

Chorus-like synchronized vocalizations (Big Chorus) in budgerigars

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Abstract

A number of recent studies have reported how budgerigars (*Melopsittacus undulatus*) are capable of mimicking various behaviors, and that individual vocalizations are strongly influenced by those of other conspecific birds in their vicinity. We examined this effect by placing four budgerigars in separate cages adjacent to each other, and then recording and analyzing all of their vocalizations over a two-week period. Time-based comparisons of the amount of time spent performing warble-songs over a 10 min period revealed a strong correlation between the duration of vocalization when all of the animals were males. However, no such correlation was observed when groups consisted of two males and two females. In the male-only group, whenever one male sang, the others would join in and singing would be synchronized. We repeatedly observed synchronized vocalizations where all of the birds sang together in what could be described as a chorus. While we were unable to demonstrate the functional significance of this behavior, since budgerigars are flocking birds, these synchronized vocalizations were not considered to function as territorial calls or for courtship.

Keywords : Budgerigars, Vocal, Warble-song, Chorus-like synchronized,

Introduction

Budgerigars, the smallest parrots in the order Psittaciformes, live in large flocks in Australia and are known to mimic the sound patterns of conspecific individuals^{1,2)}. A recent study reported that when budgerigars were shown a video of other budgerigars standing on, and pecking at, a screen, they mimicked the behavior of their counterparts³⁾. Furthermore, observations of multiple budgerigars have suggested that the actions of stretching and yawning may also be copied by other birds⁴⁾. These behaviors are not limited to budgerigars; a male Eleonora cockatoo (*Cacatua galerita eleonora*) named Snowball and a male African grey parrot (*Psittacus erithacus*) named Alex, both in the order Psittaciformes, were observed to move spontaneously and in sync with music in a manner similar to dancing in humans⁵⁾. Indeed, Snowball was observed to moderate his behavior in response to variations in the tempo of the music⁶⁾. In a study investigating whether dancing animals on the video-sharing website YouTube were moving in time to the music, an Asian elephant (*Elephas maximus*) and 14 parrot species capable of vocal learning were seen to move in chorus.

In addition to music, budgerigars are capable of

synchronizing their behaviors to rhythmic changes in artificial light and auditory stimuli⁷⁾. Thus, while these birds can mimic and synchronize their behaviors, the manner in which they are influenced by the vocalizations of their neighbors has not yet been clarified. We therefore analyzed the vocalizations of four budgerigars that were raised in the same soundproof box⁸⁾ using vocalization data containing warble-songs⁹⁻¹¹⁾ and investigated whether their vocalizations were synchronized and whether one of the birds was leading the others.

Materials and Methods

a. Experimental animals and groups

The experimental animals consisted of seven, two-year-old budgerigars (four males and three females) that were purchased from a pet shop in Tokyo in 2009; all of the animals had been used in a previous experiment⁷⁾. Four males were assigned to a male-only group (male group) and two males and two females were assigned to a male-female group. Experimental recordings of sound were performed twice in the male group and three times in the male-female group to give a total of five recording sessions in 2011 (Table 1)⁸⁾.

Table 1 Sex composition and experimental structure and duration

ID	Group (Trial)	Members	Acclimatization	Experiment	Analysis
A	M (1 st)	M1, M2, M3, M4	4/10-4/27	4/28-5/6	4/28-5/4
B	M-F (1 st)	M2, F1, F2, M3	7/23-8/8	8/9-8/23	8/9-8/22
C	M (2 nd)	M1, M2, M3, M4	9/10-9/17	9/18-10/3	9/18-10/1
D	M-F (2 nd)	M1, F1, F2, M4	10/12-10/18	10/19-11/3	10/19-11/1
E	M-F (3 rd)	M1, F1, F3, M4	11/11-11/20	11/21-12/7	11/21-12/6

In the male-female group (3rd trial), the data from 30 November to 1 December was damaged and could not be used ; consequently, the data from 2 to 6 December was used. M : male birds, F : female birds, Trial: trial number. Animal IDs correspond to those in the graphs below.

b. Experimental equipment and recording system

In this experiment, we used the same equipment employed by Abe & Sakurai (2014) (Fig. 1) ⁸⁾. Budgerigar behavior was monitored and recorded using a video camera. The photoperiod inside the soundproof box was 12L:12D. When the light was on, the luminance at the center of each cage was 40 lux (LX-100, Lutron Electronic Enterprise Co., Ltd., Taiwan) , which is approximately the same as the brightness under a streetlight at night. The animals could see and hear their neighbors within each soundproof box, but they could not hear any sounds outside the box. Audio software (Avisoft Recorder, Avisoft Bioacoustics, Berlin, Germany), a unidirectional microphone (PRO 35, Audio-Technica, Japan), and an amplifier (Xenyx 802, Behringer, Germany; Fast Track Ultra, M-AUDIO, RI) was used to record bird calls and warble-songs.

