

Effects of competitive prey capture on flight behavior and sonar beam pattern in paired big brown bats, *Eptesicus fuscus*

Chen Chiu^{1,2,*}, Puduru Viswanadha Reddy³, Wei Xian¹, Perinkulam S. Krishnaprasad^{2,4} and Cynthia F. Moss^{1,2}

¹Department of Psychology, University of Maryland, College Park, MD 20742, USA, ²Institute for Systems Research, University of Maryland, College Park, MD 20742, USA, ³Department of Econometrics and Operations Research, K519, Tilburg University, PO Box 90153, 5000 LE Tilburg, Netherlands and ⁴Department of Electrical and Computer Engineering, University of Maryland, College Park, MD 20742, USA

*Author for correspondence (chiuchen@gmail.com)

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SUMMARY

Foraging and flight behavior of echolocating bats were quantitatively analyzed in this study. Paired big brown bats, *Eptesicus fuscus*, competed for a single food item in a large laboratory flight room. Their sonar beam patterns and flight paths were recorded by a microphone array and two high-speed cameras, respectively. Bats often remained in nearly classical pursuit (CP) states when one bat is following another bat. A follower can detect and anticipate the movement of the leader, while the leader has the advantage of gaining access to the prey first. Bats in the trailing position throughout the trial were more successful in accessing the prey. In this study, bats also used their sonar beam to monitor the conspecific's movement and to track the prey. Each bat tended to use its sonar beam to track the prey when it was closer to the worm than to another bat. The trailing bat often directed its sonar beam toward the leading bat in following flight. When two bats flew towards each other, they tended to direct their sonar beam axes away from each other, presumably to avoid signal jamming. This study provides a new perspective on how echolocating bats use their biosonar system to coordinate their flight with conspecifics in a group and how they compete for the same food source with conspecifics.

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Key words: bats, classical pursuit, flight behavior, sonar beam pattern, jamming avoidance.

INTRODUCTION

Individual animals that fly within a group coordinate trajectories with other individuals. Each individual in the group senses the movement of other sufficiently close group members, and adjusts its own flight behavior in order to avoid collision and to maintain group coherence. Many animal species, such as fish (Parrish and Hamner, 1997), birds (Lebar Bajec and Heppner, 2009) and bats (Betke et al., 2007; Dechmann et al., 2010; Richard et al., 1962), aggregate in groups. When an echolocating bat flies in the same air space as conspecifics, it must both coordinate its flight path with others and adapt its echolocation calls to minimize interference from calls produced by conspecifics.

Previous research has demonstrated that the big brown bat uses a constant absolute target direction (CATD) flight strategy, which is nearly time optimal, to intercept its insect prey (Ghose et al., 2006). However, it is still an open question as to whether the big brown bat applies the same strategy when interacting with conspecifics. Two flight control strategies, classical pursuit (CP) and CATD, are examined here as possible strategies the bat may use to interact with another bat. The CP strategy refers to a configuration in which one animal always points its velocity vector towards the position of a target animal (Klamkin and Newman, 1971; Wei et al., 2009). When bats exhibit CATD, the lines joining the two animals' flight trajectories are parallel at any time, and hence the angle between the conspecific and a fixed reference is constant (Justh and Krishnaprasad, 2006). Based on the prior work, we are led to predict that paired big brown bats employ the same CATD strategy when they fly together as the strategy they use to pursue insect prey.

An animal in a group uses sensory input (e.g. vision, hearing or lateral line in the case of fish) to sense conspecifics' movements and to adjust its own movement (Parrish and Hamner, 1997). Because echolocating bats rely largely on listening to echoes reflecting from objects to track prey and other conspecifics/heterospecifics, the directional aim of the bat's sonar beam shows how the bat guides its flight through biosonar. The big brown bat emits sonar calls through the mouth, and its sonar beam is therefore aligned with its head. Prior research has demonstrated that the big brown bat's head leads the body as it flies, and tracks and intercepts insect prey (Ghose and Moss, 2006). However, the bat's sonar beam direction with respect to neighboring conspecifics has not been previously reported and is one focus of the present study. We hypothesize that the bat points its sonar beam alternately between the conspecific and the prey in order to track their positions and movements.

Because calls produced by echolocating bats are directional, it has been hypothesized that a bat can point its sonar beam away from conspecifics to avoid signal jamming with conspecifics (Simmons et al., 1995). Several jamming avoidance strategies used by echolocating bats have been reported, and all of these strategies involve modification in temporal/spectral features of self-generated signals (Bates et al., 2008; Chiu et al., 2009; Gillam et al., 2007; Obrist, 1995; Ulanovsky et al., 2004) or timing of signals (Chiu et al., 2008). However, no research so far has measured the sonar beam axes of two bats flying together and whether they adapt the directional sonar beam control to avoid signal interference. We predict that directing sonar beam axis away from another bat is

another jamming avoidance strategy the bat uses when flying with conspecifics.

In this study, we investigated flight trajectories and the sonar-beam-directing behavior of paired bats that were competing for a single prey item. Results from this study demonstrate how the big brown bat competes for a food source and coordinates its flight behavior with a conspecific nearby, what kind of pursuit strategy is used to interact with another conspecific, and how the bat controls its sonar beam to track objects of interest and avoid signal jamming.

MATERIALS AND METHODS

Animals

Five big brown bats, *Eptesicus fuscus* Beauvois, were used in this experiment and formed four pairs of bats. These bats were collected in Maryland, USA (collection permit #SCO 42501) and housed at the University of Maryland, College Park, MD, USA. Temperature and humidity were maintained constant at 24–28°C and 30–50%, respectively. The light:dark cycle in the housing facility was reversed by 12 h to ensure that bats were at their most active period during the behavioral experiments. Food (mealworms) and water (tap water/vitamin water) were provided on a daily basis. During training and experimental trials, food was only provided as a reward to motivate the bat to perform the required tasks. The mean mass for an adult big brown bat was 14–16 g, and the food deprivation was stopped if the bat lost 20% of its baseline mass. All animal care and experimental procedures were approved by the Institutional Animal Care and Use Committee at the University of Maryland, College Park, MD, USA.

