



Response of Male Dusky Warblers (*Phylloscopus fuscatus*) to Invaders with Different Song Length

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ABSTRACT

Aggressive signals in songbirds have received extensive attention. Several song features, such as the syllable rate, song matching, song type switching, and song overlap, are used in aggressive signalling in songbirds. However, in the territorial dusky warbler (*Phylloscopus fuscatus*), which includes trills in its song, it is unclear whether song length meets the context, prediction and response criteria of aggressive signal needs further study. We studied the responses of males to invaders with different threat levels by playing back songs of various length during the breeding season of the dusky warbler in Saihanba National Forest Park. We observed no significant differences in physical and song behaviours in male dusky warblers in response to simulated intruders with different song length. However, there was a tendency for both the physical and song behaviours of males to enhance as the song length of intruders grew. In addition, the mean song length of territorial males increased during competition with intruders, and maximum song length was positively related to a stronger song response by territorial males. Our results suggest that dusky warbler song length does not meet the response criteria for classification as an aggression signalling mechanism. However, our results suggest that song length may be an indicator of the fighting ability of male dusky warbler and may function in short-term communication.

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Authors' Contribution

JH designed the study. JW and LM performed the field experiments. SL analyzed the data. JW and LM carried out statistical analyses. JH and LM wrote the draft manuscript. All authors approved the final submission.

Key words

Acoustic communication, Song length, Territorial competition, Fighting ability, Playback

INTRODUCTION

The bird songs carry very important biological information (Kroodsma and Byers, 1991; Catchpole and Slater, 2008; Tryjanowski *et al.*, 2018; Wang *et al.*, 2022). Birdsong is divided into songs and calls. Songs are mainly made by males during the breeding season and function in attracting mates and defending territories. Conflict among animals based on competition for resources (including territory, food, and mates) is ubiquitous, and many researchers have studied vocal communication in a wide variety animal under competition for territory, including birds, frogs, and toads (Arak, 1983; Robertson, 1986; Cardoso *et al.*, 2007; Geberzahn *et al.*, 2009, 2010; Linhart *et al.*, 2012; Moseley *et al.*, 2013; Linhart and Fuchs, 2015). Songs can convey information regarding the sender's body size (Liu *et al.*, 2017), body

condition (Wang *et al.*, 2019), fighting ability (Linhart *et al.*, 2012), and threat level (Jin *et al.*, 2020). If competitors can recognise the information regarding the threat level of other individuals based on songs, they can adjust their behaviour appropriately (Searcy *et al.*, 2006; Hardouin *et al.*, 2007; Geberzahn *et al.*, 2009; Linhart *et al.*, 2012; Linhart and Fuchs, 2015), making it possible to resolve the conflict through acoustic communication, thereby reducing or avoiding harm caused by competition (Smith and Price, 1973).

Songs are multi-layered and highly flexible signals that provide information regarding the sender's probability of attacking (Searcy and Beecher, 2009). Different mechanisms may be used to signal aggression in different bird species during competition for territory. Multiple song properties, such as the syllable rate, song matching, song type switching, and song overlap, are potential aggressive signals in songbirds (Todt and Naguib, 2000; Catchpole and Slater, 2008; Searcy and Beecher, 2009; Szymkowiak and Kuczyński, 2017). However, for most presumably aggressive signals, established criteria for a signal to be aggressive are not all met (but see e.g., Naguib and Mennill, 2010). Searcy and Beecher (2009) proposed that three criteria must be satisfied for a signal to be considered aggressive. First, the signal should increase during aggression on both sides of the competition (conditional criterion). Second, the signal should predict whether the

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sender of the signal will escalate the fight (prediction criterion). Finally, the recipient should respond differently to varying signal intensities (response criterion).

Song length is a feature that can vary during competition for territory. Numerous studies have shown that song length carries important biological information for songbirds. For example, studies of willow warblers (*Phylloscopus trochilus*), bobolink (*Dolichonyx oryzivorus*), and white-crowned sparrows (*Zonotrichia leucophrys*) have shown that short songs may signal aggressive intentions (Järvi *et al.*, 1980; Capp and Searcy, 1990; Nelson and Poesel, 2012). In the great tit (*Parus major*), song length is a signal of male quality (McGregor and Horn, 1992). However, in the territorial chiffchaffs (*Phylloscopus collybita*), song length may signal its motivation to escalate conflict (Linhart *et al.*, 2012). In addition, in a non-passerine bird, the Hoopoe (*Upupa epops*), male song length is correlated with sexual selection (Martin-Vivaldi *et al.*, 1999). The roles of song length may differ among species; thus, more empirical studies are needed to verify whether song length can reliably predict male aggression during competition for territory.

