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大彎嘴 (*Pomatorhinus erythrocnemis*) 雄鳥 歌曲歌型對應與歌曲重疊之意義

Song type matching and overlapping in the song contests of male Black-necklaced Scimitar Babblers

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本論文係王怡茹君（R97B44011）在國立臺灣大學生態學與演化生物學研究所完成之碩士學位論文，於民國一百零一年七月三十一日承下列考試委員審查通過及口試及格，特此證明

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中文摘要

先前的研究認為，雄性鳥類歌曲的對應 (song matching) 以及歌曲重疊 (song overlapping) 是具有攻擊意味的溝通訊號，然而，關於歌曲對應與歌曲重疊兩訊號之間的相互關係卻研究的非常少。為了解兩訊號間是否存在關係，本實驗設計對雄性大彎嘴進行回播操作。首先，我們探討歌曲歌型對應 (song type matching) 或者歌曲重疊 (song overlapping) 在大彎嘴 (*Pomatorhinus erythrocnemis*) 中是否具有意義。其次，我們將兩訊號結合，探討兩訊號加疊後，攻擊意味是否會增強。最後，我們在歌曲歌型對應操作中的後半段，加入歌曲重疊，探討經由循序漸進地將此兩訊號加疊，是否能增強攻擊意味。

大彎嘴為具較強領域性的鳥種，且平均個體所擁有的歌型數適中，適宜進行回播操作。本實驗以大彎嘴為對象，於 2010 至 2011 的繁殖季，在台灣新北市烏來山區對成年雄性個體進行回播，並同時錄製它們的歌聲與紀錄行為。回播所使用的大彎嘴歌型來自新竹、雲林以及嘉義的大彎嘴個體。

結果顯示，大彎嘴雄鳥在接受歌曲歌型對應回播時，其歌間間隔時間變化幅度會增加 (P=0.011)，且停留在距離播放器 10 公尺半徑內的時間較長 (P=0.039)。雄鳥在接受歌曲重疊時，並沒有產生任何不同的反應。然而，當歌曲重疊與歌曲歌型對應同時發生時，雄鳥的歌聲變短 (P=0.030)；當歌曲歌型對應已回播一段時

間之後再加入歌曲重疊時，雄鳥會增加唱歌次數 (*P*=0.0005) 且於回播時 (*P*=0.033) 及回播後 (*P*=0.033) 停留在距離播放器 10 公尺半徑內的時間較長。

根據結果，我們做了以下結論：大彎嘴雄鳥的溝通行為中，歌曲歌型對應為一具有攻擊意味的訊號。歌曲歌型重疊只有在歌曲歌型對應同時發生；或者歌曲歌型對應已發生一段時間後加入，才為一具有攻擊意味的訊號，即歌曲歌型重疊為第二級訊號，當有必要表現出更強的攻擊意味時，才會伴隨著歌曲歌型對應出現。

關鍵字：大彎嘴、歌曲歌型對應、歌曲重疊、攻擊意味訊號、階層訊號、鳴禽

Abstract

Song type matching and song overlapping have been considered as aggressive signals in male songbirds. However, no studies have focused on the relationship between these two types of signals. To determine whether exposure to combine signaling increases aggression in songbirds, first, we evaluated the functions of song type matching and song overlapping in the Black-necklaced Scimitar Babblers (*Pomatorhinus erythrocnemis*). Second, we combined song type matching and song overlapping to examine is the combination a more aggressive signal. Lastly, we added overlapping in contest after type matching has already used for a while to examine that is song overlapping a second graded signal to escalate aggressive intention in the Black-necklaced Scimitar Babblers.

The Black-necklaced Scimitar-Babblers, which exhibits strong reaction to intruders and possessed medium sized repertoire, was chosen as our subject. In the treatments interactive playback was used for recording their singing and behavioral responses. Field experiment was conducted during the breeding seasons of 2010 and 2011 at Wulai, New Taipei City, Taiwan. Interactive songs for playback were collected in Hsinchu, Yunlin and Chiayi.

The results show that the male Black-necklaced Scimitar Babblers exhibited greater variation of song interval (*P*=0.011) and spent more time in a 10-meter circle from the speaker (*P*=0.039) when song-type matching treatments were conducted. Males did not exhibit responses that were different from control treatments compare to song overlapping treatments. However, when song overlapping and song type matching happened simultaneously, males exhibited shorter songs (*P*=0.030); when song overlapping was added in after song type matching had continued for a while, males responded stronger that they exhibited more number of songs (*P*=0.0005) and spent more time in a 10-meter circle from the speaker during playback (*P*=0.033) and post-playback period (*P*=0.033).

We conclude that in song contests of the male Black-necklaced Scimitar Babblers, song-type matching may serve as an aggressive signal. Overlapping may serve as an aggressive signal if happens with song type matching simultaneously or with song type matching continues for a while. We conclude that song overlapping is a second graded signal to escalate aggressive intention in the Black-necklaced Scimitar Babblers if necessary.

Keywords: *Pomatorhinus erythrocnemis*; song type matching; song overlapping; aggressive signal; graded signal; songbird

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Introduction

Communication plays an important role of information exchange in animals (Hauser, 1996; Bradbury & Vehrencamp, 1998). The vocal communication systems in birds have been well studied so that we could know many functions of countersinging interactions in songbirds (Searcy & Andersson, 1986; McGregor & Peake, 2000; Todt & Naguib, 2000; Searcy & Nowicki, 2005; Rindy et al., 2007; de Kort et al., 2009; Searcy & Beecher, 2009). During countersinging interactions, territorial male songbirds often use different strategies to compete with other males or to attract females (Searcy & Andersson, 1986; Naguib & Todt, 1997; Otter et al., 1999; Todt & Naguib, 2000; Peake et al., 2001; Mennill et al., 2002; Searcy & Nowicki, 2005; Searcy & Beecher, 2009). All the different strategies can be separated into two types: by changing the type of signal (pattern-specific responses) or by shifting the timing of songs (time-specific responses) to convey information between interacting individuals during song contests (Todt & Naguib, 2000).

Song matching is a pattern-specific response which occurs when one individual replies to another with the same type of signal as the signal that the other bird just sang. Evidence supports that song matching is an aggressive signal in song contests of territorial male songbirds (Krebs et al., 1981; Beecher et al., 2000b; Burt et al., 2001;

Molles & Vehrencamp, 2001; Vehrencamp, 2001; Beecher & Campbell 2005; Vehrencamp et al., 2007; Searcy & Beecher, 2009; Hsieh, 2010) There are many forms of song matching, including the matching of song types (Krebs et al., 1981; Burt et al., 2001; Molles & Vehrencamp, 2001; Vehrencamp, 2001; Vehrencamp et al., 2007; Hsieh, 2010), the matching of song repertoire (Burt et al., 2001; Molles & Vehrencamp, 2001; Beecher & Campbell 2005), the matching of strophe length (McGregor & Horn, 1992), and the matching of song frequency (Shackleton & Ratcliffe, 1994; Mennill & Ratcliffe, 2004a). Song overlapping is a time-specific response which occurs when an individual starts to sing while another has not completed its song. In other words, overlapping masks part of another individual's song which might limit the information transmiting to others. Similar to song matching, song overlapping has been hypothesized to be an aggressive signal in previous investigations (Todt, 1981; Dabelsteen et al., 1997; Naguib & Todt, 1997; Todt & Naguib, 2000; Mennill & Ratcliffe, 2004a; Naguib & Kipper, 2005; Schmidt et al., 2007). However, the function of song overlapping as a signal is still debated recently (Searcy & Beecher, 2009; Naguib & Mennill, 2010).

The functions of matching and overlapping have been examined extensively in the song contests of birds (Todt & Naguib, 2000; Searcy & Beecher, 2009). However, few studies have examined the relationship between song matching and song overlapping to see if there is any relative function between these two signals (Mennill &

Ratcliffe, 2004a). Mennill and Ratcliffe (2004a) have examined the relationship between song frequency matching and song overlapping in the Black-capped Chickadees, *Parus atricapillus*, by using interactive playback. The results showed that frequency matching and overlapping convey information independently on the male Chickadees' vocalization, which means that these two signals are two distinct functional signals of vocal interaction. However, by using Acoustic Location System, Fitzsimmons et al. (2008) have concluded that song frequency matching and song overlapping are graded aggressive displays in the Black-capped Chickadees. In the Black-capped Chickadees, overlapping functions as the first aggressive signal and frequency matching been added in the communication would escalate aggressive intention as the second aggressive signal. Results in these studies indicate that some relative functions may exist in song matching and overlapping, but we still know remarkably little about the relationship between two signals, especially in songbirds which do not use song frequency matching strategy. In this study, we evaluate the functions of song type matching and song overlapping in the Black-necklaced Scimitar Babblers (*Pomatorhinus erythrogenys*). The Black-necklaced Scimitar Babblers can sing a variation of different song types so they can choose different song type to match other male's song type, which is very different from the Black-capped Chickadees that matching by shift the song frequency. In this study, we designed experiments and expected to know if there is any relationship between song type matching and song overlapping, which has never been studied yet.

The male Black-necklaced Scimitar Babblers provides a unique system for examining the relative functions of song type matching and song overlapping because it exhibits strong reaction to intruders and it possess medium sized repertoire (<15 songs) that are not too complex as other songbirds (Price, 2011). The average repertoire size of male is seven (Chiang, 2009), and therefore they can use different song types when countersinging with others. The main structure of their songs has two notes, and the frequency range of songs can differ from 840 Hz to 2200 Hz. Besides, the male Black-necklaced Scimitar Babblers have strong territoriality. If a male intrudes and sings in the owner's territory, the territory owner will approach the intruder very fast and countersing to repel the intruder. Moreover, unlike other birds, the male Black-necklaced Scimitar Babblers rarely move with others except their own mate, so we can conduct experiments with each male separately.

To investigate the functions of song type matching and song overlapping in the Black-necklaced Scimitar Babblers, interactive playback was used to simulate an intruder in each male's territory to record the terrirory owners' vocal and behavioral responses. There are five treatments in this study (**Fig. 1**). Based on the results of earlier studies that song type matching is more aggressive than song non-matching

(Vehrencamp, 2001), we hypothesized that males treated by song type matching intruders would show more intense responses than males treated by non-matching intruders. Based on the earlier results that song overlapping is more aggressive than song non-overlapping (Todt, 1981; Naguib & Mennill, 2010), we hypothesized that males treated by song overlapping intruders would show more intense responses than males treated by non-overlapping intruders. And we also hypothesized that when song type matching and song overlapping happen simultaneously, which means that when combining these two signals, males would show more intense responses than males treated by the control treatment. Also, we hypothesized that when song type matching and overlapping happen simutaneously, males would show more intense responses than males treated by only non-matching or non-overlapping treatments. Moreover, we hypothesized that the treatment which begins with song type matching in the first half part of contest then adding song overlapping in the later half 15 minutes of contest would be more aggressive than only song type matching happens. This hypothesis is consistent with field observations of communication in the male Black-necklaced Scimitar Babblers. We have observed that males would escalate aggressive intention by adding song overlapping in contest that only song type matching was used before. Lastly, we hypothesized the treatment which beginning with song type matching in the first half part of contest, then adding song overlapping in the later half part would be more aggressive than non-song type matching happens with non-overlapping treatment.

Materials and Methods

Study areas

The study area locates in Wulai, New Taipei City, Taiwan (24° 52'N, 121° 32'W), where is located in north direction of Snow Mountain (Fig. 2). A heavy-humid subtropical climate was found in this region with rain all the year round (Chang, 2002). The annual average temperature ranges from 16.3 to 20.5 ° C and the annual average rain fall is 4600 millimeters (Yang, 1997) with elevation ranges from 150 to 460 meters. Wulai is subtropical forest with Lauraceae and Moraceae as dominant plant families (Yang, 1985). During 2009 bird survey in TounHou, 53 species were recorded which included 19 conservation species, 7 endemic species and 18 endemic subspecies (Chang et al., 2009).