The Avisoft Recorder was set to record sounds longer than 0.05 s with an energy of $\geq 0.5\%$ and a noise level of $< 90\%$ at a sampling frequency of

16 Hz (range 1-8 kHz). When one of the birds produced a sound that met these criteria, the sound recording was made for 1 s starting 0.3 s prior to initiation of the sound. If another sound occurred during this 1 s, the recording was made for an additional 1 s. A number was then assigned to each sound and the sound was saved as an audio file (Fig. 2).

The birds were acclimatized to the experimental environment for approximately 2 weeks prior to conducting the experiment. During this acclimatization period, the experimental equipment was adjusted to limit noise contamination in the form of other bird sounds to less than 5%, while all of the target vocalizations were recorded all day for 1 to 2 weeks. Care was provided once every 2 days for a period of 5 min when all recordings were stopped and the food and water was changed without any human contact. In this study, if the interval between two audio files was < 4 sec, then this was regarded as the same vocalization. In addition, continuous vocalizations ≥ 10 s were taken

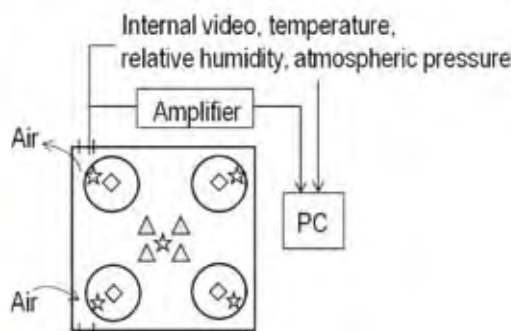


Fig. 1 Experimental setup and equipment

Left : Photograph of the soundproof boxes ; Right : Spatial relationship of objects inside each soundproof box. Diamonds : microphones, stars: lights, triangles; cameras, parallel lines : wiring ports.

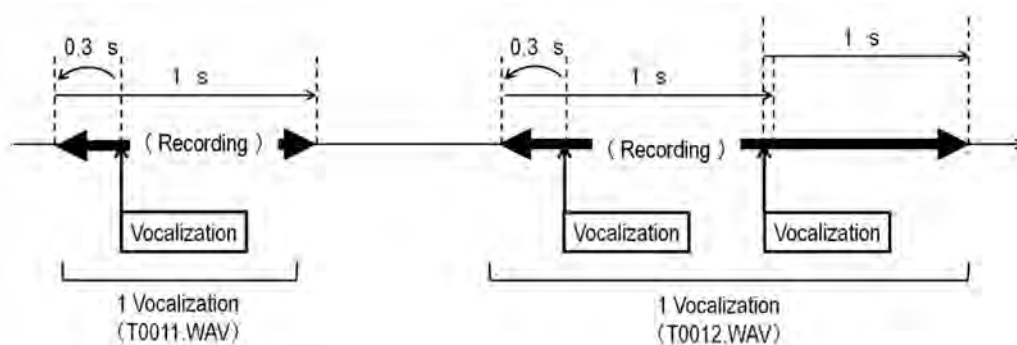


Fig. 2 Method for separating recordings

as a warble-song⁸⁾. We restricted our analyses to warble-song data.

c. Initiation and frequency of warble-songs among individuals in a group

We referred to any individual that initiated warble-songs as a leader if another individual in the same group also started singing within 3 s. We estimated the total number of warble-songs and the frequency of leading any of the three other individuals. The frequency of leading other individuals was counted as “1” even if one of the other three individuals sang the warble-song multiple times within the reference warble-song (the warble-song of the individual that began singing). The number of individuals that can be led by a single warble-song ranges from a minimum of 0 to a maximum of 4. Using this counting methodology, counting was performed for each warble-song initiated by each individual. If an individual rejoined a warble-song, then the score for that individual was taken as 1. The frequency of leaders’ warble-songs was analyzed by one-way ANOVA with Bonferroni correction.

