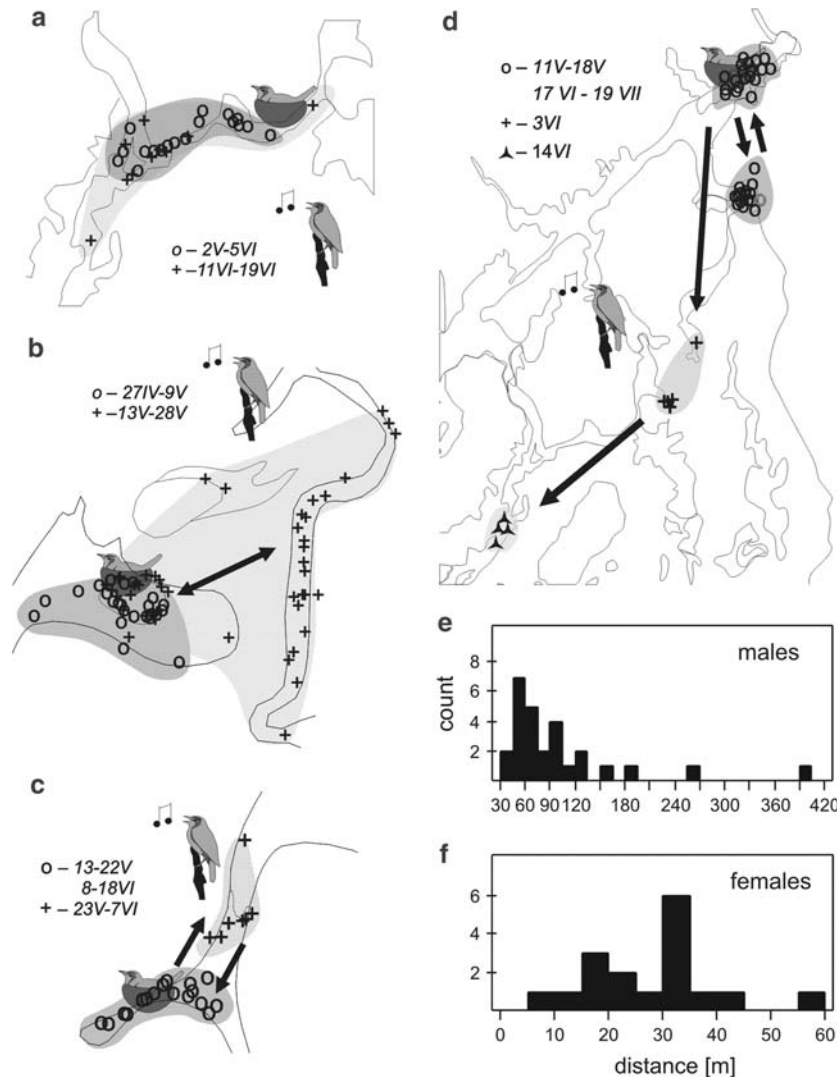
In females, the average radius of activity was 28.3 m (SD = 11.95, *n* = 17; Fig. 1f) from the centre of all

**Table 1** Population size and numbers of males of various mating status in the studied population of Sedge Warblers *Acrocephalus schoenobaenus* from 1996 to 2005

Year	Number of breeding pairs	Number of males resuming song	Number of polyterritorial males	Number of polygynous males	Number of non-breeding males
1996	29	0	0	0	15
1997	23	2	2	0	21
1998	12	5	3	0	36
1999	16	4	2	0	9
2000	13	4	2	0	15
2001	21	5	1	0	18
2002	25	6	2	1	6
2003	11	9	8	2	8
2004	15	5	4	4	11
2005	21	6	3	3	11
Mean	18.6	4.6	2.7	1.0	15.0
SD	6.08	2.41	2.17	1.49	8.72
<i>n</i>	186	46	27	10	150

observations. The radius of activity in displaying males was only slightly greater (36.7 m,  $SD = 36.05$ ,  $n = 186$ ). If it is thus assumed that the territories of the male and female overlap, the centre of the second territory of the male is in terms of distance three times greater on average than the

maximum radius of activity of the female from the first territory. The maximum radius of female activity may vary within a considerable range: for a female active within the smallest area it was 9 m whereas for another female, with a large home range, it reached 59 m. Extra-territorial forays