Study Species

The Black-necklaced Scimitar Babblers is an endemic species in Taiwan (Collar & Robson, 2007). Its natural habitats are subtropical or tropical moist lowland forests and subtropical or tropical moist montane forests where it can line up to 2500 m. Their body size is medium (24 cm), with a fairly long, curved bill. The average repertoire size is seven per male, in other words, the average numbers of different songs a male can sing is seven (Chiang, 2009). Since song type matching has been well studied in birds that have small to moderate sized song repertoires (<15 song types) (Todt & Naguib, 2000; Catchpole & Slater, 2003), the Black-necklaced Scimitar Babblers with moderate repertoire size is suitable for studying the function of song type matching. Although male and female cannot be distinguished by their outlook, they can easily be distinguished by their totally different songs or calls. The main structure of male's songs range from one to three syllables with frequency range from 840 Hz to 2200 Hz. The Black-necklaced Scimitar Babblers have strong territoriality. A previous study has showed that territory area of the male Black-necklaced Scimitar Babblers ranged from 0.57 ha to 3.09 ha and there is no overlapping between males' territories (Chiang, 2009). If one male intrudes into another male's territory, the territory owner will approach the intruder very fast to repel the intruder by singing or approaching. The male Black-necklaced Scimitar Babblers provides a unique system for examining the relative functions of song type matching and song overlapping because it exhibits strong reaction to repel intruders and it possess medium sized repertoire. Even though the Black-necklaced Scimitar Babblers is a common species in Taiwan, however, little research has focus on it. In this study, we focused on song type matching and song overlapping strategies of the male Black-necklaced Scimitar Babblers to investigate the functions of signals.

General Methods

The interactive playback was used to simulate male as an intruder from 5:30 a.m. to 10:30 a.m. during the breeding seasons between March and early September of 2010 and 2011. In order to make sure that one individual would not receive the same treatment, the locations of all the treatments were separated at least 200 meters distance since a previous study showed that the shortest distance between two male Black-necklaced Scimitar Babblers was 150 meters (Chiang, 2009). Besides, the experimental treatments were conducted in different males' territories but were conducted at the same location to make sure that there is only one individual in one territory so that we could control the treatments which each individual received. Moreover, we checked if there is one individual's territory by playing back to measure how close the males would approach. If males have approached the speaker in 10 meter circle, we can assume that the location was the male's territory. Since we did not have the information of our subject's territories range, we cannot make sure the locations where we playing back are at the same locations of territories of different males.

To find the male Black-necklaced Scimitar Babblers for conducting field experiments, investigators patrolled with the motorcycles and tried to detect the Black-necklaced Scimitar Babblers, mainly by sounds, along the paved roads within the study areas. If a singing male was close to the road, we set our playback equipment very soon and carefully while approaching the subject as close as we can, trying to avoid disturbing the male by our approaching. If the male was not close enough to the road, we would use playback to induce it approaching the speaker. The playback equipment included one MP3 player (Philips SA2120 or FunTwist D-Chord 288), one speaker (TATUNG loudspeaker TBA-810), one 15-meter cable which connected the player and the speaker and one Black-necklaced Scimitar Babbler specimen (**Figure. 3**). The investigators hid behind a shelter, usually a large tree trunk or rock to operate the player. In 2010, if there was no male been found after we patrolled longer than 4 hours in the morning, we used playback to stimulate the male Black-necklaced Scimitar Babblers to enhance the detection rate.

Interactive Playback

We used the male Black-necklaced Scimitar Babblers' songs collected from Jiashih Township in Hsinchu County; HuBen Village in Yunlin County and LanTan in Chiayi County of Taiwan (**Figure 2.**) by Kung-Kuo Chang, Ruey-Shing Lin and myself between 2007 and 2010. Since those places are at least 50 kilometers from the study area, we can make sure that the playback stimuli created by these songs was strange songs to males in Wulai. Those songs were recorded in 16 bits at a range from 8000 to 48000 Hz sample rate. To prepare stimulus songs, we first classified all of the collected song records by investigating spectral shapes. Twenty different song types were classified (**Figure 4.**). Then we chose the most high quality sounds in each class to represent the specific song type. Later, we used GoldWave software (GoldWave Inc. version 5.55) to amplify every sound to 100 dB which is normal sound amplitude of the male Black-necklaced Scimitar Babblers in natural condition we have measured by decibel meter.

There are five treatments: (1) non-type matching and non-overlapping subject's song (2) type matching and non-overlapping the subject's song (3) non-type matching and overlapping the subject's song (4) type matching and overlapping the subject's song (5) type matching the subject's song in the first half part of playback contest, then added overlapping in the later half part of playback contest as a graded aggressive singing response. Type matching means the playback intruders produced the same type of song as the subject's song. In non-type matching treatments, we chose different type of song from the subject's song as the playback intruders. Overlapping means the playback intruder sang before the subject's song has been completed so the song would overlap the subject's. To avoid overlapping the subject's song, the playback intruder delayed singing response about 2 seconds later when subject's song has been completed, which was similar to the responses of males in natural condition in.

To make sure the same type of song as the subject's song was used in song type matching treatment in the field, sound records were checked again when we were back to the laboratory by comparing spectrum shapes using Syrinx-PC software (J. Burt, University of Washington, Seattle, U.S.A.; Mennill & Ratcliffe, 2000) and by listening again. After checking by both seeing spectrum and by listening, we could make sure that the songs we used by playing back were the same types as males songs, otherwise the non-matching data would not be used to do further analysis. To make sure we overlapped the subject's song successfully, the spectrum was checked to make sure playback's song overlap subject's song. To make sure the subject's songs were overlapped by our playback, sound records were checked again when we were back to the laboratory by seeing spectrum shapes using Syrinx-PC software. In the total 15 minutes playback period, the proportion that songs sung by the male Black-necklaced Scimitar Babblers' songs were overlapped by our songs must be over one-third, otherwise the data would not be used to do further analysis.

Playback treatments continued 15 minutes in each treatment. The fifth playback treatment was separated into two parts. Song type matching was conducted in the first 7.5 minutes, and then song overlapping was added in the later 7.5 minutes. After playback finishing, we stayed at the same location and continued to record subject's songs and behavior as the 15 minutes post-playback period.

Measuring Responses to Playback

To evaluate male singing responses, we recorded males' songs and behavior during playback and post-playback period. We used Marantz PMD 671 and PMD 660 sound recorders (Marantz Inc.) and Telinga twin-science microphone recording the Black-necklaced Scimitar-Babblers' songs in the field. Songs were recorded in 16 bits at a 44000 Hz sample rate. We used Syrinx-PC sound analysis software to reduce the background noise in 30 minutes records. We used Avisoft-SASLab Pro to analyze the males' song spectrum by automatic measurement. The parameters we measured were (1) total number of songs, (2) number of song type switching, (3) number of song type, (4) song length average, (5) song length coefficient of variation, (6) song interval length and (7) song interval length coefficient of variation (**Fig. 5**).

To evaluate males' behavioral responses, we record the subject's distance from speaker. We judged the distance by seeing the subjects directly or by hearing their songs. Distance was separated into two categories: less than 10 meters from speaker and over 10 meters from speaker. We also recorded the time they spent in each category, then we transfer data into (1) proportion of playback period spent less than 10 meters from the speaker and (2) proportion of post-playback period spent less than 10 meters from the speaker. Moreover, we recorded subject's (3) number of passes over and (4) closest approach distance during the whole 30 minutes playback and post-playback period.

We gave 51 playback trials to 26 male Black-necklaced Scimitar Babblers between 2010 and 2011. On average, each individual received two different playback treatments. None of them received the same playback treatment more than once. To avoid males would weary with playback, the interval between treatments for each individual was at least one week long. The responses of the same males intrigued by different treatments were assumed independent.

Statistical Approach

According to our hypotheses, we tested seven singing parameters and four behavioral parameters to see is there any difference between: (1) non-matching plus non-overlapping treatment and matching plus non-overlapping treatment. (2) non-matching plus non-overlapping treatment and non-matching plus overlapping treatment. (3) non-matching plus non-overlapping treatment and matching plus overlapping treatment. (4) matching plus non-overlapping treatment and matching plus overlapping treatment. (5) non-matching plus overlapping treatment and matching plus overlapping treatment. (6) non-matching plus non-overlapping treatment and matching then added overlapping in the later 15 minutes treatment. (7) matching plus non-overlapping treatment and matching then added overlapping in the later 15 minutes treatment.

Statistical analyses were performed using the SPSS statistics package (version 20). First, we test if our data fit the assumption of parametric analysis. The result showed that data does not fit normal distribution, which means data does not fit the assumption of parametric analysis. Because of the reason, we used non-parametric Kruskal-Wallis One-Tail Test to analyze data.

Results

Male Singing Responses

Results showed that subjects who received song type matching treatments gave significantly greater coefficient of variation of song interval (*P*=0.011) (**Fig. 6g, Table 1.**). Subjects who received overlapping treatments did not exhibit any significant differences in singing responses (**Fig. 6, Table 1.**). Subjects who received song type matching plus overlapping treatment exhibited significant shorter average song length (*P*=0.030) when compared with non-song type matching plus non-overlapping treatment (**Fig. 6d, Table 1.**). Subjects who received song type matching plus overlapping treatment did not exhibit any significant differences in singing responses when compared with song type matching plus non-overlapping treatment or non-song type matching plus overlapping treatment (**Fig. 6, Table 1.**). Subjects who received type matching in the first half part and then added overlapping in the later half part did not exhibit any significant differences in singing responses when compared with non-song type matching plus non-overlapping treatment (**Fig. 8, Table 1.**). Subjects who received type matching in the first half part and then added overlapping in the later half part exhibited significant more songs when compared with song type matching plus non-overlapping treatment (*P*=0.0005) (**Fig. 8a, Table 1.**).

In summary, subjects' singing responses were influenced by intruder song type matching where subjects exhibited greater variation of song interval. Moreover, subjects' singing responses were also influenced by intruder which combined song type matching and song overlapping: subjects were influenced by intruder song type matching plus song overlapping where subjects exhibited shorter song; subjects were also influenced by intruder song type matching in the first half part then overlapping added in the later half part where subjects increased their number of songs.

Male Behavioral Responses

The results show that subjects who received song type matching treatments spent less time staying outside 10-meter circle during post-playback period (*P*=0.039) (**Fig. 7b, Table 2**). Subjects who received overlapping treatments did not exhibit any significant differences in behavioral responses (**Fig. 7, Table 2.**). Subjects who received song type matching plus overlapping treatment did not exhibit any significant differences in behavioral responses when either compared with non-song type matching plus non-overlapping treatment (**Fig. 7, Table 2.**), song type matching plus non-overlapping treatment (**Fig. 7, Table 2.**), or non-song type matching plus overlapping treatment (**Fig. 7, Table 2.**). Subjects who received song type matching in the first half part and then added overlapping in the later half part spent more time staying inside 10-meter circle during post-playback period (*P*=0.033) (**Fig. 9a, Table 2.**), and during post-playback period (*P*=0.033) (**Fig. 9b, Table 2.**) when compared with non-song type matching plus non-overlapping treatment. Subjects who received type matching in the first half part and then added overlapping in the later half part did not exhibit any significant differences in behavioral responses when compared with song type matching plus non-overlapping treatment.

In summary, subjects' behavioral responses were influenced by song type matching intruder where subjects spent more time in 10-meter circle from the speaker during post-playback period. Subjects' behavioral responses were also influenced by intruder who type matching in the first half part and then added overlapping in the later half part where subjects spent more time in 10-meter circle from the speaker during both playback and post-playback period.

Discussion

Our study provides a prospective view of the relationship between song type matching and song overlapping, especially in birds which can sing a variety of songs. The responses of the male Black-necklaced Scimitar Babblers to territorial intruders varied with song type matching and song overlapping strategies of the intruders. Males gave more variable song interval during song contests with song type matching versus non song type matching intruders, in other words, they changed their song rhymes more frequently in contests with a song type matching opponent. Males also behaved different responses that they spent more time close to opponents toward song type matching intruders versus non song type matching intruders. Males did not give more song performances or behaved differently in contests with song overlapping intruders, however, when intruders used strategy which combining song overlapping and song type matching, males showed distinct responses. When intruders used song type matching and overlapping strategies simultaneously, males gave shorter songs during song contests comparing with non-song type matching plus non song overlapping intruders. When intruders used song type matching strategy firstly and then added in song overlapping strategy with song type matching simultaneously lately, males gave more songs comparing with song type matching intruders. Males also behaved different responses that they spent more time close to opponents comparing with non-song type matching plus non-song overlapping intruders during both playback and post-playback period. In conclusion, males' responses to interactive playback treatments demonstrate that song type matching conveys information; song overlapping only conveys information when happening with song type matching simultaneously or when song type matching has already used for a while.

