The role of territory choice, mate choice and arrival date on breeding success in the Savi's Warbler *Locustella luscinioides*

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We investigated how territory quality, settlement date and morphometry affected several components of yearly breeding success of a Swiss population of Savi's Warblers *Locustella luscinioides*. Territories occupied by males differed from unoccupied sites of similar size and location by having higher and denser reeds, a more extensive straw litter, and a thicker cover of dead sedge leaves. Territories with these characteristics were the ones first chosen by males upon spring arrival. These males, however, did not differ in morphometry from those that arrived later. Availability of suitable nesting sites, rather than food availability, appears to be an important choice criterion for territories. Early arriving males had higher breeding success than late males because of a higher mating success and more successful clutches. The positive correlation between male breeding success and territory quality was thus mediated through their common dependence on occupancy date. Female breeding success decreased with the date of first-clutch laying, mainly because late-nesting females fledged fewer broods. Breeding success in either sex did not correlate with morphometry. Our results provide clear support for territory choice by males, but not for mate or territory choice by females, and show the crucial role played by individual settlement date on many aspects of the breeding cycle of both sexes. We propose a lottery model of mate choice: arriving females obtain the best available territories even without choosing mates or territories; since males occupy territories sequentially and in order of decreasing quality, the few unpaired males available at any moment also occupy the best available territories.

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In many bird species, nesting adults need breeding territories to rear offspring successfully, and males often play a major role in acquiring and defending them against competitors. Territories may vary greatly in quality, as measured by food availability or exposure to predators (Hildén 1965, Brown 1969) and this variability affects male fitness. When searching for mating partners, females are expected to select males either by their quality or by their territory, since their own fitness depends on it (Orians 1969, Burger 1985, Yasukawa and Searcy 1986). Acquiring a good territory should help males to attract more and/or better females. Male and female fitness is influenced by offspring survival,

which depends directly on food availability and predation risk. In fact, all components of male yearly breeding success (mating success, number of clutches per female, clutch sizes as well as hatching rate, nestling success and postfledging survival) can be expected to depend to some degree on territory quality. The same is true for females, apart from mating success. Therefore, access to a good territory is of crucial importance to both sexes.

Territorial defence, however, may require good fighting ability if competition is strong. In migratory species, early arrival at the breeding sites allows first access to the best territories (Wallgren 1956, Brooke 1979, Urano
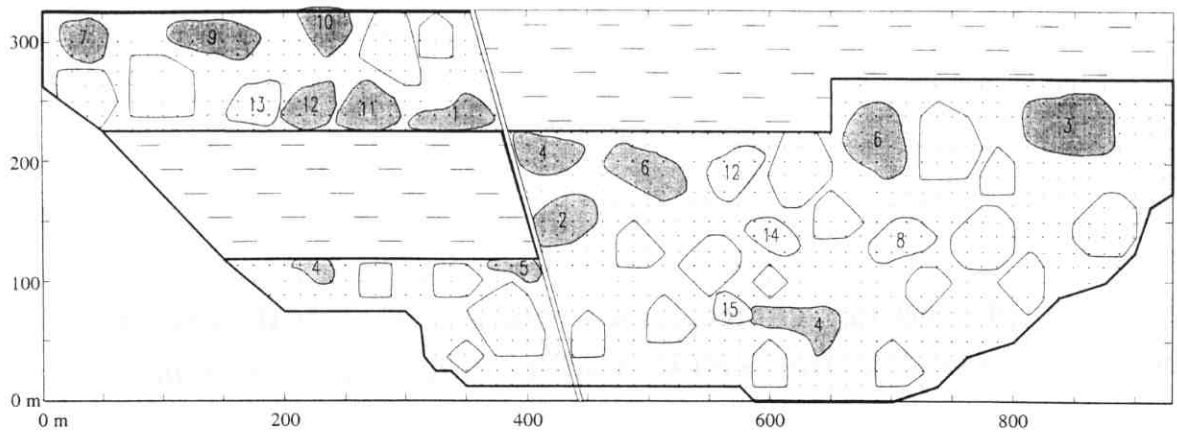
Fig. 1. Study area with territories of paired males (dark grey), bachelors (light grey) and pseudo-territories (open). Numbers within territories correspond to ranked arrival dates. Dots are the sampling points and dashed areas are mown parcels.

1985, Bensch and Hasselquist 1991) but early migration may also incur some costs that only healthy individuals can afford to pay (e.g. Ketterson and Nolan 1983, Arvidsson and Neergard 1991). Thus, the relationships between arrival date, body condition, territory quality and breeding success are critical for the settlement tactics of migratory territorial birds.

Here we present the results of a study of the Savi's Warbler *Locustella luscinioides*. The questions we specifically tried to answer are: (1) by which criteria do individuals choose territories or mates; (2) does breeding success depend on territory quality, mate quality or settlement date; and (3) which components of breeding success are actually affected.