The dusky warbler (*Phylloscopus fuscatus*) (Passeriformes, Sylviidae) is a small, long-distance migratory bird. The dusky warbler has a polygamous mating system, with male competition for territories largely determining social mating success, resulting in a strong territoriality throughout the breeding period of this species (Forstmeier, 2001). In addition, most of the songs of the warbler contain a trill (a continuous structure resulting from the repetition of several identical syllables) (Ivanitskii *et al.*, 2012; Liu *et al.*, 2016). Song length plays a very important role during competition for territory (McGregor and Horn, 1992), providing a basis for our analysis. In this study, synthetic sounds of different song lengths (as measured by the number of syllables) were used to simulate intruders of different threat levels, and the role of these signals in competition was verified by playback experiments. During songbird territory defence, both physical and vocal behaviours are generally employed (Gorissen *et al.*, 2006; Baldassarre *et al.*, 2016; Hill *et al.*, 2018). Therefore, we verified the role of song length of male dusky warblers in response to different invaders by observing changes in both their physical and song behaviours as well as the relationship between these behaviours. We predicted that territorial males would respond more strongly to intruders singing longer songs than to those singing shorter songs and would increase their song length during competition; additionally, we predicted that territorial males that respond with longer songs may also be more aggressive.

MATERIALS AND METHODS

Study area and species

The study area was located in Saihanba National Forest Park (42°02′–42°36′N, 116°51′–117°39′E), Chengde, Hebei Province, China. The climate in this area is quite cold, with an average annual temperature of -1.4°C , a frost-free period of 60 days, and a snowpack period of up to 7 months, and it is characterised as having a cold-temperate continental monsoon climate (Liu *et al.*, 2017).

The species studied is the dusky warbler, a small passerine bird with a single body colour. It is a migratory summer bird native to this region. It breeds annually from late May to early September, mostly in bushes, and often emits loud songs during the breeding season.

Production of playback song

A total of 11 highly clear recordings were selected from spontaneous song of dusky warblers recorded in 2016 in the study area. These 11 males were marked with coloured foot rings and were not present in the study area in 2017. We selected high-quality recordings with a duration of 10 min. The lowest and highest frequencies of dusky warblers were 1.75 ± 0.30 kHz and 7.04 ± 0.89 kHz, respectively (Liu *et al.*, 2016, 2017); thus, background noise below 1,500 Hz and above 9,000 Hz was removed. If other types of bird sounds or noise overlapped with the male dusky warbler's song, then the overlap was removed, leaving the song rate unchanged as much as possible. Next, two syllables were then copied or removed from each of the 11 sound samples, with the copied or removed syllables occurring between the second and third syllables, producing 11 playback sounds each of extended and shortened song length. The reason for copying or deleting two syllables was that the number of syllables in the spontaneous state of the dusky warbler was 6.50 ± 1.91 , with a dispersion of 2. All 33 sounds were produced using Raven Pro (version 1.4, Raven, USA), with a duration of 5 min and a volume setting close to the natural level (sound volume of approximately 80 dB at a distance of 1 m from the target) (Forstmeier and Balsby, 2002). The number of syllables produced for the playback of shortened song length was 3.97 ± 0.38 , the number of normal syllables was 5.98 ± 0.62 , and the number of syllables for extended song length was 8.10 ± 0.61 (Fig. 1). The song length of all played sounds was within the range of the natural song of the dusky warbler.

Playback experiments

In July 2017, playback experiments were conducted for 33 dusky warblers in the Saihanba area of Hebei, China, from 5:00 to 10:00 each day in good weather conditions

