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Original article

Adaptive settlement in sedge warblers *Acrocephalus schoenobaenus*—focus on the scale of individuals

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ARTICLE INFO

Article history:

Received 1 April 2004

Accepted 20 July 2005

Available online 19 January 2006

Keywords:

Habitat heterogeneity

Habitat selection

Pre-emption

Mating

Site dependence

Population regulation

Experience

Sedge warbler

Acrocephalus schoenobaenus

ABSTRACT

Breeding site selection can be linked to population dynamics through pre-emptive site selection, by which an individual selects the best (in terms of fitness) available site, preventing others from sharing it. We examined the pattern of territorial settlement and its fitness consequences during a study of sedge warblers *Acrocephalus schoenobaenus* inhabiting two study plots in the Nida Wetlands (southern Poland). Throughout all 7 years of the study (1997–2003), male sedge warblers repeatedly occupied sites in sequence from best to worst, according to the amount of cover by reedmace and common reed on one plot, and the amount of common reed on the other plot. As individuals aged, they occupied sites with increasingly higher proportions of reedmace and common reed. On the first plot, where the within-habitat heterogeneity was greater, settlement date and consequently reedmace and common reed cover at the sites occupied by a male had a positive influence on that male's fitness components: the probability of mating, nesting success, and the number of offspring recruited to the breeding population in succeeding years. On the second plot, which was more homogenous, there was no such evident relationship between fitness and the proportion of cover by reeds.

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1. Introduction

Within a population there is usually considerable variation in reproductive success, attributable to differences between individuals in access to resources. Finding and occupying a site of the highest possible quality is basic to successful competition. Choosing a place to settle is an important decision, since it largely determines the chances of survival and successful breeding, often for a lifetime.

Ideal free distribution (IFD, Fretwell and Lucas, 1970) is probably the best-known model of habitat selection. According to this model, habitats best suited for reproduction should be occupied first. Thus, individuals choose between habitats, and all individuals within the same habitat have equal reproductive success. IFD also assumes a regulative

role for crowding. The mean success of individuals occupying the best habitat decreases as more individuals settle, which has the effect of reducing success in this habitat to such a level that it becomes more beneficial for a newcomer to occupy a habitat of evidently lower initial quality. When the territorial behaviour of settled individuals restricts newly arriving individuals to poorer habitats, IFD is altered to an ideal dominance distribution (IDD, Fretwell and Lucas, 1970). In the latter model, habitat suitability decreases due to increasing density of individuals, causing an increase in the resistance of established individuals to newcomers. This leads, as in IFD, to an equilibrium, where habitat suitability is equalised over all occupied habitats.

However, a considerable number of field studies have shown that the assumption of within-habitat homogeneity is not realistic. On the contrary: individual-scale studies have revealed significant within-habitat heterogeneity. This finding has opened new possibilities of explaining population processes by considering settlement patterns. Incorporating

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individual differences in reproductive success within a heterogeneous habitat, Pulliam and Danielson (1991) presented a simple alternative to the IFD model. They assumed that it is adaptive to choose between sites within a heterogeneous habitat and to occupy them sequentially from the best to the worst. This pattern was termed “ideal pre-emptive distribution”. The essential difference between this model and the earlier model of IFD is its focus on individual site characteristics and within-habitat heterogeneity. This increases variation in the fitness of individuals when habitats are heterogeneous. The mechanism of individual site pre-emption within heterogeneous habitats can contribute to regulation of population numbers, even without taking into account the negative effects of crowding. These concepts, presented in a number of publications (e.g. Łomnicki, 1998; Pulliam, 1988; Dhondt et al., 1992), have been synthesised by Rodenhouse et al. (1997) in a site-dependent model of population regulation. This model assumes that fitness is related to site quality, and that progressively inferior sites are used as population size increases. In this model, the mean reproductive success of a population depends on the relative proportion of breeding sites of differing qualities and on the proportion of all sites that are actually occupied. This mean reproductive success will often be lower and have much higher variance than that calculated for the best sites in the IFD model or for all occupied habitats in the IDD model. When population density is low, only the best sites are occupied, resulting in higher mean reproductive success and population growth. Rodenhouse et al. (2000) point out that the site dependence model is an important improvement, because a “focus at the spatial scale of the individual site was being overlooked”. Moreover, “the link between individual performance and site characteristics was also being lost”. McPeck et al. (2001) also emphasised that studies of habitat selection should concentrate on assessing whether individuals make adaptive choices of where to breed.

It is safe to assume that site suitability generally varies continuously (e.g. Kristan and Boarman, 2003), and that differences between habitats can be a consequence of different distributions of site suitability within these habitats. One cannot be sure whether the variability of suitability within a given habitat is greater than that between habitat patches. When it is greater, we need to focus on individuals and their choice of breeding sites if we are to understand the relationships between habitat quality and population numbers.

Following the work of Pulliam and Danielson (1991); Rodenhouse et al. (2000); McPeck et al. (2001), here we study the mechanism of pre-emption, and in particular the link between the performance of the individual and the characteristics of the site it occupies. Such links are critical to the fundamental model presented by Fretwell and Lucas (1970) as well as the ideal pre-emptive distribution (Pulliam and Danielson, 1991) and site-dependence models (Rodenhouse et al., 1997; McPeck et al., 2001). According to these models, some verifiable predictions can be formulated pertaining to the pre-emptive use of sites and adaptive settlement in heterogeneous environments:

1. Settlement should be based on repeatable rules that different individuals follow, and the resulting distribu-

tion of individuals in space should be non-random and repeatable between years for different sets of individuals, even for time scales longer than individual lives.

2. The settlement rules and resulting pattern should be adaptive—birds should settle preferentially at sites that bring about higher fitness.

The aim of this study is to test the assumptions of pre-emptive site occupation in the migratory sedge warbler *Acrocephalus schoenobaenus* population that we studied in the Middle Nida Wetlands (southern Poland). We wanted to test whether site selection by individuals of this species is (1) determined by characters objectively measurable in the field, (2) pre-emptive in nature, and (3) adaptive, that is, whether individuals occupying a preferred type of site attain higher levels of fitness.

