JOURNAL OF AVIAN BIOLOGY

Article

Song performance is a condition-dependent dynamic trait honestly indicating the quality of paternal care in the bull-headed shrike

Yuusuke Nishida and Masaoki Takagi

Y. Nishida (http://orcid.org/0000-0001-5237-407X), Osaka City Univ., Dept of Biology and Geosciences, Osaka city, Osaka, Japan. – M. Takagi (http://orcid.org/0000-0001-8308-899X) (mtakagi@eis.hokudai.ac.jp), Hokkaido Univ., Dept of Natural History Science, Sapporo, Hokkaido, Japan.

The good parent hypothesis in sexual selection predicts that if females can increase their fitness by mating with males who provide high-quality parental care, then female preferences for male phenotypes honestly indicating the quality of paternal care will evolve. In order to test this hypothesis, we investigated correlations between male song, the timing of pair formation of males, male feeding rate, and reproductive success, in the bull-headed shrike *Lanius bucephalus* (an altricial oscine passerine with biparental care). Analysis revealed that although the timing of pair formation was not correlated with most song characteristics (e.g. repertoire size), male morphological traits (e.g. tail length), or male territory size, it was negatively correlated with male singing tempo (i.e. the number of notes uttered per second). Those males that sang at higher speeds were in better body condition (i.e. body mass standardized by tarsus length^3 was higher), fed their chicks frequently during the nestling period, and raised heavy chicks. These results show that in the bull-headed shrike male singing tempo is a condition-dependent dynamic trait honestly indicating the quality of paternal care, and strongly supports the good parent hypothesis.

Keywords: good parent hypothesis, sexual selection, bull-headed shrike

Introduction

Male song in oscine passerines is a sexually selected trait that has dual functions: female attraction and territory defence (Andersson 1994, Searcy and Nowicki 2005, Catchpole and Slater 2008). Sexual selection theory predicts that if male songs honestly indicate their genetic quality and/or ability to provide direct reproductive benefits, female preference for such songs will evolve (Andersson 1994). One of the potential direct benefits is the quantity and quality of parental care (Hoelzer 1989). In oscine passerines where most of the species is altricial birds with biparental care (Cockburn 2006), parental provisioning greatly influences the growth and survival of offspring (Alatalo et al. 1982, Smith et al. 1982, Sasvari 1986, Wolf et al. 1988, 1990). Thus, if male song honestly indicates the quality and quantity of paternal care, then female preference for male song will evolve (good parent hypothesis: Hoelzer 1989).

In order to confirm that song is a reliable indicator of a good father, it is necessary to demonstrate that: 1) females choose their mates based on certain song characteristics, 2) such characteristics reflect the quantity and quality of paternal care, and 3) females mating with such males obtain high reproductive success (Hoelzer 1989, Johnstone 1995). Many authors have submitted data showing that song characteristics reflect the quantity and quality of paternal care in various bird species by using song output (Greig-Smith 1982, Welling et al. 1997, Hofstad et al. 2002, Dolby et al. 2005) and song complexity (Buchanan and Catchpole 2000, Bartsch et al. 2015). For example, song rate in stonechat *Saxicola torquata* (Greig-Smith 1982) and repertoire size in common nightingale *Luscinia megarhynchos* (Bartsch et al. 2015) were found to be positively correlated with male feeding rates. However, so far only one study has successfully verified all conditions of the good parent hypothesis (sedge warbler *Acrocephalus schoenobaenus*: Buchanan and Catchpole 1997, 2000). Buchanan and Catchpole (1997, 2000) found that female sedge warblers chose their mates based on male repertoire sizes, which reflected male provisioning rates; females mating with such males raised heavy chicks. Therefore, the good parent hypothesis using male songs in oscine passerines has not yet been adequately verified.

Multi-year field studies are necessary in order to accurately verify the good parent hypothesis. Song output is known to reflect male feeding effort in willow tit *Poecile montanus* (Welling et al. 1997) and snow bunting *Plectrophenax nivalis* (Hofstad et al. 2002). However, they provided no evidence that females mating with such males obtained greater reproductive success (e.g. increased number of fledglings or greater chick weight). One possible reason is that most parents were able to nurture all of their chicks successfully because of coincidental food abundance during the one or two years when the studies were conducted (Welling et al. 1997). Multi-year field studies will enhance the power to detect the true correlation between male songs and reproductive successes.

