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Can simple songs express useful signals for mate choice?

Nan Lyu, Jinlin Li and Yue-Hua Sun*

Abstract

Background: As one of the most elaborate and diverse sexual signals, bird songs are prominent among mate choice criteria. Females generally prefer mates with larger repertoire size, which promotes the evolution of song complexity. However, there are also some songbirds that have far simpler and less diverse vocalizations, which have not been the focus of scientific scrutiny. Most *Phylloscopus* warblers are accomplished singers with complex songs. In contrast, Hume's Warbler (*P. humei*) has extremely simple songs. In order to explore the song's function, its evolutionary significance and particularly to assess its possible relationship with parental investment, we studied mate choice of the subspecies *P. h. mandellii* in Lianhuashan National Nature Reserve, Gansu, China.

Methods: We recorded body measurements and songs of breeding males and then explored their relationships with the date of clutch initiation, reasoning that the characteristics of males that are involved with early nesting activities reflect female mate preferences. We also recorded egg size and body measurements of nestlings to assess the relationship between parental investment and mate choice.

Results: We found that male wing and tail lengths were positively correlated with early clutch initiation as were songs characterized by short duration and rapid rise to maximum amplitude. We also found that early-breeding females did not lay large eggs, but produced more surviving young, which grew up faster.

Conclusions: Female mate choice criteria in this bird include both visual signals and song characteristics. Our study supports the hypothesis that females may judge male quality from quite subtle differences. In order to reduce the risk of predation, a preference for such inconspicuous male characteristics may be partially driven by high vulnerability of this warbler to predators as a ground-nesting species.

Keywords: Bird song, Sexual selection, Mate choice, Parental investment, Hume's Warbler

Background

Mate choice is one of the main sexual selection mechanisms and can lead to the evolution of conspicuous or even excessive phenotypic characteristics in animals (Andersson 1994). Bird songs tend to be long and complex vocalizations produced by male individuals during the breeding season (Catchpole and Slater 2008) and are prominent criteria in the mate choice (Searcy and Andersson 1986). Females generally prefer mates with a large sized repertoire, promoting the evolution of song complexity (Searcy 1992). In contrast, some songbirds

have far simpler and less diverse vocalizations (Byers and Kroodsma 2009). The function and evolution of such "simple songs" and their relationship to sexual selection have attracted little attention (Cardoso and Hu 2011) and our understanding of mate choice of these species is therefore limited, besides its potential significance to the exploration of avian song evolution.

Generally in nature, conflicting pressures of sexual selection as well as in natural selection have long been viewed as a means to stabilize the evolution of sexually selected signals, such as ornaments and songs in birds (Andersson 1994; Gray and Cade 1999). Females can reap benefits both directly and indirectly through an appropriate mate choice (Møller and Thornhill 1998), e.g., getting better food resources, nest sites, nuptial gifts and also

*Correspondence: sunyh@ioj.ac.cn

Key Laboratory of Animal Ecology and Conservation Biology, Institute of Zoology, Chinese Academy of Sciences, Beijing 100101, China

better genes for their offspring. Furthermore, parental investment strategies of both sexes may be influenced by their choice in mates, which in turn affects the survival of their offspring (Mitchell et al. 2007; Ligon and Hill 2010). For example, female Common Moorhens (*Gallinula chloropus*) compete for relatively fat males that are more persistent incubators (Petrie 1983), while female Common Stonechats (*Saxicola torquata*) prefer males with higher song rates, which apparently signals that they are more diligent in feeding offspring and in nest defense (Greig-Smith 1982). Male Great Tits (*Parus major*) with a large central black breast-stripe are also more likely to defend their brood (Norris 1990). Moreover, females can alter egg size (e.g. Cunningham and Russell 2000; Rutstein et al. 2004; Bonato et al. 2009) or feeding effort (e.g. Linville et al. 1998; Ligon and Hill 2010) according to the quality of their mates.

Most of the *Phylloscopus* warblers are accomplished singers with remarkable and impressive songs. In the Hume's Warbler (*P. humei*), however, only two

simple songs have been reported (Baker 1997). They are described either as a double whistle note or as a drawn-out descending buzz. Furthermore, for *P. h. mandellii*, it had been discovered that this subspecies only issues the buzz song type (Fig. 1), but has five types of call (Bi 2004). It is still unclear why the songs of *P. humei* are so different from other apparently closely related *Phylloscopus* species (Baker 1997; Bi 2004).