2. Materials and methods

2.1. Study area

A population of sedge warblers was studied during 1996–2004 in a large wetlands area situated in the Nida River valley, southern Poland (50°33′–50°35′N, 20°28′–20°32′E). The study area is located between two side arms of the river, where permanently flooded old anastomosing river arms and local depressions are surrounded by temporarily inundated sedge areas and dry grasslands in slightly higher places. The sedge warblers were studied on two plots (Fig. 1), labelled PPL (since 1996) and PCZ (since 1998), where detailed observations were made. The plots differed in their surface features and vegetation. Plot PPL covered a 36.5 ha flat area encompassing an irregular network of old river beds with some small permanently inundated areas. Reedmace (broadleaved cattail, *Typha latifolia*) was the predominant species in the old river beds and permanently inundated areas, whereas the rest of the area was covered by various species of sedges, dominated by *Carex gracilis*. The higher places were overgrown with meadows. Plot PCZ was smaller (10.8 ha) and more homogenous. Most of PCZ was covered with sedges and a few large beds of common reed (*Phragmites australis*), but there were also three small patches of *Typha* and a single patch of sweetgrass (*Glyceria maxima*). Two small clusters of young alders (*Alnus glutinosa*) occurred in the central part of PCZ. The rest of the study area was covered with meadows and pastures, with single trees along the side arms of the river. More details of the plots are given in Bielański et al. (2005).

Before each breeding season, a new detailed map of the study area was prepared, in order to account for changes in the vegetation distribution between particular years. The shape of the riverbeds and the vegetation cover was precisely mapped (1 m accuracy) by means of a GPS receiver (Geoplotter II), and categorised according to distinguished land cover types (wet meadow, sedge, sweetgrass, reedmace, common reed, alder woods, open water, and dune with dry meadow). Table 1 shows the proportions of land cover types in the study area, averaged for the study period. After mapping,

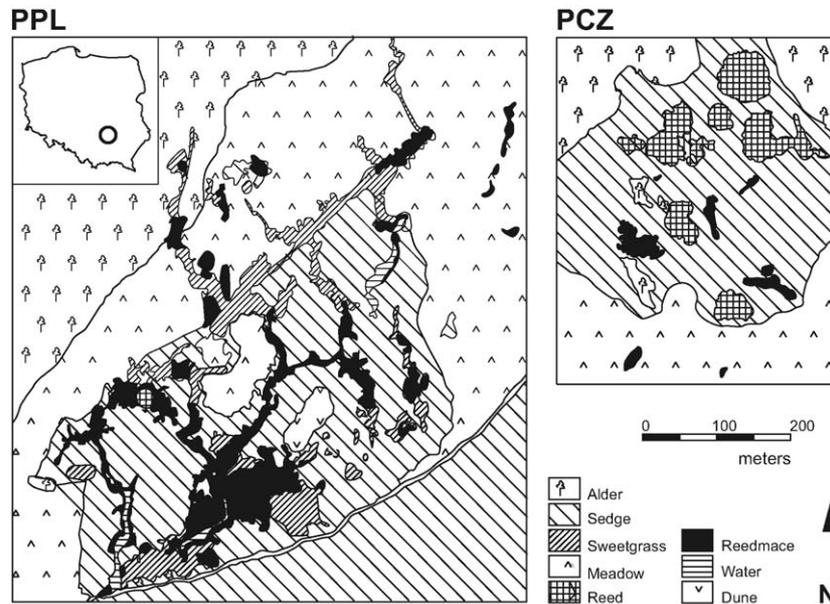


Fig. 1 – Schematic map of the two study plots, PPL and PCZ, in the Nida River valley (southern Poland) with six main types of vegetation (meadows, sedges, sweetgrass, reedmace, common reed, and alder) and open water.

the demarcations and land cover attributes of the subdivisions were imported to GIS (ArcInfo), under which a detailed digital map of the study area was developed.

The degree of land cover heterogeneity on the two studied plots was examined in areal samples (circles, 30 m radius) randomly selected by means of GIS software (50 samples per study plot). The number of all types of land cover in each sampled unit was determined, and the mean number of land cover types was compared between study plots. Another measure of habitat heterogeneity was based on the fact that the patches deviate in shape from a circle, and this deviation increases the length of its perimeter versus a circle, which of course has the shortest possible perimeter (Hinsley et al., 1995). A patch boundary complexity index was calculated as the ratio P_m/P_c , where P_m is the perimeter of each land cover patch (vegetation or body of water), and P_c is the perimeter of a circle having the same area as the patch.

2.2. Field protocol

Before the breeding season, the whole study area was surveyed regularly three to five times a week for arriving sedge warblers. After their arrival, all birds were immediately mist-netted, ringed with a numbered aluminium ring and a unique combination of three colour rings. The captured birds were sexed on the basis of cloacal protuberance (Svensson, 1992), and the sex of these individuals was subsequently verified on the basis of their behaviour during the breeding season. There are no morphological characters indicating the age of sedge warblers, thus any information on age comes from individuals ringed as nestlings. Mist-netting had no effect on the territorial males' behaviour, as they usually re-

turned to the same place after being released and soon started singing again.

Over the course of the breeding season, detailed surveys of the study plots were made at least three times a week; the position of all colour-ringed individuals and their behaviour were plotted on the map of vegetation. Altogether, during the 7 years of the study, 10,256 records of sedge warblers were gathered, including 5980 records of territorial male behaviour. Most of the nests were found on the basis of earlier observations of females carrying nest material. In order to reduce the chance of predation, visits to nests were kept to a minimum. The nests were carefully inspected at late stages of incubation and at the time of the expected hatching date. On the eighth day after hatching, the nestlings were ringed with a numbered aluminium ring.

2.3. Individual site characteristics

In order to study land cover correlates of site pre-emption, it is necessary to sample the land cover at the sites occupied by males objectively, in a protocol repeatable for different individuals. In this study the composition of land cover was examined in units of space delimited on a digital map of the study area around all male song posts on the first day after arrival (Fig. 2). The land cover structure was analysed within a 30 m radius (area 2826 m²) around a male's song post. Such an area corresponds to the average size of territory for sedge warblers (2888 m²) estimated in homogenous vegetation at plot PCZ (Król et al., 2002). This procedure yielded a quantitative characteristic for an averaged area unit ("site") occupied by the single male, roughly overlapping with its territory and immediate surroundings.

