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Mate choice in the willow warbler – a field experiment

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Summary. Females may choose a mate on his own quality or on the quality of his resources, i.e., his territory. We removed willow warbler males and allowed new males to settle, before the arrival of females, in order to test whether the proximate cue for female choice was any male trait or territory characteristics. The experiment indicates that females base their choice on some male trait. No correlation was found between male settlement order and size (tarsus length, wing length), but males arriving early were in better body condition than males arriving late. The most likely male trait for female choice was singing rate, which was a good indicator of male settlement date. The duration of time between mating and egg laying was shorter in early territories, both in the observational and the experimental data. Since male song rate was correlated with territory quality (e.g., food abundance) the ultimate benefit to females choosing males with high song rates could be a high quality territory.

Introduction

The evolution of male attributes, such as ornamentation and display behavior, can be explained by sexual selection theory. If female choice of mate is the main selective force, attributes attracting females are expected to evolve. If on the other hand females choose a specific site for breeding, behavioural mechanisms that enhance the competitive ability of males are expected to evolve through intra-sexual selection (Partridge and Halliday 1984). In order to understand how sexual selection acts, it is thus of great importance to determine whether females choose mates or breeding sites.

In species where males provide material benefits, it is often unclear whether females choose mates or breeding sites. Some experiments demonstrate that females choose a territory of high quality (Pleszczynska 1978; Alatalo et al. 1986; Slagsvold 1986; Warner 1987) while others suggest that females base their choice on some male trait (Downhower and Brown 1980; Alatalo et al. 1990).

Males of migratory passerines generally arrive earlier than females at the breeding areas in spring. In most species males immediately establish a territory; when females arrive they may choose among males or territories. Several studies have demonstrated a positive correlation between male arrival order and mating order (Brooke 1979; Alatalo et al. 1984, 1986; Gottlander 1987; Radesäter et al. 1987), but if males occupy territories in a decreasing order of quality (e.g., food abundance) it is difficult to determine whether females actually choose a male or the resources defended by the male. Male display rate has been shown to correlate with arrival order (Gottlander 1987; Radesäter et al. 1987) and food abundance (Ydenberg 1984; Davies and Lundberg 1984; Tamm 1985; Radesäter and Jacobsson 1988; Strain and Mumme 1988; Alatalo et al. 1990). After a male has obtained a mate, his song rate may decline significantly (Jakobsson 1987; Stenmark et al. 1988). A female choosing the male with the highest song rate among those available may thus come in possession of an unmated male of high quality, a territory of high quality, or a combination of both (Searcy and Andersson 1986).

Our study was designed to test whether female willow warblers (*Phylloscopus trochilus*) base their choice on any male characters or on the resources defended by the male. Since male quality and territory quality probably are intercorrelated, we tried to break up this connection by removing territorial males and allowing new males to settle before the arrival of females.

Methods

Field procedures. The willow warbler populations were studied at two different plots close to Gothenburg, southwest Sweden. Experiments were performed in one of these plots while the other was unaffected by experiments. The study area consists of some small meadows and woodland dominated by oak (*Quercus robur*), birch

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(*Betula pubescens*), alder (*Alnus glutinosa*), hazel (*Corylus avellana*), and in moist places willows (*Salix spp.*). Between 1984 and 1988 the study plots were searched daily from 20 April to the first week of June, when no more females arrived. Newly arrived territorial males were easy to detect since they sang vigorously. Most of them were captured on the day of territory establishment or on the next day and ringed with a unique combination of color rings. At the same time weight was measured to the nearest 0.1 g, tarsus to the nearest 0.1 mm, and wing length to the nearest 0.5 mm. Territory size was determined with play-back technique and measured on a map with a planimeter (see Arvidsson and Klaesson 1986).

Mating was easy to detect since males nearly stopped singing on the pair-formation day. In most cases females immediately began nest building, making it easy to find the nests and to determine the date of egg laying.

In 1986–1987 the time budgets of 12 males were measured during the pre-mating period in the control plot using the point sample method (Martin and Bateson 1986). Activities of different males were registered daily in two 15-min periods, one in the morning and one in the afternoon, in a random order (unpublished data).

Males arrive on average 2–3 weeks before females. The density of males 1984–1987 was 94±5 (mean±SD) territories/km^2 but in 1988 when the experiment was conducted the density was only 55 territories/km^2 (11 territories in the experimental plot; mean size±SD = 1.4±0.4 ha). Polygyny was never observed, and normally there was a surplus of territorial males (unpublished data).