Phylloscopus humei was originally considered as conspecific under the name of Yellow-browed Warbler *P. inornatus* (Voous 1977) but, based on acoustic, molecular, morphological and behavioral evidence, it is now accorded full species status (Irwin et al. 2001). Two disjunct subspecies are recognized: *P. h. humei* in India and *P. h. mandellii* in central China (Baker 1997). It is monomorphic, lacking obvious sexual ornaments but males, competing for territories early in the breeding season, display their pale wing-bars in *P. h. humei* (Marchetti 1993, 1998). Hitherto, only some basic descriptions about population status and breeding are available for the

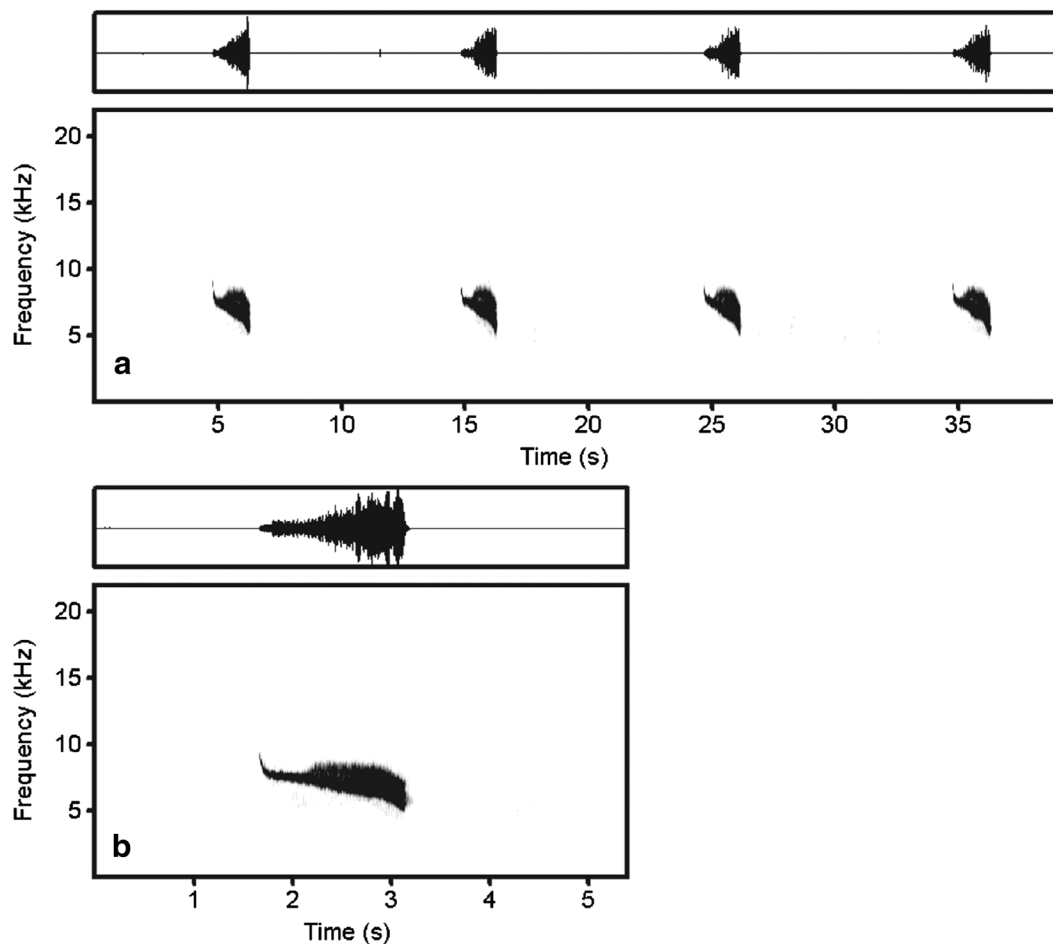


Fig. 1 Song spectrogram of *P. h. mandellii*. **b** is the magnified spectrogram of the third note in **a**

Chinese subspecies (Bi et al. 2009). In order to explore the possible relationships between mate choice and the simple song of *P. humei*, we conducted a field study of *P. h. mandellii* in the Lianhuashan Nature Reserve, Gansu, China. We specifically studied (1) preferences of females in their mate choice (considering both visual and song characteristics) and (2) whether the survival and development of their offspring is related to their mate choice.