Table 1 – Spearman rank correlations (r_s) between the date of settlement of a male and the fraction of a given land cover type in a unit of area (“sites” 30 m in radius and 2826 m² in area) delineated around song posts of males on the first day after arrival; determined during 1997–2003 in PPL and 1999–2003 in PCZ. In the “Naïve” males group, only the earliest breeding season was considered for each individual. Birds retrapped in their second breeding season (“Experienced”) were analysed for all years together, due to the smallness of sample sizes within each considered year. For “Lifetime” data, the mean lifetime date of arrival of each male was correlated with the mean fraction of land cover at all sites it occupied during its life. The percentage of each land cover type in the total area of the respective study plot is given in Table headings. The remaining types of vegetation, not listed in table (*Juncus*, *Alnus*, *Phalaris*, *Salix*, *Urtica*, psammophilous vegetation and others) account for the remaining area (1.5% on PPL and 2% on PCZ)

Plot	Year	N		Meadow	Sedge	Sweet-grass	Reed-mace	Reed	Open water
		Naïve	Experienced	51%	30%	8%	7%	0.5%	2%
PPL	1997	29	15	0.21	0.10	-0.01	-0.49**	-0.26	0.10
	1998	43	5	0.25	0.06	-0.14	-0.40**	-0.27	-0.14
	1999	14	8	0.31	0.15	-0.17	-0.43	—	0.06
	2000	22	0	0.49*	0.26	-0.19	-0.56**	-0.32	0.20
	2001	33	3	0.44**	0.26	-0.17	-0.48**	-0.23	-0.05
	2002	18	12	0.12	0.46	-0.57*	-0.23	-0.44~	-0.11
	2003	12	2	0.49	-0.49	-0.28	0.26	0.28	0.15
	All years “Naïve”	171		0.30***	0.08	-0.20*	-0.36***	-0.28***	-0.02
	All years “Experienced”		44	0.42**	0.22	-0.09	-0.46**	-0.31*	-0.19
	“Lifetime”	171		0.30****	0.09	-0.18*	-0.34****	-0.30****	-0.09
Year	N		Meadow	Sedge	Sweetgrass	Reedmace	Reed	Alder	
			3%	65%	5%	3%	20%	2%	
PCZ	1999	27	4	0.48*	0.31	—	-0.07	-0.68***	—
	2000	29	5	0.05	0.28	—	0.03	-0.39*	—
	2001	33	4	0.11	0.04	—	-0.31	-0.40*	—
	2002	18	5	-0.06	0.24	-0.06	0.39	-0.26	0.19
	2003	18	9	0.40	-0.36	-0.15	0.09	-0.42~	-0.50~
	All years “Naïve”	125		0.14	0.12	-0.01	-0.02	-0.35***	-0.01
	All years “Experienced”		27	0.18	0.35	0.10	0.23	-0.51**	0.30
	“Lifetime”	120		0.19*	0.12~	-0.02	-0.003	-0.37****	-0.86

N – number of males, ~ 0.06 < P < 0.05, * 0.01 < P < 0.05, ** 0.01 < P < 0.001, *** P < 0.001, **** P < 0.001, “—” sample too small.

2.4. Estimating reproductive success

To verify whether the noted site choices are adaptive for each male, the relationship between its fitness components and the land cover structure at the site it occupied was tested. We investigated the basic measures of male reproductive success: mating success, and nesting success for mated males, including clutch size and number of hatchlings and fledglings. Male mating success (mated or non-mated) was determined by direct observations in the field. A male was considered mated when he was observed guarding a female or when nest building was noted or a new nest was found in its territory. A male was considered polygynous if it had mated and already had one nest, and then was observed mate-guarding with a second female, and that female’s nest was also built within its territory. The male’s parentage was subsequently verified during nestling feeding. Clutch size was estimated for nests found during incubation. The number of young hatched in nests was estimated during visits to the nests near the expected hatching dates. Fledgling number was estimated on the basis of the number of nestlings observed on the eighth day after hatching; no later checks were done because it might have led to premature fledging and an artificial increase in the mortality of nestlings (Król et al., 2002). Local recruitment of the young hatched in 1997–2003

was analysed for all studied males, mated or not, also taking into account the information on recruits recorded in 2004 and fathered by males from previous seasons.

2.5. Data analysis

The data were analysed separately for each study plot. The relationship between settlement date and land cover was tested using Spearman rank correlations because the majority of the land cover proportions had non-normal distributions. The proportions that describe land cover structure within each analysed site (circle, 30 m radius) sum to 1. A consequence of this constraint is that an individual’s preference of one land cover type will lead to an apparent avoidance of other types. Because of that non-independence, only one measure of land cover can be handled at a time.

The correlations between settlement date and the proportion of a particular type of land cover at the site of a given male was analysed for three data sets:

1. “Naïve” males, having no previous experience in the study area. Since we knew nothing about the age and previous history of the birds studied in the first year of observations at each plot, data from those years (1996 at PPL and 1998 at PCZ) were excluded from the analysis. Since the probability that a male sedge warbler

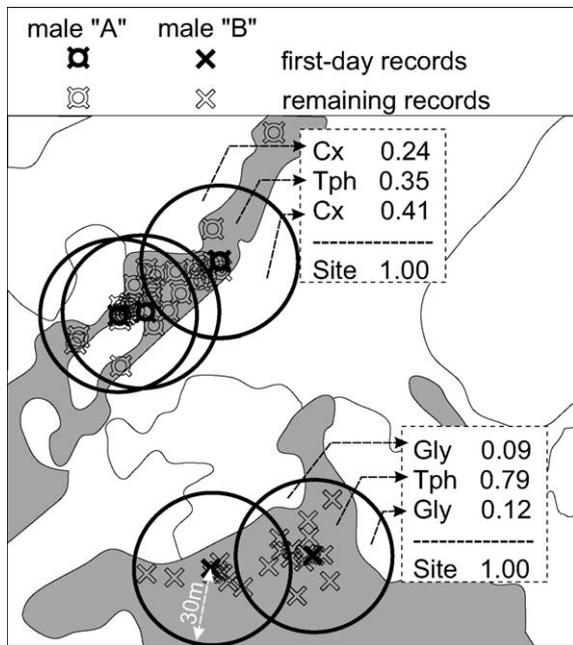


Fig. 2 – Method of sampling land cover structure of sites occupied by male sedge warblers on the first day after arrival. In order to quantify the characteristics of the sites occupied by settling males, the land cover structure was analysed within a 30 m radius around all song posts identified for a male on the first day after arrival. Black symbols denote song posts used on the first day after arrival, while light symbols denote later records of the same males; large black circles around black symbols delimit units of space in which the area of all types of land cover was measured by means of GIS. For simplicity, the boundaries of vegetation patches falling outside the analysed space are marked with thin lines. Data on land cover composition were averaged for each male's song post area on the first day after arrival, giving a reliable estimate of land cover structure in the area corresponding to the territories occupied by males and their immediate surroundings, thereafter referred to as a "site". These procedures enabled quantitative estimation of patch size and land cover composition at the sites in a way that was comparable between males without confounding the effects caused by elongated shapes of territories, or by extension of a territory between a few small patches. Cx – sedge *Carex* sp., Gly – sweetgrass *Glyceria* sp., Tph – reedmace *Typha* sp.

survives to the third year is ca 5% (own data), exclusion of the first years significantly reduced the probability that males classified as naïve in the next years (1997 at PPL and 1999 at PCZ) were in fact experienced males from before the colour-ringing began. Naïve birds are the most numerous group among the studied males, so the analysis was done both for each year of the study separately and for data pooled for all years (see Table 1).