We studied bull-headed shrikes *Lanius bucephalus* for six years (2012–2017) in Japan. In the bull-headed shrike, both parents provision their chicks (Takagi 2003a), and parental feeding is one of the factors determining starvation and survival of chicks (Takagi 2001). During the breeding season, territorial male shrikes sing during courtship and until they mate with females (Yamagishi and Saito 1985, Harris and Franklin 2000), suggesting that females choose their partners based on their songs. Therefore, we considered that the bull-headed shrike was a good model organism to investigate the good parental hypothesis, and our long-term field data made the verification of the hypothesis possible. Our purpose in this study was to investigate whether or not male song is a reliable indicator of a good father in the bull-headed shrike. We predicted that: 1) female shrikes might choose their mates based on male song characteristics, 2) male song characteristics reflect paternal feeding effort, 3) females mated with such males achieve high reproductive success (e.g. greater chick weight, larger number of fledglings).

Material and methods

Study site and species

The bull-headed shrike is a monogamous, altricial oscine occurring throughout Japan (Ornithological Society of Japan 2012). Male and female bull-headed shrikes are easily distinguished in the field based on their morphological traits. Male shrike has a black mask over eyes and ear-coverts, and his wings are dark brown with a distinct white patch on primaries; female shrike is similar to the male, but has a brown mask, and her wings are dark brown without a white patch on primaries (Harris and Franklin 2000). We carried out field observations in an area of small-scale agricultural fields (ca 2 km^2) in the southern part of Osaka, Japan (34°28′N, 135°35′E). Shrikes arrived in the area during September and October (Yamagishi et al. 1992). Males establish their wintering territories mainly in areas of agricultural fields, whereas females establish theirs mainly in forest and residential areas. Males do not sing when they are competing for territories during the non-breeding season. Individual males and females overwinter in their own territories until the breeding season begins (i.e. until January of the following year) (Yamagishi et al. 1992). Each female mates with a territorial male, then breeds in his winter territory during the period from February to May (Yamagishi and Saito 1985). Shrike pairs build open-cup nests in shrubs or bamboo clumps, produce clutches of 4 to 6 eggs, which females incubate alone for about 15 d. Eggs hatch asynchronously over one to three days (Takagi 2001). For about one week after the first egg hatches in each clutch (i.e. during the early nestling period), mothers brood and fathers mainly feed their chicks. For one week after the early nestling period (i.e. during the later nestling period), both parents provision their chicks (Takagi 2003a). When parents are unable to provide adequate food for their offspring because of inclement weather, such as heavy rain, chicks starve to death in order beginning with the lightest (Takagi 2001). Both parents continue to provision their offspring in the vicinity of their nests for about two weeks after fledging (Yamagishi and Saito 1985).

Territory mapping

In order to measure male territory size, we conducted territory-mapping surveys from 1 October to 31 November from 2012 to 2016, when male shrikes established their wintering territories. We selected one male at random for each survey, tracked him for four hours beginning at sunrise using binoculars (10.5 × 44), and recorded the locations where he perched during that time on a map. A male territory was defined as the area within the polygon of the outermost perch sites. By means of a combination of field surveys and aerial photographs, we classified the types of habitat in each male territory as: vegetable field, rice field, orchard, forest, abandoned farmland, road, or artificial building. The area of each habitat type within each territory was calculated using Quantum GIS 2.10.1 software (<www.qgis.org>).

Our observations of 37 colour ringed males showed that in no case did males move their territories from winter to spring. Therefore, we can use the position of the male's territory (which we surveyed during the non-breeding season) as a marker for ID, and it is possible to assure accurate data (timing of pair formation, male song, reproductive success, etc.) assignment to individual birds.

Timing of pair formation

In the bull-headed shrike, the mating relationship between a male and a female is formed through three stages: 1) courtship, 2) consorting, 3) reproduction (egg laying, incubation, nestling). For several days after the day on which a female arrives in a male's territory, he frequently courts her (Yamagishi and Saito 1985). We defined the period as the courtship stage. After the male no longer courts the female the courtship stage ends; however, the male continues to accompany the female for several weeks until reproduction begins. We defined the period as the consorting stage. During this stage, we observed 11 pairs (with colour leg rings) and then confirmed that 91% of them (i.e. 10 pairs) advanced to the reproduction stage (egg laying, incubation, nestling). Therefore, if we confirmed that a male no longer courted a female in his territory, but was seen to be continually consorting by her, we considered that they had formed a mating relationship. Since a pair during the consorting stage always accompanies each other, 10 minutes is easily sufficient to confirm whether pair formation occurs.

In order to identify the timing of pair formation, we divided the breeding season (the period from 1 February to 31 May from 2013 to 2017) into 30 four-day intervals (e.g. 1st interval: the period from 1 to 4 February; 2nd interval: the period from 5 to 8 February; 3rd interval: the period from 9 to 12 February; and so on), and once during each interval we observed each male for 10 min from a distance of ca 20 m. When a male was seen to be accompanied by a female in his territory and did not court the female during the 10-min observation, pair formation was considered to have occurred. We then identified during which interval pair formation had occurred, and used the timing of pair formation as the indicator of a pairing date. For example, if a male mated with a female during the 1st interval (i.e. the period from 1 to 4 February), the timing of pair formation of the male was recorded as '1'; if a male mated with a female during the 3rd interval (i.e. the period from 9 to 12 February), the timing of pair formation of the male was recorded as '3'. Thus, the timing of pair formation was noted as a relative pairing date, not an actual pairing date.