The male Black-necklaced Scimitar Babblers tended to response to song type matching intruders with more highly aggression. The results support our hypothesis that males treated by song type matching intruders would show more intense responses than males treated by non-matching intruders. Intense responses aroused from song type matching opponents were manifested most obviously in males' staying longer close to opponents during post-playback and changing singing rhythm more frequently. Song type matching arouses similar levels of responses in other bird species. The Banded Wrens, *Thryothorus pleurostictus*, the Great Tits, *Parus major*, and the Song Sparrows, *Melospiza melodia*, stay longer close to the speaker when aroused by song type matching strategy during playback and post-playback (Krebs et al, 1981; Vehrencamp, 2001; Vehrencamp et al., 2007). Strong approach increases the risk of being attacked and also increases the risk of fighting. Interactions by using matching signal associated with the highest probability of aggression and will escalate aggressive level to more threatening (Krebs et al., 1981; Burt et al., 2001; Molles & Vehrencamp, 2001; Vehrencamp, 2001; Vehrencamp et al., 2007; Searcy & Beecher, 2009; Hsieh, 2010). The Black-capped Chickadees gave higher variability of song interval aroused by song type matching strategy during playback period (Mennill & Ratcliffe, 2004a). However, there is no other investigations measured the variation of song interval when conducted matching treatments; instead, this parameter was mostly measured and used to explain the results in conducting song overlapping strategy. Since our result showed that song type matching significantly aroused more variation of song interval in songbird, we suggest that more investigations of song type matching with measuring variation of song interval are needed in the future. It seems possible that singing with changing rhythm frequently can avoid songs being type matching by intruders or even can type match the intruder's song instead. Song type matching has been considered a signal used to show aggressive intent (Beecher et al., 2000b), directing individuals (Todt & Naguib, 2000), or an index signal which allows participants of interaction or bystanders to assess the signal quality and to judge singer's quality (Logue & Forstmeier, 2008). Song type matching also has been shown to serve as a conventional signal of aggressive intentions (Molles & Vehrencamp 2001; Vehrencamp 2001) in songbirds. Our results support that song type matching is a signal which can exhibit aggressive intent during communication and also serves as a conventional signal of aggressive intentions.

Since the male Black-necklaced Scimitar Babblers did not response to song overlapping intruders with significantly higher aggression, our results do not support the hypothesis that song overlapping intruders would arouse more aggressive responses. In previous studies overlapping has been hypothesized that it serves as an aggressive signal (Todt, 1981; Dabelsteen et al., 1997; Naguib & Todt, 1997; Todt & Naguib, 2000; Mennill & Ratcliffe, 2004a; Naguib & Kipper, 2006; Schmidt et al., 2007), however, there is still some controversy among scientists. Searcy & Beecher (2009) have another opinion with overlapping that in their review they concluded there is little evidence that overlapping is associated with aggressive responses since there are also many results showed overlapping does not coincide with aggressive responses (Dabelsteen et al., 1996; Dabelsteen et al., 1997; Mennill & Ratcliffe, 2004a; Hall et al., 2006; Vehrencamp et al., 2007). On the other hand, males' responses to song overlapping are more ambiguous than males' responses to other signals. Naguib & Mennill (2010) hold a contrary opinion to Searcy & Beecher's reviewing conclusion about song overlapping. They pointed out that most studies showed birds changed towards more intense singing and approach to the overlapping intruders. The function of song overlapping still remains uncertain and needs more investigations to provide more clearer understandings. In conclusion, song overlapping is not an aggressive signal in the male Black-necklaced Scimitar Babblers and we suggest that more studies are needed for understanding the function of overlapping in bird's song contest.

The male Black-necklaced Scimitar Babblers tended to response to intruders who combined song type matching and song overlapping strategies with more highly aggression. Our results support our hypothesis that males treated by song type matching plus song overlapping intruders would exhibit more intense responses than males treated by non-matching plus non-overlapping intruders or treated by matching intruders. Intense responses were manifested most obviously in males' shortened songs. In the Black-capped chickadees and the Nightingales, males shortened their songs when overlapped by intruders (Hultsch & Todt, 1982; Mennill & Ratcliffe, 2004a). It seems possible that shortening songs can avoid songs being overlapped by opponents' songs and thus can protect information they want to convey in their songs s. Moreover, results also give strong support for our hypothesis that males treated by song type matching happened first then overlapping added in the later part would exhibit more intense responses than males treated by non-matching plus non-overlapping intruders or treated by only matching intruders. Intense responses were manifested obviously in males' singing more songs and staying longer close to opponents during both playback and post-playback period. In the Great tits, males also sing more songs when aroused by song type matching signal (Krebs et al., 1981). Singing more songs is possible a way to show aggressive intention to repel intruders while staying closer distance trying to repel the intruder. In our results we can see: when overlapping was added in the later part, males showed more significant responses in both singing and behavioral responses than overlapping happened with song type matching simultaneously. We conclude that song overlapping signal is with function when happens with or after song type matching and serves as stronger aggressive signal when happens after song type matching. The reason why using two strategies serves as a more aggressive signal is probably because that it requires rapider neural integration to response thus males which can use both strategies pretend to be more intelligent. From our results, we can see that when song overlapping happened after song type matching to serve as the second graded signal, males' responses would be aroused with more significantly aggression than song overlapping happened with song type matching simultaneously. Graded aggressive displays also exist in other bird species. In the Black-capped Chickadees, matching and overlapping serve as graded signals that overlapping is the first aggressive response and matching is the second aggressive response (Fitzsimmons et al., 2008), beginning with overlapping and escalating to matching if necessary in graded contest escalation. This communication strategy is totally contrast with the strategy we found in the Black-necklaced Scimitar Babblers that song type matching is the first aggressive responses and overlapping is the second aggressive response. In the studies of graded signals, the non-matching, repertoire matching and song type matching system has been studied as graded aggressive signals in the Song Sparrows and the Banded Wrens (Burt et al., 2001; Molles & Vehrencamp, 2001). In the Common Nightingales (*Luscinia megarhynchos*), song type matching and song overlapping function very similarly as graded signals that they use higher levels of song type matching in their first breeding season and then song overlapping in their second breeding season (Sarah et al., 2011). Since we still understand very little about the relationship between matching and overlapping, our study provides a valuable perspective on the relationship between these two signals.

In our experiment design, we simply separated 15 minutes into 7.5 minutes and 7.5 minutes and then addied overlapping in the later 7.5 minutes to mimic graded signal. However, this is not the best idea for mimicking the natural condition of communication between two male Black-necklaced Scimitar Babblers. In natural condition, males would add in the second graded signal after the first graded signal when two males approach each other very closely while already communicated for a while by using song type matching. Since we did not consider the distant between two males when adding the second graded signal, it might be a reason that the males' responses were not strong enough as our expectation.

In our study, we measured the number of pass over and closest approach distance as parameters to represent behavioral responses, however, male Black-necklaced

Scimitar Babblers did not show any significant differences when comparing between different treatments. It might be possible because in our observation when males were aroused by playback intruders, males would try to approach the speaker, however, males seldom flight through the speaker directly but mostly circled around the speaker instead. It is possible the reason why the number of pass over did not show significant different when comparing different treatments since males circled around instead flight through the speaker directly. Moreover, we have never seen the males attacked our specimen when conducted the field playback experiment. Males aroused by our playback would approach the specimen, however, since our specimen did not move as normal birds, it is very possible that males felt abnormal with the intruder so gave up the attacking intention. In other laboratory, a robot bird were invented which can operate by remote control to mimic a real bird. The robot bird was designed by hiding remote control car within a box which a bird specimen was put on. Since it is not so difficult for making a robot bird, we suggest that next similar experiment can try to use a robot bird as an intruder to arouse males' stronger responses.

In summary, our results reveal that the male Black-necklaced Scimitar Babblers can use both song type matching and song overlapping strategies to interact with other males. Song matching is a meaningful signal of aggressive intentions; song overlapping is meaningful only when it combines with song type matching. It is more possible that song overlapping strategy serves as the second graded signal to escalate aggressive intention after song type matching in the male Black-necklaced Scimitar Babblers, which consists with our nature observation.

Since our study is based on playback experiment, further research into naturally occurring contests is suggested. Moreover, more studies are still needed so that we could know more about the communication system of the Black-necklaced Scimitar Babblers to build accurate models of dynamic signal behaviors.

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Tables

Table 1. Seven singing responses of the male Black-necklaced Scimitar Babblers (*Pomatorhinus erythrocnemis*). *P*-value based on non-parametric Kruskal-Wallis One-tail Test.

		Parameters representing singing responses						
Comparing Two Treatments		Number of songs	Number of song type switching	Number of song types	Song length average (s)	Song length coefficient of variation	Song interval length	Song interval length coefficient of variation
No match No overlap	Match No overlap	0.131	0.086	0.086	0.093	0.348	0.278	0.011*
No match No overlap	No match Overlap	0.466	0.370	0.241	0.303	0.303	0.365	0.466
No match No overlap	Match Overlap	0.150	0.348	0.463	0.030*	0.337	0.482	0.161
Match No overlap	Match Overlap	0.268	0.285	0.273	0.222	0.357	0.263	0.379
No match Overlap	Match Overlap	0.087	0.449	0.308	0.500	0.409	0.500	0.379
No match No overlap	Match Overlap in later	0.057	0.484	0.101	0.134	0.168	0.119	0.070
Match No overlap	Match Overlap in later	0.0005*	0.125	0.483	0.268	0.235	0.419	0.105

Table 2. Four behavioral responses of the male Black-necklaced Scimitar Babblers (*Pomatorhinus erythrocnemis*). *P*-value based on non-parametric Kruskal-Wallis One-tail Test.

Comparing Two Treatments		Parameters representing behavioral responses: < 10m proportion (%)	< 10m proportion (%) post-playback	Number of pass over	Closest approach distance (m)
No match No overlap	Match No overlap	0.074	0.039*	0.329	0.390
No match No overlap	No match Overlap	0.109	0.083	0.449	0.249
No match No overlap	Match Overlap	0.209	0.182	0.390	0.235
Match No overlap	Match Overlap	0.322	0.469	0.213	0.370
No match Overlap	Match Overlap	0.235	0.444	0.444	0.370
No match No overlap	Match Overlap in later	0.033*	0.033*	0.500	0.312
Match No overlap	Match Overlap in later	0.324	0.216	0.355	0.268

Figures

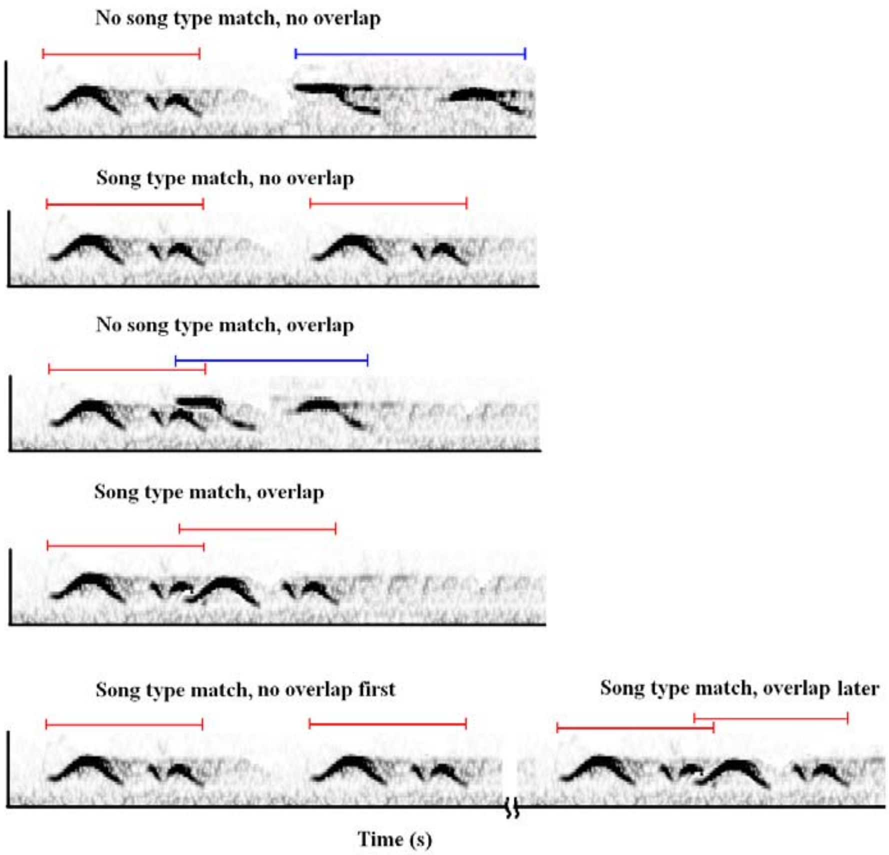


Figure. 1 Sound spectrum of the male Black-necklaced Scrimitar Babblers (*Pomatorhinus erythrocnemis*) for five interactive playback treatments. To type match the subject's song, the playback intruder produced the same type of song as the subject's song. To avoid type matching the subject's song, the playback intruder produced different type of song as the subject's song. To overlap the subject's song, the playback intruder sang before the subject's song was complete. To avoid overlapping the subject's song, the playback intruder delayed singing response and start singing in the silent interval. To overlap the subject as a graded aggressive singing response, the fifth treatment began with song type matching in the first half part of contest, and then overlapping was added in the later half of contest.