Behavioral tasks

Experiments were conducted between July and September in 2005 and 2006. Each big brown bat was first trained to capture a tethered mealworm separately until the success rate to capture the worm was over 80%. Data recording began after all bats were fully trained. Two bats were released from the same spot in the flight room simultaneously to compete for a single tethered mealworm. The worm position changed between trials to prevent both bats from using spatial memory to localize the target. Trials ended when one bat made contact with the mealworm. Fifteen trials per day over a minimum of three test days, yielding at least 45 trials per bat pair, were recorded. Around 15–20 trials per bat pair were selected for detailed analyses because of their high-quality audio and video recordings.

Experimental setup and data recordings

All training and experiments occurred in a large flight room (7 m × 6 m × 2.5 m; length × width × height), lined with acoustic foam (Sonex, Illbruck, Minneapolis, MN, USA). Two high-speed cameras (240 frames s⁻¹; Kodak MotionCorder, San Diego, CA, USA) were placed in adjacent corners of the room to record the positions of bats, the tethered mealworm and the microphones. Only long-wavelength lighting (>650 nm) was available during data recording to restrict the bat from using visual cues to localize the target and conspecifics (Hope and Bhatnagar, 1979). Video recordings were later used to reconstruct the 3-D flight trajectory of each bat by a custom MATLAB (Mathworks, Natick, MA, USA) program. Three ultrasound-sensitive microphones (UltraSound Advice, London, UK) were placed on the floor to take calls produced by each bat and then stored in a Wavebook (IOTech, Cleveland, OH, USA; sample rate 250 kHz per channel). Audio recordings were analyzed by another custom MATLAB program. A 16-microphone (Knowles FG3329, Itasca, IL, USA) array was positioned along three walls

of the flight room to record the intensities of the bat's sonar emissions. The height of each microphone in this array was 0.9 m above the room floor and the spacing between two adjacent microphones was 1 m. Audio, recorded from three ultrasound-sensitive microphones on the floor and the microphone array on walls, and video recordings were simultaneously end-triggered after one bat made contact with the mealworm, and the preceding 8 s (240 frames s⁻¹) of data were stored.

Sonar beam direction analysis

The big brown bat's biosonar is directional, and the axis of sonar beam indicates the most intense part of its sonar emission. The direction of each vocalization's beam axis can be computed *via* intensities recorded by microphones on the U-shaped array. The sound intensity at each microphone was corrected for spherical loss and atmospheric absorption. Each vector length in Fig. 1 represents the corrected intensity of one sonar emission, and the vector direction is from the bat position toward each microphone on the array. The sum of these 16 intensity vectors yields the direction of the sonar beam axis. Detailed methods on correcting and normalizing sound intensities at each microphone and computing sonar beam axis have been reported previously (Ghose and Moss, 2003). The angle between the sonar beam axis and target of interest is the tracking angle, and two targets of interest in this study are the tethered mealworm and the moving conspecific.

Bat–bat pursuit strategies

Here we examine two pursuit strategies, CP and CATD, which the big brown bat may apply when pursuing conspecifics. We defined the leader as the bat that flew ahead and the follower as the bat that flew behind. These roles were defined strictly by the bats' relative positions and could be reversed at any time in the trial, e.g. when the follower overtook the leading bat. Two cost functions, Λ and Γ , were computed to examine how closely the leader–follower relationship matched, respectively, the CP and CATD strategies (Justh and Krishnaprasad, 2005; Reddy et al., 2006; Reddy, 2007; Wei et al., 2009). The cost function Λ is the cosine of the angle between the paired bats' separation vector and the vector representing the velocity of the follower. The cost function Γ is the cosine of the angle between the paired bats' separation vector and the vector representing the rate of change of this separation. The follower is in the CP state when $\Lambda = -1$ and it is in the CATD state when $\Gamma = -1$.

RESULTS

Flight behavior

Four pairs of big brown bats, including two male–male pairs, one female–male pair and one female–female pair, were analyzed in this study. The flight behaviors of paired bats can be categorized into three types, converging, diverging and following flight, according to the inter-bat heading angle (the angle between each bat's velocity vectors), and the angle between the paired bats' separation vector and velocity vector (Table 1). Detailed definitions of these flight behaviors were published in Chiu et al. (Chiu et al., 2008). Following flight refers to the flight behavior when one bat was behind the other bat and both flew in a similar direction (i.e. inter-bat heading angle smaller than 90 deg). During converging flight, the two bats flew towards each other, and during diverging flight the bats flew away from each other. On average, 75% of the time paired bats were in following flight, 16% of the time they were in converging flight, and the remaining 9% of the time they flew in diverging flight. The proportion of following flight is significantly

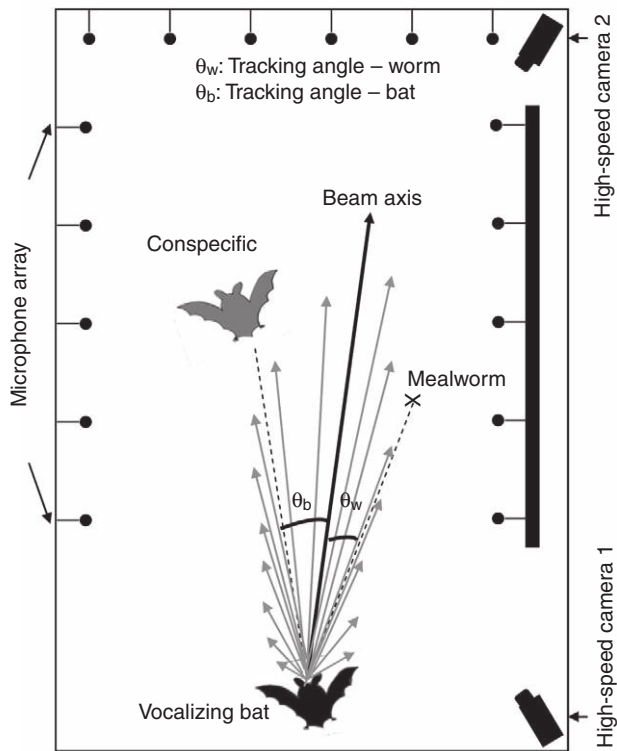


Fig. 1. Schematic of sonar beam pattern reconstruction for one bat. The vocalizing bat (color black) produced one vocalization. Each gray vector shows the intensity of this sonar emission received by each microphone on the array, and the direction of the sonar beam axis (thick black vector) indicates the direction of acoustic gaze. The sonar beam axis is the sum of these 16 intensity vectors. The tracking angle to the bat is the angle between the other bat and the sonar beam axis, while the tracking angle to the worm is the angle between the tethered mealworm and the sonar beam axis.

larger than the other two flight patterns [one-way analysis of variance (ANOVA), $P < 0.05$, Scheffé test for *post-hoc* test].