In order to break up any intercorrelation between arrival order and territory quality, four males were removed on 6 May 1988; an additional male disappeared on 8 May. The aim was to remove the earliest males, but in order to avoid the surrounding males to enlarge their territories and thereby inhibit the settlement of new males, all males in the part of the study plot with the earliest mean date of establishment were removed. Before the first females arrived on 12 May, one male changed territory location and five new males established territories with approximately the same size and location as the originally established territories (Fig. 1). The number of unmanipulated control males was six.

Assumptions and predictions. A female choice based on territory quality was tested by analyzing the relation between mating order and the order in which territories primarily were occupied. Settlement order was assumed to reflect territory quality, with early males in high quality territories. Replacement males were predicted to occupy territories in the same order as the removed males in case territory quality affects male mating success. The importance of male quality was tested by analyzing the correlation between mating order and the order of male arrival. Assuming that early arriving males are of higher quality, we predicted that early males should mate earlier if male quality was assessed by females. By removing early males and allowing replacement males to settle, we broke the correaltion between male quality and territory quality allowing late males, presumably of low quality to settle in good territories.

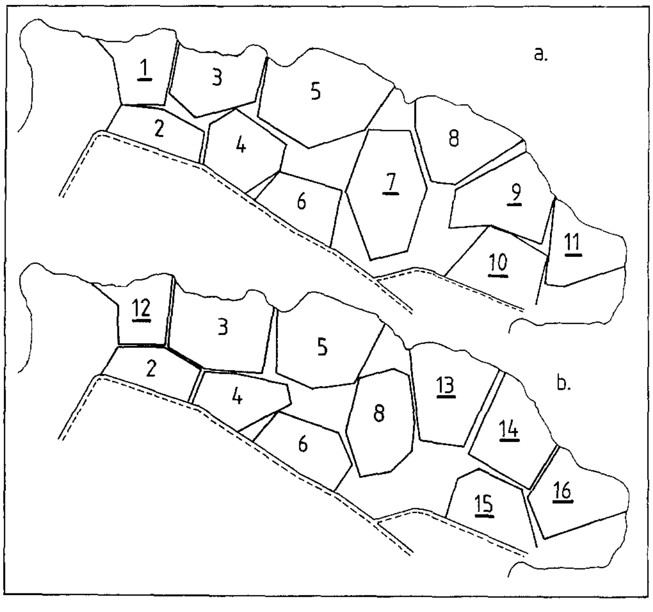

Fig. 1 a, b. Location of willow warbler territories before **a** and after **b** removal in the experimental plot. *Underlined* individuals removed respective replacements

Data from earlier seasons without experimental manipulation and from the control area was used to test: (1) if settlement order of males and mating order were correlated, (2) if male size, condition or singing rate was correlated with the settlement date, i.e., if they were possible cues for female choice, and (3) if time from mating to egg laying was correlated with territory settlement date, i.e., if females gained an ultimate benefit from choosing early males.

Since the distribution of several variables deviated from normality, nonparametric statistics were used (SAS 1985; Siegel and Castellan 1988). In cases when data from several years were pooled, they were first standardized in relation to annual means.

Results

Mating order

The mating order was significantly correlated with male arrival order (considering only males arriving before the first female) in 4 years in the control plot (Table 1); males that established territories early also mated early.

In the experimental plot, mating date also correlated significantly with the arrival date of the males (Fig. 2,

Table 1. Spearman rank correlations between male settlement order and mating order in the control plot 1985–1988. Only males that arrived before the first female were included

Year	*n*	r_s	*P*
1985	18	0.66	0.0031
1986	14	0.57	0.0322
1987	15	0.90	0.0001
1988	15	0.55	0.0349

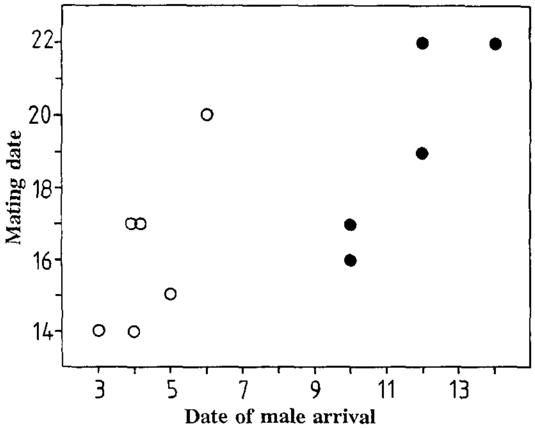

Fig. 2. Female mating date (1 = 29 April) in relation to the arrival date of willow warbler males in the experimental plot 1988. *Filled dots* = manipulated territories; *open dots* = unmanipulated

