



Whistle duration and consistency reflect philopatry and harem size in great reed warblers

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The great reed warbler, *Acrocephalus arundinaceus*, is one of the most intensively studied species in the area of vocal behaviour and an important model in studies of sexual selection. We evaluated performance of the whistles produced by different males and examined whether individuals improved their performance over consecutive seasons. Finally, we tested whether the performance of whistles reflected males' philopatry and harem size. We assessed whistle performance based on duration and consistency. Our analyses showed that great reed warbler males improved the performance of their whistles in subsequent seasons. Whistles became both longer and more consistent from one year to the next. We also found that males' harem size was significantly related to whistle performance, which in turn reflected philopatry. Subsequent analyses revealed that the performances of polygynous and philopatric males differed significantly from those of monogamous, unpaired and new males. As philopatry is preferred by great reed warbler females, it is in the males' interest to advertise this feature. Coding philopatry in the songs of individual males seems to be an easy and efficient way of informing females about males' familiarity with the breeding grounds. The proper performance of difficult double-element whistles, the mastery of which may be time consuming, seems to be a good candidate for indicating males' philopatry. If so, the quality of whistle syllables may also reflect differences in the general quality of individual males as high performance levels may be associated with both males' longevity and their ability to learn.

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Numerous recent studies have shown variation in vocal behaviour among individuals in a species or a population (O'Loughlen & Beecher 1999; Gentner & Hulse 2000; Molles & Vehrencamp 2001; Ballentine et al. 2004). This variability has been found in many different features of vocal communication and may serve distinct functions (Baptista & Gaunt 1994; Vehrencamp 2000; Forstmeier et al. 2002; Aubin et al. 2004; Węgrzyn et al. 2009). The main functions of birdsong are territory defence and mate attraction through advertisement of the quality of the singing male (Catchpole 1983; Andersson 1994; Searcy & Yasukawa 1996). Different parameters of the song are considered to reflect the male's physical condition, parental care ability, age, experience, gene quality and immunity, as well as the quality of his territory (Loffredo & Borgia 1986; Hasselquist et al. 1996; Hasselquist 1998; Buchanan & Catchpole 2000; Duckworth et al. 2001; Marshall et al. 2003; Garamszegi et al. 2004; Mays & Hill 2004). Thus, vocal

behaviour is considered to be subject to intense sexual selection (Catchpole 1986, 1987; Catchpole et al. 1986; Garamszegi et al. 2003, 2004), but the structural features of a song that determine its attractiveness to females and the mechanisms that underlie female choice often remain unknown.

The expression of the song features preferred by females shows a high level of diversity owing to the different performance abilities of males. Besides costly handicap signals, such as song rate, repertoire size or song length (Searcy & Yasukawa 1996; Vehrencamp 2000; Ward et al. 2003; Berg et al. 2005), the performance of a song or its elements may also convey information reflecting the male's quality. A growing number of studies have provided substantial support for this view. For example, singing males may reach physiological limitations during sound production (Lambrechts 1996; Podos 1996, 1997, 2001; Suthers & Goller 1997), and males may differ in how far they can push these limits. In species such as the swamp sparrow, *Melospiza georgiana*, or the canary, *Serinus canaria*, there is a performance trade-off between trill rate and frequency bandwidth, and females prefer males that can produce trills closer to the performance limit (Drăgănoiu et al. 2002; Ballentine et al. 2004). A study by Forstmeier et al. (2002) demonstrated that the ability of male dusky warblers,

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*Phylloscopus fuscatu*s, to maintain high sound amplitude during singing correlated with their longevity and with extrapair paternity. In the brown-headed cowbird, *Molothrus ater*, the majority of the acoustic features found to elicit sexual displays involve the relationship between the low- and high-frequency notes that the bird produces in special note clusters using the two sides of the syrinx (King et al. 1980; Allan & Suthers 1994). The production of physically challenging songs may also signal male quality during male–male conflicts as males performing songs near the performance limit can be perceived as a greater threat by male territorial owners. Experiments by Illes et al. (2006) demonstrated that male ringed wrens, *Thryothorus pleurostictus*, discriminated and responded differently to songs based on their vocal performance. The above-mentioned studies show that male quality might be judged from subtle differences in the sounds they produce.

The great reed warbler, *Acrocephalus arundinaceus*, is an intensively studied species in the area of vocal behaviour and an important model in studies of sexual selection. Both captive studies (Catchpole 1986) and field observations (Catchpole 1983; Ezaki 1987; Bensch & Hasselquist 1992) have indicated that the song of great reed warbler males is subject to female preference. However, the most frequently analysed aspect of the great reed warbler song, the size of the syllable repertoire, does not always correlate with males' mating and breeding success (Forstmeier & Leisler 2004). Therefore, female preferences with respect to the qualitative features of the song, such as the performance of some song elements, may be an alternative explanation of attractive aspects of the great reed warbler song.

There are two possible mechanisms underlying female choice based on performance assessment. First, well-performed song elements might be a direct signal of male quality if they are costly to produce. Second, a particular set of syllables might indicate a local dialect (O'Loughlen & Rothstein 1995), allowing females to recognize males better adapted to a local environment or better at interacting with neighbours, which may have crucial importance in territory maintenance.

Great reed warbler males sing two types of syllables: rattles and whistles (a detailed description and sonagram are in Węgrzyn & Leniowski, in press). We chose whistles for our analyses as we demonstrated in our previous study that they are more shared among males than rattles. We also showed that the composition of the whistle repertoire of individuals was more repeatable within and between seasons than the composition of the rattle repertoire. Additionally, within-season similarity of an individual's whistle repertoire to that of other males is correlated with harem size, but the similarity of the rattle repertoire is not (Węgrzyn & Leniowski, in press). Low changeability of whistle repertoire composition among individuals and between years in the studied population enabled both longitudinal and cross-sectional analyses in the present study. We assessed whistle performance by calculating the relative duration and consistency of whistle reproduction for particular males. We suggest that this is a good measure of singing performance in great reed warblers for several reasons. First, the analysed whistles consist of two elements of different fundamental frequencies, so it is very likely that they are produced by two successively activated bronchi. Poor motor coordination may lead to the absence, shortening or overlapping of elements of the whistle, resulting in a decrease in overall whistle duration (illustrated in the Methods). The described variation in whistle production was frequently observed on sonagrams of songs in the studied population. Second, our preliminary analyses showed that duration was the only measured bioacoustics parameter for which variation was observed in the same direction in all studied whistle types. As we were interested in measuring a universal parameter to permit assessment of whistle performance irrespective of whistle

type, we focused on whistle duration. The other parameter used in our study to assess whistle performance, consistency in note production, has been shown in other species to improve with age, probably as a result of practice (de Kort et al. 2009). Thus, it may play an important role in great reed warbler female choice, which has been reported to depend on the males' age (Leisler et al. 1995) and philopatry (Bensch et al. 1998; Hansson et al. 2004). However, it is not clear what feature the females use to recognize older and/or returning males. If more time is needed to master the proper production of some syllables, both older and philopatric males may be distinguished from the young and immigrant individuals by differences in syllable performance.