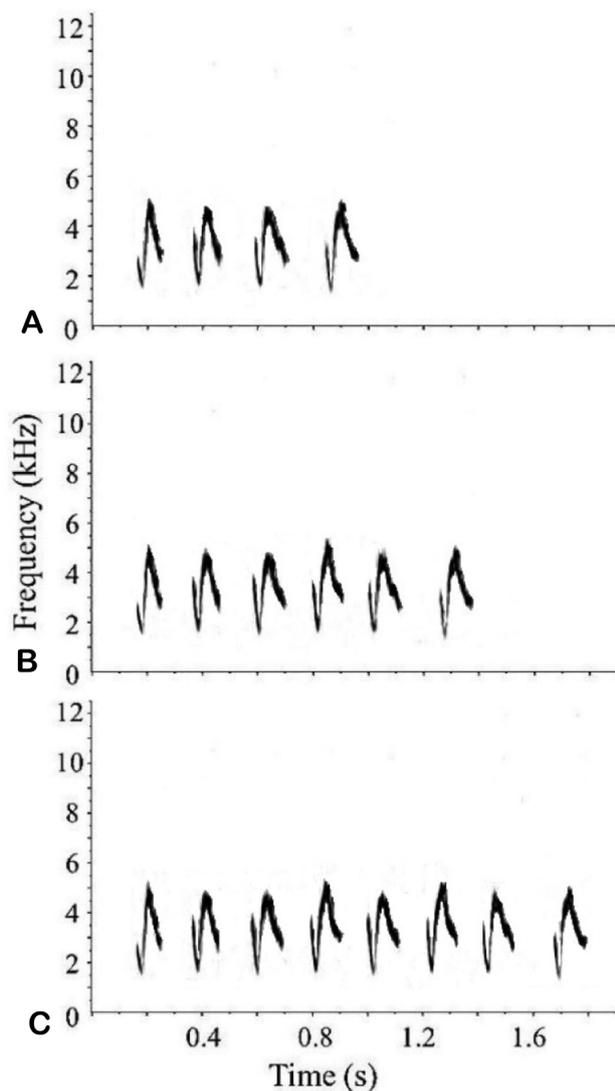


Fig. 1. Sounds with three different song length for playback. A, shortened song length; B, normal song length; C, extended song length.

(no wind or rain). The study targets were identified by song localisation. Once the study subject was identified, a Bluetooth audio player (SONY, SRS-XB2, Japan) was immediately placed in the centre of the bush where the bird was singing, and wooden sticks were used to mark a 3 m area around the bush (Funghi *et al.*, 2015). After the device was placed, the observer waited for 15 min to avoid disturbing the study subjects. The observer then concealed themselves in a secluded area 10 to 15 m away from the player and recorded the target dusky warbler's song using a portable digital recorder (Tascam, Model DR-600, Japan) and an external strong directional microphone (MKH416 P48, Sennheiser Electronic, Germany) before

playing back the sound. The sample width was set to 16 bits and the sampling frequency was set to 44.1 kHz. The recording time before playback was 5 min. One of the 33 playback sounds was randomly selected for playback, each male sound was played back once, and each playback sound was used only once. The recorded behavioural parameters were as follows: time elapsed before the bird sang (s), time elapsed before the bird moved within 3 m of the speaker (s), time elapsed before the bird flew over the speaker (s), time spent within 3 m of the speaker, number of flights over the speaker, number of songs sung, and song duration. The behavioural responses of birds were narrated verbally using a recorder while the song of the measured male bird response was recorded by the observer. Playback durations were 5 min, and neighbouring male songs were not played back on the same day. Recordings continued for 5 min after playback.

Song measurements

Sounds recorded 5 min before, 5 min during, and 5 min after the playback of dusky warbler sounds used were imported into Raven Pro to generate spectrogram for analyses. The parameters for spectrogram generation were set to fast Fourier transform (FFT length)= 256 points, Hann window (Hann window), overlap (overlap)= 50%, frequency resolution = 172 Hz, and time resolution = 2.9 ms. The mean song length (number of syllables) and maximum song length for each territorial male were recorded before, during, and after playback. Maximum song length was chosen because our previous studies of dusky warblers showed that the maxima of song characteristics are constrained by male condition (Wang *et al.*, 2019); thus, extreme values may be an important indicator for dusky warblers.

Statistical analysis

The principal components of the seven response variables were extracted for males during playback by a principal component analysis. A generalised linear mixed model was used to analyse the responses of male dusky warblers to intruders of different song length, using each of the three extracted principal components as a response variable, playback type (shortened, normal, and extended song length) as a fixed factor, and male dusky warbler identity as a random variable. Since three dusky warblers did not sing in response to playback, data for these three dusky warblers were excluded, after which mean song length, and maximum song length, were analysed as response variables. We also analysed whether the date of the experiment (setting the first day the experiment was conducted as 1) had an effect on the intensity of the male response, and found that the date of the experiment had

no significant effect on either behaviour or song (all $P > 0.05$).

Then the effect of playback on territorial male dusky warbler song length was verified; since three males did not sing during playback, data for these three males were excluded from the analysis. Subsequently, mean song length and maximum song length were used as response variables, respectively, playback stage (before, during, and after playback) as a fixed factor, and male dusky warbler identity as a random factor. Results of multiple comparisons were tested using the least significant difference (LSD) method.

