Female choice in the sedge warbler, *Acrocephalus schoenobaenus*: multiple cues from song and territory quality

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SUMMARY

Recent models of animal signalling emphasize the evolution of complex displays containing 'multiple messages'. A variety of potential cues used in female choice were investigated during a three-year field study of the sedge warbler, *Acrocephalus schoenobaenus*. Twelve possible cues were investigated, and three were found to have a significant influence upon pairing date. Two were different measures of song (repertoire size and song flighting) and one a measure of territory (territory size). Repertoire and territory size had a significant influence on pairing date in all three years, and song-flighting in two. The three cues were not intercorrelated and so had independent effects upon pairing date. We suggest that females select males upon multiple cues as these reflect different aspects of male and territory quality.

1. INTRODUCTION

Recent years have witnessed an explosion in studies of sexual selection (reviewed by Andersson 1994; Andersson & Iwasa 1996), and it has become almost routine to demonstrate female choice for males with exaggerated traits. In birds, most studies have found it convenient to focus on one particular male trait, such as tail length or plumage coloration. However, there are strong intuitive and theoretical reasons to suspect that females should use the maximum amount of available information when assessing potential mates. One way of achieving this is to use multiple cues from the different kinds of signals males produce. Earlier models of signalling (e.g. Grafen 1990) have generally assumed that only one kind of display is involved. It is only recently that several models (Iwasa & Pomiankowski 1994; Sullivan 1994; Johnstone 1995, 1996) have started to explore the implications for signal design of mate choice involving multiple cues.

These ideas can clearly be applied to sexually selected traits such as the complex songs of male birds (Searcy & Andersson 1986; Catchpole 1987). Indeed, the bird song literature is replete with studies on female choice emphasizing single traits such as song repertoire size or song rate (Catchpole & Slater 1995). However, no single study has yet considered both the quality and quantity of male song in relation to female choice, even though these could potentially convey quite different kinds of information important to prospecting females. It may also be possible for females to obtain access to both direct and indirect benefits by selecting males on particular cues (Kirkpatrick & Ryan 1991).

The complex song of the male sedge warbler, *Acrocephalus schoenobaenus*, is known to be important in female choice. In a field study (Catchpole 1980) males with larger syllable repertoires were found to attract females earlier, and in a laboratory study captive females displayed more to recordings of larger repertoires (Catchpole *et al.* 1984). However, no other aspects of song or territory quality were investigated in parallel, and many questions still remain about other possible cues that females may be using. Sedge warblers are cryptic and monochromatic, and in this species male plumage has not been targeted by sexual selection. When males advertise for females they take up territory, sing intensively, and also perform elaborate song flight displays. These observations and the earlier results suggest that females select males directly upon the basis of cues contained in their singing behaviour, indirectly upon the quality of their territories, or perhaps a combination of these.

The main objective of the present study was therefore to investigate the relative importance of potential cues from song and territory quality on female choice. As in the 1980 study, we measured repertoire size and used pairing date as a measure of female choice. But this time we also measured other aspects of song quality and quantity, including song-flighting behaviour, and also several aspects of territory quality.

2. METHODS

The study area was Wraybury Lakes, a series of flooded gravel pits situated in the Thames Valley, southern England. A marked population of sedge warblers was studied throughout the breeding season in 1994, 1995 and 1996. Sedge warblers are migrant species, and males arrived and occupied territories during April. Males were caught in mist nets soon

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after arrival and marked with a unique combination of coloured plastic rings to facilitate individual identification. Females arrive later and pairing is clearly indicated by cessation of male song (Catchpole 1980). The site was visited on a daily basis to record all the males, collect behavioural data and locate nests.

(a) *Song quality and quantity*

Males sing vigorously after arrival and songs were recorded using a Sennheiser microphone, a parabolic reflector, and a portable Marantz tape recorder. From each male we recorded 15–30 min of continuous, spontaneous song, early in the morning 1 or 2 d after arrival. Songs were analysed blind later in the year using a Kay DSP Sonagraph. From a sample of 20 songs we estimated the following measures of song structure and complexity. Repertoire size was estimated as the total number of different syllable types found within the sample (see also Catchpole 1980). We also measured the mean number of syllable types per song, mean song length and mean length of the complex middle section. Sonographic analysis of repeat samples from a small sample of males has shown that repertoire size remains constant from day to day and that the other measures show minimal variation.