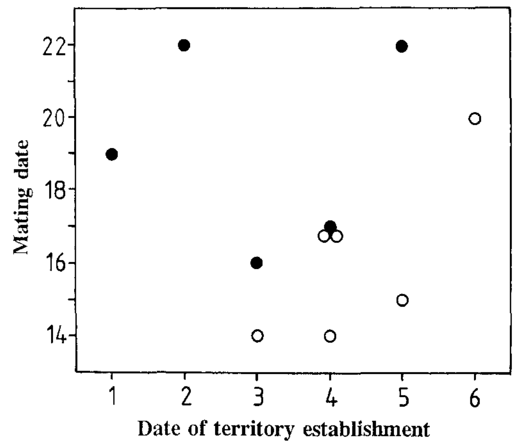

Fig. 3. Female mating date (1 = 29 April) in relation to the date willow warbler territories first were established in the experimental plot 1988. *Filled dots* = manipulated territories; *open* = unmanipulated

Table 2. Territory settlement date, male arrival date, and mating date in the experimental plot 1988 (1 = 29 April)

Group	n	Settlement ±SE	Male arrival ±SE	Mating ±SE
Unmanipulated	6	4.3±0.42	4.3±0.42	16.2±1.24
Manipulated	5	3.0±0.71	11.6±0.75	19.2±1.24
Wilxocon test (W_x)		22.5	45	39
Significance (P)		0.11	0.002	0.06

Table 3. Spearman rank correlations between territory settlement date (dependent variable) and different measures of size and condition of willow warbler males in the control plot 1985–1988. Data from all years pooled after being standardized by annual means

Independent variable	n	r_s	P
Tarsus	72	0.195	0.10
Wing length	72	−0.074	0.54
Cond 1 (weight$^{1/3}$/tarsus)	44	−0.326	0.03
Cond 2 (weight$^{1/3}$/wing length)	44	−0.257	0.09

Spearman rank correlation, $r_s = 0.76$, $P = 0.007$, $n = 11$). No such correlation was found between mating date and the date territories first were established (Fig. 3, $r_s = 0.06$, $P = 0.86$, $n = 11$), suggesting that females base their choice on some male trait and not on any territory characteristic. To test this result further, territories were divided in two groups, unmanipulated and manipulated. Late males in manipulated territories were mated nearly significantly later than early males in unmanipulated territories, despite the tendency of late males occupying territories originally established earlier (Table 2).

The predicted positive correlation in the order of territory occupation between removed and replacement males was not found ($r_s = 0.15$, $P =$ n.s., $n = 5$); however, sample size was too small to draw any safe conclusion.

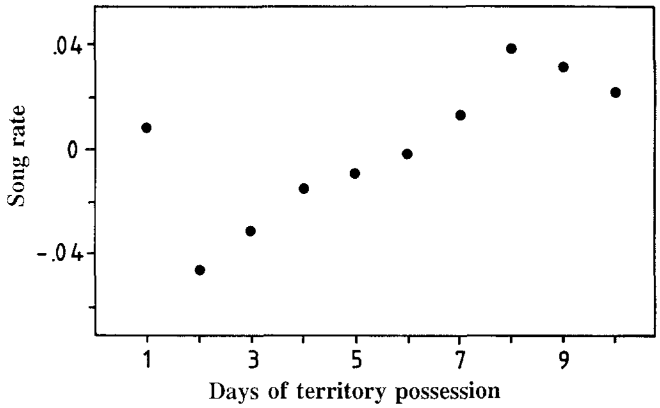

Fig. 4. Mean song rates (values standardized by annual means and the effect of temperature excluded) of willow warbler males in relation to territory possession time (days) in the control plot 1986–1987