In addition, the relationships between the song length of male dusky warbler during playback and response variables were evaluated using linear regression to verify whether the song length predicted aggressive responses. The statistical analysis was performed using SPSS 25.0 for Windows (IBM Inc., USA). All the data are presented as mean \pm SD, and all statistical tests were two-tailed, with a significance level of $P < 0.05$.

RESULTS

Extraction of principal components for response variables

Three principal components were extracted for the seven response variables elicited by sound playback with different song length in the tested males (Table I), explaining 93.338% of the total variance. The Kaiser-Meyer-Olkin measure of sampling adequacy was 0.544, indicating adequate sampling. The Bartlett's test of sphericity was significant: $\chi^2 = 256.323$, $df = 21$, $P < 0.001$.

The first principal component extracted from the response variables for different song length explained 40.777% of total variance, with higher values representing stronger responses (i.e., longer songs, greater number of songs sung, and shorter song latencies), and we define the

first principal component as an indicator of song response. The second principal component explained 28.782% of the total variance, with lower values representing stronger responses (i.e., shorter fly over latencies and greater number of flights), and we defined the second principal component as an indicator of flight response. The third principal component explained 23.780% of the total variance, with higher values representing stronger responses (i.e., longer dwell times within 3 m and shorter times approaching within 3 m), and we defined the third principal component as an indicator of approach response. PC 1 was the acoustic behaviour, PC 2 and PC 3 were the physical behaviours (Table I).

Response of male dusky warblers to playback type

The GLMM results showed that playback type (shortened, normal, and extended song length) did not differ significantly for male dusky warbler responses in terms of song response ($F_{2,30} = 0.378$, $P = 0.688$), flight response ($F_{2,30} = 2.265$, $P = 0.121$), or approach response ($F_{2,30} = 1.816$, $P = 0.180$). However, as the song length of intruders increased, the song response, flight response and approach response of territorial males tend to become stronger (Fig. 2).

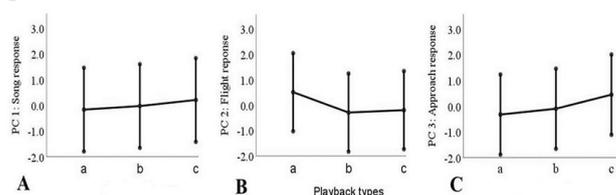


Fig. 2. Song response, flight response, and approach response of male dusky warblers to intruders with different sentence lengths. A, shortened song length; B, normal song length; C, extended song length.

Table I. Results of a principal component analysis to extract response variables during playback.

	PC1 song response	PC2 flight response	PC3 approach response
Duration of song (s)	0.980	-0.033	0.123
Time elapsed before the bird sung (s)	-0.977	0.013	-0.109
Number of songs sung	0.929	0.043	0.118
Number of flights over the speaker	0.001	-0.965	-0.016
Time elapsed before the bird flew over the speaker (s)	-0.016	0.947	0.033
Time elapsed before the bird moved within 3 m of the speaker (s)	-0.063	0.186	-0.956
Time spent within 3 m of the speaker (s)	0.269	0.386	0.842
Eigenvalue (% variance explained)	2.854 (40.777)	2.015 (28.782)	1.665 (23.780)

The three principal components with eigenvalues > 1 are shown, with bold indicating values with absolute values of loadings greater than 0.800.

In addition, we analysed the song length by territorial male dusky warblers during playback. Three dusky warblers did not sing in response to playback (two did not sing during playback of shortened song length and one did not sing during playback of normal song length); thus, we excluded data for these three warblers. The results of our analysis revealed that the playback of different song length did not have significant effects on mean song length ($F_{2,27} = 0.758, P = 0.478$) and maximum song length ($F_{2,27} = 0.223, P = 0.801$) of territorial males. However, territorial males responded to extended song length intruders with the longest song, i.e., the mean number of syllables of male dusky warblers responded to shortened song length intruders with 5.94 ± 0.92 , to normal song length intruders with 5.78 ± 0.90 ; and to extended song length with 6.24 ± 0.80 . Additionally, as the length of the replayed song is longer, maximum song length of the territorial male response tends to increase gradually ($P > 0.05$, LSD) (i.e., the maximum number of syllables of territorial male in response to shortened song length was 9.67 ± 1.73 , in response to normal song length was 9.70 ± 4.08 , and in response to extended song length was 10.55 ± 3.72).