**Fig. 1** Typical examples of territorial behaviour shown by song resuming males in a population of Sedge Warblers *Acrocephalus schoenobaenus*, in the middle Nida Wetlands. **a** Male code GOG, in 2002 began singing and display flights on this territory on 2 May and ended on 5 June, later observed with a female during mate guarding. The female began incubation around 10 June, the chicks hatched on 26 June. The male resumed singing and display flights (11–19 June), but the range of his territory was close to the first one. This male did not mate again. **b** Male code BWB, established a territory around a cattail patch on 27 April 1998 and was displaying until 9 May. After the female began incubation, he extended the range of his activity (from 13 May) onto a nearby canal and a patch of cattail. However, he displayed in both the new and old territories, precisely up until the date of hatching in the first nest (28 May). This male did not mate again. **c** Male code WWW, in 1998 had sung from 13 to 21 May on the first territory where he mated. The female began incubation of the

eggs on 22 May and the male shifted onto an evidently separate territory some 50 m distance away where he displayed intensively (from 23 May to 7 June). This male did not mate again. **d** Male code ROG, in 2005, after settling on 11 May in a patch of cattail, displayed intensively, occasionally using a song post in another patch of cattail, some 100 m south. From 21 May he stopped displaying although he was observed frequently, including mate guarding in the northern patch where his female built a nest. After incubation started, the male was observed on 3 May, displaying intensively on a small territory situated ca. 260 m south of the nest, and later, on 14 June, intensively displaying again on yet another small territory, situated ca. 400 m southwest of the nest. From 17 June, he returned to the first female. **e** The distribution of distances between the first and the second territory of polygynous males in the studied population. **f** The distribution of female territory radius

extending 60–64 m from the centre of all observations ( $n = 3$ ) were recorded, and in one case even reached 148 m from the centre of activity of the female.

### Song resuming

The average proportion of song resuming in the years of study was 0.30 (SD = 0.218, range: from 0 to 0.82) of the number of breeding males (Table 1). The number of resuming males did not show a significant correlation with the numbers in the breeding population, although a negative trend close to the level of significance was found ( $r = -0.60$ ,  $n = 10$ ,  $P = 0.069$ ).

The males arriving earlier resumed singing significantly more often than other males [logistic regression model: status of male (0, not resuming; 1, resuming song), as the dependent variable vs settlement date and year as independent variables; for the settlement date:  $B = -0.055$ ,  $SE = 0.025$ , Wald statistics = 4.81,  $df = 1$ ,  $P = 0.028$ ,  $n = 112$ ]. Song resumption did not show any correlation with the quality of the first territories of males, calculated as measured by the proportion of tall wetland vegetation, reedmace and common reed [logistic regression model: status of male (0–1), as the dependent variable vs the sum of reedmace and common reed area, within a site and year as independent variables; for vegetation:  $B = 1.635$ ,  $SE = 1.217$ , Wald statistics = 1.81,  $df = 1$ ,  $P = 0.18$ ,  $n = 112$ ].

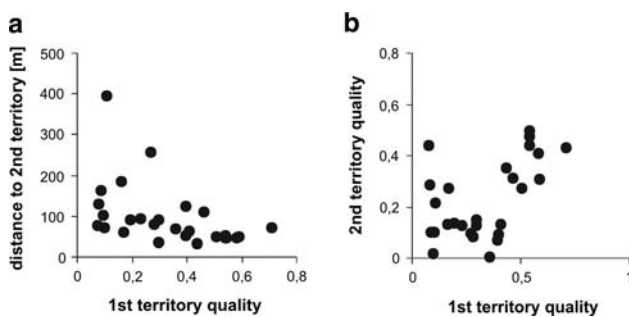
### Polyterritorial behaviour

The average proportion of polyterritorial males compared to the number of breeding males in a given season was 0.19, with great variability between the study years (Table 1); from complete lack of polyterritorialism up to