To determine the relationship (order) in the experimental group, we compared the number of warble-song leaders and followers by Fisher's exact test. The frequency of leading warble-songs was then calculated for two individuals (e.g. M1 and M2), and not for three individuals as above. Thus, the frequency of M1 leading M2 and of M1 not leading M2 was calculated. Individuals with consistently high rates of leading were considered to be dominant.

d. Statistical analysis

Analyses were based solely on data collected while the boxes were illuminated. We used Fisher's exact test to examine the difference between the synchronized (big chorus) and unsynchronized vocalizations of the four budgerigars. In terms of the temporal cross-correlation and the correlation between the duration of vocalization of each budgerigar, we used the Mann-Whitney U test to compare differences between the male and male-female groups.

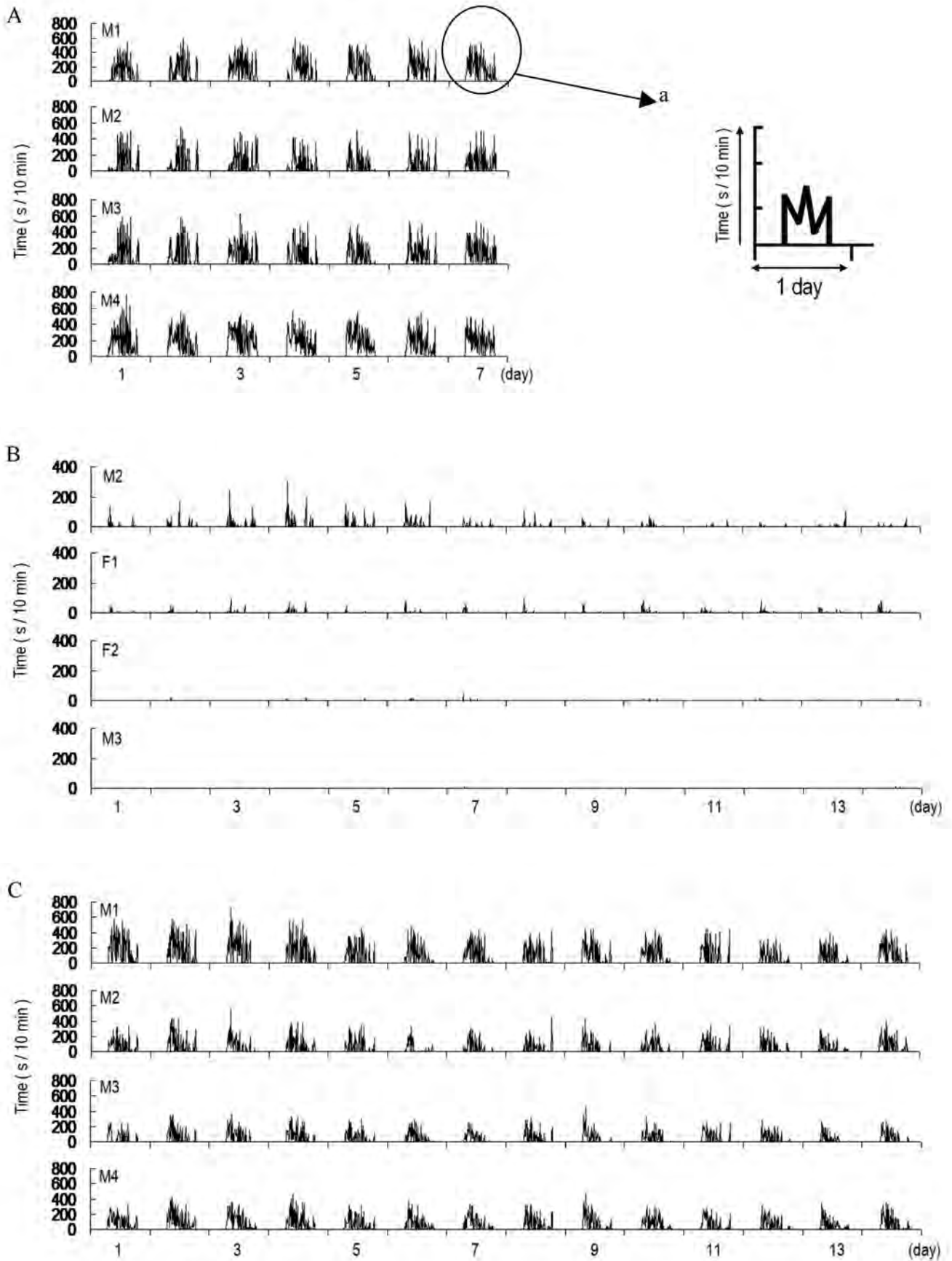
Results

1) Intergroup comparisons of the length (time) warble-songs during a 10-min period

After dividing the entire recording into 10-min sessions and then comparing the duration of warble-songs in that 10 min period (time: s/10 min), all of the birds in the male group exhibited similar shifting patterns on a graph representing the duration of vocalization (Fig. 3, A, C). When one budgerigar started singing, another bird and then another began singing in chorus, until all of the birds were singing in a synchronized chorus (big chorus). This behavior was not observed in the male-female group (Fig. 3, B, D-E).