Effect of playback on song length in territorial males

The GLMM results showed that the experimental stage (before, during, and after playback) had a significant effect on the mean song length of territorial male ($F_{2,87} = 29.100, P < 0.001$; Table II). Multiple post-hoc comparisons (LSD) showed that the mean song length of male dusky warblers before playback was significantly lower than those during playback ($t = -7.589, P < 0.001$) and after playback ($t = -3.117, P = 0.002$), and the mean song length of male dusky warblers was significantly higher during playback than after playback ($t = 4.472, P < 0.001$; Fig. 3). However, there was no significant effect of experimental stage (before, during, and after playback) on maximum song length for territorial male ($F_{2,87} = 1.867, P = 0.161$; Table II).

Table II. Generalised linear mixed model for mean song length and maximum song length in dusky warblers.

	F	df1	df2	P
Model for mean song length				
Experimental stage	29.100	2	87	< 0.001
Model for maximum song length				
Experimental stage	1.867	2	87	0.161

Prediction of behavioural responses by song length in territorial males

Mean song length had no effect on song response

($F_{1,27} = 2.776, P = 0.107$); however, the maximum song length had a significant effect on song response ($F_{1,27} = 10.102, P = 0.004$). Linear regression revealed a positive correlation between maximum song length and song response ($t = 2.783, P = 0.010$; Fig. 4), i.e., individuals with a longer song length exhibited a stronger behavioural response.

Neither mean song length ($F_{1,27} = 1.087, P = 0.306$) nor maximum sentence length ($F_{1,27} = 0.427, P = 0.519$) had a significant effect on flight response. In addition, neither mean song length ($F_{1,27} = 0.965, P = 0.335$) nor maximum sentence length ($F_{1,27} = 0.444, P = 0.511$) had a significant effect on approach response.

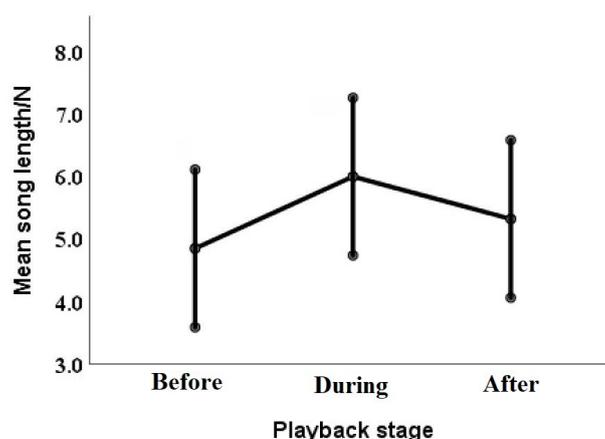


Fig. 3. Mean song length of male dusky warblers at three playback stages.

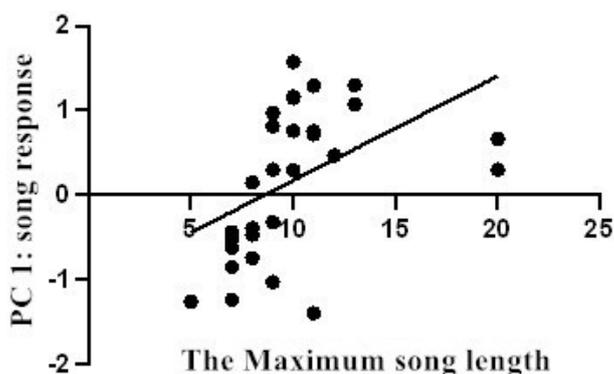


Fig. 4. The relationship between maximum song length and PC1 (song response).

DISCUSSION

The results of this study showed that physical and song behaviours of male dusky warblers did not differ in response to simulated intruders with different song length

during competition for territory; therefore, the response criteria for aggressive signals were not satisfied. However, there was a tendency for both physical and song behaviours of territorial males to increase as the length of the intruder's song increased. In addition, the song length of territorial males during competition with intruders would increase, moreover, maximum song length of territorial males is positively correlated with their song behaviour, thus satisfying both the condition and prediction criteria. Our study showed that song length is not an aggressive signal in dusky warblers.