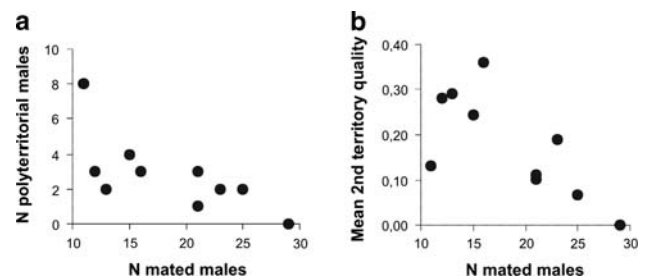
the proportion of polyterritorial males reaching 0.70 (2003 in Table 1). The males which arrived earlier did not establish second territories more frequently than other males [logistic regression model: territorial status of male (0, male with one territory; 1, male with second territory) as the dependent variable vs settlement date and year as independent variables; for the settlement date:  $B = -0.029$ ,  $SE = 0.027$ , Wald statistics = 1.157,  $df = 1$ ,  $P = 0.282$ ,  $n = 112$ ]. Similarly to song resumption, there was no significant effect in terms of the quality of the first territory, on the probability of being polyterritorial [logistic regression model: territorial status of male (0–1: see above) as the dependent variable vs. the sum of reedmace and common reed area within a site and year as independent variables; for vegetation:  $B = 2.328$ ,  $SE = 1.466$ , Wald statistics = 2.520,  $df = 1$ ,  $P = 0.112$ ,  $n = 112$ ].

When the quality of the first and second territories was compared for the same males, the second territories were deemed to be significantly poorer in terms of preferred types of vegetation (Wilcoxon matched pairs test:  $Z = 2.86$ ,  $n = 27$ ,  $P = 0.004$ ). The quality of the second territories ( $n = 27$ ) and territories of the non-breeding males ( $n = 150$ ) occurring in the same population did not differ significantly ( $H_{1,177} = 0.04$ ,  $P = 0.84$ ). The distance between the first and second territory is related to the quality of the first: if the first territory is good, than the distance to the second is smaller ( $r_S = -0.62$ ,  $n = 27$ ,  $p = 0.0006$ ; Fig. 2a). However, despite the differences, the quality of the first and second territory is correlated ( $r_S = 0.44$ ,  $n = 27$ ,  $P = 0.022$ ; Fig. 2b).

During each season, the number of polyterritorial males shows a statistically significant negative correlation with the number of breeding males ( $r = -0.70$ ,  $n = 10$ ,  $P = 0.023$ ; Fig. 3a). Another statistically significant negative correlation was found between the average quality of the second territory and the number of breeding males in a given year ( $r = -0.68$ ,  $n = 10$ ,  $P = 0.030$ ; Fig. 3b).



**Fig. 2** The relationships between the first and second territory quality: **a** the correlation between first territory quality and distance to the second territory, **b** the correlation between first territory quality and second territory quality



**Fig. 3** Effect of population size on a number of territorial males and quality of the second territories: **a** scattergram of numbers of polyterritorial males in relation to the population size of mated males in the years 1996–2005, **b** scattergram of mean second territory quality in given year, in reference to the population size of mated males



## Polygyny

Among 186 males mating throughout the whole period of this study, the significant effect of different territorial behaviour on the probability of polygyny can be seen:

- males resuming ( $n = 46$ ): eight males mated two females each; among the males for whom no observation of song resuming were made ( $n = 140$ ), only two males were polygynous (Fisher exact test,  $P < 0.0001$ ).
- polyterritorial males ( $n = 27$ ): six mated with the second female on the second territory, and among the remaining males in whom no polyterritorialism was observed ( $n = 159$ ), the polygamous status was attained only by four males (Fisher exact test,  $P = 0.001$ ).
- males resuming only in their first territory ( $n = 19$ ): two mated polygynously; whilst eight among the remaining males ( $n = 167$ ) were polygynous. This difference is not statistically significant (Fisher exact test,  $P = 0.27$ ).