Figure. 2 The red circle is the location of study area. The study area located in Wulai, New Taipei City, Taiwan (24° 52’N, 121° 32’W). The red stars are locations where playback songs came from. From top to bottom the places are Hsinchu County, Yunlin County and Chiayi County.

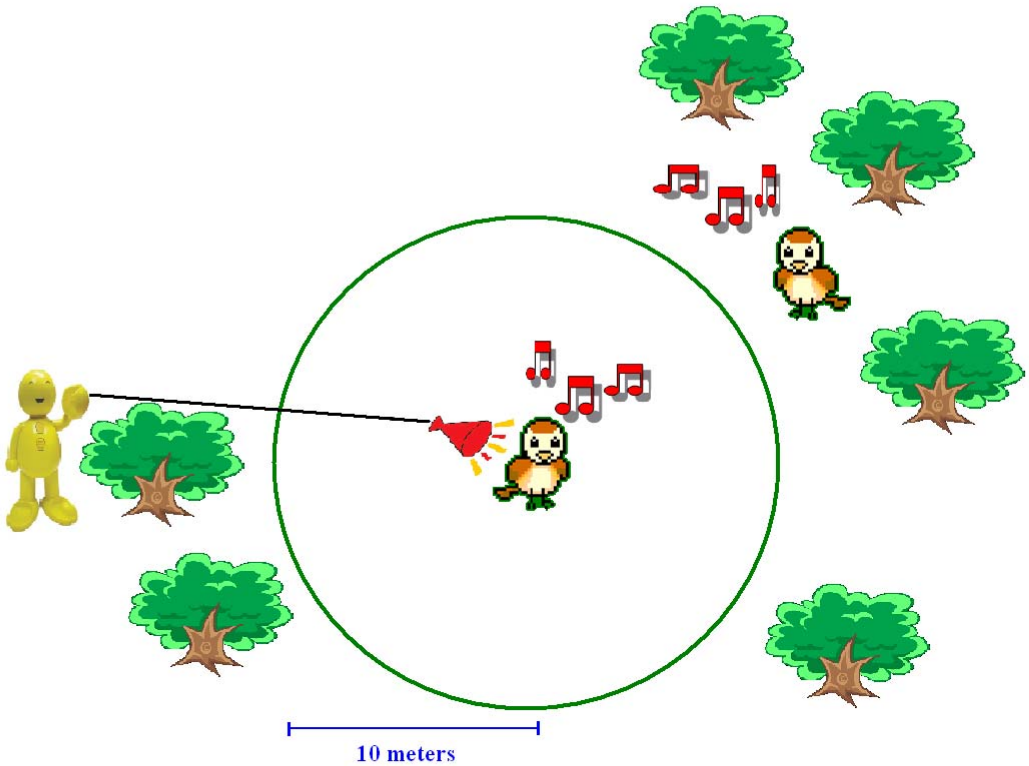
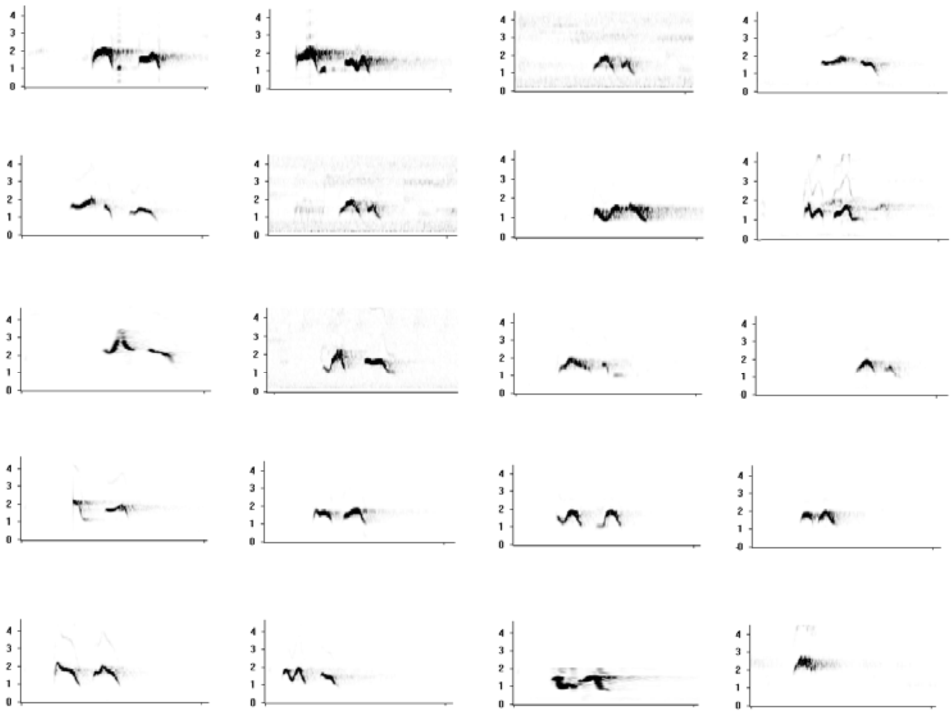


Figure. 3 The speaker was hided beside our bird specimen and connected with MP3 player by 15-meter cable. MP3 player was operated by the investigators hid behind a shelter. Meanwhile, investigators recorded their songs and behavior to evaluate their responses.



Time (s)

Figure. 4 Twenty different song types of the male Black-necklaced Scrimitar Babblers (*Pomatorhinus erythrocnemis*) were classified from sound records collected from Jiashih Township in Hsinchu County, HuBen Village in Yunlin County and LanTan in Chiayi County of Taiwan between 2007 and 2010. Those songs were used to create playback stimuli as stranger intruders to male Black-necklaced Scimitar Babblers in Wulai.

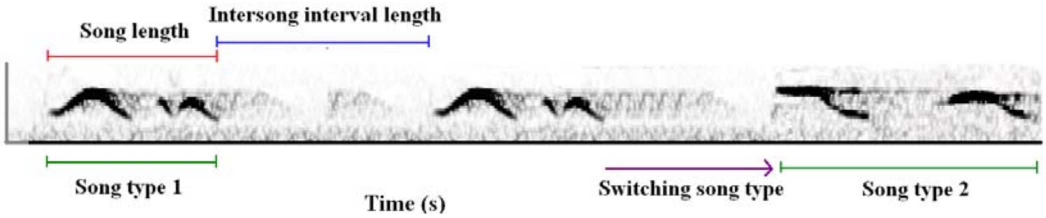
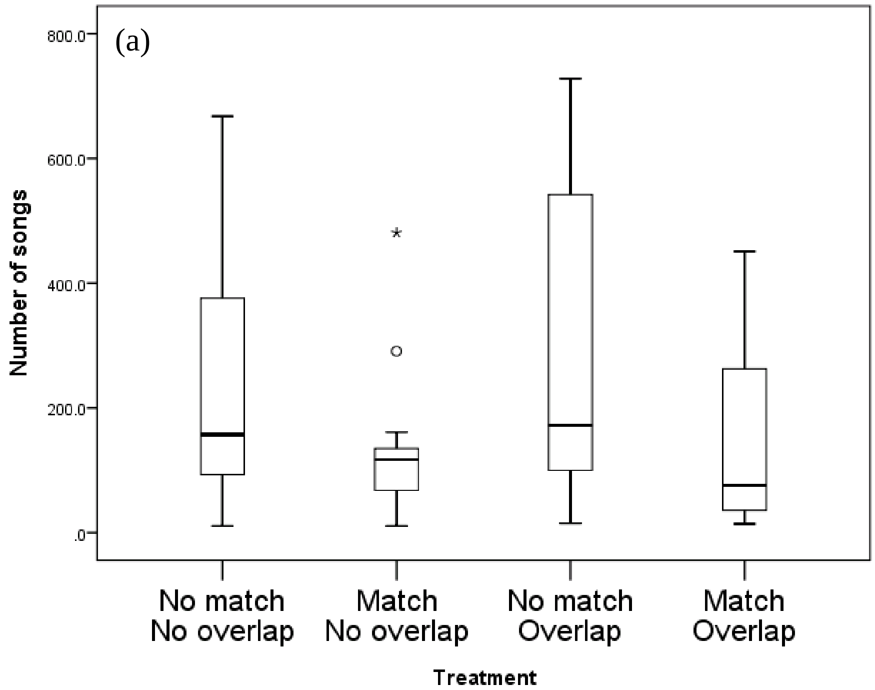
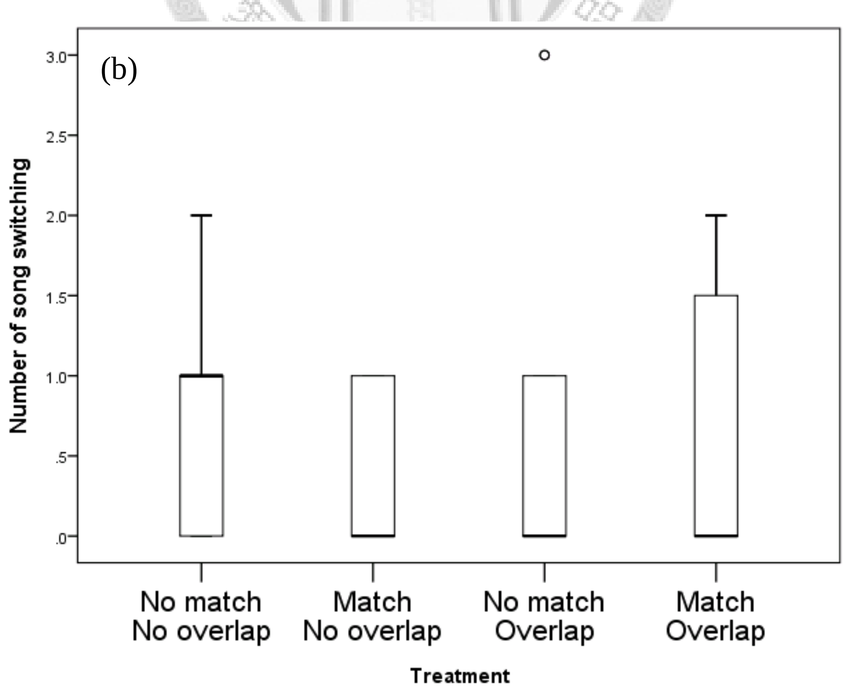
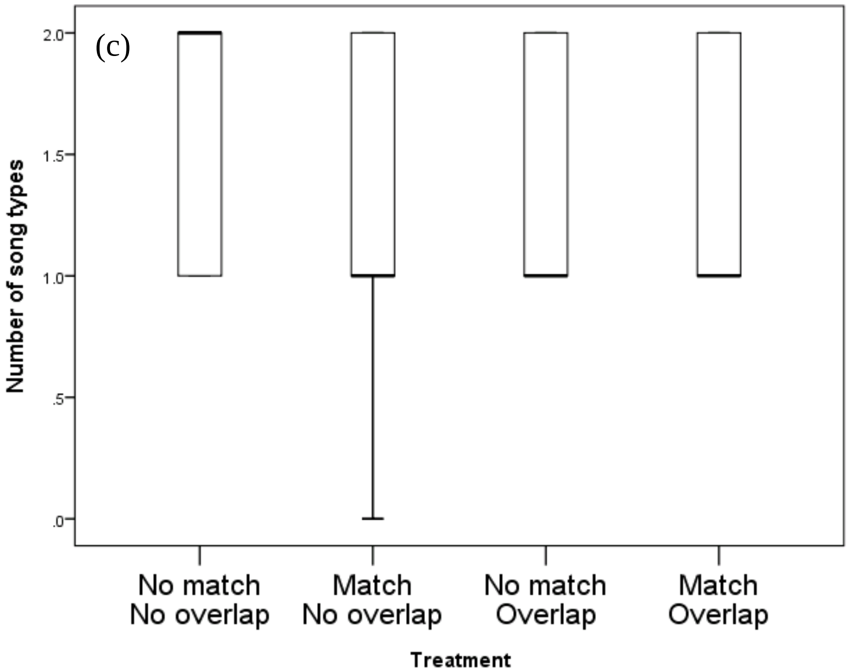
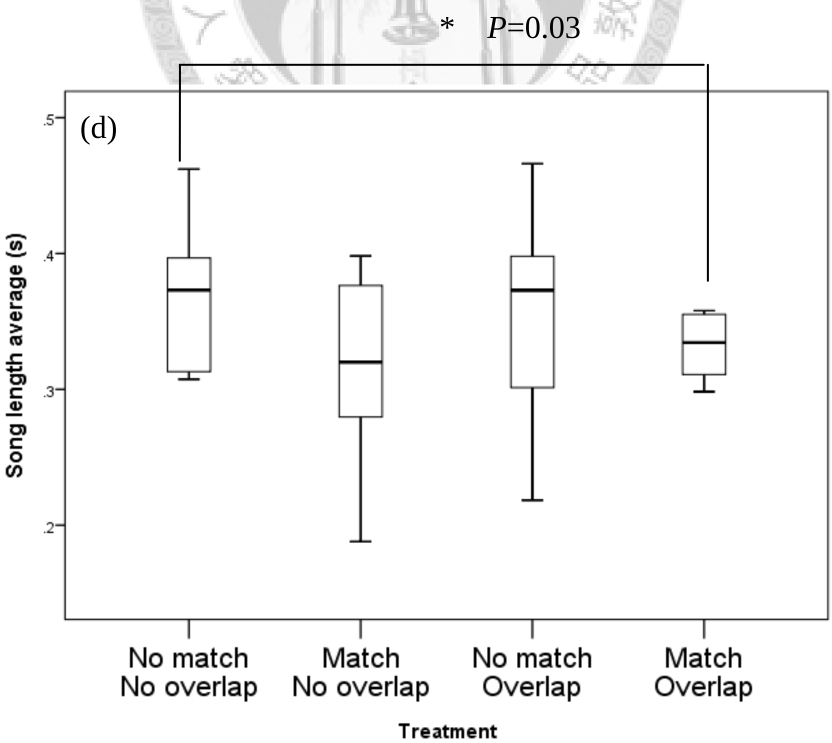