2. "Experienced" males, returning to the study area for the first time. Males returning in subsequent years were not included, as it would lead to non-indepen-

dence of the annual samples. Because for single years the samples of experienced males were small in this group (Table 1), this analysis was done only for data pooled for 1997–2003 from PPL and 1999–2003 from PCZ.

3. "Male lifetime data", in which the settlement dates and land cover proportions at sites occupied by the male throughout its life were averaged (Hasselquist, 1998). Arrival dates were standardised separately within each year of the study (the date of settlement of the earliest arriving male was taken as day 0). Then the standardised dates were averaged for the male's lifetime and were correlated with the mean fraction of the site covered with each land cover type at all sites the male occupied during its life. Data from 1996 at PPL and 1998 at PCZ were excluded from this analysis because the previous experience of the males was unknown. Lifetime reproductive success could not be calculated for males that survived to 2004, since it was not known whether they would continue to breed in subsequent seasons. For this reason, these males were also excluded from this data set.

The number of successful nests for a single year was too low to allow reliable analysis of the correlates of male breeding success for each year separately. For this reason we analysed male lifetime breeding success, that is, the total number of eggs laid by a given male's mates in all breeding seasons, and the total number of hatched nestlings and fledglings. These variables were correlated with lifetime data on land cover and the arrival date of each male, standardised and averaged as described above.

The relationship between mating success (binary variable: 1 – mated males; 0 – unmated males) and land cover at a site was analysed using a logistic regression, with male mating status as the dependent variable, with settlement date and the sum of land cover types preferred by settling males as independent variables, and with the influence of year (categorical variable) controlled. For lifetime data, mating success described as a binary dependent variable (0 – males that never mated, 1 – males that mated at least once in the lifetime) was analysed in relation to standardised and averaged land cover features, settlement date and the male's longevity as independent variables. Longevity was defined as the number of breeding seasons in which a male was recorded at the study site. Therefore this measure could also be used to describe a male's experience category, and there was no need to additionally distinguish between naïve and experienced males in this analysis.

In order to study the relationships between land cover type and recruitment, logistic regression models were constructed with the same layout as in the mating models, that is, they used the same groups of males (data for naïve males and lifetime data for males). The models tested the relationship between local recruit production for males (1 – males producing recruited offspring, 0 – males with no recruited offspring) as binary dependent variables in relation to land cover and settlement date as independent variables, and they controlled for the influence of year in naïve males. Similarly to the mating analysis, the model for lifetime data on

recruitment included land cover, settlement date and longevity as the independent variables.

3. Results

3.1. Heterogeneity of the study plots

Heterogeneity of land cover, measured as the average number of land cover types in a random sample of units of space, was significantly greater at PPL (2.72, S.D. = 1.01) than at PCZ (1.96, S.D. = 0.70; $t = 4.37$, $N = 100$, $P = 0.0003$). Differences in heterogeneity between the study plots were confirmed by the perimeter/area ratio of land cover patches (P_m/P_c ; 1.87 at PPL and 1.50 at PCZ; $t = 2.8$, $N = 174$, $P = 0.007$).

3.2. Settlement rules

The pre-emption hypothesis predicts that settlement patterns should be non-random and repeatable. In both study areas the settlement pattern of males was related to the site's land cover features, and this relationship was repeated for different sets of individuals recorded in different years (Fig. 3). On each study plot, larger patches of tall wetland vegetation (i.e. reed, reedmace) were occupied first, and then areas with smaller and smaller patches of tall wetland vegetation were colonised in turn. This general pattern, shown in Fig. 3 for both study plots, was repeated through all the years of the study. Earlier settlement in tall vegetation was confirmed by the statistically significant correlations between

the dates of the males' arrival (data for naïve and experienced males, as well as lifetime data pooled for all years of the study) and the fractions of land cover types in the site occupied (Table 1). For the PPL plot, analysis of all data sets revealed a significant negative correlation between settlement date and the area of cover by tall wetland vegetation (particularly for reed and reedmace) within their sites. In contrast, late dates were positively correlated with meadow vegetation. Analyses limited to naïve birds for separate seasons gave significant negative correlations for reedmace in most of the study years. For the PCZ plot, all analysed data sets showed a negative relationship between settlement date and the fraction of cover by reeds within the sites, and this relationship also held for naïve bird data analysed in each year separately.

The rules for selecting sites and the general spatial pattern of settlement functioned on a time scale far longer than the average longevity in the studied population. Most of the birds of known age (24 of 29 recruits, or 76%) appeared at the study site for only one season to breed.

3.3. Age and settlement

The pre-emption hypothesis predicts that as males become older and more experienced, they should occupy sites of progressively higher quality (in this case expressed as the proportion of tall wetland vegetation). Out of 171 naïve birds ringed at PPL, 44 males were retrapped in the second breeding season, 12 in the third year, and only one in the fourth. For the 125 naïve male birds ringed at PCZ, the corresponding numbers are 27, 6 and 1.