Male song

We recorded the songs of 58 male bull-headed shrikes for several minutes during 2 February to 9 March during the morning (06:00–12:00), using a LisN parabolic microphone (Fuji Planning, Tokyo, Japan) and an Olympus LS-7 solid-state recorder (Olympus, Tokyo, Japan), with a sampling rate of 44.1 kHz and 16-bit resolution. The songs were converted into spectrograms (window type: Hann; window size: 512; overlap: 50%; filter and width: 248 Hz) using acoustic analysis Raven Pro 1.5 beta software (Cornell Laboratory of Ornithology, USA).

We defined an uninterrupted sound on the spectrogram as a 'syllable' (Fig. 1a). A syllable was composed of a fundamental tone and harmonic tones (Fig. 1a). Since the harmonic tones were often not recorded due to the environmental conditions (e.g. humidity, temperature, biotic and abiotic noise, etc.), we have used only the fundamental tone in the following analysis. Hereafter, the fundamental tone is referred to as a 'note' (Fig. 1a).

We sampled a total of 490 ± 103 notes from each male, and measured the following eight song characteristics because these were known to be important variables of vocal communication in passerines (Catchpole and Slater 2008, Searcy and Nowicki 2005): 1) high frequency (kHz) (the highest frequency of a note); 2) max frequency (kHz) (the loudest frequency of a note); 3) low frequency (kHz) (the lowest frequency of a note); 4) frequency bandwidth (kHz) (the difference between the high and low frequency of a note); 5) note duration (seconds) (the length of a note) (Fig. 1a). We defined a sequence of notes given at shorter than 0.5-s intervals as one song and measured 6) song duration (seconds) (the length of a song) (Fig. 1b). We compared the shape of notes on the spectrograms and measured 7) repertoire size (the number of different note types an individual utters). Finally, as an indicator of the singing speed of males,
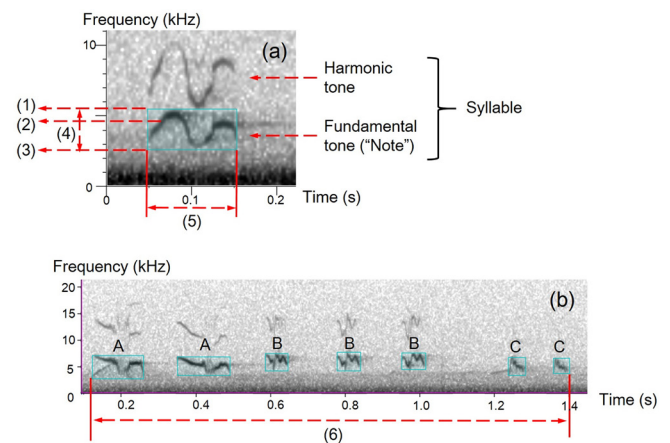

Figure 1. Examples of measured song characteristics of the bull-headed shrike. The horizontal axis, vertical axis, and colour density of the spectrograms show time, frequency, and amplitude of male song. A syllable is composed of a fundamental tone (i.e. note) and harmonic tones. Each number in parentheses and arrows indicate the measured song characteristics: (1) high frequency (kHz), (2) max frequency (kHz), (3) low frequency (kHz), (4) frequency bandwidth (kHz), (5) note duration (s), and (6) song duration (s). On the spectrogram below, (7) the repertoire size is three (note types A, B, C), and (8) tempo (/s) is 5.6, because the number of notes uttered was seven and the time taken to utter the notes was 1.25 s.

we measured 8) tempo (/second) (the number of sampled notes/the time taken to utter all of the sampled notes). The recording date was not correlated with any song characteristics (Supplementary material Appendix 1 Table A1).

Podos (1997) measured vocal performance as a trade-off between tempo and frequency bandwidth. In order to preliminarily check whether this definition can also be used in the bull-headed shrike, we analysed the correlation between tempo and frequency bandwidth. Tempo proved not to be correlated with the frequency bandwidth (Spearman's rank correlation, $r_s = -0.051$, n = 58, p = 0.702), indicating that Podos's definition could not be used in the bull-headed shrike. Therefore, we used the tempo as an indicator of vocal performance which was independent of the frequency bandwidth.