Bats in this study maintained small inter-bat distances and angular separations. The inter-bat distance in this study was rarely longer than 3 m, and the longest inter-bat distance was 4.18 m. Two

bats kept a distance shorter than 1 m over half of the time (60%), 30% of the time from 1 m to 2 m, and the rest of the time (9%) more than 2 m. Paired bats tended to maintain a small angular separation. Almost half of the time (48%), the angle between the two bats' heading directions was between 0 deg and 30 deg, 25% of the time between 30 deg and 60 deg, 11% of the time between 60 deg and 90 deg, and 16% of the time was over 90 deg.

Relative position of paired bats and their prey-capture performance: the whole trial

Big brown bats in this study flew mostly in following flight but their flight behavior and the relative position of paired bats were influenced by conspecifics. The relative position of paired bats affects an individual bat's prey-capture performance and there are potential advantages for both the leader and the follower. The bat flying in the lead may be able to capture the food reward more frequently than the follower, because it is closer to the tethered mealworm. However, the follower has the advantage of tracking the position of the leading bat. Therefore, the follower could capture the worm when the leader was away from the worm.

Fig. 2 shows the flight behavior, relative position of paired bats and their prey-capture performance for each pair of bats. Three male bats were studied in two male–male pairs, M1–M3 and M2–M3. About 82% of the time, bat pair M1–M3 flew in following flight and bat M3 flew behind M1 most of the time (90.49%) during following flight (Fig. 2A, left). Bat M3 also had a significantly higher prey-capture rate than bat M1 ($\chi^2 = 19.7$, $P < 0.0001$, Fig. 2A, right). Another male–male pair, M2–M3, showed different flight behavior from the M1–M3 pair. About 70% of the time they were in following flight and two-thirds of the time M2 was the follower (Fig. 2B, left). The prey-capture performance for bat M2 and M3 showed no significant difference between these two bats ($\chi^2 = 1.2$, $P = 0.27$, Fig. 2B, right). Bat M3 was paired with bat F2 to examine the interaction between male and female bats. The male bat M3 spent two-thirds of the time trailing the female bat F2 (Fig. 2C, left), and M3's prey-capture performance was significantly higher than the female bat F2 ($\chi^2 = 12.3$, $P < 0.0001$, Fig. 2C, right). However, when the female bat F2 was paired with another female bat F1 (Fig. 2D, left), almost 75% of the time it followed F1, and F2 also captured significantly more worms than bat F1 ($\chi^2 = 5.82$, $P < 0.05$, Fig. 2D, right).

Table 1. Definitions and examples of three different flight behaviors; following, converging, and diverging

Flight behavior	θ_1 and θ_2^*	α^\dagger	Example
Following	$\theta_1 \geq 90$ deg and $\theta_2 < 90$ deg or $\theta_2 \geq 90$ deg and $\theta_1 < 90$ deg	$\alpha < 90$ deg	
Converging	$\theta_1 < 90$ deg and $\theta_2 < 90$ deg	$0 \text{ deg} \leq \alpha \leq 180$ deg	
Diverging I	$\theta_1 \geq 90$ deg and $\theta_2 < 90$ deg or $\theta_2 \geq 90$ deg and $\theta_1 < 90$ deg	$\alpha \geq 90$ deg	
Diverging II	$\theta_1 \geq 90$ deg and $\theta_2 \geq 90$ deg	$0 \text{ deg} \leq \alpha \leq 180$ deg	

* θ_1 and θ_2 are the angles between each bat's velocity vector and the paired bats' separation vector, respectively. The subscript number indicates different bats.

$^\dagger \alpha$, angle between velocity vectors of the bats (inter-bat heading angle).