In the years when many males resumed singing there was also more males that obtained polygynous mating ( $r = 0.76$ ,  $n = 10$ ,  $P = 0.016$ ).

No statistically significant differences were found in the breeding success for the whole season between primary and secondary females, except for the difference in recorded clutch size, which was close to being statistically significant. Primary females laid on average 6.4 eggs (SD = 1.96) per season (including two second clutches of primary females), whereas the secondary females laid 4.6 eggs (SD = 1.84) per season (Wilcoxon matched pairs test  $Z = 1.89$ ,  $n = 10$ ,  $P = 0.059$ ). The difference disappears at fledging: the primary females fledged 3.9 chicks (SD = 2.88), whereas secondary females fledged 4 chicks (SD = 2.26; Wilcoxon matched pairs test  $Z = 0.21$ ,  $n = 10$ ,  $P = 0.83$ ).

## Discussion

Song resuming was a fairly common phenomenon in the studied population of Sedge Warblers, as ca. one-third of all males resumed singing. A similar proportion of song resuming males was found by Borowiec (1999) and Hasselquist and Langefors (1998) 30 and 38%, respectively. The aim of resumed singing is to obtain additional mating, because the song-resuming males are more often polygynous.

If spring migration represents a process verifying the quality of a male, and the date of arrival reflects this quality extremely well (Møller et al. 2004), one may infer that the males resuming song have significantly higher individual quality than the remaining males (see also Borowiec 1999). However, in our study the higher individual quality of resuming males is not significantly reflected in the higher quality of their territories.

Most of the song resuming involves resumption on a separate territory. Our finding that males resuming song only within their initial territory are usually not successful in attracting another mate seems to be of key importance. Only an additional territory increases the probability of polygyny. The effectiveness of the second territories can be explained by the issue of female–female aggression (Yasukawa and Searcy 1982). The second territories, where males acquire an additional female, are situated outside the extent of the home range of the primary female (Figs. 1e, f). The distance to the second territory established is affected by the quality of the first one: the better the first territory is, the closer the second territory. One may suppose that in richer territories the issue of female–female aggression is less significant, thus the second territory may be situated a little closer. The existence of female–female aggression in polygynous species has been a matter of discussion, especially in flycatchers *Ficedula* spp. (Slagsvold and Dale 1995; Ratti et al. 1995). However, there are also good indications that this phenomenon occurs in *Acrocephalus* warblers. In Great Reed Warbler *Acrocephalus arundinaceus*, nests of primary and secondary females were situated at the maximum possible distance within the male's territory (Catchpole et al. 1985). In the same species, infanticide was also suggested, with secondary females destroying eggs of primary females (Hansson et al. 1997).

The possibility of occupying the second territory and thus attaining polygyny depends on the total number of individuals in the population. This is confirmed by the negative correlation between the number of polyterritorial males and the number of breeding males, as well as by the negative correlation between the average quality of a polyterritory and the breeding population number. With a high number of breeding males, the resuming males have little space to set up second territories because at the time their females begin incubation all available places might be already occupied by other males, or the males must face intensive competition with new settling males. This may make the establishment of the second territory unprofitable because of conflicts and the energy expenditure involved.

The higher the numbers in a breeding population, the lower the quality of places available for the establishment of a second territory. As a result, with the rise in population numbers, males can establish their second territories only in places of increasingly inferior quality. On the other hand, the quality of the second territory is correlated with the quality of the first territory: thus in a free competition for vacant places, these sites are acquired by those males which have already competed successfully when settling on their first territories.

