

Paper:

# Absence of Jamming Avoidance and Flight Path Similarity in Paired Bent-Winged Bats, *Miniopterus Fuliginosus*

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[Received January 12, 2021; accepted March 19, 2021]

Echolocating bats perceive their surroundings by listening to the echoes of self-generated ultrasound pulses. When multiple conspecifics fly in close proximity to each other, sounds emitted from nearby individuals could mutually interfere with echo reception. Many studies suggest that bats employ frequency shifts to avoid spectral overlap of pulses with other bats. Technical constraints in recording technology have made it challenging to capture subtle changes in the pulse characteristics of bat calls. Therefore, how bats change their behavior to extract their own echoes in the context of acoustic interference remains unclear. Also, to our best knowledge, no studies have investigated whether individual flight paths change when other bats are present, although movements likely reduce acoustic masking. Here, we recorded the echolocation pulses of bats flying alone or in pairs using telemetry microphones. Flight trajectories were also reconstructed using stereo camera recordings. We found no clear tendency to broaden individual differences in the acoustic characteristics of pulses emitted by pairs of bats compared to bats flying alone. However, some bats showed changes in pulse characteristics when in pairs, which suggests that bats can recognize their own calls based on the initial differences in call characteristics between individuals. In addition, we found that the paired bats spend more time flying in the same directions than in the opposite directions. Besides, we found that the flight paths of bats were more similar in “paired flight trials” than in virtual pairs of paired flight trials. Our results suggest that the bats tend to follow the other bat in paired flight. For the following bat, acoustic interference may be reduced, while the opportunity to eavesdrop on other bats’ calls may be increased.

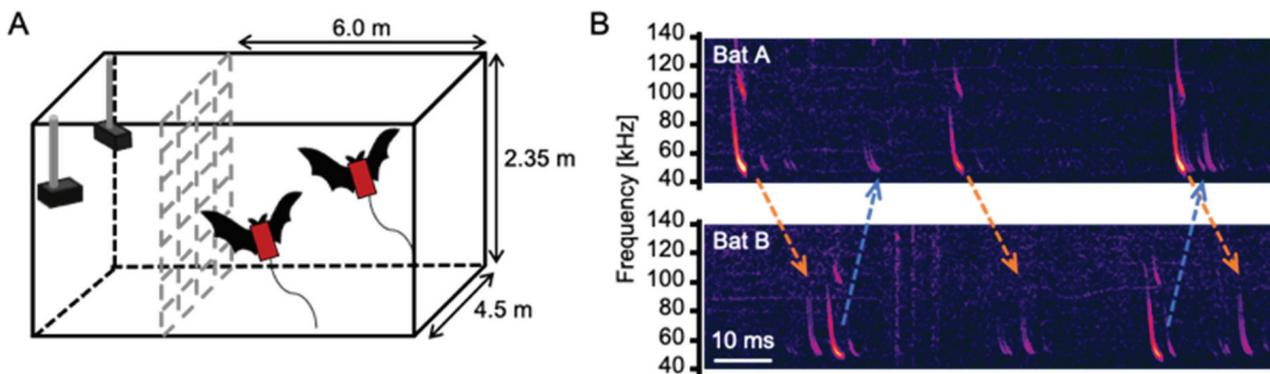
**Keywords:** bats, echolocation, flight dynamics, jamming

## 1. Introduction

Echolocating bats emit ultrasound pulses and perceive the surrounding environment by listening to echoes [1]. Some species of bats roost in very large colonies; tens of thousands of individuals can cohabit in narrow and dark caves [2]. Bats also often fly with conspecific individuals [3, 4]. Therefore, bats are likely exposed to acoustic interference when echolocating, such as pulses (and the echoes thereof) emitted by other bats, as well as behaviorally irrelevant echoes from background objects [5–7]. Even in such an acoustically complex situation, however, bats are able to fly without colliding into other bats or obstacles. Recorded sounds with a fixed microphone can be distorted to some extent by the Doppler effect and atmospheric attenuation. Also, individual identifications by sounds could be difficult in group flying bats. These technical constraints have made it challenging to capture subtle changes in acoustic characteristic of pulses emitted by a group of bats. Therefore, it remains unclear how they extract behaviorally relevant information from their echoes under conditions of acoustic jamming.