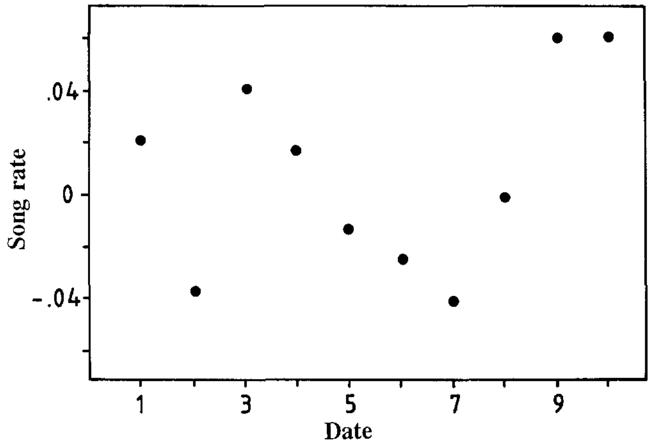

Fig. 5. Mean song rates (values standardized by annual means and the effect of temperature excluded) of willow warbler males in relation to date in the control plot 1986–1987

Male characters

Although females seemed to choose males rather than territories, we did not find any significant correlation between measures of size and arrival order; however, males arriving early were in better body condition at the time of arrival than males arriving late (Table 3).

Song rate

The singing pattern of willow warbler males depended on temperature and how long the male had been established as a territory owner. Song rate (with the effect of temperature removed) in the control population increased significantly with the duration (days) of territory possession (Fig. 4, $r_s = 0.77$, $P = 0.009$), but not with date per se (Fig. 5, $r_s = 0.27$, $P = 0.45$). The time males allocated to singing was inversely correlated with feeding time (Fig. 6, $r_s = -0.92$, $P = 0.0001$, $n = 11$), indicating that

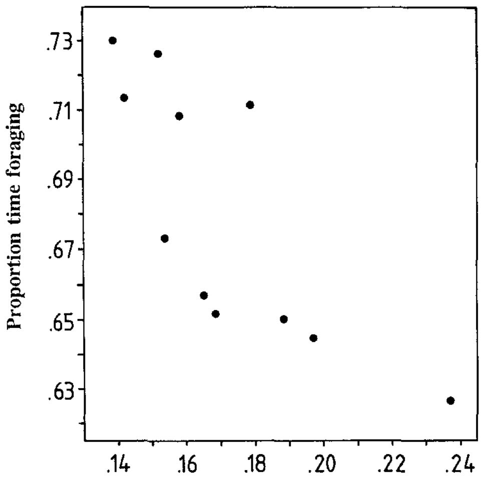

Fig. 6. Relation between the proportion of time singing and feeding time of willow warbler males in the control plot 1986–1987

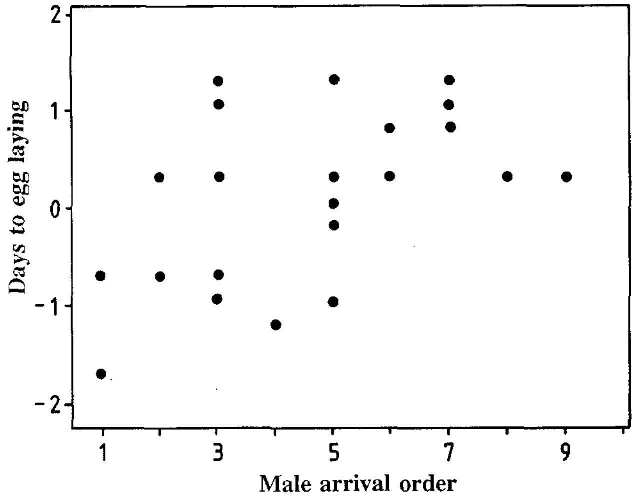

Fig. 7. The number of days from mating to egg laying (values standardized by annual means) in relation to the arrival order of willow warbler males in the control plot 1985–1988

males with high song rates had territories rich in food resources.

Time required for egg production

There was a strong correlation between male settlement date and the number of days from mating to egg laying in the control plot (Fig. 7, $r_s = 0.70$, $P = 0.0001$, $n = 24$), indicating that females mated with early males enjoyed better foraging conditions or were in better body condition. The reason was not male settlement day or mating day per se because females mated with late settling replacement males in the experiment area produced clutches within a shorter time period than females mated with control males that settled earlier (Fig. 8, mean replacements 6.4 days, mean control 7.8, Wilcoxon two-sample test, $P = 0.017$). The shorter delay between mating and laying normally shown by females mated with early males is thus probably a consequence of these males ability to pick territories with rich food resources.