In the present study, we evaluated performance of the whistles produced by different males and examined whether individuals improved their performance in consecutive seasons. Finally, we tested whether the performance of whistles reflected males' philopatry and harem size.

METHODS

Study Area and Population

The study was conducted from the end of April to the beginning of August in 2002–2005. The study area consisted of 10 fish ponds in Korniaaków Północny near Rzeszów, southeast Poland (50°07'N, 22°22'E). In the 4 years of our study, we mist-netted and colour-ringed all territorial males present in the study area (42 males) and seven males that did not establish territories and disappeared shortly after ringing. Three territorial males occupied inaccessible territories in 2002 and thus were not recorded. We recorded and analysed songs from the remaining 39 males. All territories were monitored every 2–4 days each year from the end of April to the middle of July, and records of identity, status of males and their vocal behaviour were taken. In 2002 we only recorded the vocal behaviour of males, but in 2003–2005 we also estimated each male's harem size and ringed nestlings. Nests were located by searching the reeds and observing females during nest building or while feeding their young. Two researchers searched for nests during all seasons after a particular male had stopped singing (this is a signal of pairing in great reed warblers). As a number of great reed warbler males are polygynous, we recorded whether the paired male resumed singing and we searched for the next female and nest if he ceased singing again. If a nest was depredated, we searched for a rebuilt one after a substantial period of time had passed. We searched for nests by approaching the most probable parts of the territories (dense, thick reeds) from the water's edge and pulling the reeds apart with a 3 m long bamboo stick. We penetrated the reeds as described every 1 m. This method allowed detailed search without destroying breeding territories. Observation of adult behaviour allowed us to find nests built further than 3 m from the water's edge as well as those in atypical places (bushes and nettles). After the breeding season each year, we carefully checked all monitored territories to make sure that we had not missed any nests during the season. The only nests we found in after-season inspections of which we had been unaware were abandoned by females while still under construction (unfinished nests). Thus, we believe that the number of nests we found in each season reflected the real number of great reed warbler nests in the studied population. Nests were checked every 3–6 days, and nestlings were ringed between 5 and 9 days old, except for two nests from which nestlings were mist-netted and ringed shortly after they had fledged. In 2003–2005 we ringed 191 nestlings. Nestlings were ringed and measured at their nests, and the procedure took no longer than 5 min. Parents visited the nest shortly after we put the nestlings back and moved away from the

nest. Feeding of the young was resumed in 15–25 min. There were no cases of nest abandonment after the ringing. We did not approach nests with nestlings older than 9 days to avoid frightening them away. None of the ringed nestlings tried to escape from their nests before or after ringing.

Male pairing success was measured in terms of the number of females attracted (given by the variable Harem). We defined a male's harem as the number of females that were nesting together with him (males defend the nests of their females). 'Harem' was estimated for all territorial males in 2003–2005.

In the *Acrocephalus* species it is not possible to age individuals using plumage, as birds in their first year and older look exactly the same. According to EURING age codes every adult great reed warbler individual ringed in spring is aged as 4 (hatched before current calendar year, exact year unknown). Indeed, the colour of the iris allows one to distinguish young birds from those older than 4 or 5 years old (personal observation) but this is insufficient to age individuals precisely. The returning rate of ringed nestlings in the studied population was very low (two of 191 ringed in 3 years), and as a consequence, we did not know the ages of the recorded males. Thus, to estimate changes in syllable performance over time, we used the number of seasons in which the male was present in the study area ('Returns'). Males spotted only once were scored as R0. Males that we recognized another time in subsequent seasons based on their coloured rings were scored as R1, R2 or R3.

In the analyses of the effect of philopatry on whistle performance, we divided males into two groups: philopatric (R1, R2 and R3) and newcomers (R0). We excluded the year 2002 (the first year of the study) from the analysis of the effect of the philopatry as all males observed in 2002 were spotted for the first time, making it impossible to distinguish the philopatric males from the newcomers. We ringed all territorial males in 2002–2005 and all nestlings found in 2003–2005, and therefore the probability that a male without a ring was new to the study area seems very high. Although we did not ring nestlings in 2002, the very low rate of returning nestlings ringed in 2003–2005 (1%) supports our assumption that a male without a ring is not philopatric. The nearest great reed warbler territories were situated about 35 km away from our study site.

All males were divided into two groups according to arrival time ('Arrival'): (1) first observed before 10 May, (2) first observed after 10 May. We used 10 May to separate early arrivals from late ones as it was the mean date of arrival for the studied population and because we observed the peak of females' arrival between 7 and 10 May (great reed warbler females arrive some days later than early males). Thus, 10 May separated males that arrived after the majority of females from those that arrived before the females.

Song Recording and Analysis

All recordings were made with a shotgun microphone AKG C568 EB and Mini Disc Sony MZR 50. Altogether, in the years 2002–2005 we collected about 40 h of recordings of the great reed warbler long song from 39 individually colour-ringed males. Each male was recorded for at least 10 min during a single session, and most were recorded for 30 min. Recordings were analysed with Adobe Audition 1.5 (Adobe Systems Inc., San Jose, CA, U.S.A.) and Avisoft SASLab Pro 3.4 (Avisoft Bioacoustics, Berlin, Germany).