One behavioral strategy to avoid or reduce acoustic interference is to change the acoustic characteristics of emitted pulses. Both playback of jamming sounds and the presence of conspecifics have been used to investigate vocal adaptation to acoustic interference. Bats that echolocate with frequency-modulated (FM) sounds change their terminal frequency when exposed to jamming sounds that mimic bat pulses [8–13], or to artificial tones and noises [14, 15]. A recent study found that eastern bent-winged bats (*Miniopterus fuliginosus*) shift the terminal frequency of their FM pulses away from each other while flying in a group of four individuals [16]. Frequency shifting behavior increases differences in terminal frequency between individuals, thereby reducing the similarity of pulses [16]. Similar behavioral adaptation could occur when clutter echoes, i.e., echoes from background objects (e.g., plant leaves), interfere with bat’s echo recep-





**Fig. 1.** (A) Schematic illustration of the experimental setup. (B) Representative spectrograms derived from the telemetry microphone recordings of echolocation pulses emitted by two *M. fuliginosus* flying together. In addition to emitted echolocation pulses and their echoes, sounds emitted from other bats were recorded.

tion. When placed in artificially cluttered environments, the terminal frequencies of two successive FM pulses emitted by big brown bats (*Eptesicus fuscus*) are shifted away by 3–6 kHz [17]. These frequency shifts likely reduce similarity between successive echoes, thus avoiding the misassignment of echoes to the original pulses [17]. Lower frequency range of pulses, including the terminal frequency, plays a significant role in target perception for echolocating bats [18]. Therefore, shifts in terminal frequency help FM echolocating bats to avoid, or mitigate the effects of, acoustic jamming caused by clutter echoes or pulses and/or the echoes of other bats.

In addition to spectral modification of echolocation pulses, temporal changes in pulse emission can also reduce jamming effects. Bats increase their pulse duration when placed in an acoustically noisy environment [15, 19, 20]. The lengthening of pulse duration increases the signal-to-noise ratio of the returning echoes in the auditory system [19, 21]. In one study, Mexican free-tailed bats (*Tadarida brasiliensis*) reduced their pulse emission rate as group size increased [22]. Similarly, flying bats decreased their pulse emission rate when exposed to jamming signals that mimic conspecific sounds [23]. Therefore, suppression of pulse emissions likely improves information throughput in a group of bats [22].

Another behavioral adaptation that could mitigate acoustic jamming during group flight is indirect alteration of echo reception by changing motor behavior. For example, appropriate flight control could reduce acoustic masking by other bats. During paired flights of big brown bats, differences in acoustic characteristics increase between individuals with a decrease in the inter-bat distance [24]. Similarly, paired big brown bats are more frequently silent when the distance between them, or differences in the angle of their orientation, decrease [25]. Mexican free-tailed bats also suppress pulse emission to a greater degree when playback of conspecific echolocation pulses is directed toward the flight path of the bat [26]. These studies suggest that the spatial relationships among bats flying in groups influence the extent to which the bats interfere with each other's echolocation. Therefore, acoustic jamming could

be mitigated not only by differentiating time-frequency characteristics of pulses each other, but also by altering the flight paths of bats flying in groups.

In the present study, we recorded the echolocation pulses and flight trajectories of bats flying alone, and in pairs, to investigate the flight strategies used by paired animals. We did not determine whether the bats changed the acoustic characteristics of their emitted pulses to a greater degree in paired flight compared to single flight. However, we found that the flight paths of bats were more similar in “paired flight trials” than in virtual pairs of paired flight trials, suggesting that flying along similar paths can reduce jamming effects caused by conspecifics.