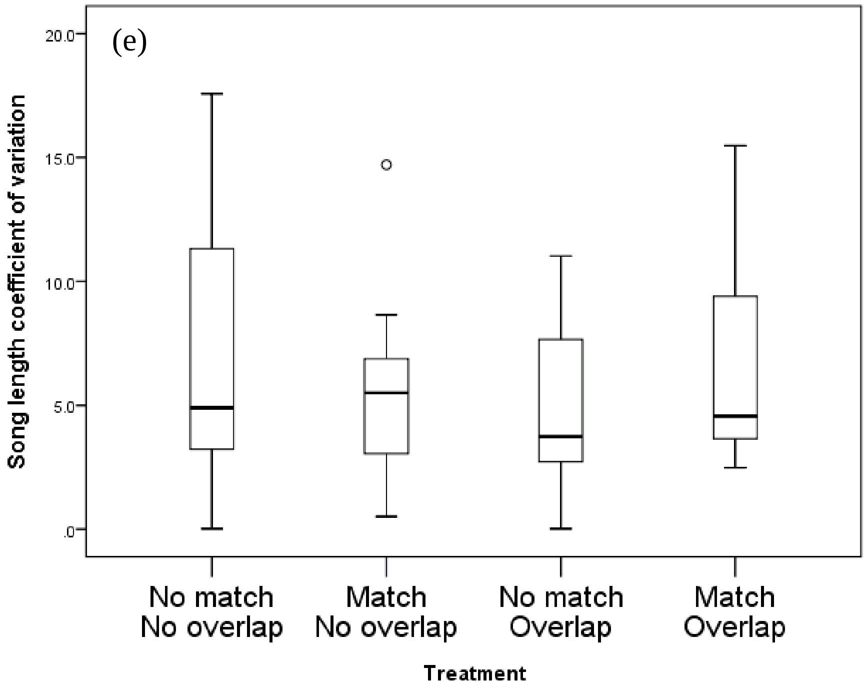
Figure. 5 To represent singing responses, some parameters were measured in male Black-necklaced Scimitar Babblers' song spectrum including: (1) total number of songs, (2) number of song type switching, (3) number of song types, (4) song length, and (5) intersong interval length.

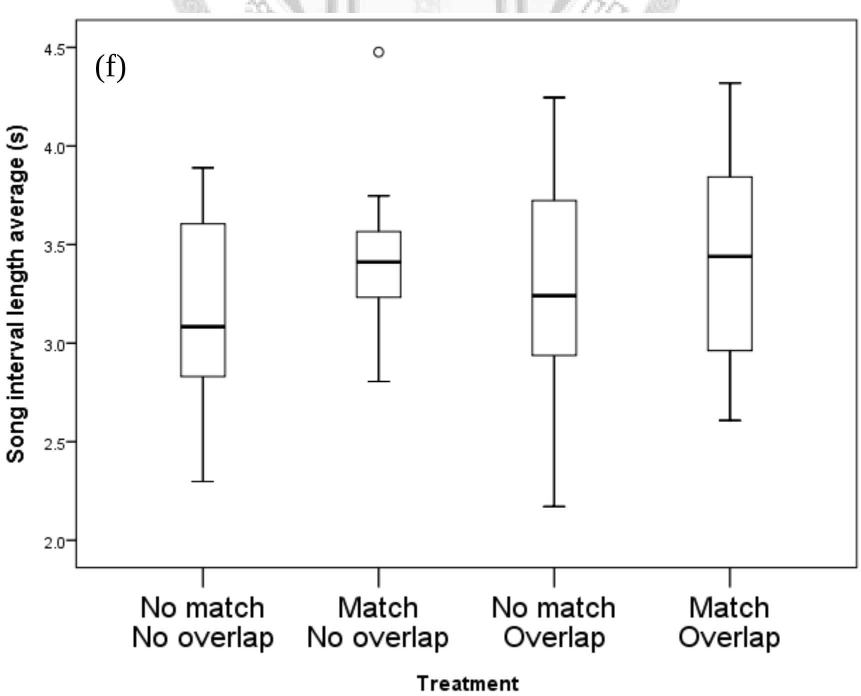

(a)
800.0
600.0
400.0
200.0
.0
Number of songs
No match No overlap
Match No overlap
No match Overlap
Match Overlap
Treatment


(b)
3.0
2.5
2.0
1.5
1.0
.5
.0
Number of song switching
No match No overlap
Match No overlap
No match Overlap
Match Overlap
Treatment


(c)
2.0
1.5
1.0
.5
.0
Number of song types
No match
No overlap
Match
No overlap
No match
Overlap
Match
Overlap
Treatment


* P=0.03
(d)
.5
.4
.3
.2
Song length average (s)
No match
No overlap
Match
No overlap
No match
Overlap
Match
Overlap
Treatment


(e)
20.0
15.0
10.0
5.0
.0
Song length coefficient of variation
No match
No overlap
Match
No overlap
No match
Overlap
Match
Overlap
Treatment


(f)
4.5
4.0
3.5
3.0
2.5
2.0
Song interval length average (s)
No match
No overlap
Match
No overlap
No match
Overlap
Match
Overlap
Treatment

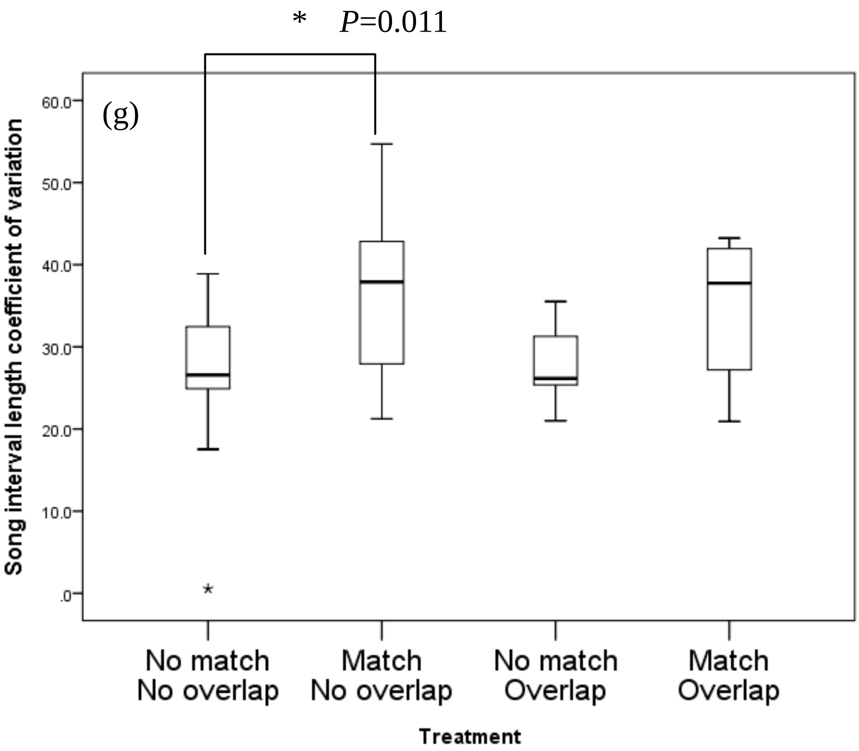
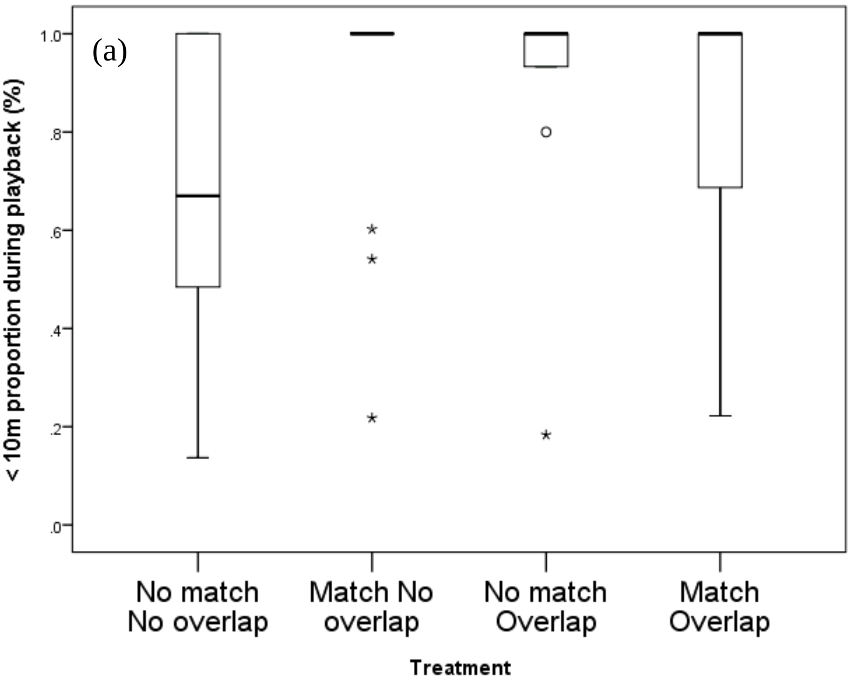
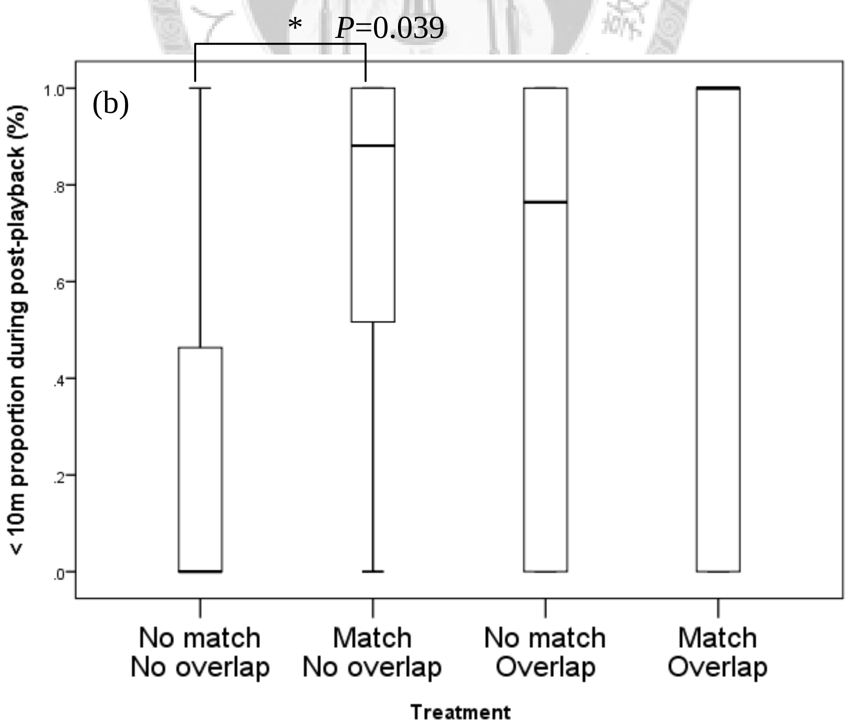
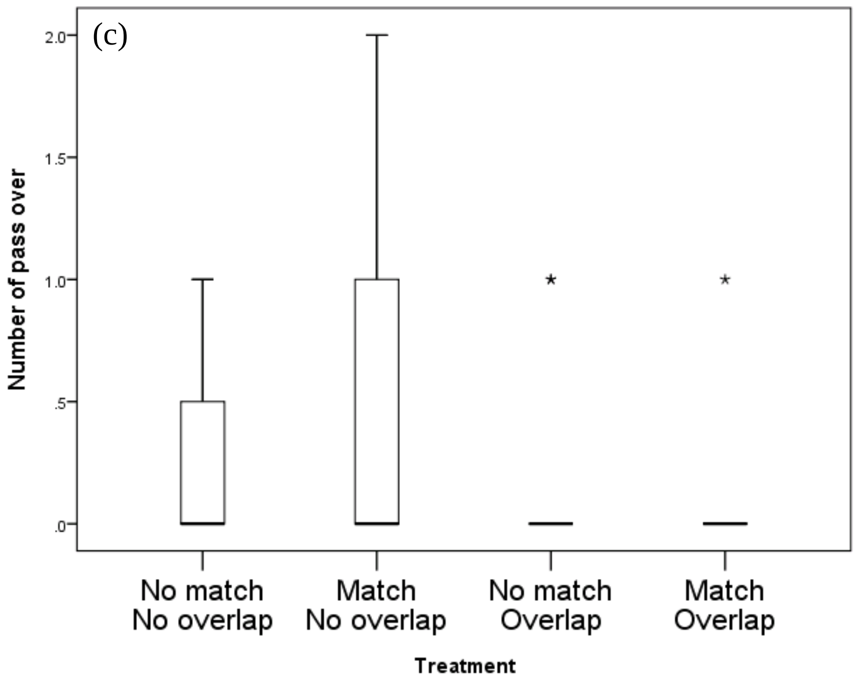