Methods

We studied breeding *P. h. mandellii* birds at Shahetan station in the Lianhuashan National Nature Reserve (34°40'67"N, 103°30'84"E) during the April–July periods in 2009 and 2010. The elevation of the station is 2850 m asl. Mature mixed forests throughout the study area are dominated by spruce, fir, willow and birch trees (Sun et al. 2003). Local ground vegetation varies from sparse vegetation to dense shrubs of different species, as well as grasses, Arrow Bamboo (*Sinarundinaria nitida*), forbs and mosses (Sun et al. 2003).

We captured a total of 55 males using mist nets and marked them with unique combinations of colored leg bands to facilitate field identification. We captured male individuals as soon as possible when we detected their singing at the beginning of the breeding season (from late April to the middle of May). We opted for three types of measurements, i.e., body characteristics, ornamental and song characteristics to assess the relationship with female mate preferences. Specifically, we measured (1) bill length (exposed culmen), wing length, tail length and tarsus length as body characteristics using a centimeter ruler to the nearest 0.1 mm; (2) eyebrow size and wing-bar size (= length × width) as the ornamental characteristics using vernier calipers to the nearest 0.1 mm. We also recorded songs from differently marked males using a Sony WM-D6 recorder and a Sennheiser directional microphone. Song recording would be conducted at least 1 day after capture. A total of 139 recordings were analyzed using Avisoft SASLab Pro v. 4.52 applying the following settings: sampling frequency 22,050 Hz, 16 bit, time resolution 5.8 ms and bandwidth 162 Hz. In order to remove background sounds (the noises and sounds of other birds), all recordings were filtered using the FIR high-pass filter in the software with a low frequency limit of 4.5 kHz before our analyses. We measured the following song parameters: duration (DUR), interval (INT), maximum amplitude (MA), distance from start to maximum amplitude (DSM), maximum frequency in the maximum amplitude (MAXMA), minimum frequency in the maximum amplitude (MINMA), frequency bandwidth in the maximum amplitude (FBMA), maximum frequency (MAXF), minimum frequency (MINF) and frequency bandwidth (FB).

We found nests by following females during the nest building period (mainly from late May to early June) and checked daily to measure the length, width and mass of newly laid eggs. In order to minimize disturbance when following females, we would check the nest after the female left. This bird has strong territorial defense behavior throughout the breeding period. In order to determine the ownership of the nest by the male, we would identify the territory of each male bird according to our field observation and as well check the color rings of male birds to verify the ownership during the incubation and/or nestling period. All nests laid eggs successfully. We calculated the egg volume as $0.457 \times \text{length} \times \text{width}^2/1000$ (Hoyt 1979). Following Marchetti (1998), we used the first egg date as a quantitative measure of female mate preference (i.e., females preferred the characteristics of males who supported the earliest possible nestings). Since the nestling period of *P. h. mandellii* is about 14 days (Bi et al. 2009), we measured the nestlings on Day 12 (bill length, wing length, tail length and tarsus length) to assess the development during the nestling period.

In order to identify the relationships among the characteristics of the body of males, egg size and fledging size, we applied a Generalized Linear Model (GLM) using R (version 2.14.1). Since multi-collinearity of independent variables can cause problems in regression models (Hosmer and Stanley 2000), we first calculated the bivariate correlations among different variables and then used a correlation coefficient threshold of 0.7 as suggested by Fielding and Haworth (1995). Fifteen variables were retained for further analysis, i.e., bill length, wing length, tail length, weight, tarsus length, eyebrow size, wing bar size, DUR, INT, DSM, MA, MAXMA, FBMA, MINF and FB. We conducted simple regression models for these variables and excluded nonsignificant variables ($p > 0.05$). Subsequently, we used a multiple regression model containing all significant variables and applied a stepwise backward procedure based on Akaike's information criterion (AIC, Akaike 1974) in order to reduce the number of variables.