## 2. Materials and Methods

### 2.1. Subjects

We collected 11 eastern bent-winged bats (*Miniopterus fuliginosus*; 6 males and 5 females) from wild colonies within an artificial cave in Fukui Prefecture, Japan; permits were granted by the government of Fukui Prefecture. All bats were housed in a temperature- and humidity-controlled room under a 12:12 h light:dark cycle at Doshisha University, Kyoto, Japan. The animals had free access to mealworms and vitamin-enriched water.

### 2.2. Experimental Procedure

Flight experiments were performed in an experimental chamber (9 m (L) × 4.5 m (W) × 2.4 m (H)) at Doshisha University. The chamber was constructed of steel plates to minimize external electromagnetic noise. Within the chamber, there was a walled flight space (6 m (L) × 4.5 m (W) × 2.4 m (H)), and a net suspended from the ceiling (Fig. 1(A)). A lighting apparatus with a filter that removed light with a wavelength below 650 nm was used to prevent the animals from relying on visual information.

All bats were randomly assigned to eight pairs. We tested the bats under two experimental conditions: single flight and paired flight. First, each bat was observed

alone in the flight space for approximately 30 s (single flight 1: S1). After the single flights, each bat was kept in an individual cage until the time of the paired flights. Next, the bats were observed in pairs for approximately 120 s in the flight space (paired flight: P). During the paired flights, one bat was released by an experimenter and allowed to fly for approximately 30 s. Then, the experimenter released the second bat. Both the single and paired flight tests were conducted within a single day for each pair. We did not perform additional single flights after paired flights because our previous studies have revealed that there are no significant changes in acoustic characteristics of emitted pulses in control conditions before and after jamming conditions [11, 12, 16].

### 2.3. Telemetry Microphone Recordings

Echolocation pulses emitted from each bat were recorded using a custom-made telemetry microphone mounted on the bat's back [16, 27]. The telemetry microphones allowed us to separately record pulses emitted from each individual (**Fig. 1(B)**). Sounds received by the microphone unit of the telemetry microphone were amplified and modulated by the frequency modulation circuit (carrier frequency = 82.2–105.5 MHz). The modulated signals were transmitted from the antenna of the telemetry microphone. A custom-made FM receiver (ArumoTech Corporation, Kyoto, Japan) with an FM+ antenna (Terk Technologies Corporation, Commack, NY, USA) received and demodulated the transmitted signals. Finally, the received signals were digitized using a high-speed USB data acquisition board (Model NI USB-6356; 16-bit, sampling frequency = 500 kHz; National Instruments, Austin, TX, USA).

### 2.4. Sound Analysis

From each recording, we analyzed 10-second sequences that had a good signal-to-noise ratio for each flight condition. The number of pulses analyzed for each pair ranged from 57 to 245. Recorded echolocation pulses were analyzed using MATLAB R2014a (MathWorks, Natick, MA, USA) using custom scripts. Each pulse was manually extracted from the oscillograms of the recordings. Then, the pulse was displayed as a spectrogram (FFT: zero-padded 2048 points, hanning window: 256 points, 96.875% time overlap). Initial and terminal frequencies were defined as the highest and lowest frequencies, respectively, of each pulse and were  $-25$  dB relative to the maximum energy portion of the spectrogram. We determined the duration of each pulse from the spectrogram and calculated the bandwidth of the pulse by subtracting the terminal frequency from the initial frequency. The interpulse intervals were defined as the period of time between onsets of successive pulse emissions.

### 2.5. Video Recordings [16]

Two video cameras (MotionXtra NX8-S1; IDT Japan, Inc., Tokyo, Japan) were placed outside the flight space

in the experimental chamber. Cameras operating at 30 frames/s captured the flight trajectories of the bats using Motion Studio software (version 2.12.6.0; IDT Japan, Inc.). The video images were recorded on a personal computer.

### 2.6. Video Analysis

Three-dimensional reconstruction of the bats' flight paths was done using DIPP-Motion Pro motion capture software (version 2.21a; Ditect Corporation, DIPP-Motion Pro, Tokyo, Japan). Direct linear transformation was performed with reference to the coordinates of a reference cubic frame.

