Low Incidence of Polygyny Revealed in a Long Term Study of the Sedge Warbler Acrocephalus schoenobaenus in Natural Wetlands of the S Poland

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Low incidence of polygyny revealed in a long term study of the Sedge Warbler *Acrocephalus schoenobaenus* in natural wetlands of the S Poland

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Abstract. In 1996–2002, 227 breeding attempts were studied in a colour-ringed Sedge Warbler population. Although 11% of males in this population resumed singing in order to mate with another female after their first females had laid eggs, only two polygynous males (i.e. 0.6%) were recorded. This is a very low value in comparison to other studies (ca. 7% on average). The low level of polygyny is attributable to the low food abundance in a natural floodplain, as the nestlings in this population were fed on predominantly small food items. Both polygynous males were recorded in 2002; this year was unusual, because flooding in early June (around the hatching date) destroyed most of the broods. This could have led to an influx of new females into the study area, a change in the operational sex ratio, and new mating opportunities for males.

Key words: Sedge Warbler, *Acrocephalus schoenobaenus*, polygyny, mating systems, flood

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INTRODUCTION

Among European *Acrocephalus* warblers, the Sedge Warbler *A. schoenobaenus* is classified as a socially monogamous species, with the highest frequency of polygyny, close to polygynous Great Reed Warbler *A. arundinaceus* (Leisler & Catchpole 1992, Leisler & Wink 2000). Results of study into the Sedge Warbler biology revealed a considerable variation in mating systems among different populations (0–19% of polygyny — e.g. Catchpole 1980, Borowiec & Lontkowski 1988, Hasselquist & Langefors 1998).

Dependence of polygyny on environmental conditions, including habitat quality, was suggested by Verner & Wilson (1966) and Orians (1969) in their polygyny threshold model (PTM). While the Sedge Warbler, with its variable mating system and broad range of habitats it occupies, appears to be a model species to test the influence of environmental correlates on the occurrence of polygyny, this issue has not sufficiently been addressed in studies to date. Instead, the main focus was on testing individual features of monogamous and polygynous males within one population (Bell et al. 1997, Hasselquist & Langefors 1998, Borowiec 1999, Buchanan & Catchpole 2000). Conversely, different aspects of habitat requirements have been dealt with in a number of studies, in which mating system was not investigated (e.g. Catchpole 1972, 1973, Thomas 1984, Shennan 1985, 1986, Anselin & Meire 1989).

The aim of this paper is to report on very low frequency of polygyny in a population of the Sedge Warbler occurring in natural habitats of the Middle Nida Wetlands and to discuss its possible ecological correlates.

STUDY AREA AND METHODS

The study was carried out between 1996–2002 in natural wetlands of the middle Nida river floodplain (20°28'–32'E, 50°33'–35', S Poland) on two plots: PPL, studied in 1996–2002, covering 36.5 ha, and PCZ, studied in 1998–2002, covering

10.6 ha. All individuals in the studied population were colour-ringed. Throughout the breeding season, during frequent (3–5 a week) controls of the study area identity of individuals, their position and behaviour were plotted on a detailed vegetation map prepared by means of a GPS receiver. Adjacent areas in which Sedge Warblers occurred incidentally were also regularly surveyed. Mating and breeding success were monitored. All data gathered in the field were analysed by means of a GIS system. Altogether, a total of 8 626 records of Sedge Warblers' identity, position and behaviour were gathered.

The diet of the Sedge Warbler nestlings was studied in 1998. On the 8th day after hatching, 2-hour time budgets were done at 10 nests, during the highest feeding activity of parents. The type of food brought to the nest was classified into 10 rough ecological types on the basis of general ecological niche (e.g. flies or caterpillars) and nutritional value (Stephens & Krebs 1986).

RESULTS AND DISCUSSION

The studied Sedge Warbler population occupied mainly edges of patches of Common Reed *Phragmites australis* and Reedmace *Typha latifolia*, surrounded by extensive sedge beds *Carex gracilis* (see Król et al. 2002 and Bielański et al. 2003 for details). Within the whole study period, 292 territories of 187 the Sedge Warbler males were recorded (some territorial males returned in subsequent years) and a total of 227 first and replaced breeding attempts were monitored. There were only two attempts of second broods, both unsuccessful.