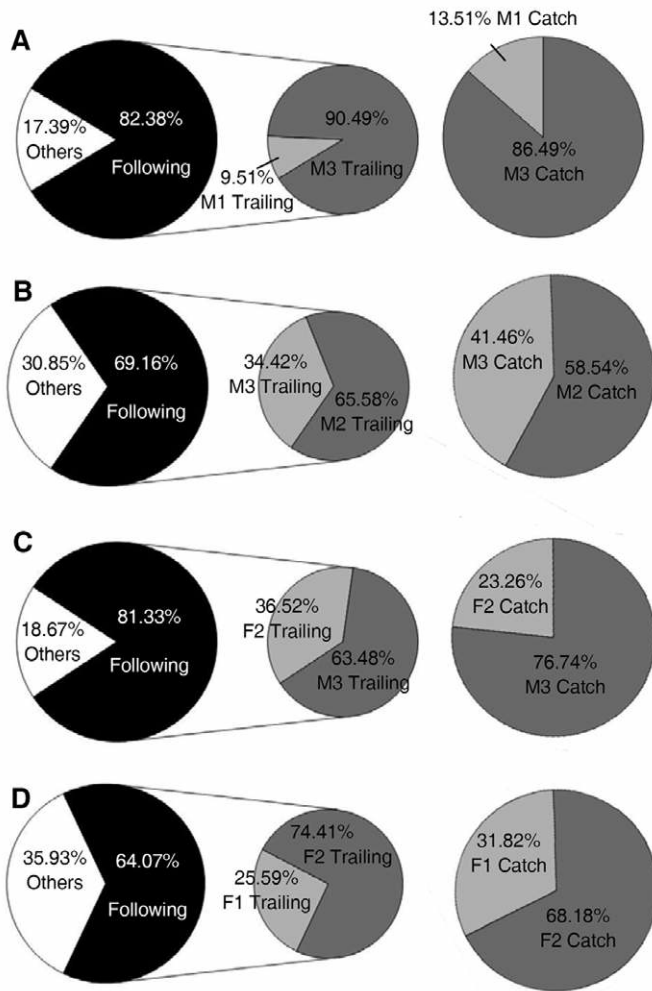


Fig. 2. The pie-of-pie charts on the left show the percentage of following flight and other flight behaviors (converging and diverging flight) for each of the bat pairs. The sub-pie charts (the pie that shows smaller values in the middle) show the relative position of each bat in a pair in following flight. The pie charts on the right show the prey-capture performance of each of the bat pairs: (A) M1–M3 pair; (B) M2–M3 pair; (C) F2–M3 pair; (D) F1–F2 pair.

The two bats in the pair competed to gain access to the tethered worm, because it was the only available food in the room and only one bat could capture it. The insect-capture success rate of a given bat depended on the individual it competed with. One bat might capture the worm most of the time when paired with a given bat but failed to capture the worm when paired with a different competitor. The prey-capture performance of one male bat, M3, was 86% when paired with another male bat, M1 (in the M1–M3 pair). The same individual only caught the mealworm 41% of the time when paired with the male bat, M2 (in the M2–M3 pair). The female bat, F2, successfully captured the worm 68% of the time when paired with the female, F1 (in the F1–F2 pair) but only caught the prey 23% of the time when paired with the male bat, M3 (in the F2–M3 pair).

Following flight was the most common flight behavior across all bat pairs. Bat pairs M1–M3 and F2–M3 showed more following flight, while M2–M3 and F1–F2 exhibited less following flight. It is noteworthy that the bat that spent more time as a follower throughout the trial had a higher prey-capture performance.

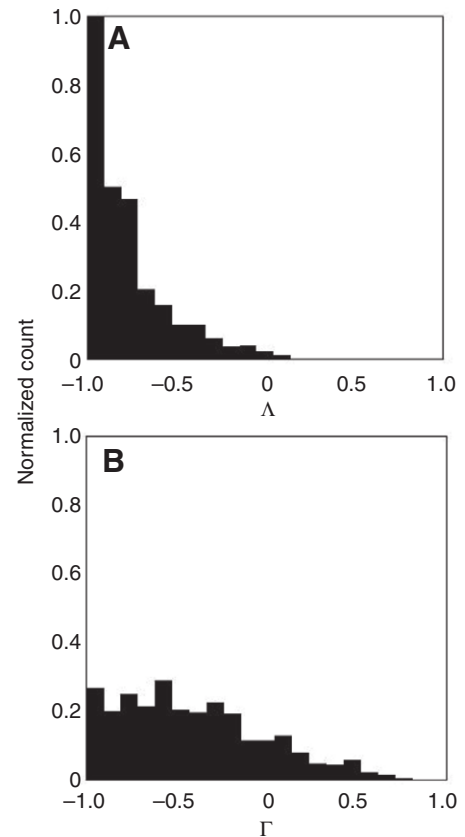


Fig. 3. Distribution of the cost function of two pursuit strategies: (A) classical pursuit (CP), cost function Δ ; and (B) constant absolute target direction (CATD), cost function Γ . The y-axis is normalized according to Δ because Δ has the maximum count.

Two females (F1 and F2) and three males (M1, M2 and M3) were used in this experiment, and a total of 10 possible bat pairs could be formed (only eight pairs were tested and four out of these eight pairs were analyzed in detail in this study). From the prey-capture performance shown in the four bat pairs above, bat F2 (68.18%) had better performance than F1 (31.82%), M3 (76.74%) was better than F2 (23.26%), M3 (86.49%) was better than M1 (13.51%), and M2 (58.54%) had a similar capture rate to M3 (41.46%). The prey-capture success rate was analyzed in the other four pairs but not their flight behavior data. We found that bat M2 (87.80%) performed better than F1 (12.20%) in the insect-capture task, M3 (85.96%) was better than F1 (14.04%), M2 (78.05%) was also better than M1 (21.95%), and M2 (66.67%) was better than F2 (33.33%). Therefore, we conclude that M2 and M3 were two bats with the best prey-capture performance among all five bats and they performed better than F2, which was better than F1. They were also more successful in catching prey than M1. However, the prey-capture performance rank is not clear between F1 and M1 or F2 and M2.

Relative position of paired bats and their prey-capture performance: within the final 1 s before prey capture

The bat that stays in the trailing position most of the entire trial was often more successful when capturing the prey than the leading bat. However, when data from the final 1 s before prey capture were analyzed separately, the leading bat had a higher prey-capture performance than the trailing bat. We divided our data into

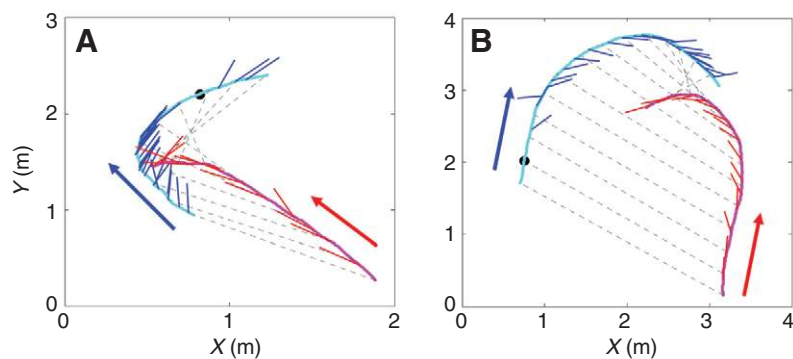


Fig. 4. Top view from two selected trials show flight behaviors and sonar beam directing patterns. Thick blue and pink lines represent flight trajectories of different bats. The black broken lines connecting these flight trajectories show the paired bats separation vector at different time indices. Each broken line is separated by 100 ms. Arrows point out the heading direction of each bat. The red and blue sticks represent the sonar beam direction of each vocalization produced by two different bats (marked in red and blue, respectively). The black dot indicates the position of the tethered worm. Different flight behaviors are shown in (A) Following flight; (B) converging and diverging flight. In both examples, the bat (marked in blue) attempted to capture the worm but failed.

three different time segments: 1000 ms, 750 ms, and 500 ms before prey capture. In addition, only data from trial segments in which paired bats flew in following behavior and when inter-bat distance was shorter than 1 m were analyzed separately here. When the bat was in the leading position 1000 ms before capturing its prey, 63.64% of the time it got the prey. The percentage of trial segments in which the leading bat captured the worm increased to 75% and 85.71%, respectively, in the 750 ms and 500 ms before target capture.