After arrival, males sang for an average period of 10 d before they paired and then became silent. Each male was visited in random order every day during the first 4 h after sunrise to take 10 min time budgets of singing behaviour. Sedge warblers sing from either a perched position or during flight. In practice, it is relatively simple to distinguish between the two and time their duration. From this record we were later able to calculate: mean singing time, singing time the day before pairing, mean song-fighting time and song-fighting time the day before pairing, all in seconds.

(b) *Territory quality and quantity*

Territory boundaries were ascertained gradually by daily observations of boundary disputes, and territory size (m²) was measured at the time of pairing. Sedge warblers prefer to nest off the ground in suitable field vegetation, and the area of potentially suitable nesting vegetation within each territory was also estimated. Nests must be well concealed to avoid predation, and a measure of shade (lux) at each nest was also taken at a standard time of day using a light meter. Sedge warblers feed particularly on emergent insects at the water margin, and the nearest distance to water (m) was our final measure of territory quality.

(c) *Female choice*

As in the earlier study (Catchpole 1980) and many others (e.g. Reid & Weatherhead 1990), pairing date was taken as a measure of female choice. However, this time later measures of reproductive success were also taken, including the date on which the first egg hatched, clutch size, and the number of young fledged.

(d) *Analyses*

Pearson correlation coefficients were used to examine covariation, and a two-tailed region of rejection was adopted throughout. To achieve normality for this analysis and later univariate and multiple regression, data were log-transformed where appropriate. All statistical tests were performed using Unistat 94 on transformed data. However, for comparative purposes and visual display, figures are shown as scatter plots with regression lines fitted to untransformed

data. Coefficients of determination (R^2) and coefficients of variation (CV) are expressed as percentages.

3. RESULTS

(a) *Correlation analysis for 1994*

We investigated the relative importance of 12 different measures of male and territory quality in a breeding population of 26 males. From the earlier study on the sedge warbler (Catchpole 1980) we predicted that syllable repertoire size would be an important cue. Our prediction was confirmed, as we found a highly significant negative correlation between repertoire size and pairing date ($r = -0.521$, $p = 0.006$) (figure 1a). However, the previous study had made no attempt to investigate other measures of song quality. For example, the number of syllable types per song can be used as a measure of inter-song complexity. Although this was strongly correlated with repertoire size ($r = 0.514$, $p = 0.008$), there was no independent correlation between syllable types per song and pairing date ($r = -0.131$, $p = 0.262$). There were also no correlations between the two measures of song length and pairing date.

We also investigated several quantitative song measures in considerable detail. The most obvious is the total amount of time spent singing, but we found no correlation between mean singing time and pairing date ($r = 0.236$, $p = 0.246$). Although overall mean song-fighting performance was not significantly correlated with pairing date ($r = -0.262$, $p = 0.196$), the more meaningful measure of song-fighting the day before pairing was ($r = -0.410$, $p = 0.038$). The latter is assumed to be the most likely time of female choice. Two males spent unusually large amounts of time song-fighting, but even when these two outliers were removed from the analysis, the correlation remained significant ($r = -0.446$, $p = 0.028$) (figure 1b).

Finally, we investigated several measures of territory quality, territory size, the amount of suitable nesting habitat, shade at the nest and distance from water. The only one of these that correlated significantly with pairing date was territory size ($r = -0.402$, $p = 0.046$) (figure 1c).

As seen in table 1, repertoire size showed the strongest correlation with pairing date, followed by song-fighting and then territory size. This was confirmed by univariate regression of all three independent variables upon pairing date as the dependent variable. Coefficients of determination (R^2) reveal that repertoire size accounted for 27% of the total variation, song-fighting 17%, and territory size 16%. When all three independent variables were entered into a multiple regression they accounted for 47% of the total variation in pairing date.

Correlation studies using pairing date as a measure of female choice face the potential problem of a confound with male arrival dates and settlement pattern. However, we found no correlation between male arrival date and pairing date, and there were also no correlations between male arrival date and any of our three main cues.

Nests were located for most of the breeding pairs, but

Figure 1. The relationships between pairing date and repertoire size, song-flighting time and territory size, 1994–96. Scatter plots are shown using original, untransformed data. Results from statistical tests on transformed data are given in the text. Song-flighting time refers to the time spent song-flighting the day before pairing.