Material and methods

General biology

Savi's Warblers are sexually monomorphic migratory birds that winter in sub-Saharan Africa, north of the tropical forest range (Bub and Dorsch 1988, Glutz von Blotzheim and Bauer 1991). They arrive at their breeding sites in Switzerland from late March to late April (Aebischer and Antoniazza 1995). Breeders occupy lowland swamps and flooded lands, nesting preferably in sedge tussocks mixed with reeds *Phragmites australis*, cattail *Typha* or fen-sedges *Cladium mariscus* (Cramp and Brooks 1992, Glutz von Blotzheim and Bauer 1991). Males occupy nesting territories within a few days after arrival, and defend them against intruders (Pikulski 1986). Females settle later (Dittberner and Dittberner 1985, own observations). The time-lag between male settlement and female arrival in Poland was 7 to 16 days, while the range of male arrival dates was 3–4 weeks (Pikulski 1986). Seasonal monogamy is the norm, but bigyny occasionally occurs (Glutz von

Blotzheim and Bauer 1991). The first nests appear within 2–3 weeks of the arrival and are mainly constructed by the females who sometimes get some help from their mates (Dirkx 1939, Mildenberger 1958). In Switzerland, usually two, rarely three clutches of 3–5 eggs are produced successively (Aebischer and Meyer unpubl.). Females perform most of the incubation, and both sexes feed the nestlings (Pikulski 1986).

Study site and environmental variables

Our study area (Fig. 1) covered 17 ha of the southern shore of Lake Neuchâtel (Switzerland). It is dominated by dense stands of sedges *Carex elata* and fen-sedges mixed with reed. Observations were carried out from March to July 1993. The daily temperatures were 1–2°C above average during breeding time. Precipitation reached average values in April and July, in May they were 81% and in June 121% of the average. We collected data on vegetation structure in March (i.e. before bird arrival). At this time the vegetation resembles what birds see when they arrive. Since territory limits were not known in March, vegetation variables were measured at 1150 sampling points situated at the nodes of a 12.5 m × 12.5 m grid covering the whole study area (Fig. 1). We sampled the following variables: (1) the proportion of open water in the square metre around the node; (2) the proportion of the square metre around the node that was covered by vegetation. For both variables, six classes were made, starting from 0 (no water or no vegetation visible) to 5 (81–100% of the square under water or covered by vegetation), going in steps of 20% (the sum of the variables (1) and (2) may not always equal 100%, e.g. in presence of mud); (3) the presence or absence of fen sedges at the node (value 1 or 0); (4) mean reed density (number of reed stalks at 0.5 and 1.0 m height on 0.25 m² around the node); (5)

144

mean reed density at 1.5 and 2.0 m height; (6) mean reed density at 2.5 and 3.0 m height; (7) mean reed height, calculated from the formula:

$$ARH = \frac{1}{RD_{0.5}} \sum_{h=0.5}^{3.5} (RD_h - RD_{h+0.5})h$$

where RD_h is the reed density at height h and h varies from 0.5 m to 3.5 m (in steps of 0.5 m); (8) the presence or absence of straw litter at the node; (9) the thickness of this layer (Fig. 2); (10) the presence of covering dead leaves from the previous year at the node; (11) the height of this cover (Fig. 2).

These last four variables reflect the availability of nest locations; nests are usually built within the straw litter and covered by dead leaves. By including all the nodes situated inside the later established territories ($\bar{x} = 10.9 \pm 4.5$ nodes), we calculated the mean value per territory for each variable.

Arrival dates and morphometry of the birds

The study area was visited every other day from late March to mid-June. During 3 hours around sunrise, we recorded the reactions of newly arrived warblers to playback of tape recordings every 30–50 m along a series of 7 parallel (50-m apart) transects (singing males can be heard from at least 200 m distance). At the beginning of the season when only few territories are occupied, playback can induce birds to leave their territory to approach the tape. Therefore, reactions to playback were only used to register the arrival dates but not to delimit territory boundaries. As soon as possible after their arrival, all birds were caught with mist nets and marked with a combination of coloured plastic leg rings to permit individual identification in the field. Birds were weighed and the lengths of bill, tail, tarsus. wing and third primary, and toe-span (including claws) were measured according to Svensson (1992). From these values, we calculated three condition factors of birds: the ratios of (body mass)$^{1/3}$ to tarsus length and wing length, respectively, and the residuals of the re-
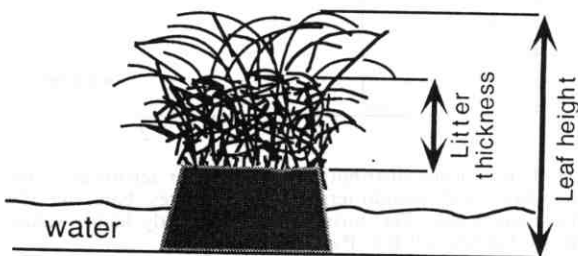

Fig. 2. Sedge tussock with descriptive variables Leaf height and Litter thickness.