When male territories are invaded, fighting often occurs because individuals must protect valuable resources that can be used to enhance reproductive success (Catchpole and Slater, 2008; Funghi *et al.*, 2015). Aggressive signalling is an important component of animal communication because it allows individuals to reduce or even avoid the cost of engaging in physical struggle during competition for resources (Bradbury and Vehrencamp, 2011). In this study, by playing back simulated intruders with different song length to territorial male dusky warblers, our results indicated that, contrary to our predictions, there were no differences in either the physical or song behaviours of dusky warblers in response to different intruders. Accordingly, this signal did not meet the response criteria proposed by Searcy and Beecher (2009). The lack of significant differences in the behaviour of male dusky warblers toward intruders with different song length in this study may be explained by the small differences in song length used for playback, with the maximum number of syllable was 8.10 ± 0.61 , whereas Liu (2016) found that dusky warblers spontaneously sing up to 16 syllables. Therefore, if the upper limit of the number of syllable is played back to male dusky warblers, significant responses may be observed. However, as the song length of the intruder increased, there was a tendency for territorial dusky warbler males to enhance both their song response and their flight and approach response. In agreement with the results of our study, a strongly aggressive intruder could provoke a strong response by wood warblers (*Phylloscopus sibilatrix*) (Szymkowiak and Kuczyński, 2017), and in parasitic common cuckoo (*Cuculus canorus*), males also responded much stronger to longer calls (Tryjanowski *et al.*, 2018); but some studies have shown the opposite (Illes *et al.*, 2006; Cardoso *et al.*, 2007; Cramer and Jordan, 2007; Nelson and Poesel, 2012). In addition, there was a tendency for territorial males to respond with greater song length and maximum song length as the song length of the intruder increased during competition, suggesting that territorial males may tend to match the song length of the intruder. In contrast to this result, white-browed scrubwren (*Sericornis frontalis*)

males do not match the song length of neighbouring invaders (Ansell *et al.*, 2020).

Consistent with our predictions, the condition criterion was met by territorial males emitting songs with significantly longer song length during male interactions than during spontaneous sing. Contrary to our findings, white-crowned bunting males reduce their own song length during male interactions (Nelson and Poesel, 2011, 2012). In addition, maximum song length of territorial males were positively correlated with their song behaviour, while flight and approach behaviours, which are indicators of aggressiveness (e.g. McGlothlin *et al.*, 2007; Rivera-Gutierrez *et al.*, 2011; Hardman and Dalesman, 2018), are unrelated. This may be because the highest song length of sound played back in our study were not sufficient to provoke aggressive behaviour in dusky warbler males. Forstmeier (2001) showed that male dusky warblers engage in more intense fighting when males chase each other while initially occupying territory during the breeding season, and direct physical conflict involving territory rarely occur during other periods. We conducted our experiments at a time when the dusky warblers completely occupied the territory (i.e., when the territory was quite stable); thus, the battle over priority singing may be more advantageous. However, Eurasian hoopoe males with longer song length would respond with a closer approach (Martín-Vivaldi *et al.* 1998, 2004).

Previous research has yielded two possible explanations for the stronger response to longer song length: (1) song length may be an indicator of combat ability during competition for territory (e.g. Martín-Vivaldi *et al.*, 2004; Lattin and Ritchison, 2009) or (2) song length may be a signal of short-term motivation (e.g. Balsby and Dabelsteen, 2001; Rios-Chelen and Garcia, 2007). Our previous research on dusky warblers has shown that individuals with more syllables in their songs were heavier and better physical condition (Wang *et al.*, 2019). In addition, in dusky warbler, an older and superior fighting ability male determine the outcome of territorial conflicts, suggesting that song length may be an indicator of fighting ability (Forstmeier, 2001). It is possible that males with longer song length may have a greater chance of winning during competitions. In a Eurasian hoopoe, call length was also positively correlated with fitness; (Martín-Vivaldi *et al.*, 1998, 2004). In addition, we found that playback influenced song length in male dusky warblers, and there was a tendency for song length to increase in response to intruders with longer songs; thus, song length may also indicate the short-term escalation of conflict during territorial competition.

CONCLUSIONS

In conclusion, our study showed that song length in a small songbird, the dusky warbler, did not simultaneously meet the three criteria proposed by Searcy and Beecher (2009) for classification as aggressive signals. Therefore, song length is perhaps not an aggressive signal in dusky warblers. While territorial males tend to show stronger physical and vocal responses to extended song length invaders, they increased song length during territorial competition, and individuals with greater maximum song length also had stronger song behaviours. Our previous research suggested that the number of syllables of songs were positively correlated with body weight and body condition. Thus, the results of this study combined with our previous research suggested that song length may carry signals for both combat ability and short-term motivation. Whether males with longer songs often win in territorial competitions remains to be studied.

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Statement of conflict of interest

The authors have declared no conflict of interest.

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