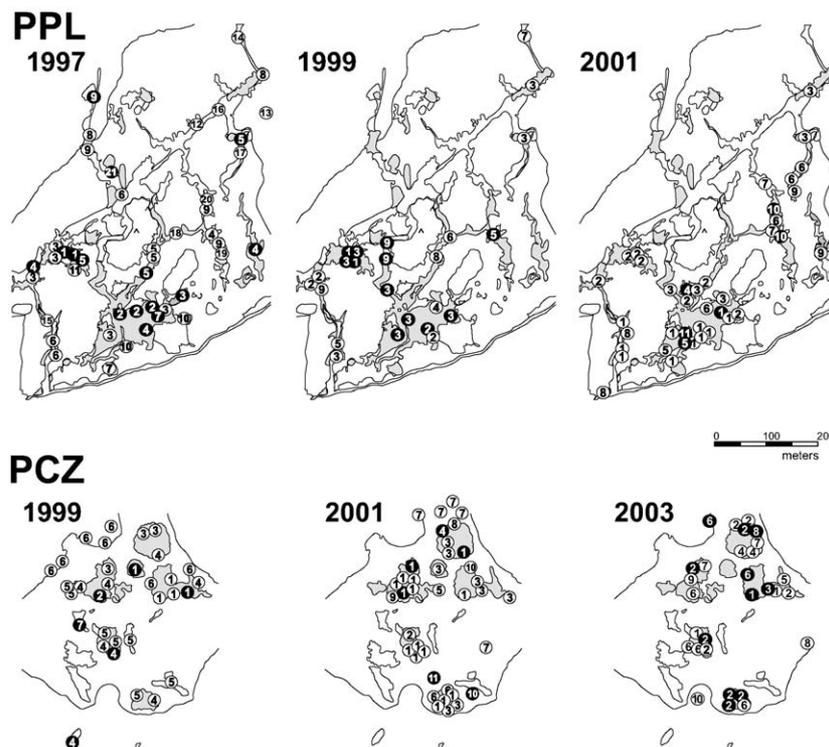


Fig. 3 – Settlement pattern of sedge warblers on the PPL and PCZ study plots in the Nida River valley (southern Poland) for years selected as examples from the entire study period (1997–2003). Light circles denote naïve males and black circles denote experienced males. Numbers reflect settlement order.

For PPL, the dates of settlement of naïve males (in year t) did not differ significantly from the dates of settlement of the same individuals in their next season, $t+1$ ($X_t = 13.20$, S.D. = 15.003; $X_{t+1} = 11.14$, S.D. = 15.384; Wilcoxon matched pairs test $Z = 1.54$, $N = 44$, $P = 0.12$). However, if only birds from the main batch of arriving individuals were considered, that is, those settling within 30 days after the first male's arrival, then the difference became significant, with older males settling earlier than naïve ones ($X_t = 9.11$, S.D. = 7.178; $X_{t+1} = 5.94$, S.D. = 6.094; Wilcoxon matched pairs test $Z = 2.16$, $N = 36$, $P = 0.031$).

At PPL, experienced males also occupied sites with a higher proportion of tall wetland vegetation (total area of reed-mace and common reed: $X_t = 0.330$, S.D. = 0.247; $X_{t+1} = 0.666$, S.D. = 0.361; Wilcoxon matched pairs test $Z = 4.178$, $N = 44$, $P < 0.0001$).

Unlike PPL, for PCZ there was no significant difference in settlement dates between naïve and experienced males ($X_t = 12.5$, S.D. = 12.04; $X_{t+1} = 9.7$, S.D. = 14.23; Wilcoxon matched pairs test $Z = 1.06$, $N = 27$, $P = 0.29$). For males settled within 30 days after the first male, there was also no significant difference ($Z = 0.92$, $N = 24$, $P = 0.36$). Similarly to PPL, site quality seemed to rise as a naïve bird gained experience, although the difference was only close to statistical significance (total area of common reed: $X_t = 0.37$, S.D. = 0.237; $X_{t+1} = 0.45$, S.D. = 0.204; Wilcoxon matched pairs test $Z = 1.90$, $N = 27$, $P = 0.058$).

3.4. Fitness consequences of settlement

3.4.1. Mating success

The distribution of mating success in the studied population was almost binary. At PPL during the 7 years of the study, 85 of 171 naïve males mated with one female per season during their lifetime. The other 86 territorial males showed no indication of mating success. Only four males mated polygynously with a second female (one naïve, three experienced). At PCZ during the 6 years of the study there, 76 males mated with one female, one naïve male mated polygynously, and 49 males were not mated at all. Because the samples were

small, polygynous males were pooled together with males mated monogamously.

To test the influence of settlement pattern on fitness, mating success was analysed as a binary dependent variable (1 – mated, 0 – unmated male) versus the arrival date and the proportion of tall vegetation at a site as independent variables, with the influence of year on naïve birds controlled (Table 2). A similar analysis was done for lifetime data, but in this model the longevity of the male was introduced as the third independent variable (Table 2). For the PPL plot, both models revealed a significant influence of the settlement date (and of longevity in the lifetime data) of the male on its mating status, with a non-significant influence of tall vegetation. For the PCZ plot, the same type of analysis showed only a relationship of tall vegetation cover to mating success, at the margin of significance.

3.4.2. Nesting success

The age of individuals had no significant influence on nesting success. At both PPL and PCZ, the nesting success (N of eggs, N of hatchlings and N of fledglings) of naïve males did not differ significantly from their success in their next breeding season (Wilcoxon matched pairs test).

Because the number of successful broods in each breeding season was too low to carry out reliable analyses of nesting success in relation to habitat cover and settlement time for each season separately, the males' lifetime data were used instead. The analysis showed no clear relationships for land cover types. For PPL there was a clear relationship between settlement date and nesting success (Table 3). There were very few significant correlations for the data from PCZ.

3.4.3. Recruitment

For the whole period of the study, 15 of 171 naïve males (9%) produced recruits in PPL, and 10 of 125 males (8%) did so in PCZ. The sites occupied by males that fathered recruits differed significantly from the sites of those that did not (Table 4). Among the naïve males on the PPL plot, the vegetation structure on the sites of successful fathers had a significantly greater proportion of reed-mace and common reed

Table 2 – Results of logistic regression analyses of factors associated with male mating success on two study plots (PPL and PCZ) for data collected in 1997–2003. The first model (“Naïve”) analyses the influence of the preferred land cover type and settlement date of naïve males on their mating success (0 – unmated, 1 – mated), with the influence of year (categorical variable) controlled. The second model (“Lifetime”) tests the influence of the preferred land cover type, settlement date (mean values for each male's lifetime) and male longevity on its mating success (0 – never mated, 1 – mated at least once during the lifetime)

Plot	Males	Model	B	S.E.	Wald	Df	P	N
PPL	Naïve	Reed-mace + common reed	4.80	3.24	2.20	1	0.140	171
		Settlement date	-0.440	0.212	4.31	1	0.038	
		Year (cat.)			16.5	6	0.011*	
	Lifetime	Reed-mace + common reed	0.574	1.109	0.268	1	0.605	171
		Settlement date	-0.442	0.134	10.9	1	0.001**	
		N of seasons of life	2.386	0.716	11.09	1	0.001**	
PCZ	Naïve	Common reed	1.695	0.878	3.73	1	0.053	125
		Settlement date	0.173	0.207	0.70	1	0.403	
		Year (cat.)			6.93	4	0.140	
	Lifetime	Common reed	0.664	0.849	0.575	1	0.448	120
		Settlement date	0.010	0.017	0.329	1	0.566	
		N of seasons of life (cat.)	20.4	7517	0.000	1	0.998	

