

Male whitethroats, *Sylvia communis*, advertise their future contribution to parental care

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Summary

In altricial species participation of males in parental care enhances reproductive success of females. How does a female select a mate who will allocate time and energy to parental effort? In the whitethroat *Sylvia communis*, a socially monogamous bird, parental performance of males might be predicted on the basis of elaborated song flights displayed in courtship. The correlation analysis revealed that males which advertised intensively needed less time to attract a female and also their parental performance was better compared to males that produced cheaper signals. In the subsequent experiment, we handicapped males by increasing their body mass by 5% with a weight attached to tail feathers. Males in the treatment group reduced the proportion of showy song flights significantly more than controls and their mating success was significantly lower. We conclude that song flights in whitethroats honestly signal male quality and that the signalling system depends on a dynamic handicap trait which responds to a relatively small change in the male.

Introduction

Hypotheses stressing the adaptive value of mate choice (Kokko et al., 2003) propose that females select mates non randomly to gain indirect fitness benefits (genetically determined high viability and sexual attractiveness of offspring), direct benefits (e.g., parental care, access to resources) or to avoid excessive costs of casual mating. In altricial species the selection for direct fitness benefits might be particularly important because participation of males in parental care enhances reproductive success of females (Artiss & Martin,

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1995; Lozano & Lemon, 1996; Wright & Brown, 2002). In birds the most demanding phase of the reproductive cycle is feeding the young (Roff, 1992; Gill, 1995; Lifjeld et al., 2002). Surprisingly, however, in a meta-analysis of 39 studies of relationships between feeding effort by males and degree of expression of sexually selected traits, the coefficient of determination was small (1.3%; Møller & Jennions, 2001). How does a female select a mate who is willing and capable of providing care to offspring?

It is believed that advertising of parental care can involve sexually selected traits like song, showy flights or bright colouration (Sætre et al., 1995; Buchanan & Catchpole, 2000). It could be anticipated that such signals must be handicaps, given the conflict of interests between prospective partners that could favour cheating (Zahavi & Zahavi, 1997). Also, we should expect that the information is conveyed in dynamic rather than static traits (*sensu* Hill et al., 1999). Parental effort is affected by body condition and health status which can change rapidly. Thus signals that reliably mirror ability to provide parental care must be capable to change on a similar time scale (Faivre et al., 2003; Torres & Velando, 2003).

Interpretation of sexual advertising should involve the context in which signals are produced. A male can often choose whether to allocate time and energy to parental effort or to mating effort, i.e. to increase the number of offspring without parallel investment in their quality. Both tactics require the same basic capacities (sexual maturity, good health, physical fitness, etc.) but are triggered by different neurophysiological processes and are difficult to pursue jointly (Ketterson et al., 1992; Cawthorn et al., 1998; Moreno et al., 1999; Stoehr & Hill, 2000; Magrath & Komdeur, 2003; but see Pitcher & Stutchbury, 2000). As a result a strongly advertising male with a perfect phenotype might invest less in paternal care than males exhibiting cheaper signals (Qvarnström, 1997; Qvarnström et al., 2000). Also, the honesty of signalling paternal ability might be corrupted by life history trade-offs between current and residual reproduction. Intense and costly signals which increase the probability of attracting a female might be in fact a kind of terminal effort by males with low chances of survival to subsequent reproductive bouts (Candolin, 1998, 1999). Kokko (1998) addresses these problems in an optimality model in which the male makes the decision on how to allocate investment to costly advertising to potential sexual partners, to paternal care and to self-maintenance. The model predicts that signals produced by

the male reliably indicate his subsequent investment in parental care if investment in multiple mating is rarely successful.

In this paper we analysed sexual signalling and mate choice for direct fitness benefits in the whitethroat *Sylvia communis*, a socially monogamous passerine bird with biparental care. In the correlation analysis we found what displays were important in determining male mating success and how they mirrored paternal effort. In the subsequent handicap experiment we determined whether changes in males' signalling effort would influence male attractiveness.

Methods

We studied a population of whitethroats near Wroclaw (southwest Poland), from 1998 to 2002. All work was carried out in a 6 km² research plot between April and June. The study site consists of uncultivated meadow with thin woody vegetation. Even though the density of our population is locally high (Halupka et al., 2002), it seems that the habitat would be able to support a much greater population.