Results

During the 2 years of field work, we found 25 nests of the 55 captured males and another 18 nests of *P. h. mandellii* without capturing the male owners. From a total of 43 nests, we identified 40 with first egg laying dates, of which 18 reared at least two fledglings successfully. None of the nests were deserted in 2009, while two nests were deserted during the egg laying period and incubation period in 2010. This may be related to the harsh climate with continuous rain during 2010. Basic information about male characteristics, eggs and nestlings are presented in Additional file 1: Tables S1 and S2.

Female mate choice

First egg dates were May 24 in 2009 and May 28 in 2010. In order to quantify the preference for a mate by a female individual, we defined these days as “1” and then transformed the first egg dates of the various nests into a numerical format (*D*). Five variables were significant ($p < 0.05$) in the simple regression analyses (Table 1). The DSM, FBMA and wing length have the highest explanatory power, with relatively large *F* values. The best multiple regression model only retained two of the five predictor variables entered ($F_{2,16} = 14.275$, $p < 0.001$), i.e., DSM and wing length (Table 1), which represent the song and body size characteristics, respectively. The DSM affected the egg laying date positively, while the wing length was negatively correlated with *D* (Fig. 2). Furthermore, we found that the wing-bar size was significantly correlated with wing length ($r = 0.513$, $n = 54$, $p < 0.001$).

Relationships between mate choice and offspring

Egg volume was correlated with egg mass ($r = 0.929$, $n = 188$, $p < 0.001$). Neither the mean egg mass ($F_{1,17} = 0.286$, $p = 0.600$) nor egg volume ($F_{1,17} = 0.124$, $p = 0.729$) were significantly correlated with first egg laying dates. However, the nestling bill length at Day 12 was negatively correlated with the first egg laying date ($F_{1,13} = 12.47$, $p = 0.004$; Fig. 3a), suggesting that early nesting may confer benefits for the offspring. Further, nestling size was correlated with egg size, given that bill length was positively correlated with egg volume ($F_{1,16} = 10.11$, $p = 0.006$; Fig. 3b).