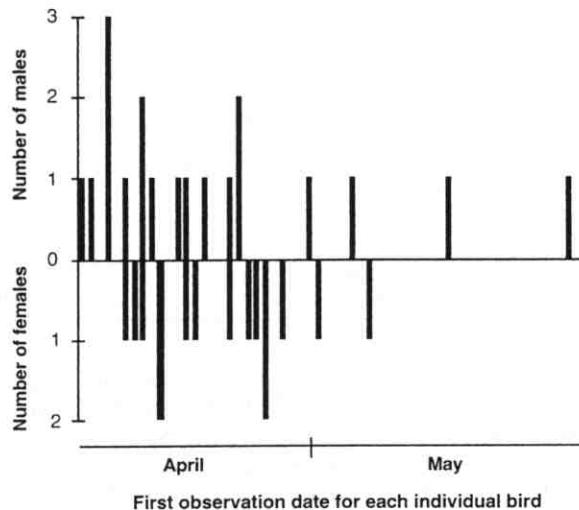First observation date for each individual bird

Fig. 3. Frequency distribution of first observation dates for males (above) and females (below) in 1993. First observation dates of males correspond closely to their arrival dates. The exact arrival dates of females are not known.

gression of (body mass)$^{1/3}$ on tarsus length. Birds were released at the point of capture.

It was impossible to determine the exact arrival dates of the females. After their arrival and until they started feeding their young, they spent most of the time well hidden in the straw litter. Calls could not be attributed to females. Thus, the females probably arrived some days earlier than first observed. However, this does not alter the finding that there was a strong overlap in the arrival dates of males and females (Fig. 3).

Territories and pseudo-territories

Two or three persons spent about 5 hours a day at least every other day from mid-April to late July on a step-ladder, to observe warblers and locate nests. The data from April and May (15–21 days per territory) were used to delimit territories. Reactions to playback and foraging activities, which often occur outside territories, were excluded. About 50–100 positions of singing or calling males were determined per territory and plotted on 1:1000 maps. Territory sizes were then measured from drawn polygons with a planimeter. Nests were found by observing females carrying nest material or adults feeding young. They were visited every other day and clutch sizes were recorded. In one territory. no nest was found until 16 July, even though the female had arrived on 26 April at the latest and had been observed regularly since. In this territory, at least one nest was presumably destroyed before we found it. This territory was excluded in analysis of the influence of egg laying dates on breeding success. All the other nests in our study area were found. 12 out of 38 during

Table 1. Discriminant function analysis comparing territories and non-occupied pseudo-territories. P-values correspond to Mann-Whitney U tests. *P < 0.05, **P < 0.01.

	P	Standardized canonical coefficients	Canonical loadings
Proportion that was flooded	0.569	−0.188	−0.078
Proportion covered by vegetation	0.119	−0.172	0.244
Average of reed densities at 0.5 and 1.0 m	0.830	−0.600	−0.111
Average of reed densities at 1.5 and 2.0 m	0.065	−0.256	0.131
Average of reed densities at 2.5 and 3.0 m	0.049*	0.526	0.251
Average reed height	0.002**	0.872	0.529
Presence of fen sedges	0.936	0.972	0.091
Presence of straw litter	0.044*	0.833	0.301
Litter thickness	0.090	0.096	0.304
Presence of covering leaves	0.207	−0.192	0.161
Height of covering leaves	0.041*	0.167	0.359

the egg laying phase, 11 during incubation and 15 during the nestling period (7 of which held the maximum number of 5 hatchlings). Since Savi's Warblers usually keep nondeveloping eggs in the nest we conclude that we have monitored practically all breeding losses.

The part of the study area not occupied by territories (more than half of the surface; Fig. 1) was used to delimit 'pseudo-territories'. These consisted of non-overlapping areas centred on randomly chosen nodes of the sampling grid, to which sizes (i.e. number of nodes) were randomly assigned from the size distribution of real territories. These areas, located in the same habitat type as real territories, were also characterised by the eleven variables described above. For each variable we calculated the mean value per pseudo-territory by considering all the nodes situated within its boundaries ($\bar{x} = 13.5 \pm 5.5$ nodes).

Statistical analysis

The relationships between phenotypic traits and arrival dates were investigated by using the data available for the period of 1992–1994. We standardized the arrival dates for each year to allow the combination of all three years into one data set.

Parametric statistics were used as long as the underlying assumptions were met. Normality was tested according to Lilliefors (1968). For the discriminant analysis we used SYSTAT 5.2.1 (Wilkinson 1992). All the other tests were performed with StatView 4.0 (Haycock et al. 1992). Statistical significance was accepted at the 0.05 level.