We recorded nine males in 2002, 21 males in 2003, 15 males in 2004 and 17 males in 2005. Some males returned regularly to the breeding grounds, so our data, for 62 male breeding seasons, stemmed from 39 males. In analyses concerning harem size and philopatry, we used recordings from 2003–2005 only (we lacked data on both harem size and philopatry in 2002). This, however, reduced the total number of analysed males only by four (from 39

to 35 recorded males) because five of the nine males recorded in 2002 returned to the study area in subsequent seasons. The total of 35 males recorded in 2003–2005 accounted for 53 male breeding seasons, in nine of which males were unpaired, in 29 monogamous and in 15 polygynous. In 30 of 53 male breeding seasons, males were philopatric, and in 23 cases they were newcomers. In longitudinal analyses of whistle performance, we used recordings of 15 returning males in 2002–2005. We recorded two males for all four seasons, five males for three seasons, and eight males for two seasons.

We chose whistles for our study of great reed warbler singing performance as low changeability of the whistle repertoire size and composition among individuals and between years in the studied population enabled both longitudinal and cross-sectional analyses. We restricted our analysis to the long, two-element whistles for which we observed relatively large individual differences. There were five types of such whistles, which we numbered 1–5. Although some males produced these whistles in a very distinct way, we were able to classify each particular whistle to a certain type based on its position in a song. Great reed warbler males share a considerable number of their songs (Węgrzyn 2006), and thus comparing the same songs from two males allows correct classification of the syllables (Fig. 1).

Measurements of Whistles and Performance Assessment

We took measurements from 10 randomly chosen whistles of each of the five types from every male recorded within a particular season, which resulted in measurements of 3100 whistles. The selected whistle types were measured in Avisoft SASLab Pro 4.4 software with the following parameters: 1024 FFT length, frame (%) = 25, window = Hamming and temporal overlap = 87.5%. This gave a 244 Hz bandwidth with 46 Hz frequency and 2.67 ms time resolution (Specht 2002). We used a one-dimensional function called Amplitude spectrum (linear) with a Hamming evaluation window and typical resolution below 3 Hz. Using this function, we measured in the power spectrum window the set of spectral characteristics for the whole syllable and for both whistle parts separately. The time parameters of whistles were measured in the sonagram window of Avisoft SASLab Pro.

In a first step, we thoroughly analysed sonagrams and variation in the acoustic measurements for each whistle type within and among males. Inspection of sonagrams revealed two sources of differences between whistles within a particular whistle type. First, variability resulted from temporal characteristics of the syllables. We observed the absence, shortening or overlapping of the elements of the whistle and, as a consequence, differences in duration between whistles of the same type (Fig. 2). Second, we observed frequency-related differences (Fig. 2). Acoustic measurements showed wide variation (measured as coefficient of variation, CV) of all analysed parameters. Preliminary analyses showed that both temporal and frequency parameters differed between males and changed with age. The changes in whistle duration were very consistent: all whistle types became longer with the age of individuals and their status (whistles of polygynous males were longer than the same whistle types of monogamous and unpaired males). The frequency parameters of whistles also differed between males and changed with age, but these changes diverged among syllable types. For example, in some whistle types the overall frequency tended to decrease with age, while in others it increased. As we were interested in a universal parameter allowing assessment of whistle performance irrespective of whistle type, we analysed only duration. Simultaneously, we observed that the consistency of whistle parameters differed between males. Renditions of the same whistle type were almost identical for some individuals, while for

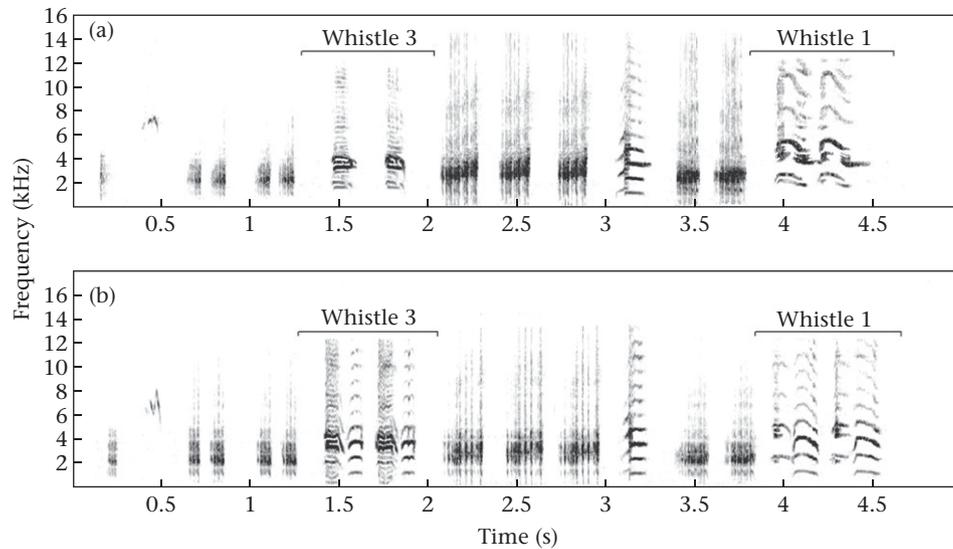


Figure 1. Example of a song shared by two great reed warbler males. The song consists of rattles (noisy syllables) and whistles (tonal syllables) repeated alternately. The positions of whistles 3 and 1 enable their correct classification despite high levels of variation in their performance between males. (a) Unpaired newcomer; (b) polygynous and philopatric male.

others consecutive renditions of the same whistle differed to some degree (Fig. 3). Studies of other species have revealed that consistency in note reproduction increases with individuals' age, probably from practice (de Kort et al. 2009). Consistency in syllable production may be important in the great reed warbler as female choice in this species is reported to depend on males' age (Leisler et al. 1995) and philopatry (Bensch et al. 1998; Hansson et al. 2004). Thus, we assessed whistle performance of great reed warbler males based on whistle duration and consistency. Whistle performance was calculated for each male and season separately. To do this, we first calculated the mean duration (mDUR) and coefficient of variation (CV) for 10 whistles of each type uttered by a male in a particular season. These values were then used to calculate grand means of duration (gmDUR) and means of CV (mCV) separately for each whistle type, resulting in an average duration and duration variability of each particular whistle type in the studied population. In the next step, we calculated the relative duration and relative consistency of each whistle type for each male in each season according to the following formulas: relative duration = $mDUR - gmDUR$ and relative consistency = $mCV - CV$.