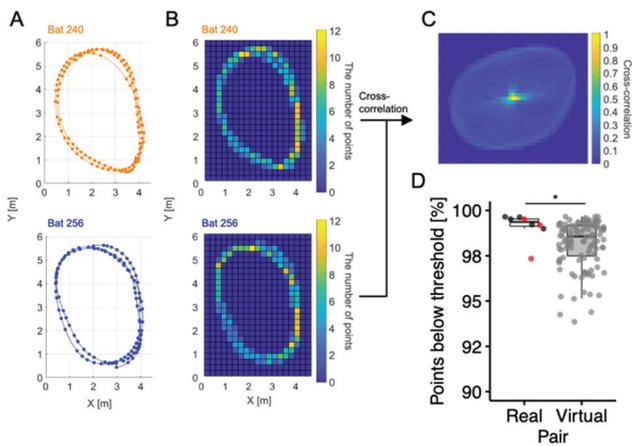
The reconstructed flight paths were fitted with tenth-order polynomials for smoothing; this was done using Igor Pro (version 5.0.3; WaveMetrics Inc., Lake Oswego, OR, USA). Each coordinate was divided into three parts (4, 4, and 2 s sequences), which were then fitted with the polynomials.

To quantify the percentages of time spent in flight in the same direction, we visually count frame by frame how long bats in each pair spent in the same direction flight, in the opposite direction flight, and in behavioral states other than flight (e.g., landing or released from an experimenter's hand). The percentages of time spent in flight in the same directions were calculated by dividing time spent in the same direction by total time spent in flight.

We focused on the horizontal plane of the flight paths to evaluate the similarities thereof between individuals, because flight dynamics are typically observed in the horizontal rather than vertical plane. The two-dimensional (2D) flight paths thus obtained were divided into  $250 \text{ mm} \times 250 \text{ mm}$  bins to create 2D histograms (**Figs. 2(A)** and **(B)**). The histograms were then normalized according to the total number of points in the flight path to create occupancy maps. Two-dimensional cross-correlation of the two occupancy maps was performed using MATLAB. We determined the similarity between occupancy maps based on criteria used in a previous study examining the flight paths of a single individual over time [28]. Similarity was defined as the number of points smaller than 60% of the maximum value of each cross-correlation (**Fig. 2(C)**). Each result of cross-correlation consisted of  $37 \times 49$  bins. The theoretical maximum similarity value was 1812, which was obtained if two individuals remained in the same bin for the entire trial ( $37 \times 49 - 1$ ). The calculated similarity values were normalized according to the theoretical maximum. To determine whether the flight paths of the paired bats were similar, we compared flight paths between individuals during both the paired and virtual pair trials. To create virtual pair data, we calculated the similarity between paired flight paths for all possible combinations of individuals.

### 2.7. Statistical Analysis

To investigate the effects of sounds emitted by other bats on the acoustic characteristics of the bats' pulses, we compared the terminal frequency, bandwidth, duration,



**Fig. 2.** Two-dimensional flight trajectories (A) and histograms (B) of Bat 240 (top) and Bat 256 (bottom) during paired flights. (C) Two-dimensional cross-correlation of the flight paths of Bat 240 and Bat 256. (D) Flight path similarity was quantified by the number of points on the 2D surface below the threshold at 60% of peak cross-correlation. Red plots indicate the pairs flew in the opposite directions and black plots indicate the pairs flew in the same directions. The gray plots show the virtual pairs. In each box plot, the horizontal bar is the median, and the box indicates interquartile range (IQR) defined as the third quartile minus the first quartile. The whiskers show the range of values within  $1.5 \times$  IQR. Asterisk indicates significant differences in flight paths similarity ( $p < 0.05$ ).

and interpulse interval of echolocation pulses emitted during single and paired flights using linear mixed models (LMMs). The fixed effects were the flight condition (i.e., single flight or paired flight), the tested bats, and interaction of these two effects. Bat ID was included as a random effect. The significance of the model was assessed using a type II Wald  $\chi^2$ -test. Post-hoc comparisons were then performed, using the Tukey-Kramer method to correct for multiple comparisons.