Figure. 6 The influence of four interactive playback treatments on the singing responses of the male Black-necklaced Scimitar Babblers: (a) number of songs; (b) number of song type switching; (c) number of song types; (d) song length average; (e) song length coefficient of variation; (f) song interval length average and (g) song interval length coefficient of variation. Non-parametric Kruskal-Wallis one-tail Test was used. The dots are outliers and the stars are extreme outliers.


(a)
1.0
.8
.6
.4
.2
.0
< 10m proportion during playback (%)
No match
No overlap
Match No
overlap
No match
Overlap
Match
Overlap
Treatment


* P=0.039
(b)
1.0
.8
.6
.4
.2
.0
< 10m proportion during post-playback (%)
No match
No overlap
Match
No overlap
No match
Overlap
Match
Overlap
Treatment


(c)
2.0
1.5
1.0
.5
.0
Number of pass over
No match
No overlap
Match
No overlap
No match
Overlap
Match
Overlap
Treatment

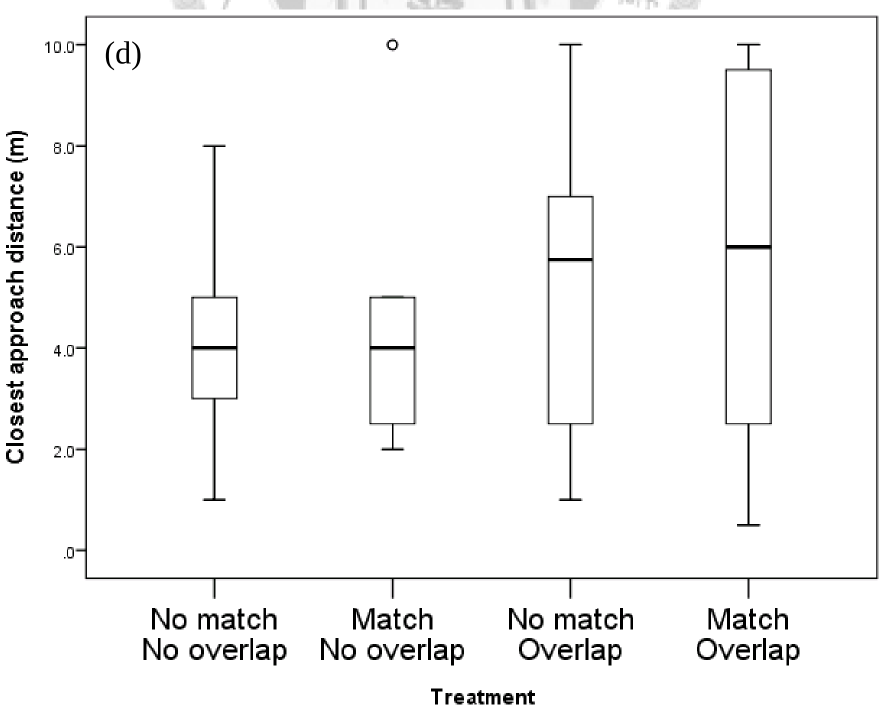
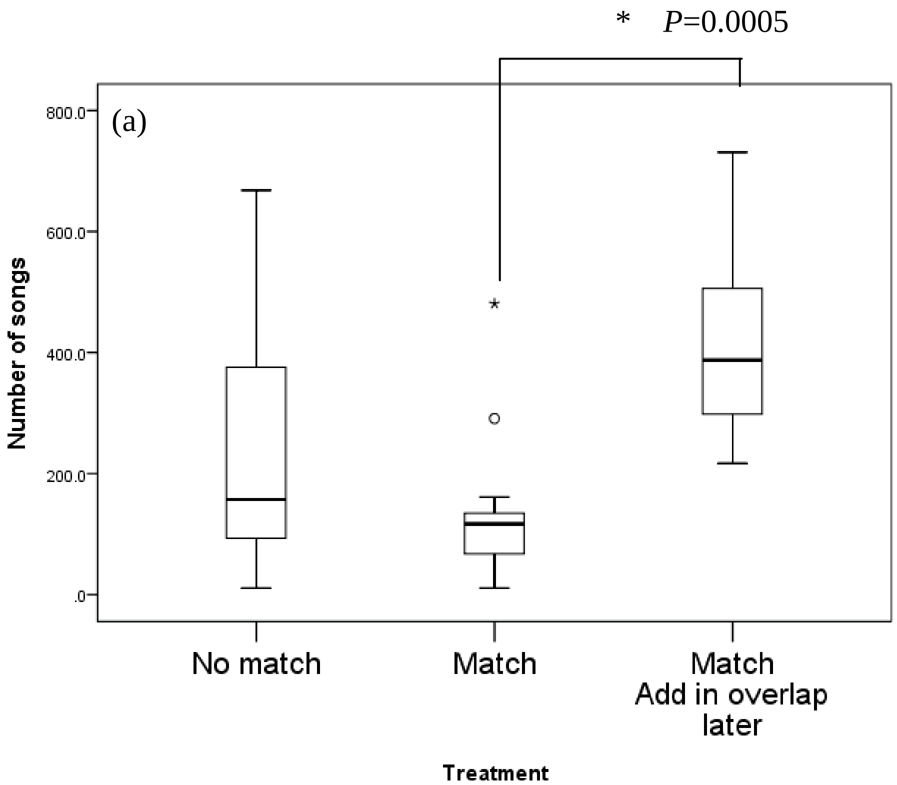
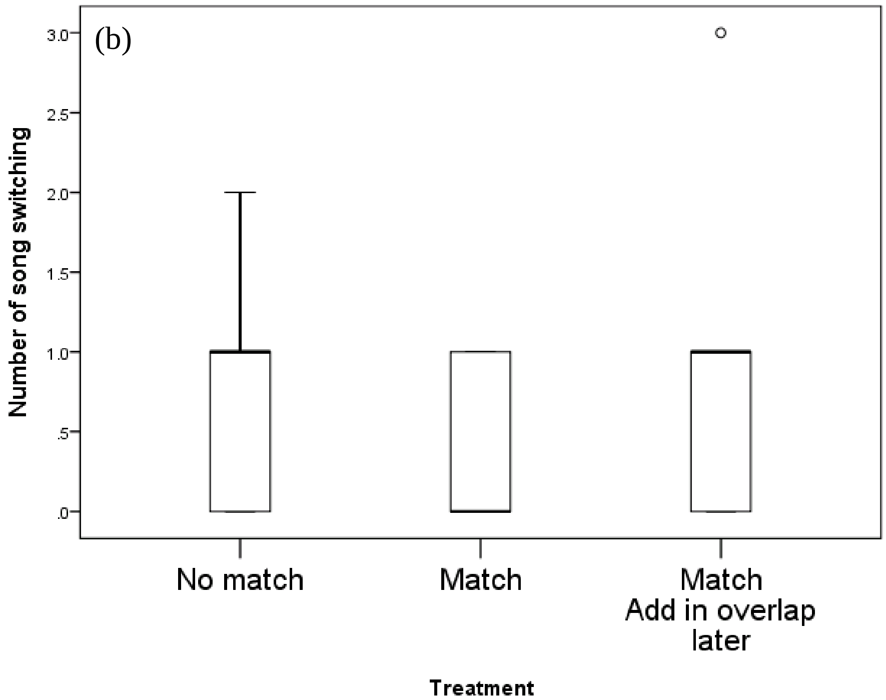
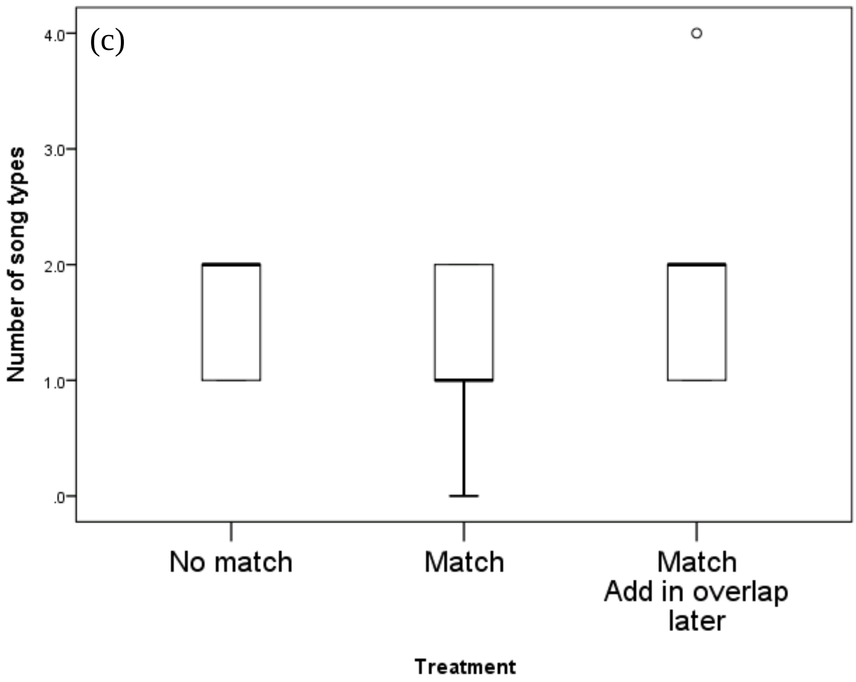
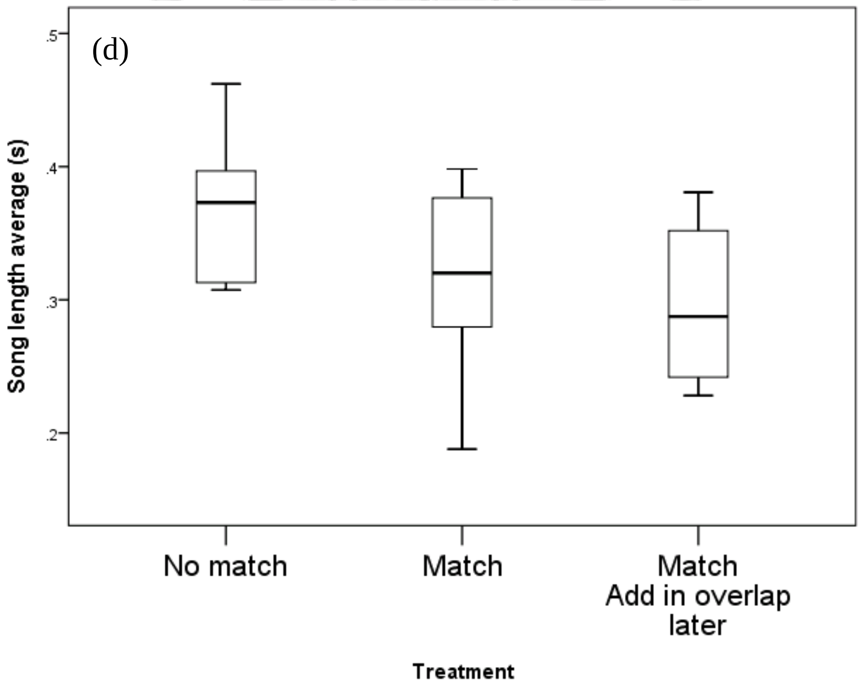