As a result, males producing a particular whistle type with a mean duration above the population average had positive values of relative duration, and those producing whistles with higher repeatability than the population average had positive values of relative consistency. For each whistle type, we scored males' performance as follows: 0 when relative duration ≤ 0 and relative consistency ≤ 0 ; 1 if (relative duration > 0 and relative consistency ≤ 0) or (relative duration ≤ 0 and relative consistency > 0); 2 if (relative duration > 0 and relative consistency > 0).

Therefore, with five types of whistles, each male could receive an overall whistle performance assessment ('Performance') between 0 and 10. The idea of assessing whistle performance by relative duration and CV is illustrated in Fig. 4. Performance was used as a variable in subsequent analyses and had a normal distribution (Kolmogorov–Smirnov test: $Z = 1.036$, $N = 62$, $P = 0.234$).

We suggest that relative duration and relative consistency are good measures of whistle performance in great reed warbler males because both components are very likely to depend on proper motor coordination of the two bronchi involved in the production of the long, double-element whistles analysed in the present study. We assume that each of the two elements of the whistle is

produced by a different bronchus because of the different fundamental frequencies of the elements (visible on sonagrams). A mechanism of syllable production with sequential activation of the left and right bronchus has been demonstrated for the northern cardinal, *Cardinalis cardinalis* (Suthers & Goller 1996), the brown-headed cowbird (Allan & Suthers 1994) and the canary (Hartley & Suthers 1990; Suthers et al. 2004). Coordinating the left and right parts of the syrinx is a difficult task for some species, involving a period of practice before the sound is properly produced (O'Loughlen & Rothstein 2003). In such cases, the performance is not physiologically constrained as it is in the swamp sparrow (Ballentine et al. 2004). Instead there is a learning constraint: individuals cannot achieve a high level of vocal performance in a short time (O'Loughlen & Rothstein 1993). We suppose that the frequently observed shortening of the whistles (for example, when the two elements overlap or one is missed) and lower consistency of whistle production may result from poor motor coordination of the syrinx in the great reed warbler as our preliminary analyses indicated that both whistle duration and consistency changed with age.

STATISTICAL ANALYSIS

We used cross-sectional analyses to test general trends of changes in performance and its components between males. In both general linear (GLM) models and correlations (Spearman), an observation of a particular male in a particular season (male breeding season) was treated as an independent unit. This widely used approach (Forstmeier & Leisler 2004; Forstmeier et al. 2006) maximizes the power for detecting patterns but assumes that there is no major effect of an individual male. We chose this approach rather than deleting repeated measures of the same male because returning males' status (in both categories: newcomer/philopatric and polygynous/monogamous/unpaired), whistle performance and arrival changed in consecutive seasons. Thus, status, whistle performance and arrival are not intrinsic and unchangeable features of a male, and using male breeding seasons in the correlations does not seem to diminish the results because of pseudoreplication. We used male breeding season as an independent unit only in the above-mentioned cross-sectional analyses.

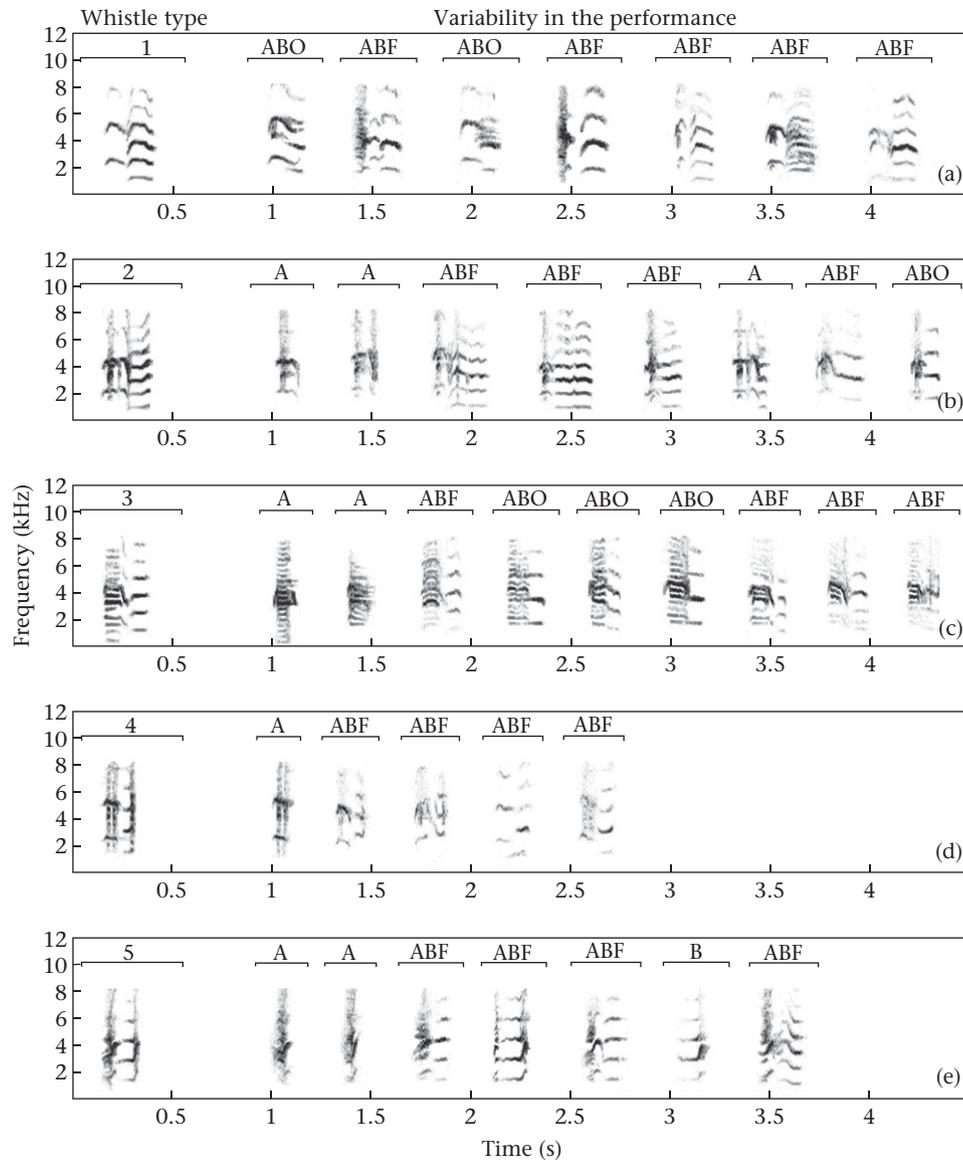


Figure 2. (a–e) Examples of variability in the performance of whistles of five types: 1, 2, 3, 4 and 5, uttered by different males. First column presents typical performance of the given whistle type by philopatric and polygynous males. A: only the first part of the whistle is produced; B: only the second part of the whistle is produced; ABO: the two parts of the whistle overlap; ABF: frequency variation in one or both whistle parts.