We used the Wilcoxon signed-rank test to determine whether individual differences in the terminal frequency, bandwidth, duration, and interpulse interval of each pair were significantly different between the single and paired flight conditions. We defined individual differences in each pair as the difference in mean value of each acoustic characteristics.

We also tested whether flight paths were influenced by the presence of other bats. A Wilcoxon rank-sum test was used to compare flight path similarity between true and virtual pairs.

All analyses were performed using R software (version 4.0.2) [29]. We used the lmer function of the lme4 package (version 1.1.26) [30] for the LMMs, and the ANOVA function of the car R package (version 3.0.10) [31] for the type II Wald- $\chi^2$ -test. The emmeans function of the emmeans package (version 1.4.8) [a] was used for the post-hoc analysis, and the wilcox.exact function of the exactRankTests package (version 0.8.31) [b] was used for the Wilcoxon signed-rank test and Wilcoxon rank-sum test.

$p$ -values  $< 0.05$  were considered significant. Results are presented as mean  $\pm$  standard deviation.

### 3. Results

#### 3.1. Changes in Spectro-Temporal Features of Echolocation Sounds

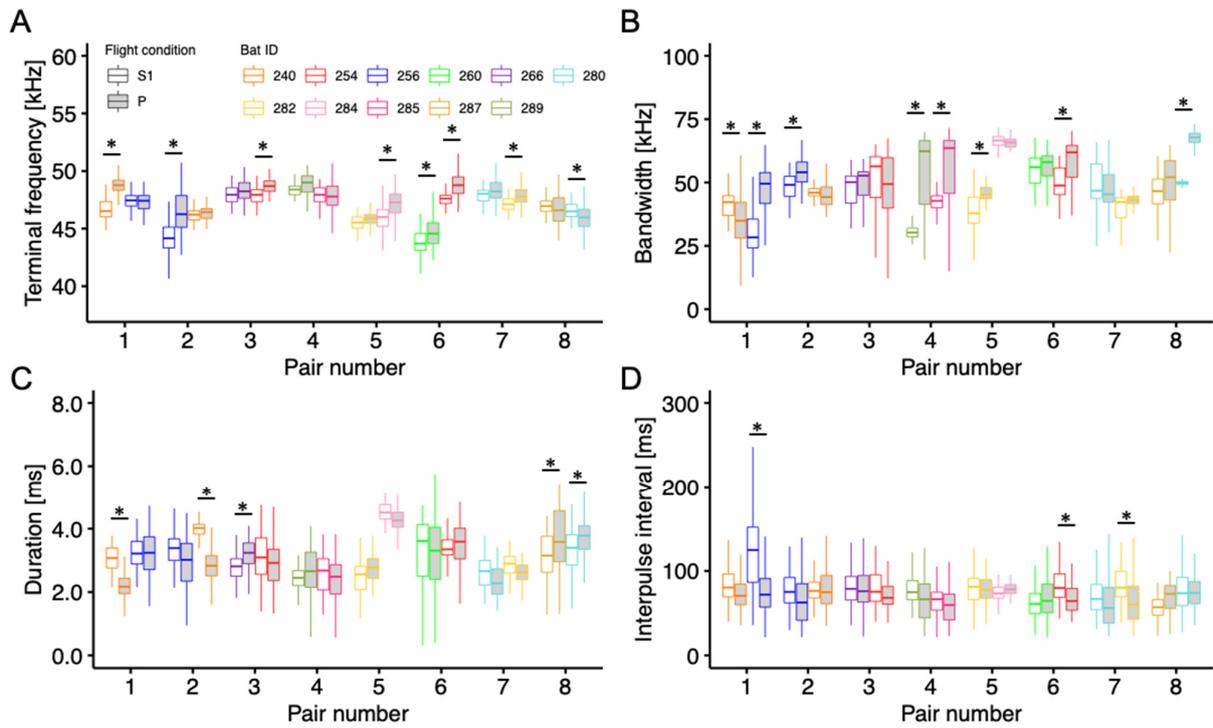
Using telemetry microphones, we successfully recorded the pulses emitted by individuals during paired flights (**Fig. 1(B)**). We compared the acoustic characteristics of the emitted pulses between single and paired flights, to investigate how they prevent or reduce acoustic jamming. For all acoustic characteristics tested, there was a significant individual  $\times$  flight condition interaction ( $\chi^2 = 480.30$ , d.f. = 15,  $p < 0.05$  for terminal frequency;  $\chi^2 = 651.22$ , d.f. = 15,  $p < 0.05$  for bandwidth;  $\chi^2 = 382.836$ , d.f. = 15,  $p < 0.05$  for duration;  $\chi^2 = 144.946$ , d.f. = 15,  $p < 0.05$  for interpulse interval).