(d)
10.0
8.0
6.0
4.0
2.0
.0
Closest approach distance (m)
No match
No overlap
Match
No overlap
No match
Overlap
Match
Overlap
Treatment

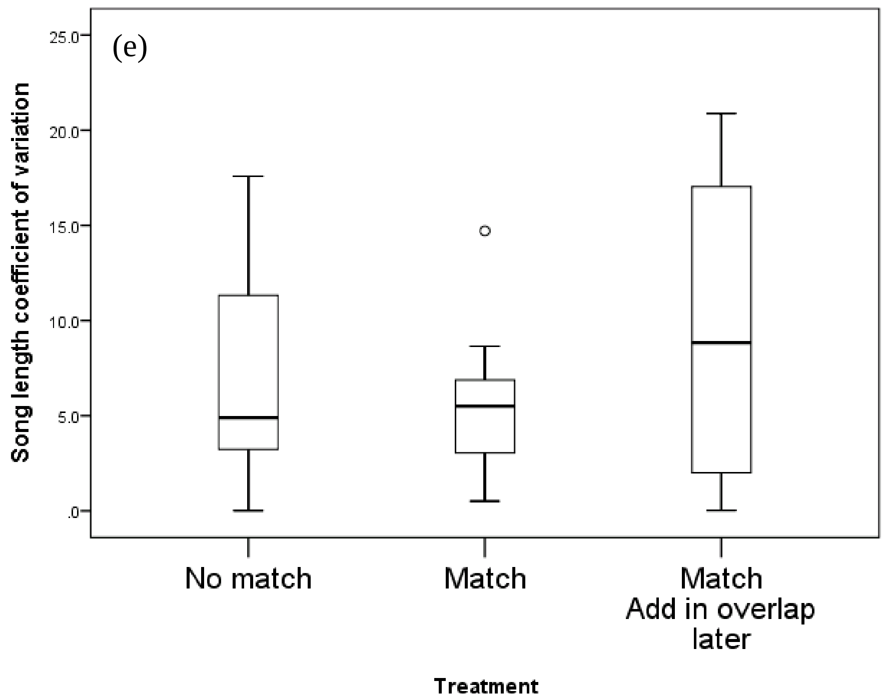
Figure. 7 The influence of four interactive playback treatments on the behavioral responses of the male Black-necklaced Scimitar Babblers: (a) proportion of the playback period spent less than 10 m from the speaker; (b) proportion of the post-playback period spent less than 10 m from the speaker; (c) number of pass over and (d) closest approach. Non-parametric Kruskal-Wallis one-tail Test was used. The dots are outliers and the stars are extreme outliers.

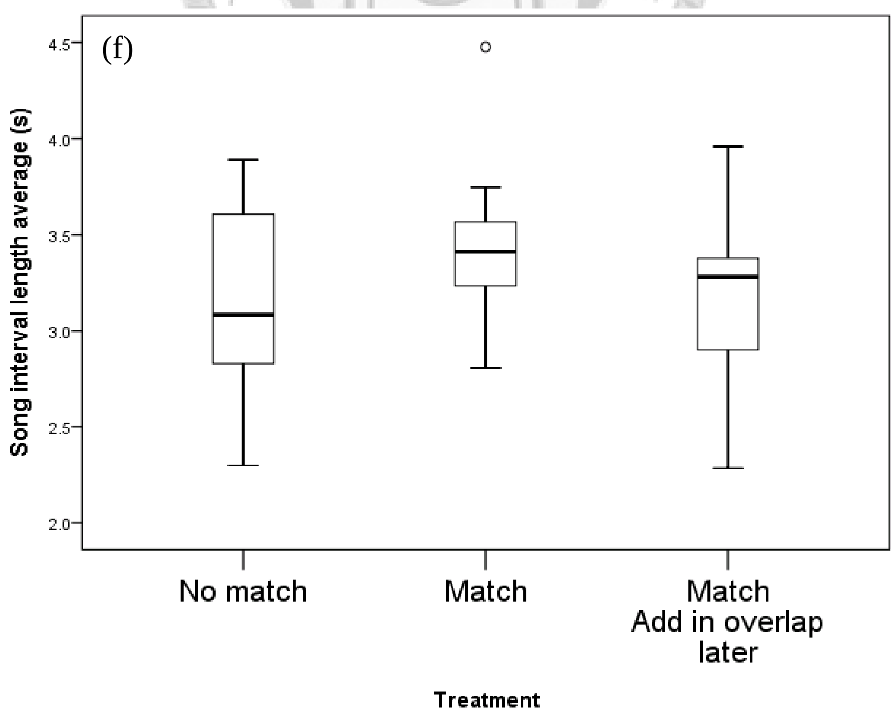

* P=0.0005
(a)
800.0
600.0
400.0
200.0
.0
Number of songs
No match
Match
Match
Add in overlap
later
Treatment


(b)
3.0
2.5
2.0
1.5
1.0
.5
.0
Number of song switching
No match
Match
Match
Add in overlap
later
Treatment


(c)
Number of song types
4.0
3.0
2.0
1.0
.0
No match
Match
Match
Add in overlap
later
Treatment


(d)
Song length average (s)
.5
.4
.3
.2
No match
Match
Match
Add in overlap
later
Treatment


(e)
Song length coefficient of variation
25.0
20.0
15.0
10.0
5.0
.0
No match
Match
Match
Add in overlap
later
Treatment


(f)
Song interval length average (s)
4.5
4.0
3.5
3.0
2.5
2.0
No match
Match
Match
Add in overlap
later
Treatment

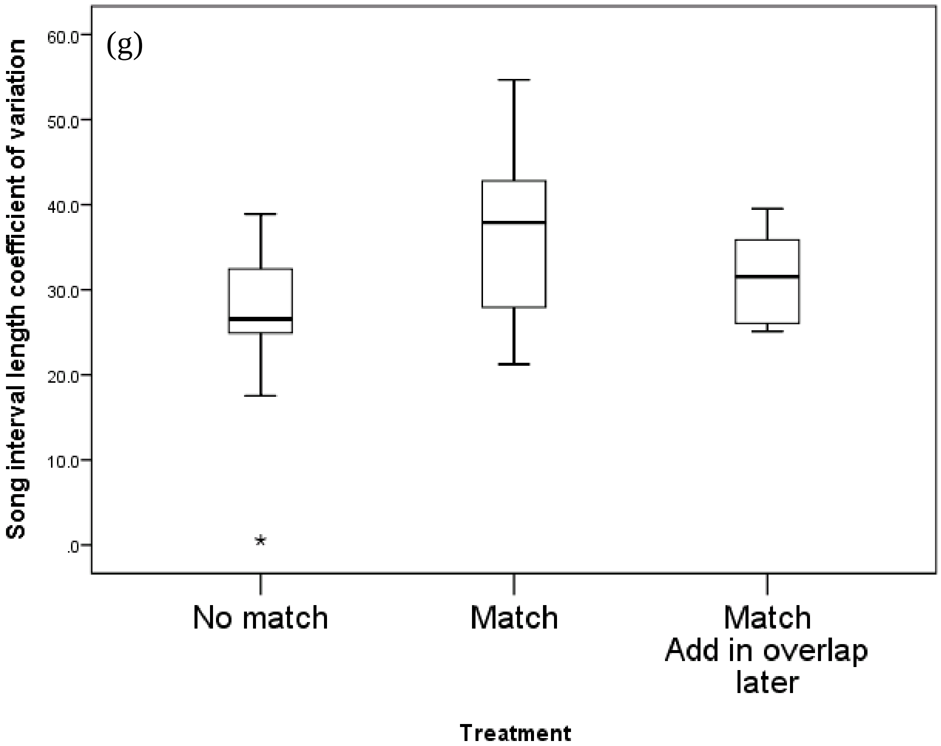
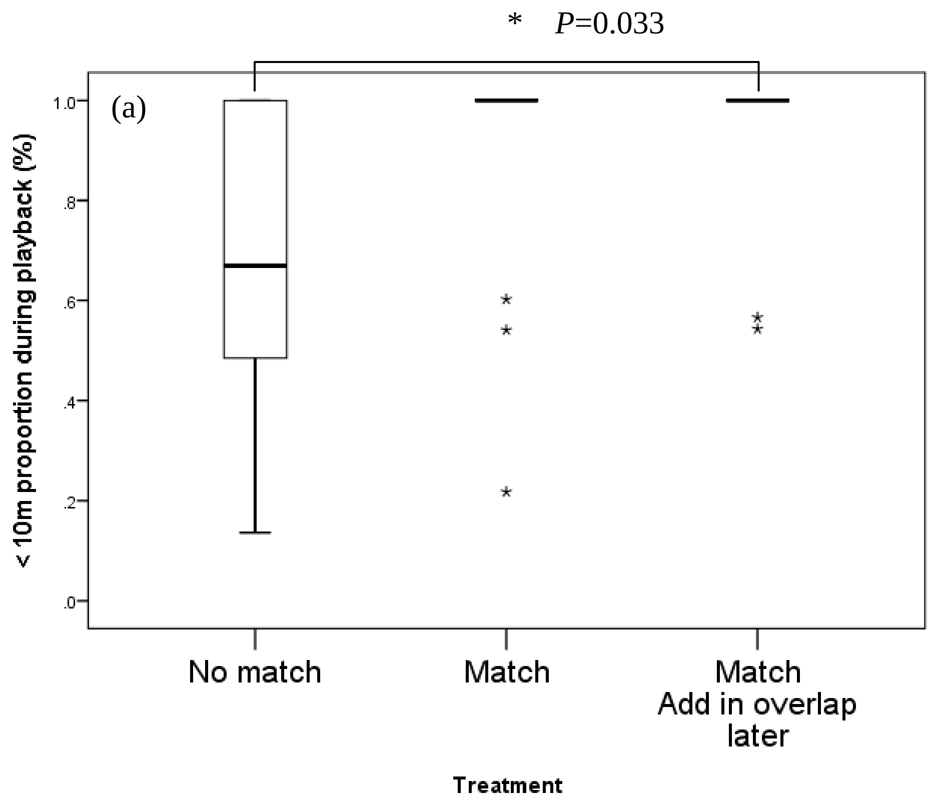
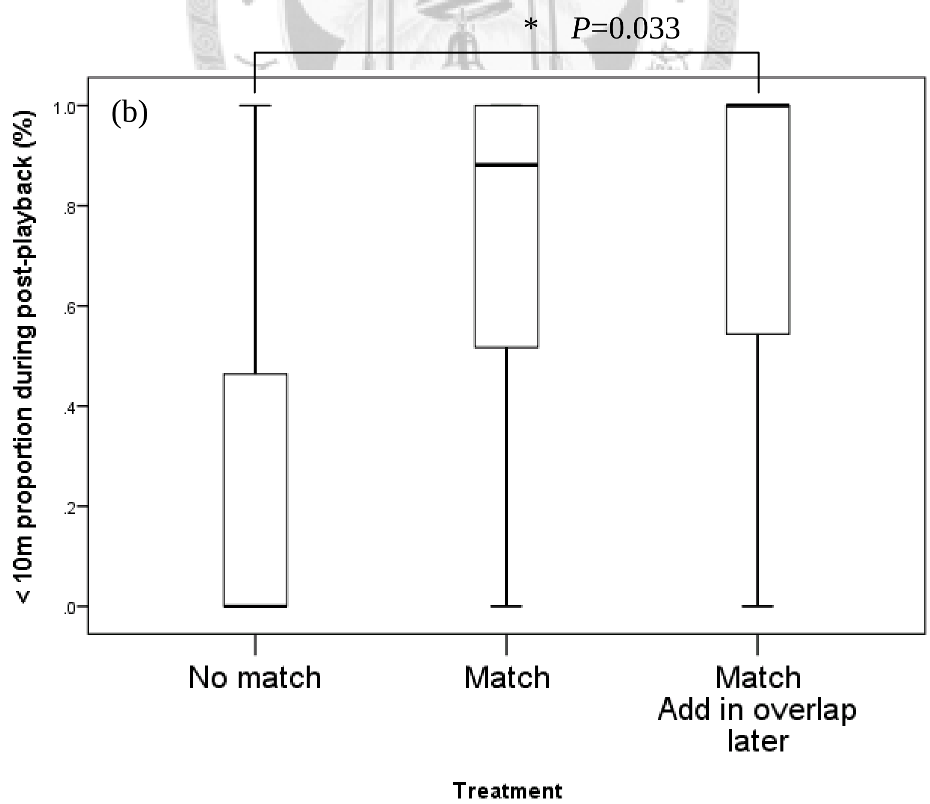
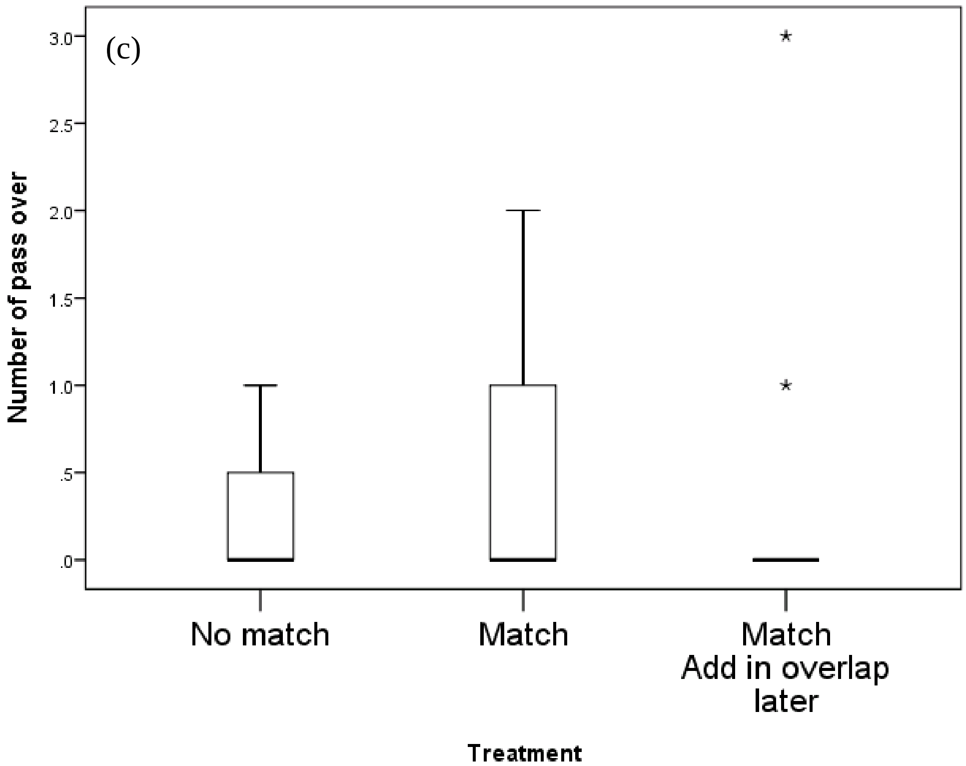