Bat–bat pursuit strategy

We analyzed the bat–bat pursuit strategy only when paired bats flew in following flight for longer than 1 s. The video segments corresponding to the terminal phase of insect capture were excluded, because the flight behavior in this trial segment is affected by the goal of prey capture. In addition, the following criteria were used to select out trial segments for analysis: (1) the spatial separation between paired bats in the selected trial segment was shorter than 1 m, and (2) the distance between paired bats was shortening.

The cost function, Λ or Γ , here is used to determine if the following bat used a CP or a CATD strategy. The trailing bat used a CP strategy to pursue the bat in front of it when $\Lambda = -1$, and it used a CATD pursuit strategy when $\Gamma = -1$. The closer the cost function was to -1 , the more the bat's flight behavior approached a pursuit strategy. Histograms of Λ and Γ are shown in Fig. 3. The peak of cost function Λ is centered on -1 , which indicates that paired bats relied most on the CP strategy to pursue the leader. The cost function Γ is more evenly distributed between 0 and -1 , which indicates that the trailing bat did not rely on the CATD strategy when pursuing another conspecific. In order to determine how long a trailing bat stayed in the CP or the CATD state when following the leading bat, the cost function value between -0.8 and -1 was selected to determine the pursuit strategy. The duration a bat pair remained in the state of CP was significantly longer than the state of CATD (CP for 50.54 ± 0.07 s, CATD for 22.42 ± 0.03 s, Mann–Whitney test, $P < 0.001$).

The direction of sonar beam emission

Six pairs of big brown bats [three pairs selected from previous study (Chiu et al., 2008) and three from this study] were chosen for sonar beam analysis, based on good signal-to-noise ratios of sonar call recordings with the U-shaped microphone array. A total of 93 trials were analyzed here. Fig. 4 shows two selected trials for different flight behaviors and the sonar beam pattern of paired bats. Fig. 4A shows an example of following flight, where one bat flew in front (leader, marked in blue) and the other bat followed behind (follower, marked in pink). A broken line connects the positions of paired bats every 100 ms, and the bat was considered to be pointing its sonar beam toward the other bat when the sonar beam direction overlapped with the broken line (± 15 deg). In this example, the leader kept its

sonar beam toward the tethered worm (the black dot) most of the time. The follower usually pointed its sonar beam toward the leading bat but also occasionally directed its beam toward the worm, e.g. note the fourth vocalization and the last few vocalizations. The leader attempted to capture the worm but failed to catch it. The second example (Fig. 4B) shows converging flight in the beginning of the trial and later diverging flight. Both bats in this example directed their sonar beams mostly away from the other individual, except the 8th to 10th vocalizations produced by one bat (marked in red). In addition, this bat pointed its sonar beam toward the prey item in the last few vocalizations in this example. The bat (not shown in the figure) but also failed to take it off the string. Please also see supplementary material Movie 1 for sonar beam pattern changes through the trial.

Sonar beam pattern, flight behavior and inter-bat distance

Data were divided into two categories according to the spatial separation of the bats and worm for each flight behavior. The left two panels in Fig. 5 show the sonar beam direction of the bat when it was closer to the tethered mealworm than to the conspecific while the right two panels show the bat's sonar beam direction when the inter-bat distance was shorter than the bat–worm distance. The tracking angle is the angle between the direction of the sonar beam and the object of interest (the conspecific or the worm). The smaller the tracking angle, the more accurately the bat directs its sonar beam axis toward that object. Bats did not show large differences in tracking angle when the distance to another bat was shorter or longer than to the mealworm, except in converging flight and part of following flight. In following flight, the leader often directed its sonar beam toward the tethered mealworm, rather than the conspecific, regardless of which object was closer (Fig. 5A). By contrast, the follower alternately pointed its sonar beam at the tethered worm and the other bat (Fig. 5B). The trailing bat directed its sonar beam axis closely toward the object of interest when that object was closer than the other one, because the peak tracking angles in both cases were centered on 0–10 deg. In converging flight, bats tended to point their sonar beams toward the worm when they were closer to the worm than the conspecific (Fig. 5C, left two panels). However, bats did not direct their sonar beam toward the other bat more often than toward the worm when the conspecific was the closer object than the tethered worm (Fig. 5C, right two panels). In diverging flight, the bat tended to point its sonar beam toward the worm rather than the other bat, even when the conspecific was closer to it (Fig. 5D). The bat often pointed its sonar beam axis toward the worm, rather than toward the other bat in most flight behaviors.