Results

Territories

Nineteen males acquired and defended territories, ranging from 500 to 3300 m² (mean = 1450 ± 680 S.D.), and

23 pseudo-territories were defined on unoccupied surfaces. Univariate Mann-Whitney statistics pointed to 4 variables (out of 11) that differed significantly between territories and pseudo-territories (Table 1): *Average reed height* was the first one (P = 0.002), followed by *Cover height* (P = 0.041), *Presence of straw litter* (P = 0.044) and *Average reed density at 2.5 m/3 m* (P = 0.049). Real territories had higher values on average for each variable. A discriminant analysis was then performed in order to find the canonical function providing the best segregation between territories and pseudo-territories. The four variables mentioned above were among those that correlated most strongly (all positively) with the discriminant function (canonical loadings in Table 1). Litter thickness also correlated with this function. Table 1 also provides the canonical coefficients of the discriminant function. The scores of territories and pseudo-territories differed significantly on the discriminant factor (Fig. 4; Wilks' lambda = 0.462, P = 0.006), with 17 territories (out of 19) and 18 pseudo-territories (out of 23) correctly attributed, i. e. 83% correct discrimination.
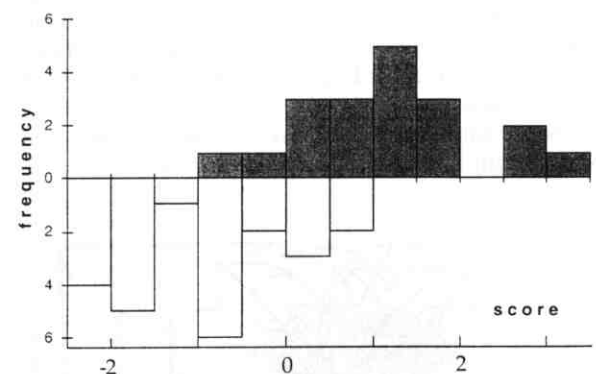

Fig. 4. Frequency distribution of scores for territories (dark grey bars) and pseudo-territories (light grey bars) on the discriminant axis. Territories have significantly higher values (Wilks' lambda = 0.462, P = 0.006).

146

Table 2. Spearman rank correlation coefficients between male occupancy date, laying date, territory score and territory size. *P < 0.05, **P < 0.01.

	Male occupancy date	Laying date of first egg	Territory score
Laying date of first egg	0.684 P = 0.023*		
Territory score	−0.741 P = 0.002**	−0.257 P = 0.394	
Territory size	−0.363 P = 0.123	−0.329 P = 0.275	0.227 P = 0.336

In 1993, the dates of territory occupancy by males ranged from 2 April to 30 May. As appears from Table 2 and Fig. 5a, these dates were negatively correlated with the territory scores (P = 0.002), but not with territory size (P = 0.12).

Breeding success

Five males remained unmated, 13 were monogamous, and one bigynous. Mating success was unaffected by territory size (P = 0.34; Table 3), but was correlated significantly with the date of occupancy (P = 0.002; Fig. 5b) and with the territory score (P = 0.021). But this latter correlation was indirect and stemmed from the correlation between occupancy date and territory score. After controlling for the effects of occupancy date, there was no correlation between mating success and territory score (partial correlation coefficient r = −0.12, P = 0.64, n = 19).

The first egg of the first clutch was laid on 26 April and the last female started laying her first clutch on 19 May. Clutch initiation dates correlated with the settlement dates of the males (P = 0.023; Table 2), but not with the territory score (P = 0.39).

The number of successful clutches per male (0 to 4, mean 1.47 ± 1.17, n = 19) correlated negatively with territory occupancy date (P < 0.001; Fig. 5d) and positively with territory score (P = 0.003; Table 3). After removing the effect of occupancy date, the latter correlation was no longer significant (partial correlation coefficient r = 0.21, P = 0.41, n = 19). The number of successful clutches per female, ranging from 1 to 3 (mean 1.87 ± 0.74, n = 15), decreased with the date of initiation of the first clutch (P = 0.006; Fig. 6a).

The mean clutch size per territory, ranging from 3.5 to 5, did not correlate significantly with either male occupancy date or territory score (Table 3), but clutch
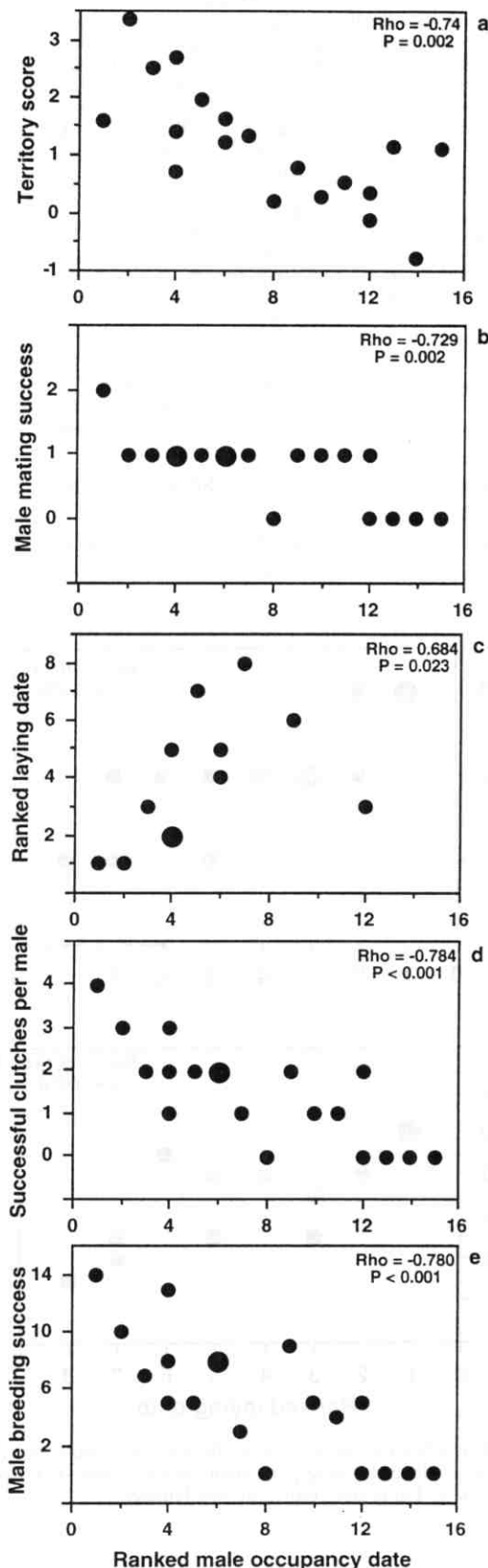