Each day we checked the study site and territories of newly arriving males were indicated on an aerial photograph. Depending on the season, 45-70% of males were individually marked with coloured leg rings. Remaining individuals were identified on the basis of their territories since male whitethroats display within a small area around their nests (Halupka et al., 2002). The behaviour of males was recorded by a focal sampling method 0-6 h after sunrise. In a preliminary study we found that signalling effort was more or less constant within this period and decreased thereafter. The observer stood 20-30 m from the focal male. We did not use hides but there were no signs that birds perceived the observer as a threat. Each observation session lasted one hour and only one session per male was made on the same day. All analyses, except of the handicap experiment (see below) included males observed for at least three sessions each, 1-5 days before the female began laying her eggs.

Male whitethroats begin advertising to females and nest building after arrival from wintering areas and cease on the day when the female begins egg laying or collects lining for the nest. Courtship in whitethroats is elaborate and consists of singing from a perch, song flights and special displays performed directly to females visiting the territory (Balsby, 2000a, b; Balsby

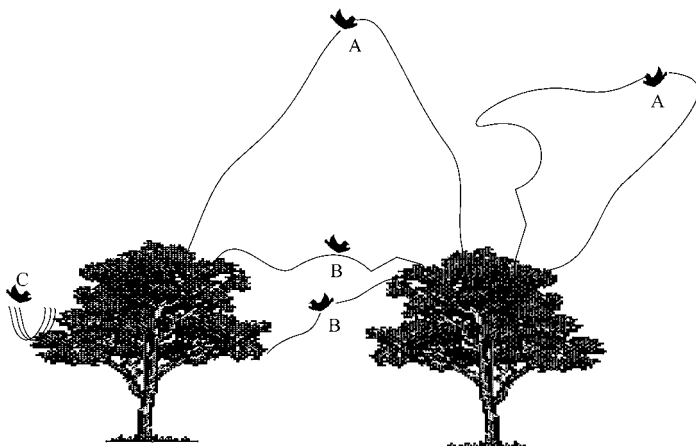


Figure 1. Exemplary trajectories of a male whitethroat performing song flights (A & B), showy song flights (A) and diving displays (C).

& Dabelsteen, 2002, 2003). Definitions of displays were as follows: ‘perch song’, the male sings while perching; ‘song flight’, the male flies between two perches and sings; ‘showy song flight’, (subclass of ‘song flight’) the male flies between two perches but the flight is exaggerated because the distance covered is not the shortest possible (Figure 1); ‘diving display’, short, usually much repeated U-shaped flights accompanied by a quiet song, made above a female hidden in vegetation (Figure 1); ‘aggressive interaction’, the male engages in a chase or physical fight with another bird.

A comparison of duration of showy and non-showy flights (M. Mandat, unpublished data) revealed that the former were significantly longer (median difference = 3.7 seconds, 95% c.l.: 2.5 to 4.9, $N = 21$ males; Wilcoxon test for matched pairs: two-tailed $p < 0.0001$). Apparently the male performing a non-showy flight simply changes the foraging posts and sings ‘by the way’. In contrast, showy flights are intended to be conspicuous. Also they are often ‘impractical’ because the displaying male starts and finishes the flight at the same place.

To quantify behaviour of males we counted the number of song flights and calculated the proportion of showy flights. Other displays (perch songs, diving displays and aggressive interactions) were recorded using one-zero sampling method for each one-minute interval of observation. Their intensities were expressed as frequencies: number of minutes with the given display observed per one hour.

Statistics were calculated using StatXact and StatsDirect software. In non-parametric tests we only used exact p values (i.e. without normal approximations).

Courtship vs attractiveness

We made an analysis of correlation between various elements of the courtship behaviour and attractiveness of males. In this part of the study, as it included unplanned tests, we used a sequential Bonferroni correction of p -values (Dunn-Šidák method described in Sokal & Rohlf, 1995) to keep the type I error constant ($\alpha = 0.05$).

Attractiveness of males was defined as nesting latency, i.e. number of days from the male's arrival to the start of breeding (when the 1st egg was laid). We assumed that attractiveness was monotonically decreasing with nesting latency. Nesting latency did not correlate significantly with the date of arrival (1998: Pearson's $r = -0.297$, $N = 21$, $p = 0.191$; 1999: $r = -0.192$, $N = 40$, $p = 0.227$) so it was not likely that our measure of male attractiveness was seriously biased due to longer nesting latency of early arriving males.