There was a significant main effect of flight condition on terminal frequency ( $\chi^2 = 351.22$ , d.f. = 1,  $p < 0.05$ ). Post-hoc comparisons revealed that seven out of the eight pairs (8 of 16 individuals) showed significant changes in terminal frequency during paired versus single flights (Tukey-Kramer post-hoc analysis,  $p < 0.05$ ; **Fig. 3(A)**). However, individual differences in terminal frequency within pairs did not significantly increase during paired flights ( $1.1 \pm 1.1$  kHz during single flight vs.  $1.2 \pm 1.1$  kHz during paired flight; Wilcoxon signed-rank test,  $V = 10$ ,  $p = 0.3125$ ).

Similarly, bandwidth increased from  $45.3 \pm 9.1$  kHz during single flight to  $50.6 \pm 7.9$  kHz during paired flight ( $\chi^2 = 286.72$ , d.f. = 1,  $p < 0.05$ ). Six out of the eight pairs (8 of 16 individuals) significantly changed their bandwidth during paired compared to single flights (Tukey-Kramer post-hoc analysis,  $p < 0.05$ ; **Fig. 3(B)**), although the individual differences in bandwidth between the paired individuals were not significant during single or paired flight ( $9.8 \pm 8.8$  kHz vs.  $8.8 \pm 7.2$  kHz; Wilcoxon signed-rank test,  $V = 20$ ,  $p = 0.8438$ ).

The pulse duration decreased from  $3.1 \pm 0.5$  ms during single flight to  $3.0 \pm 0.6$  ms during paired flight ( $\chi^2 = 38.937$ , d.f. = 1,  $p < 0.05$ ). Four out of the eight pairs (5 of 16 individuals) significantly changed their pulse duration during paired flights compared to single flights (Tukey-Kramer post-hoc analysis,  $p < 0.05$ ; **Fig. 3(C)**). However, the individual differences in duration between paired individuals were not significantly different between single and paired flights ( $0.5 \pm 0.5$  vs.  $0.6 \pm 0.5$  ms; Wilcoxon signed-rank test,  $V = 19$ ,  $p = 0.9453$ ).

The interpulse interval increased from  $88.5 \pm 26.7$  ms during single flight to  $76.4 \pm 8.8$  ms during paired flight ( $\chi^2 = 47.704$ , d.f. = 1,  $p < 0.05$ ). Three out of the eight pairs (3 of 16 individuals) significantly changed their interpulse interval during paired flight compared to single flight (Tukey-Kramer post-hoc analysis,  $p < 0.05$ ; **Fig. 3(D)**). The individual differences in interpulse interval between the paired individuals significantly decreased