Despite the 7 years of intensive studies no cases of polygyny were detected in 6 years. Only in the 7th year (2002), two polygynous males were recorded. Therefore, the average incidence of polygyny in the studied population was 0.6% (0 during 6 years and 4% in 7th year of the study). This is a very low value in comparison to results obtained in other studies (Table 1).

Polygyny in the Sedge Warbler is sequential (Buchanan & Catchpole 2000) — in an attempt to mate with a subsequent female, mated male resumes singing after his first female has laid eggs. The fraction of males resuming singing in the studied population was significant: the average of about 11% (0–24%) of territorial males followed this strategy, thus there was a potential for attracting second females. This indicates that low incidence of polygyny in the population that we studied may be determined by poor environmental quality rather than be a result of geographical differences in behaviour between populations.

Table 1. Differences in polygyny level in different Sedge Warbler populations in Europe.

Location	% Polygyny	Source
Great Britain	0	Catchpole 1980
	2–7	Kelsey after Leisler& Catchpole 1992
	7.7	Buchanan & Catchpole 2000
	11	Alker & Redfern 1996
Poland	9.8 (0–17.4)	Borowiec & Lontkowski 1988, Bell et al. 1997, Borowiec 1999
	0.6 (0–4)	This study
Sweden	14 (11–19)	Hasselquist & Langefors 1998
Mean	7 (0–19)	

According to Leisler & Wink (2000) and Leisler et al. (2002), monogamy in genus *Acrocephalus* maintains in poor environments, whereas change to better habitats is accompanied by a reduction of paternal care, allowing for attracting additional females. According to the methodology applied by Leisler et al. (2002), habitat is poor when only small food items are fed to young. Small food items are regarded as unprofitable by theory of optimal foraging, as the cost of collecting food item is very high in relation to the amount of energy gained (Stephens & Krebs 1986). In the population studied, small items dominated over other types of food (Fig. 1). This data indicates that areas occupied by this population are rather poor in terms of food abundance.

Studies into population ecology usually concentrate in areas in which densities are high. This is justified first of all by practical reasons, since large number of individuals can be studied in a small area, as well as by theoretical expectations that individuals in crowded populations exhibit social interactions, which allows for studying population mechanisms and population context of behaviour. High densities can often be found in high quality habitats in which the incidence of polygyny may not be representative for the whole geographical range of species. It can be assumed that the Sedge Warbler populations in which polygyny was recorded occupied such high-quality areas. In comparison to the results of other studies, in which 20–30 pairs/10ha were reported

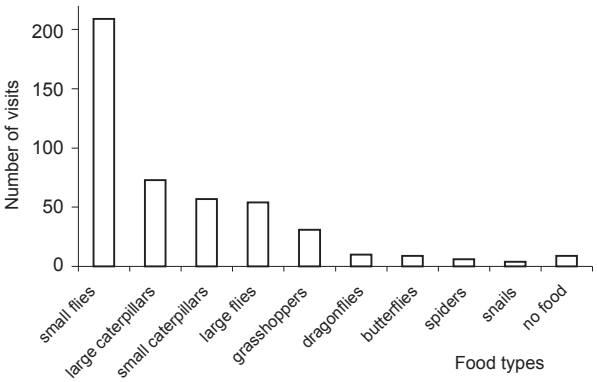

Fig. 1. Number of visits with different food types sampled at 10 nests of Sedge Warbler, during 2-hour time budgets in 1998.

(Koskimies 1991), the density of the population in the natural floodplain of the Nida was low (mean 11 pairs/10 ha, from 5.0 to 15.7 pairs/10ha, Król et al. 2002). Sample plots in our study were representative for natural floodplains, with a wide spectrum of environmental conditions. This was reflected by the distribution of quality of sites occupied by Sedge Warbler: there was a considerable number of low quality sites which were occupied only in some years, and few high quality sites occupied every year and very early in the breeding season (Bielański et al. 2003).