Reproductive success and parental feeding effort

We inspected each nest at a maximum interval of four days from 1 February to 31 May 2013 to 2017, and then determined the date of clutch initiation and clutch size. We were able to accurately record the date on which hatching occurred, because we were able to predict the date of hatching based on the date of clutch initiation and because we observed each nest every day from the predicted date. The age of each brood was counted from the hatching date of the first egg in the brood. We weighed each nestling on the 6th and 12th days after hatching, at 12:00–13:30 using a digital balance to the nearest 0.1 g. If all nestlings disappeared from a nest, it was assumed that a predator had attacked the nest.

We recorded parental provisioning behaviour at each nest in sunny or cloudy weather on the 6th and 12th days at 06:00–13:30 with a video camera HDR-CX480 (Sony, Tokyo, Japan). From the videos we observed the number of times parents attended their nests and fed their nestlings. The number of the feeds was influenced by the number of chicks in the nests (6th days: $r_s = 0.403$, $n_{nest} = 40$, p = 0.001; 12th days: $r_s = 0.346$, $n_{nest} = 34$, p = 0.045). To make it possible to analyse the correlation between the number of feeds and various variables (song characteristics, reproductive success, territory quality, etc.), we should eliminate the effect of the number of chicks on parental feeding by dividing the number of feeds by the number of chicks. For the same reason, we should divide the number of feeds by observation time of the videos. Therefore, we defined the number of feeds per nestling per hour as feeding rate (i.e. the indicator of parental feeding effort). Prey items carried by parents to their nestlings were classified into three categories: small prey < 50% of adult culmen length; medium prey > 50% but < 100% of culmen length; large prey > 100% of culmen length (Takagi 2003a). A preliminary analysis suggested that the culmen lengths of male and female parents did not differ significantly (Wilcoxon rank sum test, $W = 253$, $n_{male} = 27$, $n_{female} = 21$, p = 0.735). For both male and female parents, we calculated their feeding rates (i.e. number of feeds per nestling per hour) for each prey category, and used them for the analysis.

Morphological traits, body condition and age of parents

Male and female bull-headed shrikes were captured, using a mist net, during the nestling period. We measured body mass to the nearest 0.1 g with a digital balance, and morphological traits (e.g. tail length, natural wing length, tarsus length, total head length, total culmen length, bill depth, and bill width) to the nearest 0.01 mm with digital calipers. Body mass (g) was divided by tarsus length^3 (cm^3) in order to provide an indicator of body condition. As the body mass of male shrikes does not change within a single breeding season, whereas that of females does (Takagi 2002), we used only the body condition of male parents. We identified shrikes as 'yearlings' (i.e. those born within the previous year) or 'adults' (i.e. those older than yearlings) based on the presence or absence of buff-tipped greater primary upper coverts (Yamagishi 1982), or from the combination of colour rings attached when previously caught.

Bull-headed shrikes rarely return to their previous breeding area in subsequent years. The returning rate of males is 18% and of females 0%; even successful breeders do not always return to the area near their previous year's nesting site (Takagi 2003b). Therefore, the probability that an individual male entered twice (or more) across different years is considered very low.

Temperature

We used temperature data observed by the Japan Meteorological Agency at a site located about 15 km from the research site.

Statistical analyses

We used Spearman's correlation analysis, Wilcoxon signed-rank test, and generalized linear mixed models including survey year as a random effect with packages, 'lme4', 'lmerTest', and 'aod' in R ver. 3.1.0 software (R Foundation for Statistical Computing, Vienna, Austria). In order to examine which characteristics of male song are preferred by females, we constructed GLMM (the response variable: the timing pair formation of males; the explanatory variables: song characteristics) with a Poisson distribution and a log link function. To test whether the song characteristics preferred by females indicate parental care of males, we constructed LMM (the response variable: the feeding rate; the explanatory variables: the song characteristics) with a Gaussian distribution and an identity link function. In order to whether females gain reproductive benefits by mating with the males that have the attractive songs, we constructed GLMM (the response variable: the date of clutch initiation, clutch size, or brood size; the explanatory variables: the song characteristics) with a Poisson distribution and a log link function; GLMM (the response variable: nest predation; the explanatory variables: the song characteristics)

with a binomial distribution and a logit link function; LMM (the response variable: weight of chicks; the explanatory variables: the song characteristics) with a Gaussian distribution and an identity link function If models with Poisson distributions did not converge, due to overdistribution, we used the GLMM with a negative binomial distribution and a log link function as an alternative. Nest predation was a dummy variable, which was defined as 0 when predation occurred, and 1 when predation did not occur. Dates were counted from 1 February. The significance level for all statistical analyses was set at p = 0.05. Where there are no annotations, values represent means and SD.

Data deposition

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.c84f7c4> (Nishida and Takagi 2018).