Table 1. *Correlation coefficients 1994–96*

(Pearson correlation coefficients (r) are shown between pairing dates and the three main cues of repertoire size, song-flighting (time (s) spent song-flighting the day before pairing) and territory size (m^2). Probability levels (p) are for two-tailed tests. R^2 is the coefficient of determination and CV is the coefficient of variation (both expressed as percentages).)

cue	year	<i>n</i>	<i>r</i>	<i>p</i>	R^2 (%)	CV (%)	mean
repertoire size	1994	26	−0.521	0.006	27	14	53.08
	1995	31	−0.385	0.032	15	12	60.16
	1996	23	−0.421	0.046	18	14	66.39
song-flighting	1994	26	−0.41	0.038	17	110	14.32
	1995	31	−0.008	0.966	6	64	23.9
	1996	23	−0.419	0.046	18	99	12.12
territory size	1994	26	−0.402	0.046	16	52	824.68
	1995	31	−0.492	0.002	24	46	1047.8
	1996	23	−0.536	0.008	29	73	904.13

predation was high, accounting for many nests in any one year. In 1994, there were only two correlations with later measures of breeding success, again involving two of the three cues affecting pairing date. Territory size was negatively correlated with the date on which the first egg was laid ($r = -0.492$, $n = 19$, $p = 0.032$), and song-flighting the day before pairing was positively

correlated with clutch size ($r = 0.543$, $n = 18$, $p = 0.020$).

We therefore have three main variables that appear to influence female choice: repertoire size, song-flighting the day before pairing and territory size. None of these measures was correlated with each other, so they were all acting independently on pairing date.

(b) Matched pairs analysis for 1994

Patterns of female choice and the cues females use are usually investigated by trends observed in the population as a whole. Although this is a useful approach, such trends may obscure the fine detail and reality of individual female choice. The assumption made in models of active female choice is that when an individual female makes her decision, she has sampled and rejected all the other males in the population. Although this is a reasonable assumption, we can never be quite sure how many males and which ones are visited before a choice is made, and there is also the potential confounding effect of male arrival pattern. In 1994, our males were not dispersed uniformly over the study area, but often clumped, with some occurring in relatively isolated pairs who were observed singing and displaying against each other. It seemed to us that when the first such male paired, his female must have assessed them both and rejected one before choosing the other.

We were able to identify 11 such matched pairs in 1994, but due to a larger population and different arrival and dispersion patterns, were not able to find enough isolated pairs in 1995 or 1996. We subjected the 11 1994 pairs to a Wilcoxon matched-pairs signed-ranks test, using the same male and territory quality variables as in the correlation analysis. In this smaller sample, only one variable showed a significant effect upon pairing date, and another approached significance very closely. These were the same two singing cues revealed by the correlation analysis. In nine of the pairs the females selected the male who song-flighted most the day before pairing ($Z = -2.400$, $n = 11$, $p = 0.016$), and in seven of the pairs she selected the male with the largest repertoire size ($Z = -1.937$, $n = 11$, $p = 0.053$). Unlike the correlation analysis, there was no evidence that females in this subset selected males with the largest territories ($Z = -0.711$, $n = 11$, $p = 0.477$).

(c) Correlation analysis for 1995

In 1995, we repeated the study on a larger sample of 31 males and obtained a similar pattern. This time only two of the variables, repertoire size and territory size, were found to significantly influence pairing date. We obtained a lower but still significant correlation between repertoire size and pairing date ($r = -0.385$, $p = 0.032$) (figure 1d), but this time no correlation between song-flighting the day before pairing and pairing date ($r = -0.007$, $p = 0.483$) (figure 1e). However, territory size again showed a highly significant correlation with pairing date ($r = -0.492$, $p = 0.002$) (figure 1f). Univariate regression and calculation of R^2 values revealed that territory size accounted for 24% of the variation, repertoire size 15% and song-flighting only 6%. When all three variables were entered into a multiple regression, they accounted for 35% of the variation in pairing date.

In 1995, neither repertoire size nor song-flighting were correlated with any later measures of reproductive success. However, territory size was strongly correlated

with clutch size ($r = 0.601$, $n = 24$, $p = 0.002$) and also with the number of young fledged ($r = 0.575$, $n = 13$, $p = 0.040$).