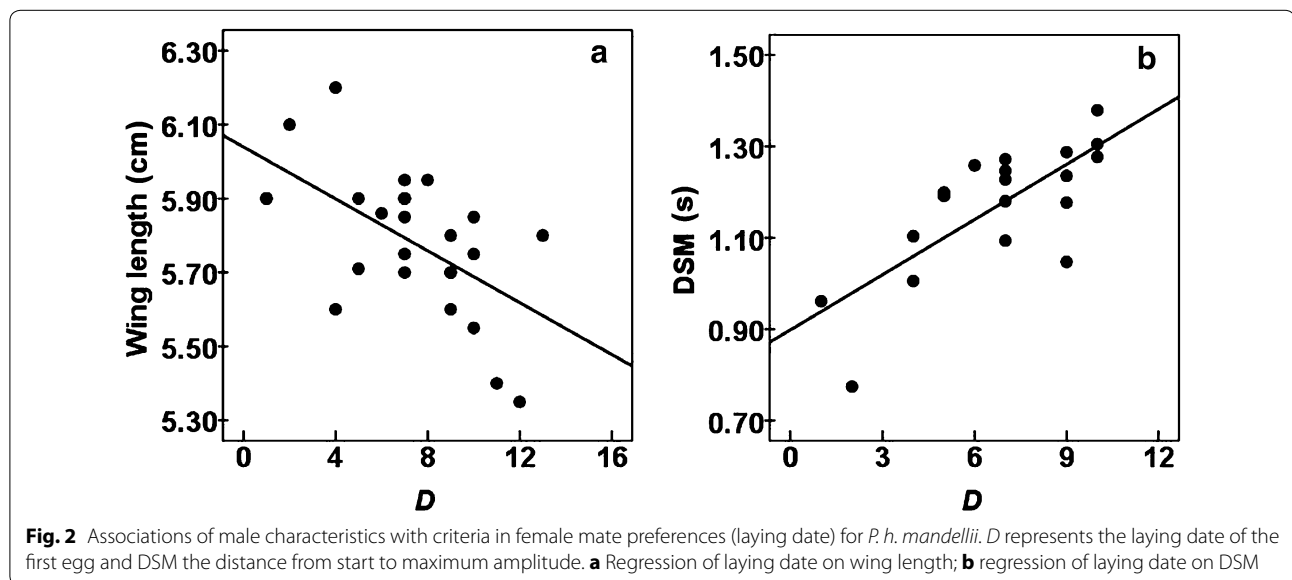
Discussion

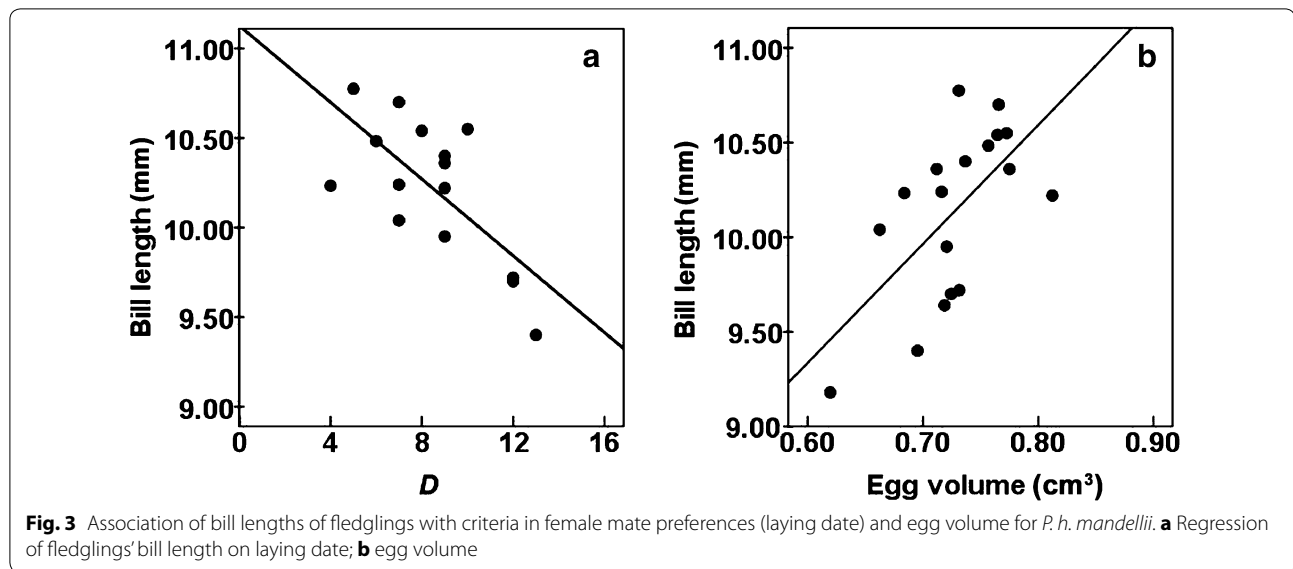
The evolution of sexual phenotypic characteristics is affected not only by sexual selection, but also by natural selection (Andersson 1982). Highly developed secondary sexual characteristics generally require large investments

Table 1 Results of the mate choice of *P. h. mandellii* birds

Variables	Simple regression models				GLM			
	Estimate	SE	$F_{1,17}$	<i>p</i>	Estimate	SE	<i>t</i>	<i>p</i>
Intercept					19.803	16.913	1.171	0.259
Wing length	−9.544	2.804	6.808	0.002	−4.650	2.625	−1.771	0.096
Tail length	−5.821	2.782	1.002	0.048				
DUR	11.542	5.153	5.016	0.039				
DSM	13.951	2.936	22.57	<0.001	11.915	2.997	3.976	0.001
FBMA	5.693	1.842	9.536	0.007				

Only significant variables ($p < 0.05$) are listed. We report the estimated coefficients (Estimate), standard error (SE), *t* values and *p* values from GLM with step backward analysis





in energy and attract predators. In either case, survival and both current and future reproduction may be adversely affected (Gray and Cade 1999).