Table 3 – Spearman rank correlation coefficients for estimates of lifetime reproductive success of males (N of eggs, hatchlings and fledglings) in relation to the average fraction of different land cover types at the sites they occupied and to the average settlement dates. Only mated birds were considered; empty nests recorded with no clutches or nestlings were excluded from the analysis. Reedbed fraction includes the sum of reedmace and common reed proportions

Plot	Male group	Fitness estimate (sample size)	Meadow	Sedge	Sweet grass	Reed mace	Common reed	Water	Reed beds	Arrival date
PPL	Naïve	N eggs (80)	0.11	-0.18	0.12	0.04	0.27*	-0.13	0.09	-0.29**
		N hatchlings (81)	-0.21~	-0.18	0.26*	0.16	0.22*	-0.04	0.19~	-0.40***
		N fledglings (85)	-0.15	-0.09	0.19~	0.11	0.15	-0.07	0.13	-0.26*
	Experienced	N eggs (27)	-0.15	0.39*	-0.48*	-0.04	0.13	-0.09	-0.02	-0.15
		N hatchlings (27)	-0.05	-0.15	-0.32	0.10	-0.05	0.13	0.07	-0.48*
		N fledglings (29)	-0.15	0.12	-0.29	0.03	-0.003	0.18	0.02	-0.36~
	Lifetime	N eggs (81)	-0.01	-0.20~	0.15	0.07	0.26*	0.003	0.11	-0.20~
		N hatchlings (82)	-0.23*	-0.19~	0.23*	0.15	0.11	0.15	0.15	-0.30**
		N fledglings (86)	-0.21~	-0.08	0.13	0.10	0.13	0.13	0.09	-0.17
PCZ	Naïve	N eggs (75)	0.03	0.15	-0.14	0.00	-0.08	0.17	—	-0.01
		N hatchlings (75)	0.01	0.09	-0.21	0.03	-0.05	0.26*	—	-0.01
		N fledglings (76)	0.05	0.12	-0.07	0.00	-0.09	0.10	—	0.03
	Experienced	N eggs (16)	-0.05	0.03	0.23	-0.27	-0.02	0.03	—	0.04
		N hatchlings (16)	0.15	-0.05	0.07	-0.02	-0.10	0.17	—	-0.23
		N fledglings (16)	0.29	0.05	-0.10	0.02	-0.16	0.24	—	0.11
	Lifetime	N eggs (75)	0.08	0.07	-0.01	0.06	-0.02	0.17	—	0.02
		N hatchlings (75)	0.09	0.01	0.03	0.13	-0.02	0.26*	—	0.001
		N fledglings (76)	0.11	0.02	0.003	0.13	-0.06	0.15	—	0.07

~ 0.06 < P < 0.05, * 0.01 < P < 0.05, ** 0.01 < P < 0.001, *** P < 0.001, **** P < 0.001, “—” sample too small.

Table 4 – Results of logistic regression analyses of factors associated with male recruitment success on two study plots (PPL and PCZ) for data collected in 1997–2003. The first model (“Naïve”) analyses the influence of the preferred land cover type and settlement date of naïve males on recruitment success (0 – males with no recruits, 1 – males that fathered at least one recruit), with the influence of year (categorical variable) controlled. The second model (“Lifetime”) tests the influence of the preferred land cover type, settlement date (mean values for each male’s lifetime) and male longevity on recruitment success

Plot	Males	Model	B	S.E.	Wald	Df	P	N
PPL	Naïve	Reedmace + common reed	15.8	6.780	5.41	1	0.020*	173
		Settlement date	-0.34	0.381	0.78	1	0.378	
		Year (cat.)			2.18	6	0.902	
	Lifetime	Reedmace + common reed	3.87	2.086	3.44	1	0.064	171
		Settlement date	-0.28	0.270	1.10	1	0.294	
		N of seasons of life	1.38	0.378	13.3	1	0.001*	
PCZ	Naïve	Common reed	-1.13	2.206	0.26	1	0.609	125
		Settlement date	-0.02	0.478	0.01	1	0.972	
		Year (cat.)			1.42	4	0.840	
	Lifetime	Common reed	-1.24	2.165	0.33	1	0.566	127
		Settlement date	-0.03	0.060	0.21	1	0.640	
		N of seasons of life	1.14	0.647	3.11	1	0.078	

than on the sites occupied by the remaining males (see Fig. 4 for raw data). There was no significant relationship between recruitment probability and settlement date. Similar though only near-significant results on vegetation structure were obtained from lifetime data analysis. There was a significant influence of male longevity, but no significant relationship of settlement date.

On the PCZ plot, the fraction of reeds at sites occupied by males that fledged recruits did not differ from the corresponding fraction at sites of males that did not fledge any recruits; the influence of male longevity on recruitment came close to statistical significance.

4. Discussion

In this study we found significant associations between male settlement date and habitat parameters over long periods and with different sets of males. Settling individuals occupied sites according to the proportion of tall wetland vegetation at sites not yet occupied by other males. The mean proportion of tall wetland vegetation at sites correlated positively with some measures of their reproductive success. These results accord with the assumptions of the pre-emptive distribution model (Pulliam and Danielson, 1991).