The number of polygynous males recorded in the majority of studies is usually low: 1–3 males (Buchanan & Catchpole 2000), mean of 3 males per year in a long term study (Borowiec 1999), 1 male in a population of 8 breeding pairs (Alker & Redfern 1996). Fairly high rate of polygyny reported in these studies may thus result from stochasticity.

The question remains why polygyny occurred at all in the studied population. One plausible explanation is natural disturbance due to flooding. The study area was regularly flooded in early spring, before Sedge Warblers arrival, and/or in summer, which frequently resulted in destroying late broods (Król et al. 2002). The year 2002, in which both cases of polygyny were detected, was exceptional in that sudden flood occurred at the time when most clutches were about hatching date (beginning of June). About 55% of nests were destroyed. After nest failure the majority of males usually stay at the study site and attempt replacement clutches, whereas most females desert breeding grounds, probably to mate and breed in other areas (Borowiec 1999, this study). As females are under severe time constraint when attempting replacement clutches, they are likely to concentrate at places which were first free of water and available for breeding. We suppose that an influx of new females from areas outside the study plots caused reshuffling of mating opportunities. Such a change in the operational sex ratio can lead to polygyny (Emlen & Oring 1977). However, this also implies that shortage of females may be responsible for low polygyny frequency. This is supported by the fact that each year a significant fraction of males in the studied population (ca. 33% on average) remained unmated throughout the breeding season.

In conclusion, we suggest that polygyny in the Sedge Warbler was often found in fragments of high-quality habitats. Large-scale approach, covering entire distinguishable natural ecosystem units, including suboptimal habitats, could reveal considerably lower rate of polygyny in the Sedge Warbler. Disturbances of the breeding cycle, e.g. due to floods, can induce higher frequency of polygyny due to change in the operational sex ratio.

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STRESZCZENIE

[Niska częstotliwość występowania poligynii u rokitniczki na rozlewiskach Nidy]

Celem pracy było przedstawienie częstości występowania poligynii w populacji rokitniczki zasiedlającej naturalne rozlewiska w dolinie rzecznej i próba określenia jej uwarunkowań ekologicznych.

Badania przeprowadzono w latach 1996–2002 w dolinie środkowej Nidy (20°28′–32′E, 50°33′–35′). Na terasie zalewowej wyznaczono 2 powierzchnie badawcze: PPL (36.5 ha, badana w 1996–2002) i PCZ (10.6 ha, 1998–2002), na których monitorowano zachowanie i sukces lęgowy 187 samców rokitniczki na 292 terytoriach (część terytorialnych samców powracała na teren badań w kolejnych latach) i 227 prób lęgowych. W 1998 r. na podstawie dwugodzinnych budżetów czasowych przy gniazdach analizowany był skład pokarmu piskląt (klasyfikowany na 10 typów).

W ciągu pierwszych sześciu lat badań nie zanotowano żadnego przypadku poligynii. W siódmym roku badań wykryto 2 poligyniczne samce, średnia częstość poligynii w badanej populacji wyniosła zatem 0.6% (od 0 do 4%). W porównaniu w wynikami innych badań (śr. 7%, Tab. 1), wartość ta jest bardzo niska. W badanej populacji próbę skojarzenia z druga samicą (wznawianie śpiewu) podejmowało średnio ok. 11% (0–24%) terytorialnych samców, których samice wysiadywały jaja.

Wśród pokarmu przynoszonego pisklętom w badanej populacji rokitniczki dominowały niewielkie muchówki (Fig. 1), co może wskazywać na niską jakość zajmowanego siedliska.

Populacja w dolinie Nidy charakteryzowała się niskim zagęszczeniem (średnio 11 par/10 ha).

Każdego roku, w badanej populacji obserwowane były nieskojarzone samce (średnio ok. 33% w ciągu wszystkich lat badań), co wskazuje na niedobór samic. Z kolei obydwa przypadki poligynii w badanej populacji stwierdzono w roku 2002, gdy na początku czerwca w dolinie Nidy nastąpiła powódź, która zniszczyła ok. 55% lęgów rokitniczki. Po ustąpieniu powodzi, na terenie badań mogły pojawić się samice, które utraciły lęgi na innych obszarach. Zmieniony w ten sposób stosunek płci mógł sprzyjać wystąpieniu poligynii.