Results

Song characteristics and timing of pair formation

The timing of pair formation was significantly correlated with tempo ($r_s = -0.561$, n = 58, p < 0.001, Supplementary material Appendix 1 Table A2 and Fig. 2) and note duration ($r_s = 0.398$, n = 58, p = 0.002, Supplementary material Appendix 1 Table A2), but not with other characteristics of
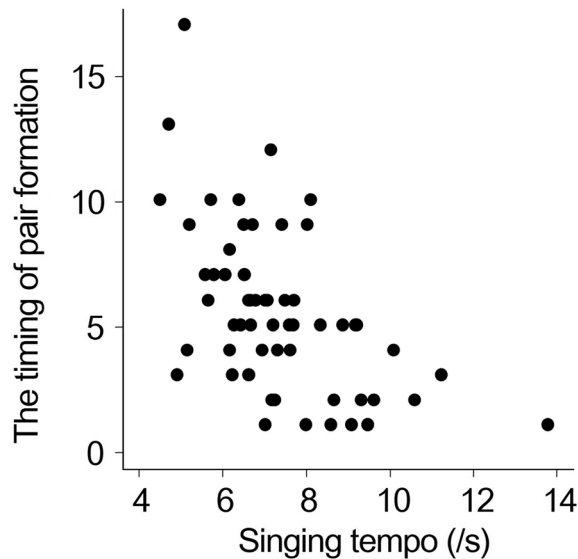

Figure 2. The relationship between male singing tempo and timing of pair formation ($n_{male} = 58$). The y-axis can reach values ranging from 1 to 30. For example, when the y-axis is 1, it indicates that a male mated with a female during the 1st interval (i.e. the period from 1 to 4 February); when the y-axis is 3, it indicates that a male mated with a female during the 3rd interval (i.e. the period from 9 to 12 February); when the y-axis is 30, it indicates that a male mated with a female during the 30th interval (i.e. the period from 28 to 31 May).

male song. The timing was not also related to male territory size or male morphological traits (Supplementary material Appendix 1 Table A2).

Because tempo was correlated with note duration ($r_s = -0.394$, n = 58, p = 0.002), we constructed GLMM to exclude the influence of statistical confounding. The analysis showed that tempo had a negative effect on the timing of pair formation (GLMM with Poisson distribution, n = 58, $slope_{tempo} = -0.202$, SE = 0.045, z = -4.521, p < 0.001, Fig. 2), whilst the effect of note duration disappeared (GLMM with Poisson distribution, n = 58, $slope_{note\ duration} = 6.375$, SE = 4.021, z = 1.585, p = 0.113).

Parental feeding effort

We recorded parental provisioning behaviour at 40 nests on the 6th and at 34 nests on 12th days. The total feeding rate (i.e. the sum of male and female feeding rate) on the 6th day of the nestling period was 1.87 ± 0.70 ($n_{nest} = 40$, male contribution: $78.5 \pm 15.1\%$) and on the 12th day was 2.38 ± 1.18 ($n_{nest} = 34$, male contribution: $47.3 \pm 19.6\ \%$) (V = 113, $n_{nest} = 34$, p = 0.023). Comparing the total feeding rate for each prey size on the 6th and 12th days, the feeding rate of large prey increased significantly over time (6th day: 0.40 ± 0.33, 12th day: 0.81 ± 0.48, V = 41, $n_{nest} = 29$, p < 0.001), but the feeding rates of small (6th day: 1.02 ± 0.58, 12th day: 0.93 ± 0.83, V = 265, $n_{nest} = 29$, p = 0.315) and medium prey did not change significantly (6th day: 0.44 ± 0.23, 12th day: 0.64 ± 0.36, V = 127, $n_{nest} = 29$, p = 0.051).

Singing tempo and parental feeding effort

Tempo was not correlated with parental (male or female) feeding rate for each prey size on the 6th day (Supplementary material Appendix 1 Table A3), nor was it related to the feeding rate of small and medium prey on the 12th day (Supplementary material Appendix 1 Table A3). However, tempo was positively correlated with the feeding rate of large prey by both males (LMM, n = 14, $slope_{tempo} = 0.097$, SE = 0.044, t = 2.216, p = 0.048, Supplementary material Appendix 1 Table A3 and Fig. 3) and females (LMM, n = 14, $slope_{tempo} = 0.097$, SE = 0.031, t = 3.125, p = 0.009, Supplementary material Appendix 1 Table A3 and Fig. 3).