2) Frequency of warble-songs and number of contributors

After examining whether there was any overlap in the singing behavior of the four budgerigars each time warble-songs were observed, we found that warble-songs were most frequently performed when all four of the birds were males (Table 2).



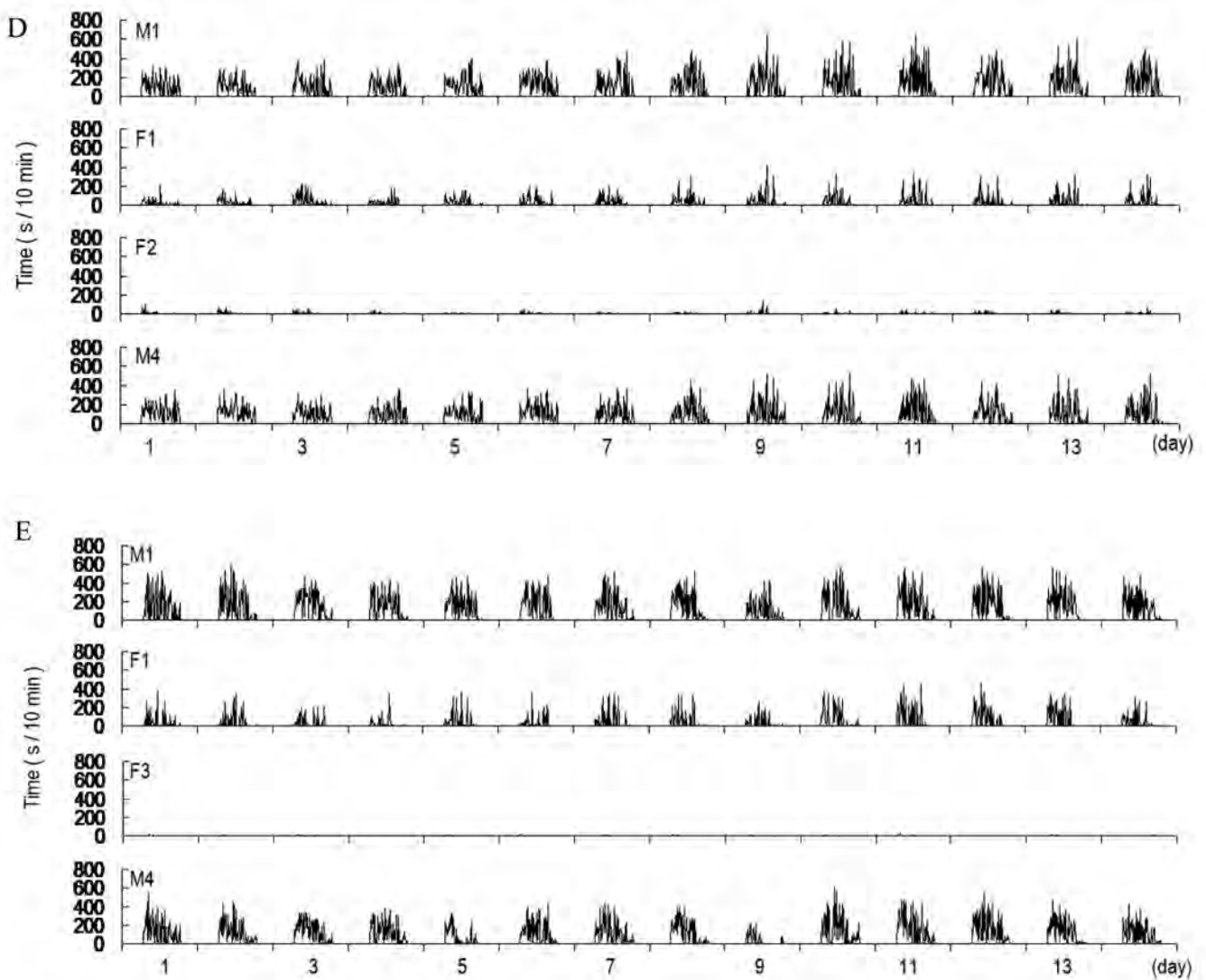


Fig. 3 Pattern of warble-songs during the experiment

a : Vocalization data represented as the total amount of warble-songs (time (s)) in a 10 min period.