(d) Correlation analysis for 1996

In 1996, we repeated the study on a sample of 23 males, and found an almost identical pattern to 1994. The same three variables again correlated significantly with pairing date and not with each other. This time repertoire size ($r = -0.421$) (figure 1g) and song-flighting the day before pairing ($r = -0.419$) (figure 1h) both affected pairing date with the same probability ($p = 0.046$), and territory size showed the strongest correlation ($r = -0.536$, $p = 0.008$) (figure 1i). Univariate regression and calculation of R^2 values revealed that territory size accounted for 29% of the variation, whereas repertoire size and song-flighting each accounted for 18%. When all three variables were entered into a multiple regression, they accounted for 46% of the variation in pairing date. Again, none of the other measurements showed any affect on pairing date. In 1996, we suffered more severe predation, and with low sample sizes of nests no correlations were obtained with later measures of breeding success.

4. DISCUSSION**(a) The importance of multiple cues**

It seems possible from our study that female sedge warblers are sensitive to at least three cues from male and territory quality. Although the nature of correlation relationships are difficult to determine in terms of cause and effect, female choice occurs only after song and territory characteristics are established. The possibility remains, however, that all three 'cues' are related to other real cues not measured in this study. This seems unlikely, as first, all the obvious male traits were investigated, and second, previous experimental work on sedge warblers has shown that captive females are responsive to variations in repertoire size (Catchpole *et al.* 1984).

There are relatively few studies that include rather than exclude or control for multiple cues, and no study on the relative importance of both song quality and quantity in female choice. In the study on the Ipswich sparrow by Reid & Weatherhead (1990), even though they included song rate and territory size, they excluded repertoire size. Cues in the pied flycatcher, *Ficedula hypoleuca*, have been investigated in considerable detail, and there is good evidence from separate studies that both song rate (Alatalo *et al.* 1990) and repertoire size (Lampe & Saetre 1995) can influence female choice. However, Alatalo *et al.* (1986) have demonstrated the importance of territory quality, and Saetre *et al.* (1994) showed that plumage coloration is also involved. Dale & Slagsvold (1996) have recently demonstrated that females appear to select males on multiple cues from plumage and territory quality, but did not include song in their study. Perhaps because there are so many cues in this species, there have been no studies that have investigated the relative im-

portance of all of them at any one time (Lundberg & Alatalo 1992; Dale & Slagsvold 1994).

The sedge warbler is a cryptic species with no detectable variation in male plumage, so we concentrated particularly on cues contained within the elaborate singing display. In all three years of our present study, repertoire size was found to be an important cue, confirming the earlier study on a different population (Catchpole 1980). In the three years of the present study, the coefficient of variation (CV) for repertoire size was similar (table 1), giving females much the same reasonable range of choice. However, the amount of song-flighting was positively correlated with pairing date in the two years in which there was also a much larger CV (table 1). This supports the findings of Reid & Weatherhead (1990), who found that the cue correlated with female choice was the one that varied most in any one year. In 1995, the only year in which song-flighting was not important, not only was there less variation in the trait (table 1), but also less time for assessment due to females arriving later. Without understanding the exact nature of the relationship between song-flighting and female choice it is difficult to say why it was not used as a cue in 1995. There are, however, several possibilities.

It is possible that song-flighting is more affected by male–male interactions, especially when many males arrive together. The late arrival of females in 1995 may have resulted in less time for assessment and female choice. Less variation in song-flighting behaviour may have increased the costs of female choice and decreased the value of the cue as an indicator of male quality. It certainly seems that in 1995 the conditions for female choice were rather different, and that our females responded by weighting the cues differently.

(b) Backup signals or multiple messages?

Several recent reviews have considered the evolution of multiple cues and the implications for both female choice and the design of male signals. Iwasa & Pomiankowski (1994) developed a new handicap model which suggested that multiple preferences could evolve as long as the additional assessment costs are not greatly increased. They then went on to show that the costs of female choice have a major influence on the evolution of multiple sexual displays (Iwasa & Pomiankowski 1995).