On the 12th day, the male feeding rate of large prey was unrelated to brood size, ambient minimum temperature, paternal morphological traits (e.g. tail length), body condition, age, or song characteristics other than tempo (Supplementary material Appendix 1 Table A4). This tendency was similar for female parents (Supplementary material Appendix 1 Table A4). However, the male feeding rate of large prey was positively correlated with the areas of vegetable fields ($r_s = 0.659$, n = 16, p = 0.006, Supplementary material Appendix 1 Table A4) and roads in each male territory ($r_s = 0.628$, n = 16, p = 0.009, Supplementary material Appendix 1 Table A4), and the female feeding rate of large prey was positively correlated with the area of vegetable fields ($r_s = 0.735$, n = 16, p = 0.001, Supplementary material Appendix 1 Table A4).
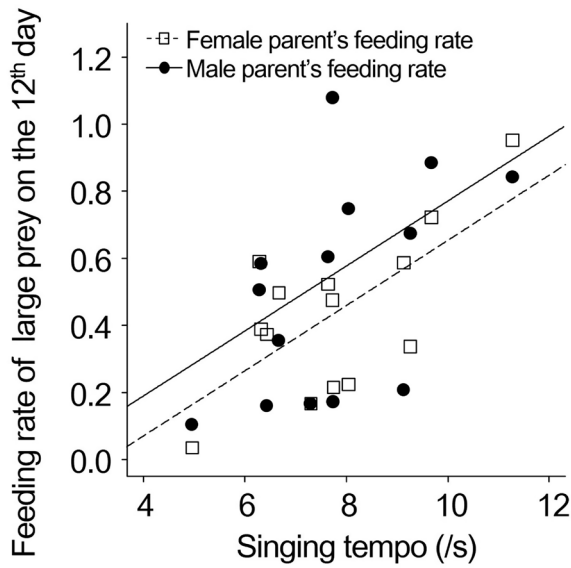
Figure 3. The relationships between male singing tempo and male (filled circles and solid line) and female (open squares and dotted line) feeding rate (the number of nest attendances for provisioning per nestling per hour) of large prey on the 12th day ($n_{nest} = 14$). Prey size was classified into three categories: small prey < 50% of culmen length of parents; medium prey > 50% and < 100% of culmen length; large prey > 100% of culmen length.

The areas of vegetable fields and roads were correlated with each other ($r_s = 0.495$, n = 58, p < 0.001), so we constructed LMM to exclude the influence of statistical confounding. The analysis showed that vegetable field area had a positive effect on male feeding rate of large prey on the 12th day (LMM, n = 16, $slope_{vegetable\ field} = 0.103$, SE = 0.035, $t = 2.952$, p = 0.011), whilst the effect of road area disappeared (LMM, n = 16, $slope_{road} = 0.133$, SE = 0.072, $t = 1.848$, p = 0.088). Similarly, vegetable field area had a positive effect on female feeding rate of large prey on the 12th day (LMM, n = 16, $slope_{vegetable\ field} = 0.162$, SE = 0.040, $t = 4.024$, p = 0.001). Tempo was related to vegetable field area (LMM, n = 38, $slope_{tempo} = 0.338$, SE = 0.140, $t = 2.406$, p = 0.021, Supplementary material Appendix 1 Table A5), but not to other habitat areas.

Singing tempo and reproductive performance

Tempo was positively related to average chick weight (LMM, n = 16, $slope_{tempo} = 0.376$, SE = 0.145, $t = 2.588$, p = 0.023, Supplementary material Appendix 1 Table A6 and Fig. 4) and the weight of the largest chick in each brood on the 12th day (LMM, n = 16, $slope_{tempo} = 0.428$, SE = 0.173, $t = 2.477$, p = 0.028, Supplementary material Appendix 1 Table A6 and Fig. 4), but not related to other aspects of reproductive performance (Supplementary material Appendix 1 Table A6).

On the 12th day, chick weight was not correlated with brood size, or the accumulated minimum temperature from the hatching day to the 12th day (Supplementary material Appendix 1 Table A7). However, average chick weight
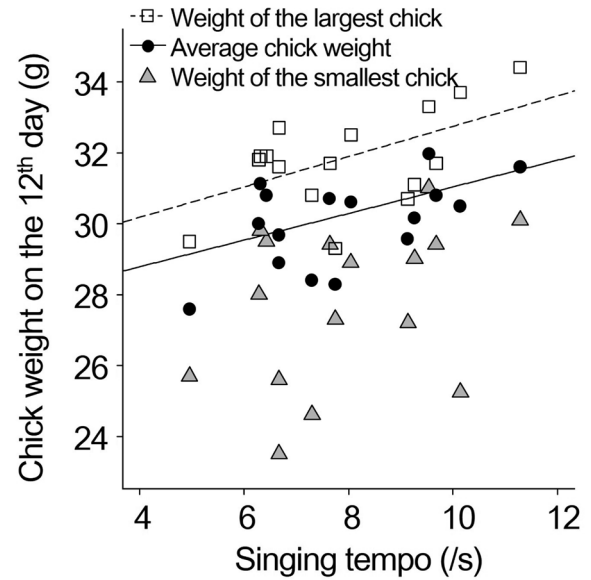

Figure 4. The relationships between male singing tempo and average chick weight (filled circles and solid line), the weight of largest chick (open squares and dotted line) and smallest chick (grey triangles) in each brood on the 12th day ($n_{nest} = 16$).