Next, we conducted longitudinal analyses as they make it possible to test changes in males' performance in relation to changes in their status (newcomer versus philopatric and unpaired or monogamous versus polygynous). Longitudinal analyses were corrected for repeated measures and carried out by means of generalized estimating equations (GEE), assuming either a normal or Poisson error distribution and an identity or log-link function. GEE are a modification of generalized linear models that accounts for the nested structure in an experimental design or repeated measures of an observational unit (for details, see Liang & Zeger 1986; Hardin & Hilbe 2003). In our case, males were the primary sampling unit, but their harem, performance, philopatry, returns and arrival were measured in subsequent seasons. Thus, we built models with the male as an object and year as a within-object variable. We assumed an unstructured correlation structure when constructing models, and we assessed the fit of the models by examining the quaslikelihood under the independence model criterion (QIC) and its corrected version (QICC), with the lowest value model having the best fit (Pan 2001). GEE results are reported

as chi-square scores, and tests were considered significant at $P = 0.05$. To keep the type I error constant ($\alpha = 0.05$), we used the Bonferroni correction if a multiple test of similar null hypotheses was carried out. P values are two tailed, unless stated otherwise. Means are quoted as \pm SE throughout.

All statistics were calculated using SPSS 16 software (SPSS Inc., Chicago, IL, U.S.A.).

RESULTS

Factors Affecting Whistle Performance

The more times males had returned to the local population, the longer and less variable were the whistles they produced, regardless of the whistle type (Fig. 5). The cross-sectional analysis demonstrated that males that had returned more often had a longer whistle duration (GLM: $F_{3,221} = 4.68$, $P = 0.003$), but it was strongly dependent on the whistle type ($F_{4,221} = 86.10$, $P < 0.001$). The CV of the whistle duration decreased with number of returns

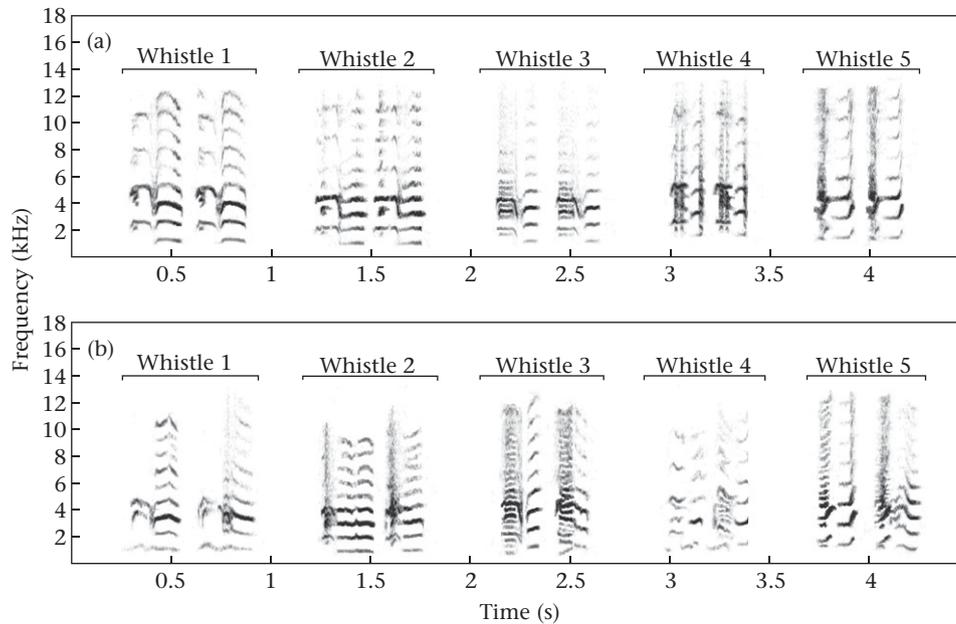


Figure 3. Differences in whistle repetition between males. (a) Whistles from males with high degrees of consistency in whistle production. (b) Whistles from males with low consistency. The repeated syllables come from single bouts.

($F_{3,221} = 7.25$, $P < 0.001$) and was independent of whistle type ($F_{4,221} = 1.94$, $P = 0.105$). This suggests that returning males improved their performance because of increases in both whistle duration and consistency.

Subsequent longitudinal analyses of 15 returning males confirmed this assumption. The average performance of whistles was significantly lower (paired t test: $t_{14} = -3.42$, $P = 0.004$) during

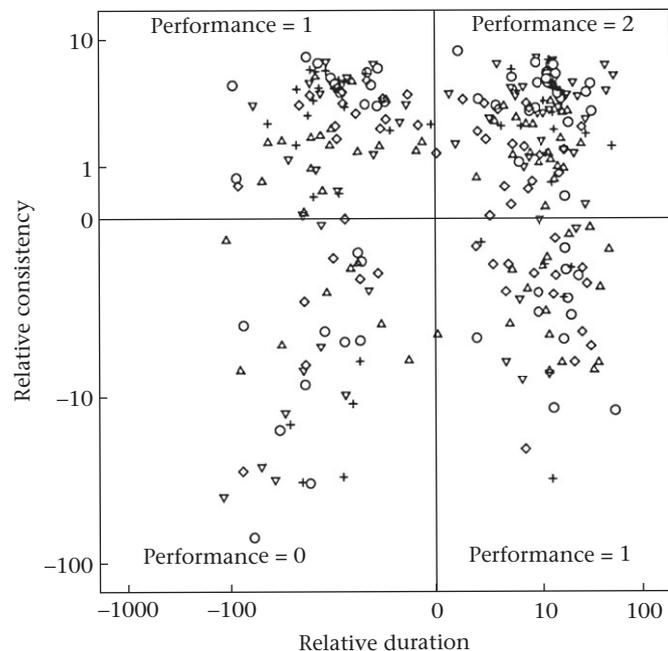


Figure 4. Illustration of the whistle syllable performance assessment. Relative duration and relative consistency axes illustrate how an average syllable duration and consistency produced by a male is shifted in relation to the grand population mean with respect to syllable type (see [Measurements of whistles and performance assessment](#)). Each whistle type is represented by a different symbol, and zeros on the X and Y axes reflect the average duration and CV of duration for the population and respective whistle type. Thus, whistles reaching values above zero on both axes had longer than average durations and were produced with higher consistency.