Fig. 5. Correlations between male (ranked) occupancy date and different breeding parameters. (a) Territory score; (b) male mating success (number of females nesting on a male's territory); (c) clutch initiation date; (d) number of successful clutches per male; (e) number of fledged young per territory. Large dots represent two males.

Table 3. Spearman rank correlation coefficients between male occupancy date, territory score, territory size and measures of male breeding success. Successful clutches = clutches in which at least one offspring fledged. Mean clutch size is the average clutch size per territory. Fledging success is measured as the number of offspring fledged per egg laid in the territory. Breeding success corresponds to the number of young fledged per territory. *P < 0.05, **P < 0.01, ***P < 0.001.

	Male occupancy date	Territory score	Territory size
Mating success	−0.729 P = 0.002**	0.545 P = 0.021*	0.227 P = 0.337
Number of successful clutches	−0.784 P < 0.001***	0.690 P = 0.003**	0.394 P = 0.095
Mean clutch size	0.082 P = 0.767	−0.029 P = 0.916	−0.176 P = 0.525
Fledging success	−0.359 P = 0.196	0.374 P = 0.177	0.135 P = 0.627
Breeding success	−0.780 P < 0.001***	0.636 P = 0.007**	0.489 P = 0.038*

Table 4. Spearman rank correlation coefficients between laying date, territory score, territory size and measures of female breeding success. Number of successful clutches = number of clutches per female in which at least one offspring fledged. Mean clutch size is the average clutch size per female. Fledging success is measured as the number of offspring fledged per egg laid. Breeding success corresponds to the number of young fledged per female. *P < 0.05, **P < 0.01.

	Laying date of first egg	Territory score	Territory size
Number of successful clutches	−0.791 P = 0.006**	0.546 P = 0.041*	0.327 P = 0.221
Mean clutch size	−0.134 P = 0.643	−0.071 P = 0.791	−0.124 P = 0.643
Fledging success	−0.418 P = 0.147	0.359 P = 0.179	0.196 P = 0.463
Breeding success	−0.751 P = 0.009**	0.433 P = 0.105	0.466 P = 0.081

size decreased with laying date (Spearman rank correlation, rho = −0.505, P = 0.021, n = 22).

The nesting site on a given territory changed from clutch to clutch, but mating partners did not: all females laid their several clutches in a single breeding territory.

Fledging success per territory (i.e. the mean number of offspring fledged per egg laid) ranged from 0.23 to 1 (mean 0.69 ± 0.23, n = 14). Weak correlations were observed with occupancy date and with territory score which, however, remained non-significant (Table 3).

Male breeding success, measured as the total number of young fledged per territory, ranged from 0 to 14 (mean 5.5 ± 4.4, n = 19). Breeding success correlated with male occupancy date (P < 0.001; Fig. 5e) and territory score (P = 0.007, Table 3). The latter, however, had no independent effect when keeping occupancy date constant (partial correlation coefficient r = 0.15, P = 0.56, n = 19). Female breeding success (i.e. the number of offspring fledged per female) ranged from 3 to 13 (mean 6.9 ± 2.8, n = 15) and correlated strongly with the date the first clutch was started (P = 0.009; Table 4; Fig. 6b). No correlation was observed with the territory score.

The correlations between occupancy date and male breeding success, and between egg laying date and female breeding success are tied to the number of successful broods. This is strengthened by the absence of significant correlations between occupancy date and number of fledged offspring per successful brood (Spearman rank correlation, rho = 0.081, P = 0.77, n = 14) and between egg-laying date and the number of fledged offspring per successful brood (Spearman rank correlation, rho = 0.013, P = 0.97, n = 13).