Correlates of proportion of showy flights

We correlated two elements of courtship behaviour which explained variation in attractiveness of males with variables which could reflect the quality of paternal care (nestling feeding, breeding success).

The proportion of feeding visits made by the male to 6-9 days old nestlings was determined from observations made from a blind placed about 20 m from the nest. We selected pairs in which the males were colour-ringed. Observations were made 3-6 hours after sunrise and lasted one hour or until the observer had collected a sample of 30 feeding visits (roughly the same time).

Handicap experiment

We used an experimental manipulation to test if sexual signals produced by males were handicaps. Individuals were randomly divided into two groups, treatment ($N = 19$) and control ($N = 24$). In both groups behaviour of males was recorded twice with 48 hours break between the sessions. Males were mist-netted immediately after the first session and marked with a combination of coloured rings. Additionally, we glued a 0.7 g lead weight to the

base of the tail feathers of individuals in the treatment group. The weight averaged between 4.4% to 5.5% of the male body mass. This method of handicapping is considered to cause neither excessive distress nor increase the mortality of experimental individuals and birds get rid of weights during the summer moult (Wright & Cuthill, 1990; Cuthill, 1991). All males caught were released within 5 minutes and they quickly resumed normal activity (singing, foraging). We expected that an extra weight would induce males to conserve energy, i.e. forage more and reduce costly sexual advertising (Gessaman & Nagy, 1988; Wright & Cuthill, 1990; Hooge, 1991). Thus, we expected a decline in mating success in the treatment group. Mating success was assessed by the second visit to the male, 48 hours after the first session. Some males ($N = 21$) did not advertise. One individual apparently moved outside the study area or died and in the remaining 20 cases males were paired already. Males which continued advertising ($N = 22$) were classified as 'unpaired' and the effect of the handicap was tested in this subsample. We expected a reduction (a one-tailed test was applied) in courtship intensity in the treatment relative to control group. We tested for such an effect by comparing percentage changes in intensity of courtship in both groups (for each display: $[(b - a)/a] \cdot 100$, where a and b were intensities observed at the first and second session, respectively).

Results

Structure of courtship behaviour in whitethroats

In a group of 72 males (each one observed for three hours) the average number of song flights equalled 13.3 per hour (SD = 7.04) including 73.6% (SD = 13.64) showy flights. Also, within one hour an average male sang for 36 minutes (SD = 12.14) from a perch and performed 1.5 (SD = 1.45) diving displays.

Courtship vs attractiveness

In a group of 37 males there were insignificant relationships (two-tailed $p > 0.05$ after the sequential Bonferroni correction) of nesting latency with the frequency of song flights (Pearson's $r = 0.269$), diving displays ($r = -0.090$) and perch songs ($r = 0.369$). Only the proportion of showy flights

was significantly negatively correlated with nesting latency (Figure 2a; $r = -0.472$, $p < 0.05$) suggesting that males that performed a high proportion of showy flights attracted females earlier.

Correlates of proportion of showy flights

There was a significant positive correlation between the proportion of nestling feedings visits by the male and the proportion of showy flights ($r = 0.695$, $N = 16$, two-tailed $p = 0.003$; Figure 2b). We also found a significant positive correlation between the proportion of showy song flights and the number of aggressive interactions with other birds ($r = 0.350$, $N = 72$, two-tailed $p = 0.003$; Figure 2c). However, the variation in breeding success was not explained by the proportion of showy flights (successful males: median = 75.5% showy flights, 95% c.l.: 72.7 to 81.8, $N = 29$; unsuccessful: median = 70%, 95% c.l.: 65 to 75.9, $N = 11$; Mann-Whitney test: $U = 120$, two-tailed $p = 0.232$).