This finding shows that when one budgerigar starts singing, a chain to utterance occurs and the four birds all start singing together. The incidence of all four birds singing in the all-male group was significantly higher than it was in the male-female group ($p < .001$; Fisher's exact test) .

3) Timing of warble-songs among budgerigars

To determine whether there was a correlation in the timing of warble-songs among individual budgerigars, we plotted the cross correlations between vocalization timing of warble-songs in the male and male-female groups (Fig. 4). The

Table 2 Number of birds and frequency of overlapping warble-songs

ID	Group (Trial)	Members	One	Two	Three	Fours
A	M (1 st)	M1, M2, M3, M4	77	63	91	268
B	M-F (1 st)	M2, F1, F2, M3	169	59	5	1
C	M (2 nd)	M1, M2, M3, M4	92	79	74	254
D	M-F (2 nd)	M1, F1, F2, M4	39	128	238	94
E	M-F (3 rd)	M1, F1, F3, M4	91	186	205	17

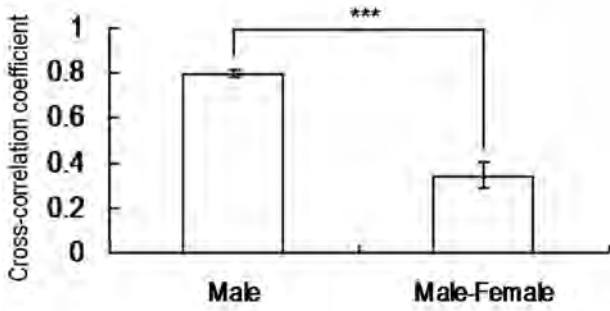


Fig. 4 Maximum difference between vocalization timing in the all-male and male-female groups (mean \pm SEM) (** $p < .001$; Mann-Whitney U -test).

maximum cross-correlation coefficient was always observed for the all-male group when there was no time lag in warble-songs. The peak value of the cross-correlation coefficient for the all-male group was significantly higher than that for the male-female group (Male : mean = .80, SEM \pm .001, Male Female : mean = .34, SEM \pm .05, $p < .001$; Mann-Whitney U -test test, Fig. 4). This finding demonstrates that budgerigars in the all-male group often sang at the same time.