Morphometry

None of the male or female phenotypic traits measured showed any significant correlation with either occupancy date, territory score, territory size, mating success, start of egg laying or, more generally, with overall breeding success (total number of offspring fledged; Table 5). Males with long tarsi tended to settle earlier
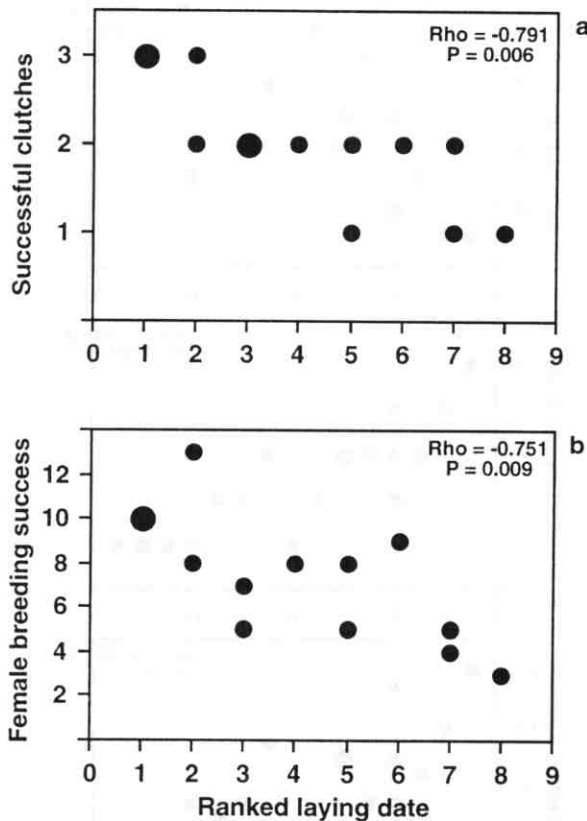

Fig. 6. (a) Number of successful clutches per female and (b) number of fledged young per female as a function of ranked laying date. Large dots represent two females.

148

Table 5. Spearman rank correlation coefficients for the morphometric traits versus mating success, breeding success and territory attractiveness (occupancy and laying date, territory score). The three condition factors correspond to the ratios of (body mass)$^{1/3}$ on tarsus length and on wing length, respectively, and to the residuals of the regression of the (body mass)$^{1/3}$ on the tarsus length. The two values per cell correspond to males and females respectively. *: $P < 0.05$. No correlation is significant after Bonferroni corrections.

	Mating success	Breeding success	Male occupancy date	Territory score	Territory size	Laying date of first egg
Tail length	−0.27	−0.29/−0.21	0.46/−0.04	−0.40/0.26	−0.45/−0.44	−0.08/0.18
Bill length	0.01	−0.18/−0.20	0.06/0.02	−0.13/−0.28	−0.22/−0.18	−0.14/−0.33
Tarsus length	0.40	0.41/0.39	−0.49*/−0.13	0.11/0.11	0.09/0.49	−0.20/−0.70*
Toe-span	−0.42	−0.22/−0.05	0.25/0.55	−0.15/−0.25	−0.26/0.06	−0.28/0.29
Wing-length	−0.22	−0.04/−0.01	0.14/−0.02	−0.06/−0.32	0.01/−0.22	−0.54/0.01
3rd primary feather	−0.12	0.06/−0.33	0.02/0.07	−0.01/−0.21	0.17/−0.44	−0.31/0.33
Weight	0.13	0.14/−0.09	−0.20/−0.33	−0.01/−0.04	−0.27/0.43	0.23/−0.45
Condition 1	−0.29	−0.30/−0.36	0.28/−0.22	−0.09/0.09	−0.52*/−0.24	0.63*/0.14
Condition 2	0.21	0.09/−0.06	−0.19/−0.27	−0.01/0.28	−0.16/0.41	0.42/−0.44
Condition 3	0.08	0.09/−0.10	−0.11/−0.33	0.06/−0.01	−0.37/0.25	0.40/−0.53

($P = 0.039$) and females with long tarsi tended to lay eggs earlier ($P = 0.035$). Males with a higher ratio of (body mass)$^{1/3}$ to tarsus length had somewhat smaller territories ($P = 0.049$) and their females tended to start egg-laying earlier ($P = 0.029$), but all these trends were not significant when applying Bonferroni corrections.

The absence of significant correlations between the phenotypic traits of the males and their arrival dates was confirmed by the results of 1992 (Spearman rank correlation, all $P > 0.3$, $n = 13$ to 16) and 1994 (all $P > 0.4$, $n = 21$).

Discussion

Territories

The territories chosen by male Savi's Warblers differed significantly from unoccupied, randomly chosen sites of similar size and location. They were characterised by higher and denser reeds, an extensive straw litter, and a thick cover of dead sedge leaves. Thus, these variables were either directly involved in territory choice, or strongly correlated with the relevant choice variables. In any case, they presumably correlated with some aspects of territory quality. Thirty-six nests (out of 38) were located within the dead-leaf litter topping sedge tussocks, which suggests that the availability of nest-site locations may be a crucial criterion in territory choice.