The tracking angle could also vary with the spacing between paired bats. Histograms in Fig. 6 show the distribution of tracking

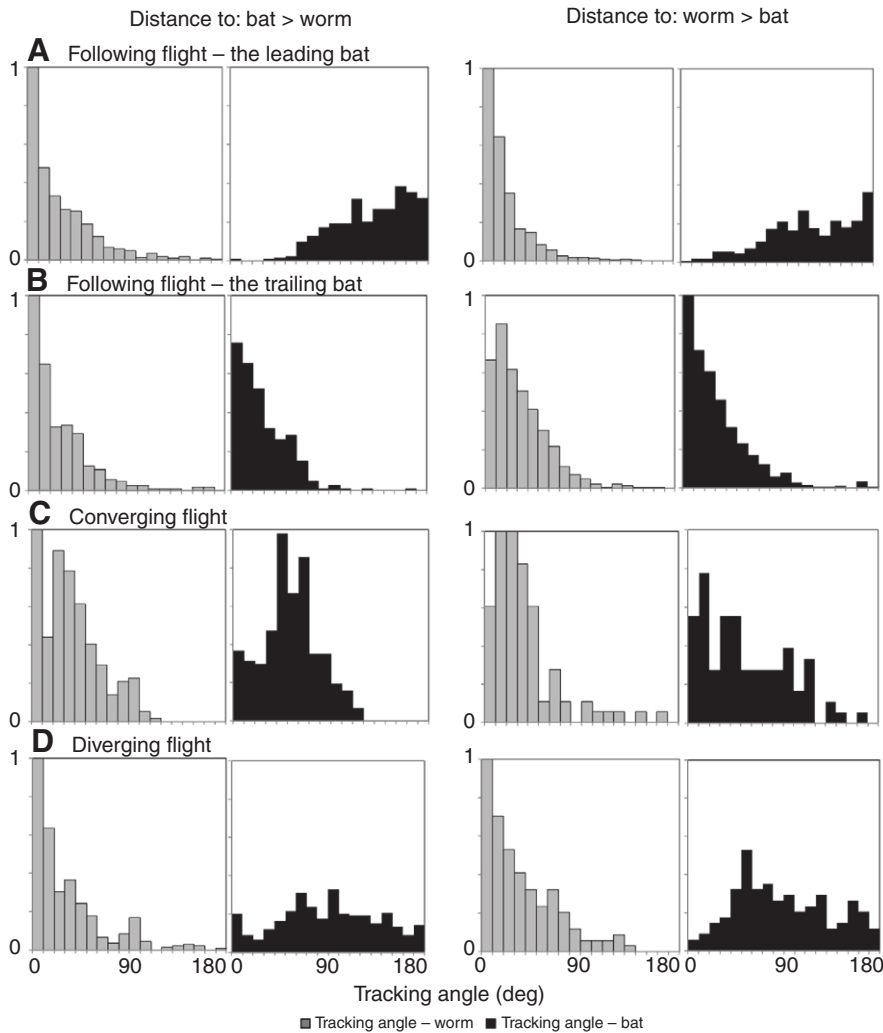


Fig. 5. Histograms of sonar beam pattern and flight behaviors when inter-bat distance was longer (left two panels)/shorter (right two panels) than the distance between the bat and the worm. The x-axis is the tracking angle toward the other bat (black) or worm (gray), and the y-axis is the normalized count. Three different flight behaviors are shown here: (A) leading bat and (B) trailing bat in following flight; (C) converging flight; and (D) diverging flight.

angles toward the conspecific at various inter-bat distances and in two different flight behaviors. Only data from converging flight and the trailing bat in following flight were analyzed here, because the position of the conspecific in these two conditions was always in front of or beside the bat. In addition, only data with both the position of the conspecific and the worm in front of the bat were chosen here in order to understand how the bat pointed its sonar beam when both objects of interest were in front. When the distance to the other bat was shorter than 0.5 m, the most frequent tracking angle toward the leading bat was between 0 deg and 10 deg (Fig. 6Ai); while the bat in converging flight pointed its beam to the side of the other bat, maintaining a tracking angle of 30–60 deg (Fig. 6Bi). As the inter-bat distance increased, the most frequent tracking angle toward the leading bat in following flight increased as well (Fig. 6Ai–Av). When two bats were farther apart, the trailing bat moved its sonar beam axis away from the leading bat. In converging flight, the most frequent tracking angle was between 30 deg and 60 deg when inter-bat distance was short, and smaller tracking angles, i.e. angle between 0 deg and 10 deg, occurred more often as paired bats moved farther apart (Fig. 6Bi–Bv).

DISCUSSION

Echolocating bats use auditory feedback to track objects of interest and to guide their flight behavior. In the present study, each bat in

the pair faced the following challenges: capturing the only prey item before its competitor, coordinating its flight behavior with that of the other individual to avoid collision, and minimizing signal interference with the echolocation calls of the conspecific.

The results of this study demonstrate that bats tended to fly in a leader–follower configuration, and individuals that spent more time as a follower throughout the trial tended to have a higher prey-capture success rate than the leaders (three out of four bat pairs showed this pattern). The flight behavior in this study can be regarded as illustrating a symmetric pursuit–evasion competition, which means that both the leader and the follower are interested in the same resource (in this case food), and the roles of the leader and the follower can be reversed between the two animals. Although one bat in a given pair tended to be a follower in most trials, their roles as the leader and the follower were sometimes changed within a trial.

Paired bats in this study did not apply the CATD strategy, as predicted before, to pursue conspecifics. Instead, they used the CP strategy when following another bat. This result suggests that big brown bats may decide in favor of different pursuit strategies when going after different targets for different purposes.

Bats of the same species usually have similar call design and the bat's echolocation can be disrupted by calls similar to its own (Masters and Raver, 1996; Masters and Raver, 2000). Because the