Similar conclusions can be drawn from the Sedge Warbler population studied by Borowiec (1999). In this population, occurring in a fairly homogeneous habitat and

having over two times higher density than the population that we studied (17.8 vs 7.1 pairs/10 ha), the share of males that resumed song outside their primary territories was very low (6.5%). Furthermore, experiments involving the artificial supply of additional breeding places, conducted on the Pied Flycatcher *Ficedula hypoleuca*, confirmed this line of reasoning. In the study of Alatalo and Lundberg (1984), in which additional excess nesting boxes were provided, the frequency of polyterritorial polygyny was significantly higher. A shift from parental to mating effort was similarly evoked in European Starlings *Sturnus vulgaris* (Smith 1995) by providing new nesting boxes adjacent to the nesting boxes of monogamous, breeding pairs. Males decreased their incubation effort in favour of singing and displaying. These two species do not defend their territories, except for the small space around the nest box, thus an excess of nesting boxes is an artificial equivalent to the additional space for polyterritory in regularly territorial species.

This kind of spatial flexibility within the territory, depending on population factors and geared to gaining additional mating, matches quite well the results of other studies of territorial behaviour. It is known that territories can expand when neighbours are removed (Krebs 1971; Adams 2001). In the species where the polygyny mechanism was studied fairly thoroughly, the singing resumed typically in the same territory, but the male concentrated his singing activity at the opposite end of his territory or in its outlying parts (Catchpole et al. 1985; Temrin and Arak 1989; Borowiec 1999). In addition, males expand their territories in the period when the female is receptive, in order to ward off any potential rivals (Møller 1990). In the marsh-nesting passerines analysed by Dyrce (1988), at a species level the increasing tendency for males to be polygynous parallels the territory size. When analysing the occurrence of territorialism in North American passerines, it was also Ford (1996) who noted the continuous nature of the transition from monoterritory to polyterritory in several species.

In the light of these observations, the mechanism of polyterritorialism may be seen as territorial expansion, on the one hand associated with the necessity to assure the second female of the space to live and to help her avoid female–female aggression, while on the other hand it is made easier by the low numbers of potential competitors for that space. This interpretation of polyterritorialism is clearly illustrated in Figs. 1b, d, where territorial expansion is evident but males do not relinquish the defence of the first territories. The transformation of the case illustrated in Figs. 1b, d into polyterritorial behaviour is easy to imagine.

Although the data collected in this study allow for an exact analysis of various forms of territorial behaviour, their ultimate consequences in the form of the mating status or reproductive success were not well-marked in the

studied population. The frequency of polygyny in this population was very low (Zajac and Solarz 2004). Also, Borowiec (1999) did not find any correlation between the number of males that resumed singing and the number of polygynous males. In contrast, in the Swedish population of Sedge Warblers, the efficiency of song resuming was very high: as much as 50% of the males that followed this strategy succeeded in attracting the second female (Hasselquist and Langefors 1998).

Because of the low number of cases, the possibility of comparing the success of primary and secondary females was very limited. We do not know whether secondary females really pay very high polygyny costs, as was previously thought (Catchpole et al. 1985; Both 2002; Garamszegi et al. 2004). There are other significant factors that may contribute to reducing costs of polygyny, such as high general productivity of habitats (Leisler et al. 2002) or female quality (Forstmeier et al. 2001).

For secondary females, the quality of the territory they occupy is of essential importance. Although the second territories are significantly worse than the first territories of the same males, they do not differ significantly from the quality of places taken for the display activities of other non-breeding males. This is concordant with the classic polygyny threshold model (Verner and Willson 1966; Orians 1969). Hence, in terms of the richness of the habitat, it may be the same for a female to become a second female for an already mated male, or the first female of a male who has not yet mated. The cost associated with this decision concerns the limitation in feeding assistance provided by the male, which can be compensated for by the higher quality of the offspring. This compensation is still controversial since the reproductive values of sons of secondary females do not outweigh the cost of polygyny, because low parental care and the consequential undernourishment of the sons of secondary females reduces their attractiveness (Gustafsson and Qvarnstrom 2006).

In case of the studied population of Sedge Warblers, there are no observations indicating “female deception”. If second territories were set up in order to hide the marital status of males, the shape of the distribution of distances between the first and the second territories of the males should be left-skewed, with most of the second territories at large distances from the first one (Temrin 1984). The results obtained in the presented study are just opposite, with the majority of second territories located just outside the first ones (Fig. 1e).