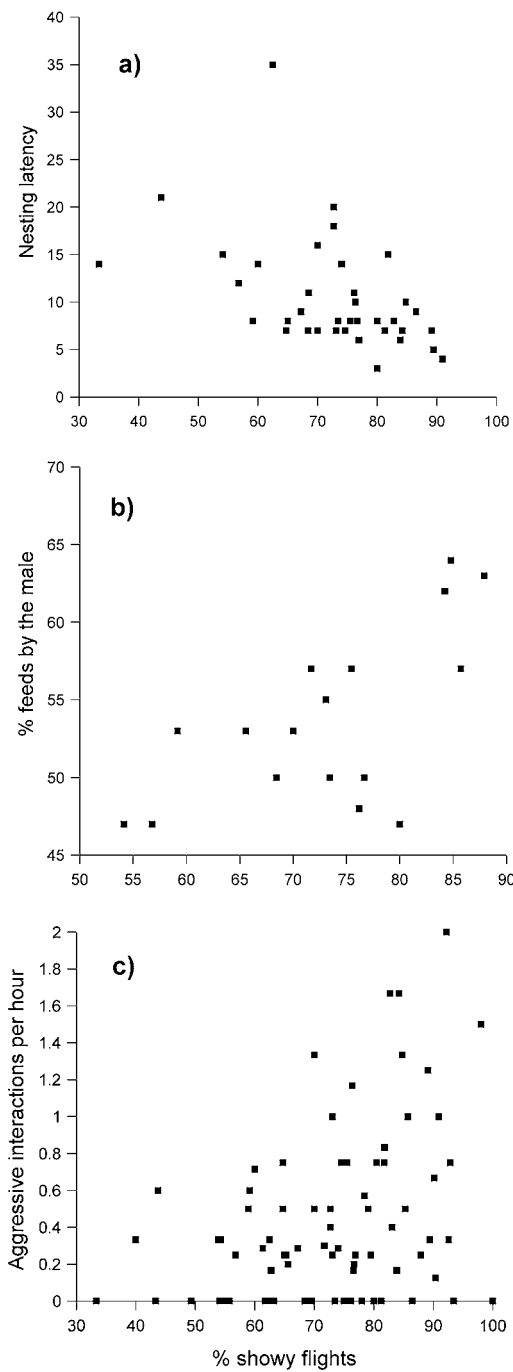
Handicap experiment

Only 5 (27.7%) of 18 handicapped males had attracted a female and stopped singing by the second observation session whereas in the control group the figures were 15 (62.5%) of 24 males (Fisher exact probability test: one-tailed $p = 0.027$).

In males that continued advertising (13 in the treatment group and 9 controls), we found no significant effect of the handicap on the number of perch songs and song flights (Mann-Whitney tests: $U = 56$, one-tailed $p = 0.448$ and $U = 53.5$, one-tailed $p = 0.391$). However, handicapped individuals reduced the proportion of showy flights significantly more than controls ($U = 25$, one-tailed $p = 0.013$).

Discussion

The key finding of this study is that in whitethroats the future parental performance of males might be predicted by females and is important in female mate choice. This was supported both by an analysis of correlation and an experiment. The behavioural trait that in the correlative part of the study determined the mating success of males and their parental effort, responded to



experimental reduction in male quality, and experimental males had lower mating success than males in the control group.

It seems that in whitethroats the two most important preconditions for the evolution of advertising paternal care are fulfilled. First, the signal is based on a dynamic handicap trait which responds to a relatively small change in the male. So this signal might respond similarly also to natural short-term changes in quality, such as wing strain or a reduction in the food supply provided by the territory. In contrast, the majority of papers testing relationship between sexual advertising and paternal care which were included in the metaanalysis by Møller & Jennions (2001), focused on static traits and this may be the basic reason why sexual advertisement seemed to be rather loosely related to parental effort (see Introduction). The most frequently analysed traits involved plumage characteristics (e.g. colour, tail length) and their expression reflect conditions during moult. Hill et al. (1999) suggests that such traits provide information about long term viability and genetic quality of the individual and are less likely to show their phenotypic value several months later, at the time of mating.

Second, after attracting a mate males have rather limited opportunities to further increase fitness through investment in mating effort. Sex ratio in the studied population is skewed and some territorial males remain unmated. Thus only a tiny fraction of individuals (less than 5%, Borowiec & Halupka, unpubl. data) are polyterritorial and attempt to attract a second female. Under such conditions, when investment in costly advertising to many females is not a profitable option, males bias their investment towards parental effort and the ability to provide care to offspring positively correlates with sexual advertisement, as predicted in the model by Kokko (1998).

Showy song flights were the only form of advertising that reliably predicted mating success and the subsequent parental care exhibited by the male (Figure 2). In the experiment, males with added weight decreased the relative frequency of showy flights even though other forms of advertising were apparently unaffected (Figure 3). Such a pattern supports the honest advertisement hypothesis (Zahavi & Zahavi, 1997). In previous studies of passerine birds, song flights have been found to predict parasitic infection (Buchanan

Figure 2. Relationships between the proportion of showy song flights given by advertising male whitethroats and (a) their nesting latency (in days), (b) chick feeding effort compared with the female, and (c) frequency of aggressive interactions with other birds (events hour⁻¹).