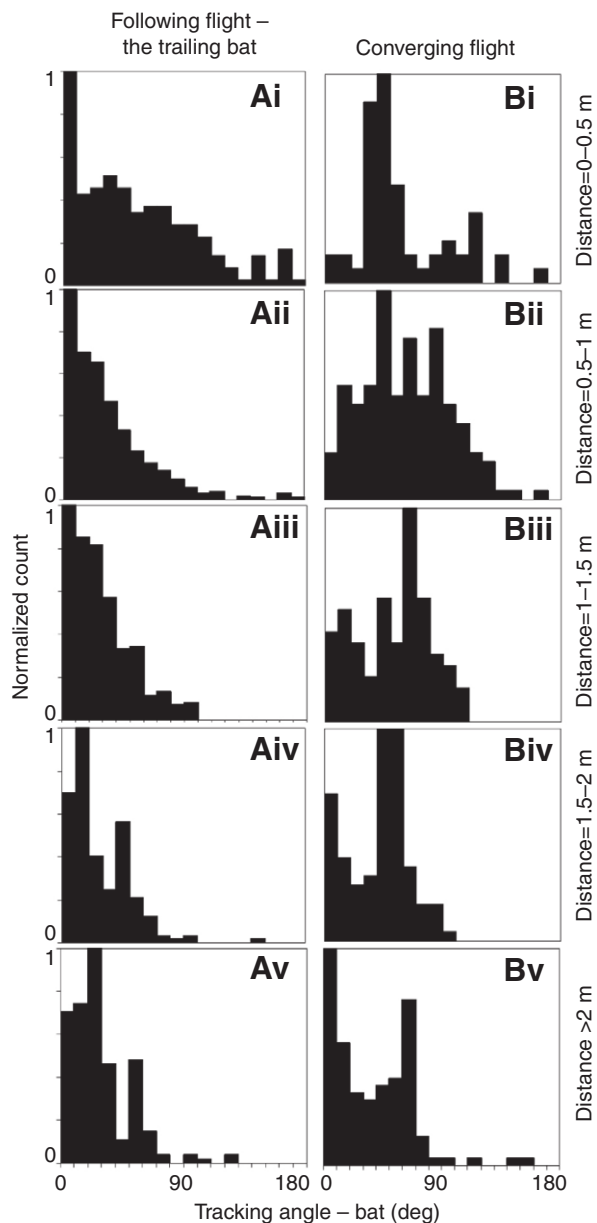


Fig. 6. Histogram of the tracking angle and the distance to the other bat when paired bats flew in converging flight and the trailing bat in following flight. The x-axis is the tracking angle toward the other bat, and the y-axis is the normalized count. Panels in the first column show the trailing bat's tracking angle toward the conspecific at different inter-bat separations: (Ai) 0–0.5 m, (Aii) 0.5–1 m, (Aiii) 1–1.5 m, (Aiv) 1.5–2 m, (Av) longer than 2 m. Panels in the second column show the tracking angle toward the conspecific at different inter-bat distances in converging flight: (Bi) 0–0.5 m, (Bii) 0.5–1 m, (Biii) 1–1.5 m, (Biv) 1.5–2 m, (Bv) longer than 2 m.

sonar beam of the bat is highly directional, the bat might point the sonar beam away from neighboring conspecifics as a strategy for jamming avoidance. When paired bats were in converging flight, they avoided pointing their sonar beams directly toward each other, presumably to avoid signal jamming. However, the trailing bat in following flight tended to direct its sonar beam axis toward the leading bat, because the trailing bat is not subject to interference from signals of the leading bat pointed in the same direction.

Following or chasing?

Bats in this study maintained close relative positions, and the follower directed its sonar beam axis toward the leader. Around 85% of the time the inter-bat heading angle was smaller than 90 deg, and 60% of the time the inter-bat distance was shorter than 1 m. Small angular and spatial separation suggests a tight flight formation between paired bats. Nearly 76% of the time one bat was following behind the other bat. The trailing bat in following flight often pointed its sonar beam toward the leading bat, and this result indicates that the trailing bat was tracking the movement of the leading bat in following flight.

It is still an open question whether the follower chased the leader or it just simply flew behind the leader. Chasing behavior is usually more aggressive than following. Following flight in this study was more likely to be a chasing behavior, especially those trials with male bats involved, because some physical contact between bats occurred and aggressive vocalizations were recorded in some trials. The bat spending more time as a follower typically showed higher prey-capture performance, which suggests that the follower may sometimes chase the leader away to intimidate it and to decrease competition for the food. Conspecific chases have been reported in several bat species, such as *E. fuscus* (Simmons et al., 2001) and *Lasiurus borealis* (Hickey and Fenton, 1990) in the field, but the purpose of this chasing behavior is still not well understood. The most likely purpose for the conspecific chasing behavior in this study is to defend the only food source and to capture the prey faster than the competitor.

Another possible explanation for following flight is that the follower wanted to conceal itself from the leader and to sneak up in order to capture the worm before its competitor. It has been demonstrated that big brown bats sometimes stop echolocation when flying in pairs (Chiu et al., 2008), and this silent behavior could also help them conceal their location from another bat in the room. Only few examples were found in this study that suggests stealth behavior; therefore, more evidence is needed to document this behavior.

Dechmann et al. reported 57% of group foraging in the bat species *Molossus molossus* in the field (Dechmann et al., 2010). They hypothesized that the purpose of this group foraging is to extend the detection distance to ephemeral food sources. However, cooperative foraging is less likely in the present study because the food source was limited. In addition, all bats which caught the tethered worms in this study produced feeding buzz, a series of short pulse interval, duration and bandwidth vocalizations generated by bats before prey capture. Therefore, extending the detection distance to prey or eavesdropping on other bats is unlikely to be the reason that big brown bats followed each other in this study. Reddy and Fenton also reported that red bats (*Lasiurus borealis*) in the field show neither cooperative foraging nor kleptoparasitism (theft of prey) behavior when conspecifics are in proximity (Reddy and Fenton, 2003).

Individual differences in flight behavior

Although males tended to show agonistic behavior when flying with conspecifics in this study, it is not conclusive whether there are sex differences in flight behavior due to the small sample size. The female–female pair showed less frequent following flight, compared with other pairs. Flight behavior and prey-capture performance are also influenced by the individual a bat was paired with. Both female bat F2 and male bat M3 modified their flight behavior when paired with different individuals. The female bat F2 often flew behind the other bat and caught significantly more worms when paired with F1. Its prey-capture performance decreased when paired with male

M3, and its role in following flight changed from the follower to the leader. Bat M3 caught significantly more worms than its competitor when paired with M1 and F2 but did not show a significantly higher prey-capture performance when paired with M2. Its relative position to the other bat also changed along with the individual it was paired with.

Previous studies have reported that female houseflies show different flight behavior than male houseflies (Wehrhahn, 1979; Wehrhahn et al., 1982; Zeil, 1986). Male houseflies usually defend their territory by chasing other males away, and they also chase other females for mating purpose. The turning angle and the turning speed of the male correlated with the error angle between the chasing and the chased flies. The same relationship was not observed in female houseflies when they flew behind another male or female. Wehrhahn et al. concluded that female tracking is less efficient than male tracking (Wehrhahn et al., 1982). Female flies do not pursue males for mating purpose; thus, the absence of a purpose for chasing may also be the reason that female houseflies did not use efficient tracking or chasing strategy.