the first season (4.6 ± 0.50) than during the last season (7.3 ± 0.43) when a particular male was recorded. To include all data in the analyses, we built a GEE model (Table 1) with Performance as a response variable and Returns and Arrival as predictors. We entered Arrival into the model as we were interested in whether early arrivals are better whistle performers, regardless of how many times they returned to the study plot. We found that number of returns significantly affected Performance (Table 1) and that Performance consistently increased with the number of males' returns to the study area (95% Wald CI of Performance: R0: 2.70–4.69; R1: 4.03–6.29; R2: 7.74–10.56; R3: 6.43–9.33). The time of males' arrival to the study area did not affect Performance significantly (Table 1).

As we were interested in whether whistle performance depends on more general factors, such as familiarity with the breeding grounds (irrespective of the level of this familiarity), we grouped the males that returned one, two or three times into a single category (philopatric) and males recorded for the first time into a separate category (newcomer). Next, we built a GEE model in which we entered Philopatry instead of Returns (Table 2). The results were similar: Performance depended on Philopatry but not on Arrival.

Philopatric males produced significantly longer (t test: $t_{257} = -3.42$, $P = 0.046$) and more repeatable (t test: $t_{257} = -3.42$, $P = 0.046$) whistles than males that were new to the study area. Performance of philopatric males was significantly better than that of newcomers (t test: $t_{51} = 4.8$, $P < 0.001$; Fig. 6a).

Altogether, from both cross-sectional and longitudinal perspectives, great reed warbler males improved whistle performance with subsequent returns to the study area (i.e. they produced longer and more repeatable whistles). Philopatry significantly affected whistle performance, irrespective of each male's number of returns.

Whistle Performance and Harem Size

In the GEE model, we tested how Performance and Arrival explained males' harem size (Table 3). We entered Arrival into the model because it is known to affect harem size in great reed

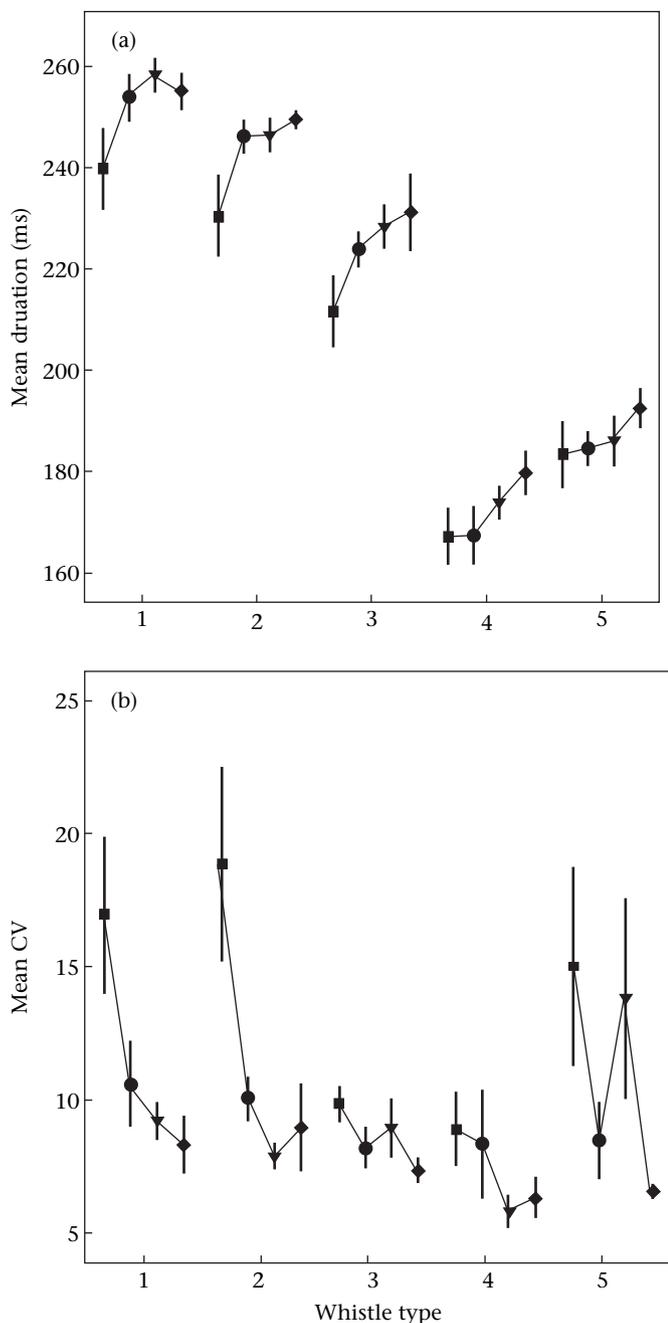


Figure 5. Mean \pm SE (a) whistle duration and (b) CV of whistle duration, calculated separately for each of the five whistle types and the number of times males returned to the local population (\blacksquare : R0; \bullet : R1; \blacktriangledown : R2; \blacklozenge : R3; R0 indicates newcomer, R1 first return, etc.).

warblers (Hasselquist 1994; Leisler et al. 1995). We found that the number of females depended on both Performance and Arrival. Differences in Performance between polygynous and other males were significant (t test: $t_{51} = -3.42$, $P = 0.046$; Fig. 6b). Whistles of polygynous males were both longer (t test: $t_{257} = -4.33$, $P < 0.001$) and more repeatable (t test: $t_{257} = 3.84$, $P < 0.001$) than those of monogamous and unpaired males.