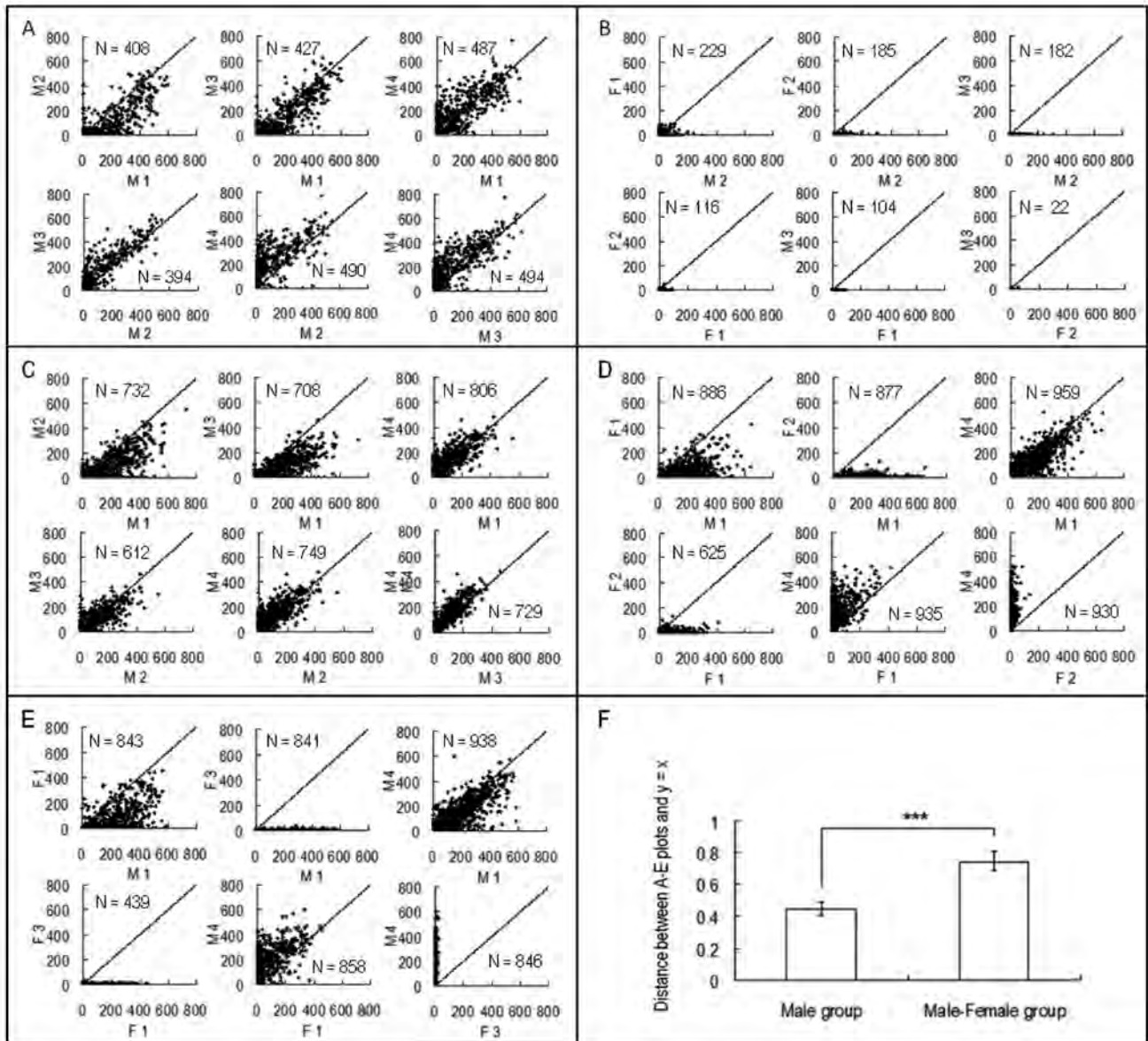


Fig. 5 Correlation between (A-E) duration of warble-songs for individual budgerigars and (F) comparison of male and male-female groups.

A-E : The X- and Y-axis units are seconds ; the density of the plots around the dotted line is correlated with the similarity of the warble-songs during a 10-min period.

F : Comparison of male and male-female groups (mean \pm SEM) ; the Y-axis shows the distance between the A-E plots and $y = x$ (** $p < .001$; Mann-Whitney U -test)

4) Duration of warble-songs of individual budgerigars

Based on the data in Fig. 3, we examined the cross-correlations between all combinations of individual budgerigars in each group. Panels A-E in Fig. 5 show the actual number of warble-songs based on the assumption that $y = x$ when the duration of warble-songs was equal among individuals. Calculating inter-individual differences in the form of distance showed that the number of warble-songs was similar for individuals in the all-male group, but that birds in the male-female group either sang on their own or differed markedly in terms of the number of their warble-songs (Male: mean = .45, SEM \pm .04., Male Female : mean = .75, SEM \pm .06., $p < .001$; Mann-Whitney U -test test., Fig. 5).

The number of warble-songs was inconsistent in the male-female group, but was similar among the birds in the all-male group, suggesting that the number of warble-songs by other birds in the group was correlated to the number of warble-songs per individual. The males exhibited a greater

tendency to synchronize their warble-songs, both temporally and quantitatively. Correlations between the timing and duration of warble-songs for the male-female group showed a weak tendency towards synchronization throughout the entire group, while the all-male group exhibited a strong tendency to sing in chorus (Fig. 4 and 5).

5) Frequencies of warble-song relationships among individuals

We investigated whether any of the budgerigars consistently initiated warble-songs within each group, and the tendency of other birds to follow this song-leading behavior (Fig. 6). Interestingly, no well-defined relationship between the initiation of warble-songs and individuals was observed in either the all-male group or the male-female group.