($r_s = 0.370$, n = 32, p = 0.037, Supplementary material Appendix 1 Table A7), and the weight of the largest chick in each brood ($r_s = 0.421$, n = 32, p = 0.016, Supplementary material Appendix 1 Table A7), were positively related to the total feeding rate of large prey. Even considering the effect of the research year on the results, the total feeding rate of large prey had a positive effect on the average weight (LMM, n = 32, $slope_{total\ feeding\ rate} = 1.570$, SE = 0.589, $t = 2.665$, p = 0.013) and the weight of the largest chick in each brood (LMM, n = 32, $slope_{total\ feeding\ rate} = 1.581$, SE = 0.557, $t = 2.836$, p = 0.008).

Singing tempo and male condition and age

Tempo was not correlated with recording date ($r_s = 0.232$, n = 58, p = 0.079), minimum temperature on the recording day ($r_s = 0.040$, n = 58, p = 0.763), or male age (Wilcox rank sum test, W = 86, $n_{adult} = 19$, $n_{yearling} = 9$, p = 1.000), but was correlated with male body condition ($r_s = 0.687$, n = 13, p = 0.010). Even considering the effect of the research year on the results, male body condition had a positive effect on tempo (LMM, n = 13, $slope_{body\ condition} = 6.186$, SE = 1.874, $t = 3.301$, p = 0.007, Fig. 5).

Discussion

We found that in the bull-headed shrike not only was male singing tempo a condition-dependent trait indicating the quality of paternal care and male territory, but also that females that chose mates based on that song characteristic increased their reproductive success. These results satisfy all
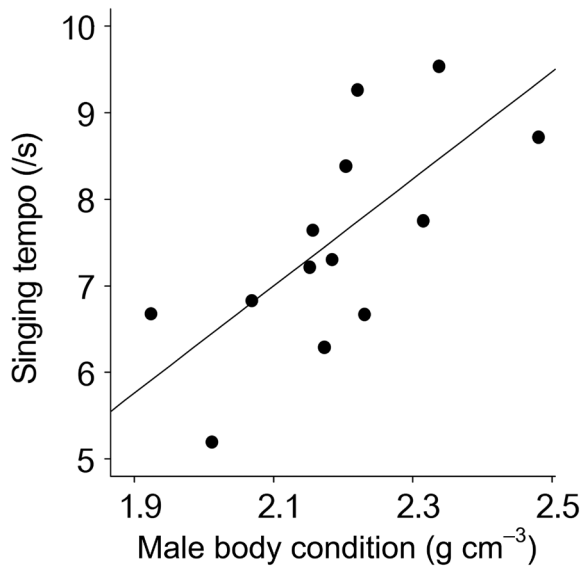
Figure 5. The relationship between male parent's body condition (body weight divided by tarsus length^3) and male singing tempo ($n_{male} = 13$).

of the conditions required by the good parent hypothesis (Hoelzer 1989, Johnstone 1995). Therefore, we conclude that male singing tempo is an honest indicator of paternal quality in the bull-headed shrike.

Song characteristics can be defined as: song output (e.g. song rate), song complexity (e.g. repertoire size), local song structure (e.g. dialect), or vocal performance (e.g. trill rate), with tempo belonging to vocal performance (Searcy and Nowicki 2005, Yamada and Soma 2016). This is the first study showing that male vocal performance is an honest indicator of a good parent in an oscine passerine. Below, we discuss in more detail the relationships between male song characteristics, female mate choice, parental feeding effort, and reproductive success.

Male singing tempo and female mate choice

We found that male bull-headed shrikes singing at high speed mated with females earlier in the breeding season than those singing more slowly (Fig. 2), but the timing of pair formation was unrelated to other song characteristics, male morphological traits, or male territory size (Supplementary material Appendix 1 Table A2). These results strongly suggest that females choose their mates based on male singing tempo. Our results, derived from field observations, provide the first example of females preferring males that sing quickly. In the bull-headed shrike, 17% of nests had extra-pair paternity (Yamagishi et al. 1992). Therefore, we cannot deny the possibility that females may choose their extra-pair partners based on their repertoire size.