See text for test statistics.

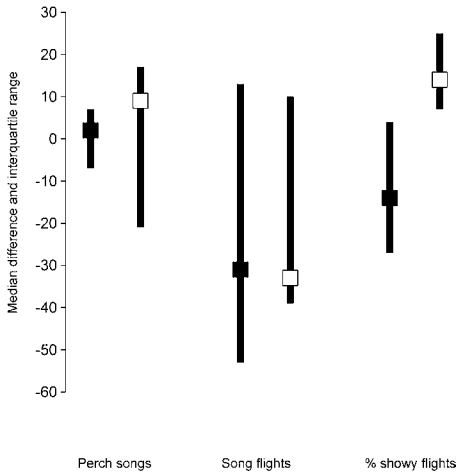


Figure 3. Median percentage changes in the intensity of courtship displays performed by handicapped (filled squares) and control (open squares) male whitethroats between two consecutive observation sessions. See text for test statistics.

et al., 1999), male condition, mating success and fledging success (Mather & Robertson, 1992).

Apparently song flights were more intensive shortly after territory establishment than two days later: a decrease in the number of song flights was recorded both in the experimental and control group (Figure 3). It might suggest that the variation in mating effort was not only determined by social status (paired/unpaired) and quality of the male but also by some seasonal effects. In sum, the total number of song flights was more or less the same in both groups but the proportion of showy flights differed significantly. Females apparently were sensitive to such a shift in behaviour of males since they preferred individuals in the control group over handicapped ones.

Observations of unmanipulated males may suggest the existence of a kind of social handicap associated with sexual advertisement. We found a significant positive correlation between the number of aggressive interactions and the frequency of showy flights (Figure 2c). This might indicate that strongly advertising males were dominant and thus willing to engage in intrasexual competition. Alternatively, this correlation could show a social cost imposed on attractive males. Strong advertising increases mating success but also results in more intrusions from other males (Balsby & Dabelsteen, 2003).

We cannot easily explain why females paid more attention to the proportion of showy flights rather than just the number. Both characteristics were

correlated ($r = 0.353$, $N = 37$, two-tailed $p = 0.032$), however only the former one allowed to predict mating success of males and their 'hidden' traits (the future parental effort and aggressiveness). Also the proportion of showy flights (and not the number) was sensitive to the experimental manipulation (Figure 3). On the other hand, the signalling system based on the proportion of showy flights may appear open to cheating. Imagine a male which made just one showy flight. This would make him very attractive for females (100% showy flights) whereas the cost of such behaviour (energy and predation risk) would be minor. We suppose that such kind of cheating has not occur. First, all males did show a reasonable number of showy song flights (on average 13 per hour — see Results) and the number and proportion of showy flights were significantly correlated. Thus the cost of advertisement has not been trivial. Second, the male can never be quite sure if his signal has reached the proper audience and/or was received errorless. Consequently the male has to repeat displays many times which guarantees the honesty of signalling (De Jaegher, 2003). Third, it is reasonable to expect that the female does not focus her attention at a single male for longer (Dukas, 2002) but rather she only glances at males while foraging in vegetation. If so, the proportion of showy flights should be important in mate choice because it directly corresponds to the probability that the female, when she looks at the particular male, observes an impressive display rather than a kind of foraging flight. Finally, by focusing on the proportion of showy flights females might get rid of confounding effects from the environment. Some habitats facilitate showy song flights (due to favourable spatial distribution of high perches) and also intensity of displays could be determined by the weather (e.g. strength of wind). As a result males are not directly comparable and the female, to assess showiness of the given individual, must use some information about a background in which displays are presented. Non-showy flights which reflect the normal activity of the focal individual (the male simply adds the song to a movement between two foraging posts) may be used as such information.

In conclusion, our data support the hypothesis that females might predict the male's future contribution to parental care, if the signal is a dynamic handicap trait and males have limited opportunities to increase fitness through advertising to other females. Some sexually selected traits might be used to advertise both the genetic quality of the male and his ability or willingness to care for the offspring. Thus, from the female point of view,

selection for direct and indirect fitness benefit need not be contradictory (cf. Fitzpatrick et al., 1995). We should rather expect that in species where contribution of males in parental care is substantial, females have evolved behavioural adaptations facilitating correct prediction of abilities and intentions of advertising males.

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