6) Duration and frequency of warble-songs

The typical length of warble-songs for domesticated budgerigars is 10 s⁹⁾. However, in the present study, the all-male group sang for ≥ 30 s. The mean duration of warble-songs in

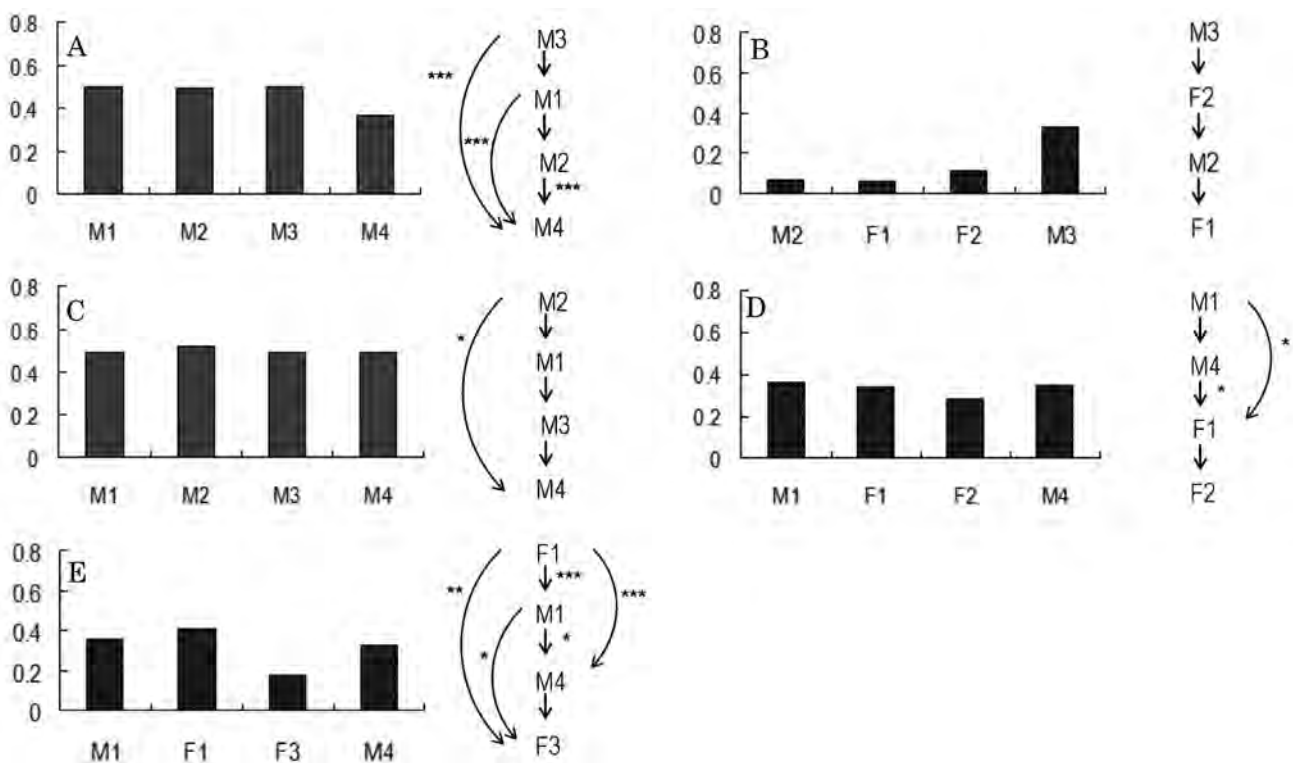


Fig. 6 Rate of incidence of song-leading among males and females in each group.

Bar graphs : Rate of leading warble-songs. The Y-axis indicates the ratio of the incidence of song-leading. After analysis by one-way ANOVA, the data were analyzed using a multiple comparison test by Bonferroni correction.

Arrows : relationship between leading and non-leading budgerigars (* $p < .05$, ** $p < .01$, *** $p < .001$; Fisher's Exact-test) .

Table 3 Mean duration (s) of single warble-songs among individual budgerigars

ID	Group (Trial)	Members	M1	M2	M3	M4	F1	F2	F3
A	M (1 st)	M1, M2, M3, M4	345.3 (2417)	160.3 (1122)	256.7 (1797)	456.3 (3194)	-	-	-
B	M-F (1 st)	M2, F1, F2, M3	-	30.4 (426)	0.2 (201)	-	14.4 (25)	1.8 (3)	-
C	M (2 nd)	M1, M2, M3, M4	209.5 (2933)	113.6 (1590)	156.2 (2187)	224.7 (3146)	-	-	-
D	M-F (2 nd)	M1, F1, F2, M4	317.9 (4451)	-	-	338.1 (1843)	131.6 (304)	21.7 (4734)	-
E	M-F (3 rd)	M1, F1, F3, M4	287.0 (4018)	-	-	303.7 (1394)	99.6 (33)	-	2.4 (4252)

Values are shown in seconds (s) and values in parentheses indicate sample size.