As in *P. h. humei* (Marchetti 1998), we found that the criteria females use in their choice of a mate in *P. h. mandellii* include both visual signals (e.g. wing length) and song characteristics. We suggest that this phenomenon is also a joint action of natural and sexual selection (Höglund and Sheldon 1998; Kokko et al. 2002). In general, two hypotheses may be applied to explain the evolution of this type of mate choice and simple songs. First, Gilliard's 'transfer hypothesis' suggests that bright ornaments and other secondary sexual characteristics (including passerine songs) may be inversely related (Gilliard 1956); e.g., males of more dimorphic species have a dominant tendency to sing short songs in 56 North American wood warblers (Parulinae) (Shutler and Weatherhead 1990). However, *P. h. mandellii* obviously does not satisfy this hypothesis, for it has quite simple songs and its plumage is even less ornamental than that of other sympatric *Phylloscopus* spp., (e.g., *P. kansuensis* with a bright median crown stripe and yellow rump).

Generally, over-developed secondary sexual characteristics may require large amounts of energy and increase predation risks (Andersson 1994), which therefore should be more costly. Another proposed explanation is that females may judge male quality from quite subtle differences, such as small variations in male songs (Forstmeier et al. 2002) or slight variations in visual signals, such as eye ring pigmentation (Pérez-Rodríguez 2008), wing patch size (Török et al. 2003) or badge size (Griffith 2000). These types of criteria in females in mate choice can clearly reduce risk of predation. For *P. h. mandellii*

females in particular, we suggest that these criteria of inconspicuous visual signals (e.g., longer wing and tail lengths) and short, inconspicuous songs may be partially related to their nesting behavior. As a ground nester, their inconspicuousness and monomorphism may be especially advantageous, as has been suggested for ground-nesting wood warblers as well (Shutler and Weatherhead 1990). Therefore, in order to reduce the probability of nest predation, *P. h. mandellii* may have evolved specific mate choice preferences in females for longer wings and smaller DSM (Fig. 2). Furthermore, given the statistically significant correlation between wing-bar size and wing length, we suggest that this bird may identify male size through the wing-bar, which should be rather easier to distinguish among individual males, as indicated in *P. h. humei* (Marchetti 1998).

With regard to song, we found that the first egg laying date was correlated with the parameters related to maximum amplitude, such as DSM, FBMA and MINMA. The most significant parameter was DSM, with early breeders having relatively short DSMs. Moreover, DUR was negatively correlated with first egg dates and DSM, suggesting that females prefer males whose songs are shorter with a faster increase in volume. Contrary to the study on *P. h. humei* by Marchetti (1998), we found that the song rate ($=1/\text{INT}$) was not correlated with the first egg date. This may be related to the multiple mate selection criteria and high plasticity in Hume's Warbler. Marchetti (1998) also found that the egg laying date was no longer correlated with song rate when wing-bar size was altered artificially. Furthermore, male songs have another important role in territorial defense. Catchpole (1983) has proposed that long songs may serve to attract mates while short songs

are used for territorial defence. The shortness of territorial defence songs could be attributed to the need in males to hear the response of their competitors (Ince and Slater 1985). We accordingly suggest that the simple song of *P. h. mandellii* should play an important role in the defence of territory.

Finally, it should be stated that although females of *P. h. mandellii* in our study did not vary their investment in eggs in relation to the first egg laying date (i.e., mate choice), we obtained some evidence of faster growth in earlier hatched nestlings. This suggests that such chicks may have benefitted from higher rates of feeding or from better food. We observed that both parents bring food and feed the nestlings cooperatively. Therefore, we suggest that the female preference for larger males (i.e., longer-winged individuals) may be driven by the greater ability of such males to provision their young. Alternatively, these individuals may be more likely to occupy better territories with better food resources and/or better nest sites. Any or all of these features should play an important role in promoting the growth of their offspring and breeding success.

Additional file

Additional file 1: Table S1. Three types of measurements for captured males including body characters, ornamental and song characters. **Table S2.** The measurements of eggs and nestling.

Authors' contributions

NL and YHS designed the study. NL and JL collected the data and performed all analyses. NL and YHS drafted the manuscript. All authors read and approved the final manuscript.

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Competing interests

The authors declare that they have no competing interests.

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