It is extremely improbable that, in the open landscape of the wetlands, the primary female does not know about the secondary mating of her male, especially because in Sedge Warbler they are preceded with conspicuous displays. The analysis of the distance between the second territory and the first one clearly indicates that any female attracted by a

resuming male has a very high probability of encountering the female from the first territory. Even more so, the instances of extra-territorial forays made by females indicate that the latter may find out that the male has mated with another female. All this happens in an open terrain where the possibilities of observing other individuals of the same species are much better than in cavity-nesters living in forests.

The situation described in the Sedge Warbler seems to be best matched by the opinion of Getty (1997), who stresses that both males and females maximise their fitness albeit both in different conditions: the richness of the habitat changes from year to year, and both population numbers and the operational sex ratio also change. In such conditions, the occurrence of seemingly ill-adapting behaviour (“deceived” females) is understandable, because the maximisation of fitness of females appears over too long time and spatial scales to be easily detected, and the variability factors are too difficult to control.

Too little is known about the proximate mechanism of these phenomena. The examples of how female settlement looks, or answers to many questions such as whether they settle on the same territory simultaneously or sequentially, whether breeding occurs synchronically in monoterritorial polygyny, or spaced over time in polyterritorial polygyny, cannot be found in the relevant body of literature. Based on the analysis of the spatial activity of male Sedge Warblers, polyterritorialism should be regarded as a behavioural adaptation, where the availability of space enables males to mate sequentially and to separate the territories of particular females in terms of space. Polyterritorialism is a specific adaptation within the flexible mating system of Acrocephaline warblers. It does not need to be pronounced in each population of Sedge Warbler. However, taking into account considerable variations in frequency of facultative polygyny reported in many species (Dyrzc 1988; Leisler et al. 2002) or even populations (Zajac and Solarz 2004), the spatial aspects of territoriality might be one of the main reasons responsible for this variation.

## Zusammenfassung

Wiederaufnahme der Gesangsaktivität und polyterritoriales Verhalten in einer Population des Schilfrohrsängers *Acrocephalus schoenobaenus*

Bei Arten mit fakultativer Polygynie scheinen Paarungs-Strategien sehr flexibel zu sein und von den örtlichen Umweltbedingungen abzuhängen. Deshalb haben wir an einer Schilfrohrsänger-Population in einem natürlichen Feuchtgebiet habitat- und populationspezifische Zusammenhänge von territorialem Verhalten und Polygynie

analysiert. Nahezu 1/3 aller männlichen Brutvögel (46 Individuen) fingen wieder an zu singen, nachdem sie mit dem ersten Weibchen verpaart waren, um ein weiteres anzulocken. Die Männchen, die erneut sangen, waren normalerweise auch die, die am frühesten angekommen waren. Es gab einen kontinuierlichen Übergang im Territorialverhalten von der Wiederaufnahme der Gesangsaktivität im ersten Revier und polyterritorialem Verhalten, mit intermediären Formen territorialen Verhaltens. 95% aller Männchen, die wieder zu singen angingen, besetzten ein zweites Revier, das deutlich vom ersten getrennt war. Das Zweitrevier lag für gewöhnlich nahe des Aktivitätsradius des ersten Weibchens. Die Qualität des zweiten Reviers hing von der des ersten ab und war signifikant schlechter. Allerdings unterschied sich die Qualität nicht signifikant von der der Reviere von nicht brütenden Männchen. Die Qualität des zweiten Reviers korrelierte darüber hinaus negativ mit der Entfernung zum ersten Revier. Polyterritorialismus hing von der Populationsgröße ab: je größer die Anzahl an territorialen Männchen, desto geringer die Anzahl an etablierten Zweit-Revieren und desto geringer auch deren durchschnittliche Qualität. Wenngleich die Häufigkeit von Polygynie in der untersuchten Population sehr niedrig lag, waren poly-territoriale Männchen signifikant wahrscheinlicher polygyn. Wir schließen daraus, dass die Häufigkeit von Polygynie deutlich von der Populationsgröße beeinflusst sein kann, die möglicherweise die Hauptursache für die Variabilität im Paarungssystem dieser Art darstellt.

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