The discriminant function, with which the above-mentioned variables correlated, offers the best expression of the differences between territories and pseudo-territories. Thus, territory scores on this axis can be taken as a global measure of the territories' attractiveness to males. This is confirmed by the strong correlation between territory scores and occupancy dates. Territories with the highest scores were clearly among the first chosen by males upon arrival and occupancy date explained more than half of the variance in territory scores. However, males that arrived

first were not of better quality, as measured by size, body mass or condition, and these phenotypic variables did not correlate with territory scores.

The only way to make sense of male preferences is to assume a close relationship between territory score and territory quality. In what follows, we will build on this assumption, and refer indifferently to either territory score or territory quality. We want to emphasise, however, that our measurement of territory quality is indirect, and that it relies on patterns of male preferences.

Only 2 out of 15 males ringed in 1992 renested in about the same territory in 1993. For 1993–94, the figure was 2 out of 14. Thus, territory fidelity is unimportant in the settlement strategy of Savi's Warbler. This is confirmed by observations at lake Neusiedl, Austria (Zwicker, cited in Glutz von Blotzheim and Bauer 1991).

Breeding success

The later the males settled, the lower was their breeding success. Similarly, the later females laid their first clutch, the lower was their breeding success. Male breeding success increased with territory score but these effects were indirect and entirely due to settlement date. Furthermore, territory score did not affect female breeding success either. Thus, good territories did not lead to the fledging of significantly more young.

Breeding success is influenced by several factors. Variation in male breeding success was essentially due to the effect of occupancy date on mating success: early arriving males were more likely to attract a female, but not a better female in terms of morphological variables or clutch-size. Furthermore, the earlier a male arrived, the earlier his female started laying eggs and the more broods they could rear. In females, the brood number was the main parameter affected by first-clutch laying date: early laying females had more time to rear a second or third brood. The only three females able to

rear three successful broods were the earliest ones to start the first clutch. Fledging success and mean clutch size per female were not influenced by the arrival date of the male or by the date when the female started laying the first clutch. However, clutch size per brood decreased with laying date. Dittberner and Dittberner (1991) also concluded from their studies in Germany that clutch size in Savi's Warbler decreased with laying date. In other species, late breeding has been shown to reduce post-fledging survival (Hochachka 1990, Verhulst and Tinbergen 1991, Nilson 1994). The advantages birds obtain by arriving early on the breeding grounds suggest the simultaneous existence of high costs that counterbalance benefits (Møller 1994). Males and females that arrive early on the breeding grounds may be exposed to adverse environmental conditions.

Lottery model

Our results can be summarised graphically (Fig. 7). As for their interpretation, the following model gives the most parsimonious account: (1) Male territory preferences are fixed, but arrival dates vary. Thus, the first males to arrive can choose among all available territories. (2) Female arrival dates, also highly variable, overlap considerably with those of males. (3) Upon arrival, females pair with any of the few unpaired territorial males available at the moment; i.e. they can not choose mates with regard to quality and/or territory.

This model obviously requires a few comments. According to the first point, early arriving males acquire better territories. The same seems generally true of other migratory territorial passerines (e.g. Wallgren 1956, Brooke 1979, Urano 1985, Bensch and Hasselquist 1991, Leugger 1993). In our case, the question arises why males should care to choose and defend good territories, if territory quality *per se* does not
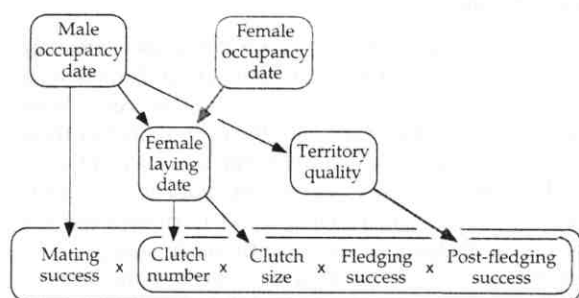

Fig. 7. Synthetic model accounting for the observed or assumed relationships between phenology, territory score, and components of breeding success. Grey lines refer to assumed relationships. Unobserved variables are represented in grey boxes. Arrows propose a causal interpretation of observed correlations. Outer box refers to male, and inner box to female breeding success.

affect breeding success. One may argue that territory quality was not accurately accounted for by our environmental variables. However, the strong correlation between arrival date and territory score contradicts this interpretation, by suggesting that most of the relevant variables were sampled. More plausible are the following three arguments:

(a) An extensive straw litter and a thick cover of sedge leaves may be a good protection against predators. The fledged offspring as well as adults spend most of the time hidden in the cover of dead leaves. Thus territory quality may affect post-fledging success and adult survival.

(b) Litter thickness and leaf height are very important for nest site selection (Aebischer and Meyer unpubl.) and are among the variables that are most strongly correlated with the discriminant scores (Table 1). Territory quality may be related to nest site quality and males may choose good nest sites. This is supported by the fact that litter thickness (Wilcoxon signed rank test, $Z = -4.71$, $P < 0.0001$, $n = 32$) and leaf height (Wilcoxon signed rank test, $Z = -4.70$, $P < 0.0001$, $n = 32$) at the nest sites were much higher than the means for the territories.