Bat–bat pursuit strategy

Two cost functions are used in this study to determine which pursuit strategy bats used when following another conspecific. When the value of cost function Λ is -1 , it means that paired bats are in the CP state and the trailing bat uses the CP strategy to pursue the leading bat. When the value of cost function Γ is -1 , it means that paired bats are in the CATD state and the trailing bat uses the CATD strategy to pursue the leading bat. We examined two pursuit strategies here and concluded that the bat stayed in the nearly CP state ($\Lambda = -0.8$ to -1) more often than in the nearly CATD state ($\Gamma = -0.8$ to -1) when following the conspecific. Past research on big brown bats has reported that they use a CATD strategy to pursue flying insect prey (Ghose et al., 2006; Reddy, 2007) (P.V.R., K. Ghose, T. K. Horiuchi, E. W. Justh, P.S.K. and C.F.M., unpublished). The CATD strategy is considered to be a more efficient means to pursue the target than the CP strategy (Glendinning, 2004). However, this study demonstrated that the bat used a different strategy when following a conspecific. The use of different strategies may be due to the different nature of predator–prey pursuit behavior and conspecific following behavior. The insect prey often moves slower than its bat predator, but the bat and its conspecifics have similar flight speeds. The follower needs to divide its attention between the prey and the leading bat, but the leading bat has its beam directed exclusively toward prey. Importantly, the bat's goal is not to intercept and capture the other bat, but to reach the worm first.

Pursuit–evasion game

The comparison between predator–prey and bat–bat pursuit may not be the most appropriate one, because of relative speeds and final goals. A better comparison with bat–bat pursuit may be the game of tag, in which one person chases another and taps that person. The role of follower and leader is reversed once the follower successfully tags the leader. Reynolds simulated the game of tag by using two virtual vehicles and discovered that it is easier and faster for a follower to accomplish the task by running faster than the leader (Reynolds, 1994). This simulation is comparable with the observation of bat–bat interactions in this study.

The successful bat captured the worm when its competitor was, on average, 1.38 m away. This suggests that the bat may have tried to elongate the distance between itself and the competitor, before it engaged in the final prey-capture process (lock beam on

prey and attack). If the competitor was too close to the bat when it was nearing the worm, the competitor may have tried to interfere with the capture attempt. The advantage of being the leading bat if its distance to the trailing bat is long is that it can access the worm first. The disadvantage of being the leading bat is that its movement can be tracked by the trailing bat, and it is also more difficult for the leading bat to localize the competitor's position behind it. The advantage of being the trailing bat is that it can potentially engage in pursuit and chase its competitor away from the food. It can also accurately track the leading bat and devise a strategy to capture the worm. In addition, the trailing bat can conceal its presence by going silent and listening to the calls of the leading bat, a strategy reported by Chiu et al. (Chiu et al., 2008). This study showed that the bat that spent more time in the trailing position over the entire analyzed trial time was more successful in capturing prey. However, the bat in the leading position within the last 1 s of prey capture showed higher prey-capture success. This result suggests that the bat's most successful strategy may be to begin a trial in the trailing position and later switch to the leading position when close to the worm.

Sonar beam direction control

The big brown bat pointed its sonar beam toward the tethered worm when approaching the prey, and the accuracy of its tracking was within 3 deg (Ghose and Moss, 2003). Another study of obstacle avoidance and prey capture showed that the big brown bat's tracking accuracy toward obstacles and prey was within 15 deg (Surlykke et al., 2009). Both studies investigated the beam-directing behavior of a single bat. However, the mean tracking angles in this study (42 deg to the worm and 27 deg to the conspecific), which involved two bats, is much greater than the previous two studies. The difference between tracking accuracy between this and previous studies may be caused by differences across these behavioral tasks. Here, the bat needed to negotiate a moving obstacle, i.e. the competitor, and to track the prey at the same time. The bat in the previous two studies only needed to deal with a stationary target or stationary obstacle and tethered prey. For a complicated behavioral task, the bat may need to direct its sonar beam toward different objects of interest and cannot accurately direct its sonar beam on one thing for an extended period of time. For instance, when the bat pointed its sonar beam toward the worm, it may also need to turn its beam toward the other bat occasionally to prevent the other bat from getting the worm first. Therefore, the difference in measured tracking angles toward different objects could decrease accuracy of beam directing behavior.

Directional control of the sonar beam to avoid signal jamming

The echolocating bat's sonar beam is directional; thus, it is possible that the bat could turn away its sonar beam to avoid signal jamming. By avoiding overlap of the most intense part of the sonar beam, paired bats may be able to limit signal jamming (Simmons et al., 1995). This study shows that when two bats flew toward each other (converging flight) they seldom pointed their sonar beam toward conspecifics. However, when one bat was following another bat, the trailing bat consistently directed its sonar beam toward the leading bat. The different sonar beam tracking behaviors in the different flight behaviors observed in this study suggests that sonar beam pointing can serve as a means for the bat to reduce signal jamming from conspecifics in its proximity. Ulanovsky et al. also suggested that the bat's directional sonar beam could suppress the interference from the sonar of conspecifics (Ulanovsky et al., 2004).

Conclusions

Simmons et al. observed two big brown bats chasing each other in an aerial dogfight in the field (Simmons et al., 2001). However, the individual's flight behavior and its position relative to neighboring conspecifics have not been addressed in previous studies of multiple bats' flight behavior. This study showed that bats tended to follow each other and maintain close relative positions when they flew in pairs. Bats used the CP strategy to follow conspecifics, rather than CATD strategy, which is used when a single bat pursues moving prey. Results from this study suggest that individual bats in a group may also apply the CP strategy in order to maintain group coherence and avoid collision with nearby conspecifics. In addition, bats could control their sonar beam direction and timing/intervals of echolocation calls to avoid signal jamming when flying in a group. This study lays the foundation for field studies of individual flight behavior and coordinated flight in groups of bats.

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