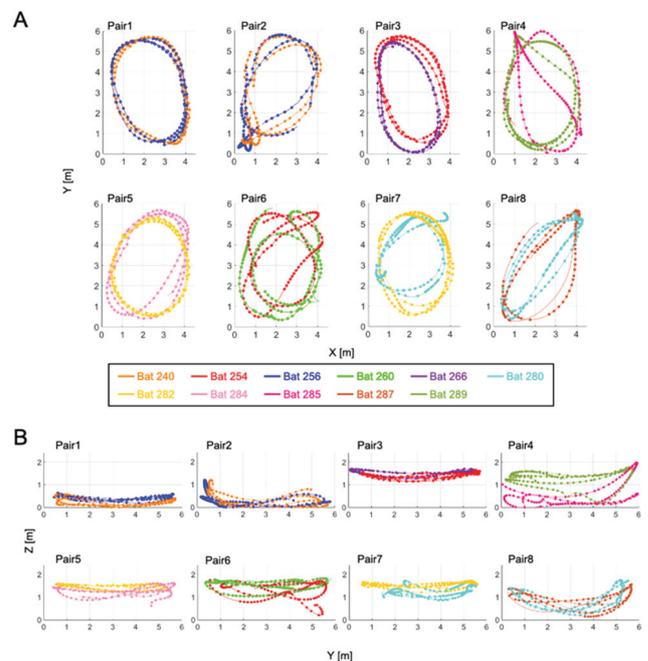


**Fig. 3.** Changes in the terminal frequency (A), bandwidth (B), duration (C), and interpulse interval (D) of the pulses emitted by each bat during single and paired flights. Asterisks indicate significant changes in acoustic characteristics according to post-hoc analysis following LMM ( $p < 0.05$ ). Line color represents bat ID. White represents single flight (S1) and gray represents paired flights (P). Of the four boxes of each pair, two boxes at left indicate a bat added first, and the others indicate a bat added next. In each box plot, the horizontal bar is the median, and the box indicates interquartile range (IQR) defined as the third quartile minus the first quartile. The whiskers show the range of values within  $1.5 \times$  IQR.

during paired compared to single flight ( $26.1 \pm 26.1$  vs.  $6.1 \pm 5.4$  ms; Wilcoxon signed-rank test,  $V = 36$ ,  $p < 0.05$ ).

### 3.2. Comparison of Flight Path Similarity Between Real and Virtual Pairs

The bats tended to fly near the edges of the flight space, in circular patterns (Fig. 4). In addition, the flight paths seemed to be similar within bat pairs. Of the eight tested pairs, five flew in the same direction, whereas three flew in the opposite direction while sound recordings were performed. We calculated the percentages of time spent in flight in the same directions by dividing time spent in the same direction by total time spent in flight. As a result, the mean percentage of time spent in flight in the same directions was  $75.2 \pm 20.2\%$  (94.3% in Pair 1, 84.3% in Pair 2, 88.3% in Pair 3, 63.9% in Pair 4, 99.3% in Pair 5, 38.0% in Pair 6, 68.0% in Pair 7, 65.7% in Pair 8). Even in the pairs where bats were flying in the opposite directions while sound recordings were performed, the percentages of time spent in flight in the same directions were 38.0%, 68.0%, and 65.7%. The results show that the paired bats spend more time in flying in the same directions. Because the flight altitudes of the paired bats were also similar, and the flight dynamics were mainly apparent in the horizontal plane, we focused on the similarity of flight trajectories in the horizontal plane. Flight path similarity was



**Fig. 4.** Flight trajectory of the bats during paired flights. (A) Top view. (B) Side view. Color represents bat ID. The bats in the Pairs 1–5 flew in the same directions while the bats in the Pairs 6–8 flew in the opposite directions.

slightly but significantly higher in the actual than virtual pairs ( $99.13 \pm 0.75\%$  vs.  $98.15 \pm 1.30\%$ ; Wilcoxon rank-sum test,  $W = 707$ ,  $p < 0.05$ ; **Fig. 2(D)**). Flight path similarity was also high within pairs of individuals that flew in the opposite direction.