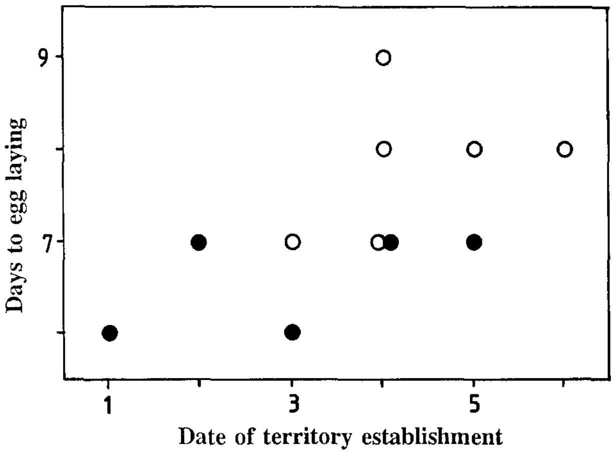

Fig. 8. The number of days from mating to egg laying in relation to territory establishment date of willow warbler males in the experimental plot 1988. *Filled dots* = manipulated territories; *open* = unmanipulated

Discussion

Our removal experiment indicates that the proximate cue for female choice in willow warblers is some male trait and not any territory characteristic. Although females preferred territories chosen by males arriving early, they selected against these territories when the original males were replaced by new males arriving late. This suggests that females do not choose territories or that territory quality changed during the period of female settlement. Willow warblers mainly feed on leaf-eating caterpillars (Arvidsson and Klaesson 1986), which develop as soon as leafing has occurred (unpublished data). The earliest territories are established in areas with early developing trees (willows, alder and young birch) while late territories are in sites with late developing trees (oak and hazel). Subsequently, the feeding conditions will vary between early and late territories until all trees have fully developed leaves in the second week of June. Since female willow warblers settle during the last 2 weeks of May, there is no reason to suspect that territorial ranks should reverse before the last female settle.

It is however difficult to decide from our experiment what male trait female willow warbles use. Since there was no significant correlation between male size and territory settlement date in any of the years, it seems reasonable to rule out size as being an important cue for female choice. Furthermore, no apparent difference in plumge coloration between early and late males was observed (personal observation). There was a negative correlation between body condition at settlement and arrival order. A better body condition could be manifested in a higher display rate, which could be a cue for female choice. One crucial assumption is that male body condition at the arrival is correlated with male body condition at the time females choose.

Male song rate is a trait that previously has been demonstrated to correlate well with food availability in the territory both in willow warblers (Radesäter and Jacobsson 1988) and in other bird species (Strain and Mumme 1988 and references therein). We did not measure song rates in our experiment; however, time budget studies in the control plot show that song rate was inversely related to foraging time. The song rate also increased significantly with duration of territory possession but not with date per se (cf. Radesäter et al. 1987). Taking individual variance into account, Radesäter et al. (1987) concluded that females would be able to determine which male has the highest song rate only after listening for about 15 min. Alatalo et al. (1990) demonstrated that experimentally fed pied flycatcher (*Ficedula hypoleuca*) males sang twice as often as non-fed males and that fed males were chosen first by females.

We cannot reject the possibility that females are attracted to males that sing frequently merely because they are more easily detected (Parker 1983). In order to prove unambiguously that females actively choose males with high song rates, we had to demonstrate that females actually reject other males (Searcy and Andersson 1986; Dale et al. 1990).

We have no direct evidence that females actually sample the singing rates of different males; however, the mating pattern strongly indicates this. An important assumption of this choice model is that females are able to measure song rates of several males simultaneously, something not yet demonstrated.

Male traits should potentially influence female choice if these traits are coupled with fitness and are possible to assess accurately prior to mating (Searcy 1979). Food abundance has a strong influence on the timing of egg laying and hence probably on reproductive success in some species (Davies and Lundberg 1985 and references therein). Since male singing rate should be an honest signal of feeding conditions, females using this trait should be able to single out territories with rich food resources. Females perform most of their breeding activities within the territory, and a female choosing a male with high song rate could ultimately gain in terms of fitness by producing more or better offsprings.

In conclusion, this study strongly indicates that the proximate cue for female choice in willow warblers is some male trait, possibly song rate. It is more difficult to be conclusive about the ultimate benefit. It is possible that territory quality is the ultimate benefit since the time required for egg production was related with the order territories were established, but male quality, affecting directly either through paternal care or through the genes they give their offspring is also a possible benefit.

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