(c) Any relationship between territory quality and breeding success is bound to be year- and site-dependent. Nest mortality was surprisingly low in our study (about 6% of nests depredated), which certainly is atypical: according to Ricklefs (1969), marsh-nesting birds suffer the highest nest-mortality rate among all temperate zone passerines, mainly through predation. Pikulski (1986) recorded 44% nest mortality in a Polish population of Savi's Warblers, more than half due to predation. Availability of good (that is protected) nest sites is likely to make a big difference when populations are more heavily depredated, or in years of bad weather conditions.

The hypothesis that good territories may offer more or better food, affecting nestling and fledgling size (Perrins, 1965, Howe 1979, Lemel 1989, Richner 1989, Smith et al. 1989, Leugger 1993) as well as adult condition, is not confirmed by our observations. In our study, better territories did not lead to more fledged offspring. In fact, territories do not coincide with the feeding ranges. During 141 hours of observations at 24 different nests we recorded 624 foraging trips by adults, 78% of which led outside the respective defended territory. Furthermore, we found no correlations between territory scores and food availability in the territories during the nestling period (Tschan et al. unpubl.). This suggests that food was not a limiting factor in our study (see also Martin 1986).

Territory quality has often been shown to correlate with mating success (e.g. Ficken and Ficken 1966, Wittenberger 1980, Urano 1985, Pikulski 1986, Ezaki 1990) or with other male traits, such as male body condition (e.g. Bibby 1982, Cody 1985, Urano 1985) or

150

intensity of song display (Catchpole 1983). In our study, territory quality correlated with the occupancy date of males. Thus, the relationship between mating success and territory quality may often be indirect, and due to their common dependence on a third variable. The use of partial correlations (present study), or experiments, should help settle the question. Arvidsson and Neergard (1991), for instance, have shown experimentally that the correlation observed in Willow Warblers *Phylloscopus trochilus* between mating success and territory quality was indeed indirect and mediated by male quality.

In our study, male arrival dates, though highly variable, did not co-vary with body condition. This contrasts with observations on other warbler species. Settlement date of male Willow Warblers, for instance, depends on body state: males in good condition settle first (Arvidsson and Neergard 1991). In some *Acrocephalus* species, older males settle first (Catchpole 1972, Dowsett-Lemaire 1981, Urano 1985); older birds often have higher breeding success (Clutton-Brock 1988). In Savi's Warbler age can only be determined if birds are individually marked as nestlings and only few yearlings return to their birthplace. At the moment, insufficient data on the age of our birds are available since we started ringing Savi's Warbler only in 1992. But preliminary results suggest that age may influence arrival date also in this species: in 1994, yearlings ($n = 5$) tended to arrive later than older birds ($n = 8$) (Mann-Whitney U test, $Z = -1.690$, $P = 0.091$). However, we do also expect much stochastic variation in arrival dates due to the hazards of migration, especially since the birds have to cross such formidable obstacles as the Sahara, the Mediterranean Sea and the Alps (Berthold and Terrill 1991). This should prevent any fine control of arrival date.

The second point of our model is supported by the correlation between the date of male settlement and that of first clutch laying.

· Finally, as our third point states, we found no evidence for mate choice. Mating success did not correlate with the male morphological traits measured. Furthermore, its correlation with territory score was entirely explained by their common dependence on occupancy date. This last effect is easily explained by the extensive overlap between male and female arrival dates and the slightly biased sex-ratio: early-arriving males simply had a higher chance to meet a female.

Obviously, complete absence of mate choice is difficult to prove. We can not exclude that females are able to discriminate between the few males or territories available at the moment of their arrival and to choose the best of them. Furthermore, females may rely on cues other than the ones we investigated. Being more plastic than morphology, behavioural traits may reflect more accurately the actual state of males. Behavioural observations may reveal correlations between mating success

and some as yet unsampled phenotypic trait, such as fighting or singing ability, as found in Red-winged Blackbirds *Agelaius phoeniceus* (Yasukawa et al. 1980), Sedge Warblers *Acrocephalus schoenobaenus* (Catchpole 1983), Great Reed Warblers *Acrocephalus arundinaceus* (Catchpole 1987) or Willow Warblers (Arvidsson and Neergard 1991). Searcy and Marler (1984) found that females in species with only one song type in their repertoire did not respond to experimental increases in repertoire size. This suggests that female choice based on male song is to be expected in species with complex songs (Catchpole 1987). Savi's Warblers have only one song type that is stereotypic with only one syllable. However, females could use song duration as a cue to male and/or territory quality. Song rate may be affected by food supply in the territory (Yasukawa 1981, Radesäter et al. 1987). Payne and Payne (1977) found that male breeding success in the Village Indigobird *Vidua chalybeata* correlated with the time spent singing. In the Yellow-headed Blackbird *Xanthocephalus xanthocephalus*, neither female choice nor reproductive success could be related to features of the males or their territories, but in contrast to our case, female reproductive success was unaffected by settlement order (Lightbody and Weatherhead 1987). It is noteworthy that the presumed absence of mate selection in Savi's Warblers coincides with complete absence of sexual dimorphism.

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