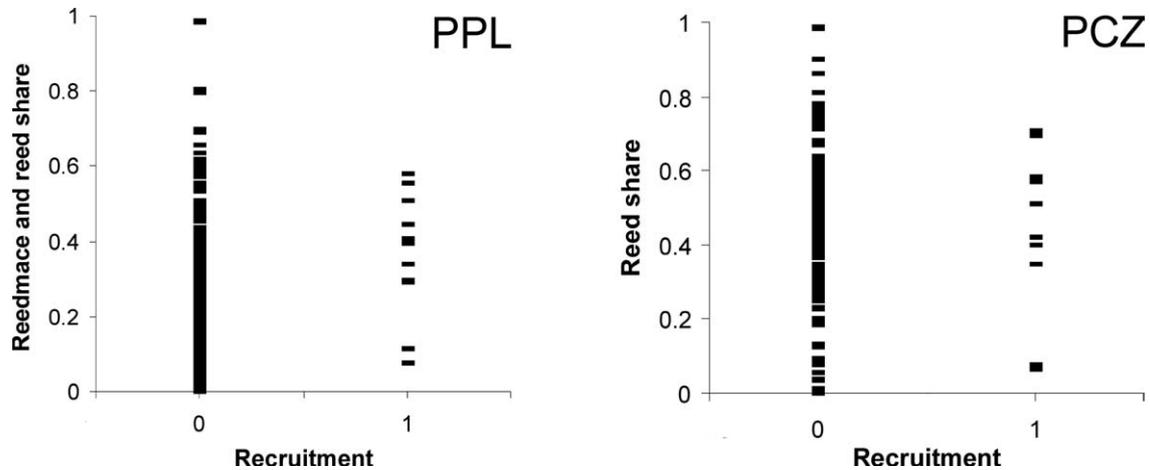


Fig. 4 – Scatter plots of site characteristics for naïve males that fathered recruits (1), versus those for males having no recruits (0), at the PPL and PCZ plots.

According to the pre-emption hypothesis, the feature that determines site choice in sedge warbler males is time of settlement. Early-arriving birds are free to pre-empt their breeding sites, whereas later arrivals have a limited choice, with no access to sites of superior quality (larger areas of tall wetland vegetation). However, in the following year, even though naïve individuals have become older and more experienced, they do not necessarily return from wintering grounds earlier than the year before; some experienced males appeared on the study plot later in the season (see male no. 11 in PPL in 2001, Fig. 3). Older individuals, regardless of the time they arrived, occupied sites with a higher proportion of tall wetland vegetation than the year before. This indicates that older males can take over more suitable sites even if they are not the earliest arrivers. It also indicates that occupation of the best sites is not determined only by arrival date or territory fidelity, but by age and experience as well.

In a heterogeneous environment like the PPL plot, settlement decisions have significant consequences for the individual's fitness. Those settling earlier than others and in larger patches of reed and reed are more successful in mating than later settlers that occupy smaller areas of tall wetland vegetation and may remain unmated. Males arriving early tend to have larger clutches and more fledglings. Although there was no straightforward relationship between nesting success and land cover type (Table 3), males occupying larger patches of tall wetland vegetation produced recruits significantly more often. Variation of fitness with site quality should lead to strong selection, increasing the male's ability to arrive at and occupy sites early, pre-empting them.

Settlement date and site land cover are highly correlated, and they probably influence male breeding success synergistically. While they are undoubtedly the two main variables, they are probably not the only parts of the synergy that shapes the males' fitness. Other variables at play may include individual male quality, conspecific attraction, and territory fidelity.

Early-arriving birds are commonly thought to be of superior individual quality, mainly due to the effects of parasitism and immune response on migration speed (Moller et al.,

2004). Early arrivers are usually older (although in this study the relationship between age and settlement date was obscured by the entry of some old males on the study plot later in the season), which means that their survival abilities have been positively tested by a variety of natural factors during their lives (Mauck et al., 2004). The higher fitness attained by long-lived individuals, such as was found in the present study, may be attributable to a number of things (see Newton, 1989 for review), including of course their longer life and greater breeding experience. The occupation of sites of increasing quality as males get older, as recorded in this study, implies that higher quality of breeding sites is another factor behind the higher breeding performance of older birds (see Currie et al., 2000).

According to the hypothesis of conspecific attraction, individuals gain from the presence of other individuals of the same species in the immediate neighbourhood (Reed and Dobson, 1993). In the studied population, the influence of conspecific attraction could not be separated from the land cover effect, because males can aggregate only if vegetation patches are large enough to allow clustering of territories. Large patches of reeds are occupied by several males per patch at first (Fig. 3), thus creating an effect analogous to conspecific attraction, which makes the two effects practically indistinguishable. If vegetation patches were small and dispersed (like those occupied late in the season in PPL, Fig. 3), no conspecific attraction could be detected because no positive effects of conspecific attraction would operate, due to the distance between patches. The dependence of the spatial arrangement of males on the land cover spatial pattern has serious implications for conspecific attraction studies, where in many cases the detected clumping of territories may in fact be a result of an uncontrolled environmental feature.

In the studied sedge warbler population, fitness correlated with the fraction of tall wetland vegetation at the male's site. Some studies have reported that individuals benefit from repeatedly choosing the same territory if they successfully raised a brood in that territory in the preceding year (Beletsky and Orians, 1994; Hoover, 2003). If the same rule is

operating in the studied population, then the males that are successful in 1 year will be the first to return to the largest patches of tall wetland vegetation. Such a mechanism would maintain the tradition of choosing to settle in the largest patches of reedbeds first, and thus would contribute to the synergistic effect of land cover patch size.

It seems difficult to disentangle the relative effects of each of the above factors on individual fitness. The multicollinearity between the two factors investigated in this study, that is, settlement date and the fraction of tall vegetation, is probably poorly discriminated by logistic regression analysis of the influence of land cover and settlement date on male fitness. These two factors largely explain the same variation in males' fitness. For instance, while settlement date was the main correlate of mating success in PPL, in PCZ the fraction of reedbed at the sites correlated with the probability of mating. Experiments may be the only way to distinguish these two effects, but it is not difficult to imagine ethological reasons why males would choose larger patches of reed and reedmace for breeding territories, besides the ones suggested above. A few are given below.

The influence of land cover type on fitness is visible mainly in mating success and recruit production. When male sedge warblers arrive at the study plots, the females are not there yet; thus the males must choose suitable sites without the benefit of direct signals from females. The females, in turn, enter the area when most of the best sites have already been occupied, and thus have no information about the differences in time of settlement of particular males. In choosing a mate, therefore, they probably rely on traits reflecting the individual quality of males (such as flight displays and/or song quality; Buchanan et al., 1999), or their decisions may be based partly on the features of the sites the males chose.

The site occupied by a male can effectively determine his mating success in a proximate way. Sedge warblers are known to have a very strong mechanism of sexual selection based on the level of male song complexity (Catchpole, 1980, 1996; Buchanan and Catchpole, 1997). On the flat, open surface of wetlands, patches with tall vegetation (2–3 m above the ground) offer the males much better conditions for song propagation (Mathevon and Aubin, 1997) than dry sedge or meadows, where tussocks or stems reach no more than 0.3 m above the ground. Sedge warblers settle before the vegetation starts to grow. Old sedges and grasses are usually flattened to the ground, having been covered by snow during the winter. Borowiec (1999) suggested a similar role for reeds at the time of male settlement.