#### 4. Discussion

Many studies suggest that FM echolocating bats shift the terminal frequency of their emitted pulses in the presence of other bats [13, 16, 32, 33] or jamming sounds [8–12]. These shifts may help the bats to reduce acoustic jamming. For example, even 1 kHz changes in the terminal frequency of pulse-like FM signals (corresponding to approximately 2% of the entire bandwidth) are sufficient to reduce the similarity between the signals [16]. In the present study, we found no significant changes in inter-individual differences in terminal frequency, although the bats tended to increase terminal frequency during paired flights compared to single flights. Acoustic characteristics other than terminal frequency also showed moderate changes. Changes in the pulse characteristics of *Carollia perspicillata*, evoked by playback of echolocation sequences as jamming signals, can vary among individuals, days, and trials, and even within trials [34]. Also, it is suggested that inter-individual frequency differences could help bats to discriminate their own sounds in acoustically complex situations [19]. We suggest that bats could discriminate their own sounds from those of other bats if inter-individual differences in pulse characteristics are sufficiently large.

Shifts in terminal frequency may be observed if the difference in terminal frequency between bats' own emitted sounds and jamming signals ranges from 2 to 5 kHz [11, 12]. The 2 kHz is relatively large relative to the inter-individual differences in terminal frequency of *M. fuliginosus* observed in laboratory flight experiments (approximately 1.2 kHz). However, we did not observe obvious frequency shifting behavior when bats flew in pairs. Several studies imply that spatial relationships among bats may play a significant role in how bats experience acoustic jamming [24, 26]. Therefore, the lack of frequency shifting observed herein could have been due to the spatial relationships between individuals.

In the present study, the paired bats spend more time in flying in the same directions than in the opposite directions. The bats showed almost circular flight paths, probably because they flew in a space without obstacles. Despite the similar circular flight paths of the different bats, the paths of bats were even more similar in the real than virtual pairs. This suggests that one bat tended to follow the other one during paired flights. In pairs of big brown bats, capture rates are higher in the following bat than in the leading bat [35]. Echolocating bats reportedly eavesdrop in certain situations, such as when hunting [4, 36] or during the mating season, i.e., when male bats need to make themselves more inconspicuous [37]. Our results imply that the following bat in a pair can eavesdrop on

the sounds of the leading bat for acoustic sensing or path planning, even when particular tasks are not being performed.

Taking a similar path may reduce acoustic masking from other bats flying together. Taub and Yovel demonstrates that when *Pipistrellus kuhlii* adjust angle of attack to improve the signal-to-noise ratio of echoes when they try to land on a small sphere placed in front of a large plastic board, where the echoes from the sphere could be masked by those of the plastic board [38]. Taking a similar path may also reduce the risk of collision, which could be more important in a larger group of bats. Further investigation is needed to confirm how flight paths that are similar between individuals are changed by bats to reduce acoustic jamming or eavesdrop on other bats.

When big brown bats fly in pairs during prey-tracking tasks, inter-individual differences in the acoustic characteristics of pulses, such as the terminal frequency and duration, increase as the distance between the individuals in the pair decreases [24]. In the present study, bats not completing particular tasks flew in a relatively large space with no obstacles. The task difficulty and interactions of individuals could affect whether acoustical jamming is avoided. To understand the perceptions of bats under conditions of acoustic interference, and their behavioral adaptation to reduce jamming, detailed examination of the relationships between the flight conditions and acoustic characteristics of echolocation pulses is necessary.

In conclusion, during paired flight, there was no clear trend for changes in the acoustic characteristics of the bats' echolocation sounds, but the flight paths of bats flying in pair became similar. We believe that spatial relationships between individuals might affect pulse acoustic characteristics. The following bat may experience less acoustic jamming and have more opportunity to eavesdrop on other bats' sounds.

#### Acknowledgements

We thank Dr. Kentaro Ito for his valuable comments and critique of the earlier draft. This work was supported by JSPS KAKENHI Grants JP16H06542 (Grant-in-Aid for Scientific Research on Innovative Areas), JP18H03786 (Grant-in-Aid for Scientific Research (A)), and JP19J02041 (Grant-in-Aid for JSPS Research Fellow).

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