Møller & Pomiankowski (1993) considered several reasons why multiple cues could be advantageous. One line of explanation involves redundancy, the more types of information the better the chances of accurate, reliable assessment—the ‘backup signal’ hypothesis. Sullivan (1994) has also explored the implications of multiple cues for female choice and the evolution of signal design. He distinguished between fixed cues, which have a fixed expression once established, and facultative cues, which vary and are condition-dependent. The former may be quickly and cheaply assessed, the latter may take longer and cost more. Johnstone (1996) has recently developed a model that suggests that both backup signals and ‘multiple

messages’ can be evolutionarily stable even when significant costs are involved. In our study we found no correlations between any of these three cues, supporting the idea of multiple messages, rather than backup signals. But what are the different messages contained within the three cues?

We found significant correlations between territory size and pairing date in all three years, and similar CVs within each year (table 1). In 1995, we also found strong correlations between territory size, clutch size and the number of young produced. It may well be that larger territories contain more resources, such as insect food, and that this has a significant effect on the number of young eventually produced. It seems that by using territory size as a cue, a female receives direct benefits (Kirkpatrick & Ryan 1991) in terms of immediate resources for her offspring.

The amount of energy a male can afford to invest in singing would seem to be an obvious indicator of his current condition. The amount of song-flighting the day before pairing was correlated with pairing date in two years of our study, and the pairs analysis also suggest that females may well use this as a cue in making a final choice between neighbouring males. Song-flighting must incur high potential costs and is thus a good candidate for an honest advertisement of male quality (Zahavi 1977; Grafen 1990). Reid (1987) has shown that the amount of song produced in Ipswich sparrows is both costly and condition-dependent. The importance of song-flighting was first suggested by the wing-clipping experiments of Møller (1991) on one of the best known song-flighting species, the skylark, *Alauda arvensis*. In our study, we found that mean daily song-flighting was positively correlated with mean daily temperature ($r = 0.432$, $n = 46$, $p = 0.010$), supporting the idea that song-flighting is condition-dependent. Mather & Robertson (1992) confirmed this in the song-flight of the polygynous bobolink, *Dolichonyx oryzivorus*, and went on to show that males who song-flighted more attracted more females and produced more young. It may be that females who use song-flighting as a cue are obtaining direct benefits for their offspring in the form of more or better male parental care.

In all three years there was a significant correlation between repertoire size and pairing date, supporting the earlier study on this species (Catchpole 1980). Although this finding now seems robust, we found no correlations between repertoire size and other aspects of male quality. Why females should choose males with large song repertoires continues to be a matter of considerable speculation (Searcy 1992; Catchpole & Slater 1995). We found no evidence that males with larger repertoires went on to breed earlier, or that they produced more young. Although our study has not run long enough to obtain good data on lifetime reproductive success or age, our older males tend to have larger repertoires. In a separate field study in Hungary, we have now obtained a correlation between repertoire size and male age (Birkhead *et al.* 1997). This suggests that larger repertoires might be a cue indicating more mature, viable males. A recent study by Hasselquist *et al.* (1996) on the closely related great

reed warbler, *A. arundinaceus*, found not only that repertoire size was correlated with age, but also that males with larger repertoires produced more viable offspring who returned to breed in subsequent years. They also found that all the males who achieved extra-pair fertilizations had larger repertoires than the neighbours whom they cuckolded. By using repertoire size as a cue, females in such species would clearly obtain indirect, genetic benefits for their offspring.

A more speculative explanation involves the idea that only older, superior quality males can afford the neural cost of the brain space necessary to store larger repertoires (Catchpole 1996). Male birds learn their songs and these are stored in a special area in the brain. A recent comparative study on *Acrocephalus* warblers (Szekely *et al.* 1996) offers some support for this. Using modern phylogenetic techniques, it revealed that during evolution, as larger repertoire size developed, one particular area of the brain, the higher vocal centre (HVC), also increased in size. We now need to establish how repertoire size relates to relative brain size within one population, how individuals inherit or develop large repertoires and how this relates to their lifetime reproductive success.

Our study suggests that assessment of multiple cues may well be involved during female choice in the sedge warbler. Further investigation is certainly necessary to confirm the exact nature of the associations between pairing date and the cues we could detect, both in terms of the benefits females obtain and the costs they may incur in assessing the different cues. Although we cannot rule out the possibility that these are backup signals, it seems more likely that the three cues involved contain 'multiple messages' relating to the different benefits females are likely to obtain.

This research project was funded by a grant from the Natural Environment Research Council. We are extremely grateful for the assistance and support of the Runnymede Ringing Group in the field.

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Received 13 November 1996; accepted 27 November 1996