Figure. 8 The influence of playback treatments designed as graded signals on the singing responses of the male Black-necklaced Scimitar Babblers: (a) number of songs; (b) number of song type switching; (c) number of song types; (d) song length average; (e) song length coefficient of variation; (f) song interval length average and (g) song interval length coefficient of variation. Non-parametric Kruskal-Wallis one-tail Test was used. The dots are outliers and the stars are extreme outliers.


* P=0.033
(a)
1.0
.8
.6
.4
.2
.0
< 10m proportion during playback (%)
No match
Match
Match
Add in overlap
later
Treatment


* P=0.033
(b)
1.0
.8
.6
.4
.2
.0
< 10m proportion during post-playback (%)
No match
Match
Match
Add in overlap
later
Treatment


(c)
3.0
2.5
2.0
1.5
1.0
.5
.0
Number of pass over
No match
Match
Match
Add in overlap
later
Treatment

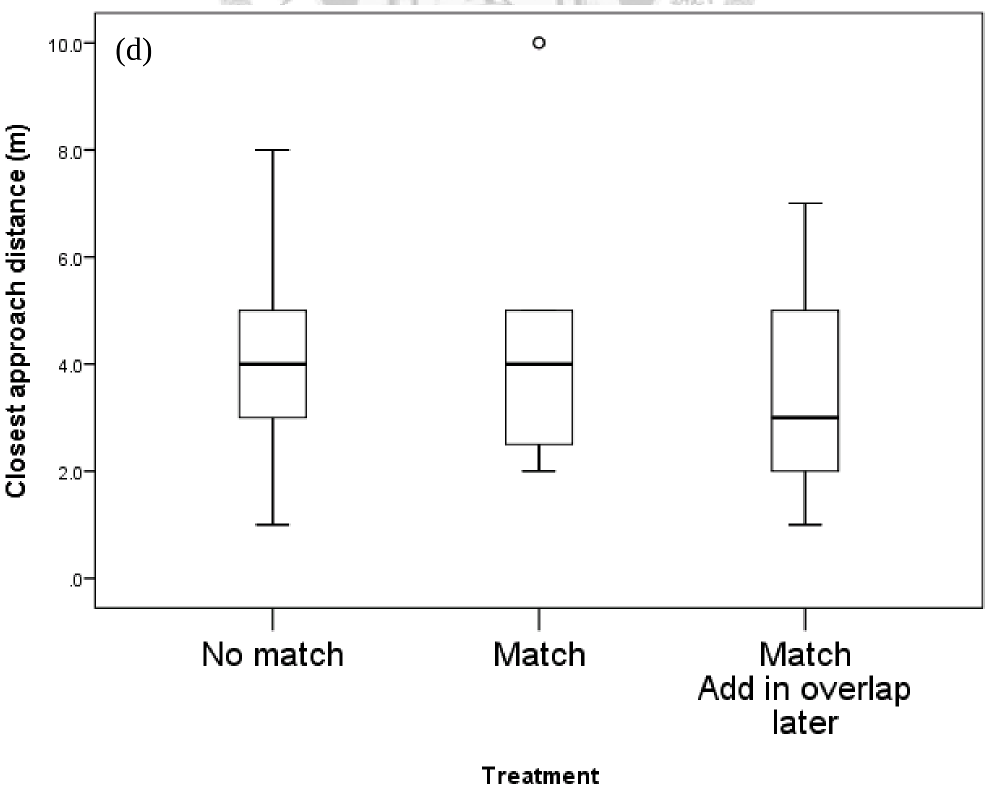

(d)
10.0
8.0
6.0
4.0
2.0
.0
Closest approach distance (m)
No match
Match
Match
Add in overlap
later
Treatment

Figure. 9 The influence of playback treatments designed as graded signals on the behavioral responses of the male Black-necklaced Scimitar Babblers: (a) proportion of the playback period spent less than 10 m from the speaker; (b) proportion of the post-playback period spent less than 10 m from the speaker; (c) number of pass over and (d) closest approach. Non-parametric Kruskal-Wallis one-tail Test was used. The dots are outliers and the stars are extreme outliers.

Appendix I

Singing responses of the male Black-necklaced Scimitar Babblers (*Pomatorhinus erythrocnemis*).

		Treatment				
		No match No overlap	Match No overlap	No match Overlap	Match Overlap	Match Overlap in later part
Number of songs	Sample size	9	13	9	7	8
	Mean±SE	262±80	139±41	280±85	162±74	417±58
	Median, Range	157, 11-668	117, 28-481	172, 15-728	76, 14-451	388, 217-731
Number of song type switching	Sample size	10	14	10	8	9
	Mean±SE	0.7±0.2	0.3±0.1	0.8±0.4	0.6±0.3	0.8±0.3
	Median, Range	1, 0-2	0, 0-1	0, 0-3	0, 0-2	1, 0-3
Number of song types	Sample size	10	14	10	8	9
	Mean±SE	1.6±0.16	1.2±0.15	1.4±0.16	1.4±0.18	1.8±0.32
	Median, Range	2, 1-2	1, 0-2	1, 1-2	1, 1-2	2, 1-4
Song length average (s)	Sample size	9	13	9	7	8
	Mean±SE	0.37±0.02	0.32±0.02	0.35±0.03	0.33±0.01	0.30±0.02
	Median, Range	0.37, 0.31-0.46	0.32, 0.18-0.40	0.37, 0.22-0.47	0.33, 0.30-0.36	0.29, 0.23-0.38
Song length coefficient of variation	Sample size	9	13	9	7	8
	Mean±SE	7.52±2.13	5.55±1.02	5.17±1.29	6.95±1.99	9.58±2.86
	Median, Range	4.90, 0.01-17.58	5.51, 0.52-14.71	3.74, 0.01-11.02	4.56, 2.49-15.48	8.84, 0.02-20.89
Song interval length	Sample size	9	13	9	7	8
	Mean±SE	3.17±0.19	3.42±1.67	3.29±2.07	3.43±1.71	3.17±1.67
	Median, Range	3.08, 2.30-3.89	3.41, 2.80-4.48	3.24, 2.17-4.25	3.44, 2.61-4.32	3.28, 2.28-3.96
Song interval length coefficient of variation	Sample size	9	13	9	7	8
	Mean±SE	26.15±3.88	36.74±2.57	27.64±1.61	34.31±3.61	31.43±1.97
	Median, Range	26.57, 0.55-38.90	37.89, 21.23-44.91	26.14, 21.00-35.52	37.75, 20.91-43.24	31.52, 25.09-39.52

Appendix II

Behavioral responses of the male Black-necklaced Scimitar Babblers (*Pomatorhinus erythrocnemis*).

		Treatment				
		No match No overlap	Match No overlap	No match Overlap	Match Overlap	Match Overlap in later part
< 10m proportion (%)	Sample size	10	13	10	7	9
	Mean±SE	0.67±0.03	0.87±0.02	0.89±0.03	0.80±0.04	0.90±0.02
	Median, Range	0.67, 0.14-1	1, 0.22-1	1, 0.18-1	1, 0.22-1	1, 0.54-1
< 10m proportion (%) post-playback	Sample size	10	14	10	7	9
	Mean±SE	0.27±0.04	0.67±0.03	0.60±0.05	0.57±0.08	0.73±0.05
	Median, Range	0, 0-1	0.88, 0-1	0.76, 0-1	1, 0-1	1, 0-1
Number of pass over	Sample size	8	11	10	7	9
	Mean±SE	0.25±0.16	0.45±0.21	0.2±0.13	0.14±0.14	0.44±0.34
	Median, Range	0, 0-1	0, 0-2	0, 0-1	0, 0-1	0, 0-3
Closest approach distance (m)	Sample size	9	10	10	7	9
	Mean±SE	4.11±0.75	4.75±0.94	5.2±0.93	5.79±1.51	3.61±0.69
	Median, Range	4, 1-8	4, 2-10	5.75, 1-10	6, 0.5-10	3, 1-7