When settling, however, the sedge warbler males not only show a preference for patches of tall wetland vegetation (such as reedmace and common reed), but also choose areas where the patches of these vegetation types are larger; this cannot be explained by better conditions for song propagation. Another explanation may be suggested: the size of the tall vegetation patch may influence female behaviour. Immediately upon arrival, in their search for a partner, female sedge warblers are subject to constraints (time, mobility, predation risk, etc.). They should therefore make their choice as soon as possible, based on the highest available number of males that can be compared in a single area (Janetos, 1980; Hutchinson and Halupka, 2004). They should be expected to

examine large patches of an attractive vegetation type, where more males can be assessed. Such a strategy would enable females to compare the individual features of many males simultaneously, and to select partners for pair bond formation (Bensch and Hasselquist, 1992) and possibly for extra-pair copulations (EPC, Neudorf et al., 1997; Buchanan and Catchpole, 2000). High-quality males should prefer this type of site, as occupying them promises successful matings. Consequently, adaptations enabling easy identification of environmental traits that ensure the achievement of higher fitness should improve site selection ability and increase the experience of males throughout their lives.

Ultimate breeding success probably was not determined during the nesting period, as the nests were usually located at the edge or just outside of the patches of reed or reedmace, in adjacent sedge tussocks (Król et al., 2002). However, fledglings leave the nest very soon and usually hide in the closest patch of tall vegetation until they are capable of making short flights. Small patches of reedbeds probably do not provide fledglings with enough cover; this is a well-known effect of habitat fragmentation (Wiens, 1994), on the scale of individual sites rather than habitats. These effects can result from the smallness of the patch area itself (e.g. increased penetration of predators and susceptibility to physical disturbances and weather effects) and from increased distance to other patches of suitable habitat (e.g. higher mortality from predation or from drowning while learning to fly). Also, the probability that the patch area will diminish or even disappear between seasons depends on its size (Bielański et al., 2005).

A remaining question concerns the mechanism of the influence of a site's land cover structure on the male's offspring recruitment in the following breeding season. This relationship may be particularly complex in the case of migratory birds such as sedge warblers, which are subject to many off-site events during migration and wintering. In the studied population, however, the relationship between site characteristics and subsequent recruitment holds despite the potential obscuring role of events occurring between fledging and recruitment. It should be remembered that some very important features of the offspring phenotype are determined in the post-fledging period, that is, within the sites occupied by the offsprings' parents. Many morphological traits (except tarsus length) are still developing after the nest is vacated (Król et al., 2002). Traits like body size and condition can influence survival during the first autumn migration. Although the natal site conditions are certainly not the only factors determining the probability of recruiting young, they undoubtedly have a great influence upon this parameter.

If the quality of a territory is evaluated only on the basis of reproductive success, choosing a good territory can never result in low reproductive success (Rodenhouse et al., 1997; McPeck et al., 2001). Describing habitat preferences on the basis of easily measurable and quantifiable features of the environment prevents the commonly committed tautology of defining suitability by the same demographic measures used to assess suitability. In our study, the differences between sites can be measured independently of the fitnesses achieved. Thus, settling preferences do not necessarily have

to imply higher breeding success. It is possible to falsify the relationship between settlement and fitness. Measuring the area of tall vegetation enables one to detect maladaptive habitat selection, possibly resulting from an “ecological trap” mechanism. This can occur when anthropogenic processes decouple the cues used for habitat selection from the fitness outcomes (Misenhelter and Rotenberry, 2000).

Apart from the micro-scale of individual sites, the influence of vegetation structure upon fitness can also be noticed at a larger spatial scale. Within-habitat heterogeneity was significantly higher at PPL than at PCZ. Such differences could influence the level of variation of the fitness achieved by individuals in each study plot. Sedge warblers preferred patches of reed at PCZ. The spatial distribution of this vegetation type, consisting of a few large patches, considerably reduced the within-habitat heterogeneity on that plot. This reduced the variation of site quality there, because most of the individuals occupied large homogeneous reedbeds (PCZ in Figs. 1b and 3). As a result, the differences in fitness between individuals were probably too small to be detected. In contrast, the within-habitat heterogeneity at PPL was high both in terms of vegetation types and in terms of their spatial distribution (many patches of various sizes and various spatial distributions, Fig. 1). This was reflected in considerable variation of site quality (PPL, Fig. 3) and, consequently, detectable differences in male fitness.

The assumptions of IFD/IDD about within-habitat homogeneity were not confirmed in this study. Even in relatively homogenous PCZ, the settlement pattern was not random but based on the same rule as in heterogenous PPL. On the contrary, the assumptions of IPD were confirmed: at the heterogenous plot the sites best for reproduction were occupied first; interestingly, however, the number of successful sites (in terms of local recruitment) was very limited.

The results of this study are potentially useful in nature conservation. According to the model of Pulliam and Danielson (1991), the consequences of habitat loss for population dynamics are weaker when individuals have greater site selection ability. Data on pre-emption can be used to estimate the relative contributions of different areas to population size and growth, and that analysis should be a key element in targeting critical areas to be protected (Pulliam and Danielson, 1991). The pre-emption model of site occupation assumes that sites occupied first usually bring about the highest fitness. The settlement pattern can therefore indicate which areas are most valuable to the species and should be prioritised in order to maintain viable populations.

5. Conclusion

Selection of breeding sites by male sedge warblers is based on small-scale features of land cover, and is repeated over periods exceeding the scale of the life span of individuals. Individuals settle first of all at sites with the largest available fraction of tall wetland vegetation. Mating success, nesting success and recruitment are negatively correlated with settlement date and consequently with the characteristics of the sites occupied by males during settlement. Males improve their breeding site quality during their lifetimes. Such

relationships are more pronounced in areas with high within-habitat heterogeneity, a finding which confirms the IPD model.

Acknowledgements

We are grateful to all those who took part in the field work, and in particular to Aleksandra Gondek, Kuba Janik, Wiesław Król and Bartek Pirga. Paweł Adamski, Mariusz Cichoń, Henryk Okarma, Paweł Olejniczak, John Rotenberry and Piotr Tryjanowski and the anonymous reviewers provided invaluable suggestions. We thank William Z. Lidicker for his keen interest and helpful comments. This study was funded by grants from the Polish State Committee for Scientific Research, no. 6P04F06412 and no. 6P04F02320.

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