Table 4 Mean daily frequency of warble-songs among individual budgerigars

ID	Group (Trial)	Members	M1	M2	M3	M4	F1	F2	F3
A	M (1 st)	M1, M2, M3, M4	34.3 (2417)	42.4 (1122)	36.4 (1797)	31.2 (3194)	-	-	-
B	M-F (1 st)	M2, F1, F2, M3	-	18.0 (426)	11.0 (201)	-	14.0 (25)	12.6 (3)	-
C	M (2 nd)	M1, M2, M3, M4	42.3 (2933)	40.3 (1590)	25.7 (2187)	26.0 (3146)	-	-	-
D	M-F (2 nd)	M1, F1, F2, M4	30.4 (4451)	-	-	25.2 (1843)	20.4 (304)	13.7 (4734)	-
E	M-F (3 rd)	M1, F1, F3, M4	39.0 (4018)	-	-	28.7 (1394)	32.9 (33)	-	12.3 (4252)

Values in parentheses indicate sample size.

the male-female group was approximately 10 s longer among the males in the group (25.37 s) than among the females (17.67 s) (Table 3, Male-Female groups 1-3, $t = 1.4845$, $df = 9.631$, $p = 0.1697$; T-test). The daily frequency of warble-songs by each group was higher for males than for females in all groups except the Male-Female Group 1 (Table 4, Male-Female Group 1).

Discussion

In the all-male group that exhibited chorus-like behavior, the warble-songs of one budgerigar would trigger singing among the other birds in the group, leading to a chorus that continued unabated for an extended period. The duration of warble-songs produced by the male group tended to be considerably longer than that for single budgerigars. The typical duration of warble-songs, which are used by budgerigars to communicate, is approximately 10 s⁹⁾. However, the overall mean duration of warble-songs produced by the all-male group that exhibited chorus-like behavior was ≥ 30 s. Among the female budgerigars, the duration of warble-songs approached 10 s, but only one bird (F1) was observed to produce a similar amount of warble-songs as her male counterparts. To the best of our knowledge, this is the first report of a budgerigar whose warble-songs increased in length

over time.

Birds belonging to the order Psittaciformes are capable of maintaining a rhythm, and budgerigars tend to synchronize their behavior with rhythms that approach the speed of warble-songs (600 ms)⁷⁾. In addition, budgerigars are more adept at synchronizing their behavior to actual warble-songs than to similar-sounding rhythms.

In many bird species, only the male learns to sing; in budgerigars females warble less than males⁹⁾. Indeed, males typically exhibit a greater capacity for vocal learning and neural control of these vocalizations than females, indicating that the neural infrastructure dedicated to vocal learning is more developed in males^{12, 13)}. Although the male and female budgerigars used in the present study both produced warble-songs, the females produced warble-songs less frequently than the males, and they were also less inclined to sing in chorus. In the Japanese quail (*Coturnix japonica*), the presence of females reportedly acts as a deterrent to vocalization among males¹⁴⁾. However, in the present study, variations in the time and frequency characteristics of warble-songs differed between the all-male group and the male-female group. This difference between groups may indicate that warble-songs might perform different functions in

these two groups.

These findings presented here corroborate those of Abe & Sakurai (2014) who analyzed calls and single utterances of single notes in budgerigars. The results presented in their study showed the existence of an order in two male groups (M1 → M2 → M3 → M4)⁸⁾. In that study, contact calls and single utterances of a single note were analyzed, but in the present experiment, only warble-songs were analyzed. The variability in the singing order observed in both groups used in the present study may be because the vocalizations employed in this study have different functions in this species, or the differences may be due to the characteristics of the individuals within each group.

In the wild, other species of birds use vocalizations to mark their territory¹⁵⁾, and some species are even known to overlay their songs with others in an attempt to interfere with the songs of rivals¹⁶⁻¹⁸⁾. However, the budgerigar is a flocking species, and is not known to exhibit territorial behavior in male/female duets or vocalizations. While warble-songs can be employed during courtship¹⁹⁾, the budgerigars in the present study were able to identify the form of the other birds so there would be no need for aggressive courtship behavior in an environment consisting solely of males.

Birds belonging to the order Passeriformes also camouflage their singing when their songs overlap with other conspecific individuals in close proximity, and they typically try to avoid singing in chorus. In the present study, we consider that the chorus-like behavior exhibited by the male group, which would be rare in the natural environment, was triggered by stress or competition, or was intended to advertise their presence to females²⁰⁾.

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