Although playback experiments have shown that in some oscines females respond actively to male high trill rate, it is not well-known whether those females benefit from greater reproductive success by preferring such song characteristics

(Vallet et al. 1998, Weiss et al. 2012). In altricial oscines with biparental care, females clearly benefit from mating with males that frequently provision chicks (Alatalo et al. 1982, Smith et al. 1982, Sasvari 1986, Wolf et al. 1988, 1990). Hoelzer (1989) predicted that females preferring male phenotypes reflecting the feeding effort of a father would evolve in such species. Therefore, it was expected that the tempo, related to female mate choice, might indicate the quantity and quality of male feeding effort in bull-headed shrikes.

Singing tempo and parental feeding effort

We found that neither brood size nor accumulated minimum temperature from hatching influenced chick weight, but chick weight was positively related to the feeding rate of large prey (Supplementary material Appendix 1 Table A7). In addition, parents increased their rate of feeding large prey to their young over the course of the breeding period. These results show that providing large prey as a food resource to their young is an effective means of promoting weight gain. We were able to show that tempo was an indicator of male and female feeding rate of large prey during the later nestling period (Supplementary material Appendix 1 Table A3 and Fig. 3), but characteristics other than the tempo was not indicators of their feeding rate (Supplementary material Appendix 1 Table A4). In other words, our results show that tempo is a true indicator of the quality and quantity of paternal care. Someone may insist that those females are capable of evaluating male feeding effort based on other song characteristics, such as repertoire size (Buchanan and Catchpole 2000, Bartsch et al. 2015). However, no song characteristics, other than tempo, correlated with male feeding rates in the bull-headed shrike (Supplementary material Appendix 1 Table A4). The result suggests that female shrikes cannot assess paternal care with reference to song characteristics other than tempo. Therefore, as we predicted, tempo (in relation to female mate choice) indicated the quantity and quality of male provisioning in bull-headed shrikes.

Interestingly, male singing tempo also correlated with female feeding rate (Supplementary material Appendix 1 Table A3 and Fig. 3), probably because males singing at high-speed held good feeding territories, from which females benefitted. Laniidae generally require open hunting grounds with a range of perch sites from which they can search for and detect terrestrial insects and small vertebrate prey (Yosef 1993, 2004, Yosef and Grubb 1994, Morelli et al. 2016). It is known that open agricultural land is an important foraging environment for the bull-headed shrike (Matsui and Takagi 2017). Our results in the present study show that the increase in the feeding rate of both male and female parents was related to the area of vegetable fields within a male's territory, suggesting that vegetable fields provide an important open foraging habitat in the population that we studied. This relationship is robust because feeding rate was unrelated to brood size, minimum temperature outside nests, parental morphological traits, body condition, or age (Supplementary material Appendix 1 Table A4). As those males that sang at

high-speed, held territories containing large areas of vegetable fields (Supplementary material Appendix 1 Table A5), it is suggested that, by mating with males singing at high speed, females are able to gain two direct benefits: male paternal care, and male territory for foraging. However, the detailed mechanism whereby vegetable field area increases the feeding rate of parents is not yet known. In the future, it will be important to investigate the number of perch sites necessary for feeding and the amount of food resources available in the field environment.

Singing tempo and reproductive success

In order to demonstrate that female preference for male sexual traits is truly adaptive, it is necessary to confirm that females gain reproductive success by choosing males exhibiting such preferred traits (Johnstone 1995). It is known that blackcap *Sylvia atricapilla* males with high song rates have nests where predation risk is lower (Welling et al. 1997). However, in the bull-headed shrike, male singing tempo was not correlated with the risk of the nest predation (Supplementary material Appendix 1 Table A6). We found that females mating with males that sing at high speed raised heavy nestlings (Supplementary material Appendix 1 Table A6 and Fig. 4). Among oscines, the heavier chicks are, the higher their survival rate as fledglings (Perrins 1965, Gustafsson and Sutherland 1988, Magrath 1991). Therefore, our study results have revealed that preference for male singing tempo is truly adaptive for female bull-headed shrikes.

Singing tempo and body condition

We have established that male bull-headed shrikes in good body condition sang at high-speed (Fig. 5). Field observations of common nightingale *Luscinia megarhynchos* have shown that heavy males sang at high-speed and their song characteristics changed dynamically during the breeding season (Weiss et al. 2012). Feeding experiments have confirmed that song performance in some oscines changes dynamically in response to changes in the singer's condition (Alatalo et al. 1990, Barnett and Briskie 2007). Therefore, we suggest that tempo in the bull-headed shrike is a condition-dependent dynamic trait. Because this dynamic trait most accurately reflects the recent quality of the male, it provides the female with useful information for evaluating paternal care. Females simply benefit by mating with males in good-condition because such males are healthy and/or have genes for parasite resistance (Hamilton and Zuk 1982). It is known that in some oscines, males with well-developed song characteristics are healthy without being affected by parasites (Buchanan et al. 1999). Therefore, in the bull-headed shrike, singing tempo may serve the function of transferring information on male health and good genes to the female.

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