The analyses in this section indicate that females preferred early arrivals and better performers. Performance in turn depended on philopatry and the number of males' returns to the study area but not on males' arrival (which we demonstrated in the previous section of the Results).

Table 1
GEE on factors affecting males' whistle performance

	Wald statistics (χ^2)	df	P
Constant	383.98	1	<0.001
Arrival	0.12	1	0.728
Returns	48.10	3	<0.001
	Coefficient estimate		SE
Constant	8.04		0.86
Arrival	-0.33		0.95
Returns			
0	-4.18		0.83
1	-2.72		0.78
2	1.27		1.00
3	0		0

Quasilielihood under independence model = 277.64; corrected quasilielihood under independence model = 234.41. Data were fitted to a normal distribution with an identity-function.

Arrival, Philopatry, Performance and Harem Size

Cumulative analyses of males' arrival, philopatry, performance and harem size showed that all parameters, except for Arrival and Performance, were highly correlated (Table 4). A detailed analysis of the relations between Arrival, Philopatry and Harem (Table 5) revealed that Arrival correlated with pairing success only in years when it was also correlated with Philopatry. In 2005, when philopatric males arrived later, Arrival had no effect on Harem. At the same time, the effect of Philopatry was significant. The above correlation analyses reveal that some important factors affecting harem size are mutually correlated and at the same time changeable between years. In the light of the complicated relationship between philopatry, arrival and harem size, the aim of our next analysis was to test whether the factors affecting harem size depend on the progress of the breeding season. Thus, we divided the males into two categories: early and late arrivals. We found that Philopatry and Performance were significantly correlated with Harem only in the group of early arrivals (Philopatry: $r_s = 0.53$, $P = 0.001$; Performance: $r_s = 0.31$, $N = 33$, $P = 0.039$), while there was no significant correlation between these factors in the group of late arrivals (Philopatry: $r_s = 0.29$, $P = 0.12$; Performance: $r_s = 0.2$, $N = 20$, $P = 0.21$). Our results indicate that within the group of early arrivals, philopatric males with a high whistle performance were more successful in mate attraction. The chances of pair formation for late males were independent of their singing performance and origin.

DISCUSSION

In the present paper, we estimated the singing performance of great reed warbler males based on the relative duration and consistency of their long, two-element whistles. In both cross-

Table 2
GEE on factors affecting males' whistle performance

	Wald statistics (χ^2)	df	P
Constant	326.73	1	<0.001
Arrival	0.47	1	0.491
Philopatry	19.51	1	<0.001
	Coefficient estimate		SE
Constant	6.93		0.51
Arrival	-0.35		0.51
Philopatry	-2.59		0.58

Quasilielihood under independence model = 228.27; corrected quasilielihood under independence model = 211.05. Data were fitted to a normal distribution with an identity-function.

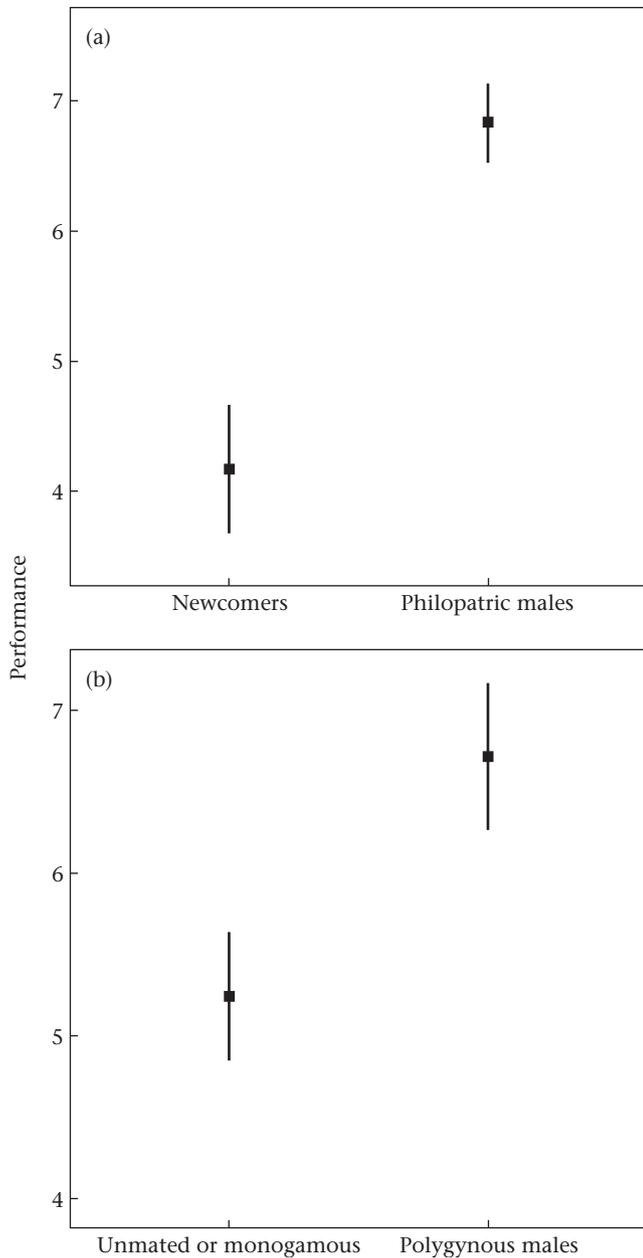


Figure 6. Comparison of whistle performance between (a) newcomers and philopatric males and (b) unmated or monogamous and polygynous males.

Table 3
GEE on factors affecting males' harem size

	Wald statistics (χ^2)	df	P
Constant	3.52	1	0.061
Arrival	16.51	1	<0.001
Performance	8.85	1	0.003
	Coefficient estimate		SE
Constant	0.60		0.32
Arrival	-0.73		0.18
Performance	0.08		0.03

Quasilikelihood under independence model = 23.59; corrected quasilikelihood under independence model = 28.22. Data were fitted to a Poisson distribution with a log-link function.

Table 4
Correlations between Arrival, Philopatry, Harem and Performance (2003–2005)

Correlated variables	Arrival		Philopatry		Harem		Performance	
	r_s	P	r_s	P	r_s	P	r_s	P
Arrival	1	0.0	0.34	0.013	0.44	0.001	0.11	0.42
Philopatry	0.34	0.013	1	0.0	0.52	<0.001	0.54	<0.001
Harem	0.44	0.001	0.52	<0.001	1	0.0	0.3	0.031
Performance	0.11	0.42	0.54	<0.001	0.3	0.031	1	0.0

N = 53.

sectional and longitudinal analyses, we showed that males improved their performance of whistles in subsequent seasons. Whistles become both longer and more consistent from one year to the next. We also demonstrated in GEE models that males' harem size was significantly related to whistle performance, which in turn reflected philopatry. Subsequent analyses revealed that the performance of polygynous and philopatric males differed significantly from the performance of monogamous, unpaired and new males.

It has been well documented so far that great reed warbler females prefer to mate with philopatric males (Bensch et al. 1998; Hansson et al. 2004). Both studies showed that lifetime fitness, measured as lifetime number of fledglings and offspring recruits, was lower for newcomers than for philopatric males, which appeared to result from reduced mating success of newcomers. The study by Bensch et al. (1998) also demonstrated that great reed warbler females are reluctant to mate with immigrant males despite their apparently similar phenotypic quality to philopatric males (in regard to life span, spring arrival date and territory quality). The question remained how great reed warbler females discriminate between returning and immigrant males. The results of our study suggest that high performance of difficult, double-element whistles may provide the females with a clue about males' origin.

As the exact age of the males in our study was unknown, the improvement of whistle performance with time might be connected to males' age and/or philopatry in terms of mastering the local dialect. In the latter case, a young but philopatric male could perform difficult local syllables more efficiently than an older newcomer. Such a situation was observed several times in the studied population: some of the poor performing newcomers were definitely older (as judged by iris colour) than some high-performing, philopatric males. This supports our conclusion that whistle performance may allow females to recognize philopatric males irrespective of their age. We suggest that comparing performance of old newcomers to young returning males is worth further investigation; however it would require more such individuals, preferably precisely aged.

On the other hand, if we consider only philopatric males, older individuals performed better than younger ones. Great reed warbler females prefer not only philopatric but also older males (Hasselquist 1998; Forstmeier et al. 2006). Female preference for older males may lead to indirect benefits such as good genes for longevity, to the extent that viability is heritable (Trivers 1972). Females may also benefit directly if older and more experienced males provide better territory, parental help or defence against predators (Alatalo et al.

Table 5
Correlations between Arrival, Philopatry and Harem in the 3 years of the study

Correlated variables	2003 (N=21)		2004 (N=15)		2005 (N=17)	
	r_s	P	r_s	P	r_s	P
Arrival*Philopatry	0.67	<0.001	0.55	0.034	0.12	0.653
Arrival*Harem	0.58	0.005	0.58	0.022	0.39	0.117
Philopatry*Harem	0.41	0.061	0.39	0.144	0.62	0.001

1986; Marchetti & Price 1989). This is especially advantageous with philopatric males because they are better adapted to the local social environment, that is, they know where to find food and nesting sites and how to avoid local predators. Thus, we may expect a feature of the males' song related to both age and philopatry to be the subject of direct female preference.

As we demonstrated that returning males with high whistle performance attract more females, we propose that a high performance of two-element whistles is the feature that allows great reed warbler females to recognize males that have returned to the breeding grounds more times than the poor performers. A competing explanation may be that philopatric males arrive first and gain better territories, which may be the subject of females' preferences in addition to the song features (Catchpole 1986; Hasselquist 1994). However, our analyses conducted separately for the early and late arrivals indicated that within the group of early arrivals, philopatric males were more successful in mate attraction than were newcomers. This suggests that arrival is not the main cue used by females to distinguish returning males from new ones. As philopatry is preferred by females, it is in the males' interest to advertise this feature. Coding philopatry in males' songs seems to be an easy and efficient way of informing females about males' familiarity with the breeding grounds without confusion with other factors (i.e. condition). The proper performance of difficult double-element whistles, mastery of which may be time consuming, seems to be a good candidate for indicating males' philopatry. If some period of practice is needed before reaching a high level of performance, the majority of the newcomers are automatically prevented from cheating.

Our analyses of the groups of early and late arrivals also revealed that the opportunities of late-arriving males for pair formation were independent of their singing performance and origin. This fact may result from different song evaluation abilities of early and late-arriving females. We suppose that the late-arriving males are more likely to pair with late-arriving females, as the early arriving females are mostly already paired when the late males arrive. The quality of the late-arriving females may be lower than that of the early ones, and this fact could be reflected in their lower ability to choose the best of the available males. In canaries, the size of the high vocal centre in the brains of females is positively correlated with the ability to distinguish between songs with and without 'sexy' syllables (Leitner & Catchpole 2002). Female zebra finches, *Taeniopygia guttata*, raised in isolation, which did not hear the songs of adult males between 14 and 40 days old, did not show preferences for high-quality songs later on. Such a preference, however, was shown for females raised with adult males that exhibited high-quality singing (Lauay et al. 2004). Therefore, it seems plausible that lower quality or less experienced females may have some problems with proper evaluation of features reflecting male quality, and as a result they may choose males more randomly than high-quality females. Another explanation is that late-arriving females may use different features from early ones to evaluate males. Other studies indicate that individual females differ within the range of preferred features. Male juncos, *Junco hyemalis*, attract females by presenting a static trait in the form of white tail coloration in addition to dynamic displays. Both elements are perceived as attractive by females, but some females pay more attention to the tail ornament and others to displays (Hill et al. 1999). The presence and the quality of the great reed warbler whistles analysed in this paper may be two of a number of cues considered by females when selecting a male, as was proven for the closely related sedge warbler, *Acrocephalus schoenobaenus* (Buchanan & Catchpole 1997). Preferred features may actually depend on the female's evaluation ability, the progress of the breeding season or other factors, giving different results among early and late arrivals.

Irrespective of the scenario, the presence of well-performed whistles in a male's repertoire and the improvement of whistle performance over time indicate males' learning ability and/or longevity. Whether the whistles serve as local dialects needs further investigation and comparison with sonagrams of songs from other populations.

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