

White-winged vampire bats (*Diaemus youngi*) exchange contact calls

G.G. Carter, M.B. Fenton, and P.A. Faure

Abstract: Temporally precise vocal exchanges, termed “antiphonal calling”, might allow pair or group members to maintain social contact with greater efficiency than when calling independently. The white-winged vampire bat (*Diaemus youngi* (Jentink, 1893)) is a group-living species that produces social calls in antiphonal exchanges. Because white-winged vampire bats can use social calls to discriminate conspecifics, we suspect that one function of these vocal exchanges is to allow group members to know who is where. Here, we tested the prediction that antiphonal calling by groups of white-winged vampire bats increases when the spatial positions of conspecifics change. We recorded social calls from groups of four individually caged bats in total darkness, with each bat located in the corner of a 4 m × 4 m room. During test trials, we shifted the spatial positions of caged bats to new positions. During control trials, caged bats were displaced an equal distance but were returned to their original positions. We found that both the number of social calls and the proportion of antiphonal exchanges were greater during test trials than during control trials. These results suggest that white-winged vampire bats use antiphonal exchanges of social calls to monitor the spatial positions of conspecifics.

Résumé : Des échanges vocaux de grande précision temporelle, appelés « appels antiphoniques », peuvent permettre à des couples ou des membres d’un groupe de maintenir un contact social beaucoup plus efficacement que les appels individuels. Le vampire à ailes blanches (*Diaemus youngi* (Jentink, 1893)) est une espèce qui vit en groupes et produit des appels sociaux lors échanges antiphoniques. Parce que les vampires à ailes blanches peuvent utiliser les appels sociaux pour reconnaître les individus de même espèce, nous soupçonnons qu’une des fonctions de ces échanges vocaux est de permettre aux membres du groupe de connaître l’emplacement de chacun des individus. Nous vérifions ici la prédiction que les appels antiphoniques par des groupes de vampires à ailes blanches vont augmenter lorsque la position spatiale des individus de même espèce est modifiée. Nous avons enregistré les appels sociaux de groupes de quatre chauves-souris dans des cages individuelles en obscurité totale, chaque chauve-souris étant placée dans un coin d’une chambre de 4 m × 4 m. Durant les essais expérimentaux, nous avons déplacé les chauves-souris encagées vers de nouveaux emplacements. Durant les essais témoins, les chauves-souris ont été déplacées d’une même distance, mais retournées à leur position initiale. Tant le nombre d’appels sociaux que la proportion des échanges antiphoniques sont plus importants durant les essais expérimentaux que durant les essais témoins. Ces résultats laissent croire que les vampires à ailes blanches utilisent les échanges antiphoniques d’appels sociaux pour connaître et suivre les emplacements des individus de leur propre espèce.

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Introduction

Some bats roost, commute, or forage in groups with stable memberships, or even coordinate their flight activity (reviewed by Wilkinson 1995; see also Brown et al. 1983; Wilkinson and Boughman 1998; Adams and Simmons 2002). Groups of bats can perform these activities in darkness, in three spatial dimensions, and through complex, cluttered environments. To accomplish such coordination, bats must identify the positions of conspecifics either by eavesdrop-

ping on their echolocation calls (e.g., Gillam 2007) or through intentional signaling with “social calls” (e.g., Wilkinson and Boughman 1998). Although researchers recognize the importance of pup isolation calls for mother–pup reunions in bats (Wilkinson 2003; Bohn et al. 2006), very little is known about if and how adult group-living bats use social calls to maintain contact (but see Wilkinson and Boughman 1998).

White-winged vampire bats (*Diaemus youngi* (Jentink, 1893)) are group-living neotropical bats that produce high-frequency echolocation calls (frequency of maximum energy ca. 63 kHz) and emit lower frequency social calls (frequency of maximum energy ca. 21 kHz). We hypothesized that social calls can function to maintain vocal contact with conspecifics because these calls attract roostmates, are produced by isolated or moving individuals of both sexes, and allow conspecifics to discriminate between individuals (Carter et al. 2008). White-winged vampire bats also participate in bouts of “antiphonal calling”, where a bat produces a social call immediately after a conspecific. We defined an antiphonal response as a social call within 500 ms of a social call from a conspecific (mean vocal latency = 230 ms, SD = 130 ms; G.G. Carter unpublished data; see also Carter

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et al. 2008). We then suggested that antiphonal exchanges allow groups of two or more bats to maintain social contact more reliably than when each individual calls independently (Carter et al. 2008). Antiphonal responses could benefit the responding bat when its vocalizations influence the initial caller's orientation, loudness, and calling rate. Two bats could therefore mutually benefit by trading cues to each other's identity and location. Such rapid feedback could help bats coordinate group activities or maintain social contact when conspecifics rapidly shift position, as when traveling or foraging in a group.

Here, our goals were to determine if groups of white-winged vampire bats would produce (i) more social calls and (ii) a higher proportion of antiphonal responses after we shifted the relative spatial positions of individuals in the group. We recorded social calls of white-winged vampire bats after two conditions. For test trials, we shuffled the relative spatial positions of four individually caged bats while holding interindividual distances constant. For control trials, we performed a sham shuffle by moving caged bats in a similar manner then returning them to their original spatial location. We predicted that during test trials, the bats would produce more social calls and also be more likely to respond to others, compared with control trials. We thus expected an increase in total social calling and the proportion of antiphonal responses (i.e., calls occurring within 500 ms of a conspecific call) relative to independent (i.e., non-antiphonal) calls.

Materials and methods

Our research was in accordance with the *Guide to the Care and Use of Experimental Animals* published by the Canadian Council on Animal Care, Ottawa, Ontario. We conducted experiments with 16 captive adult white-winged vampire bats (7 females, 9 males) housed in New Mexico (Carter et al. 2008). During experiments, we placed individual bats in soft nylon cages (36 cm × 36 cm × 64 cm; Apogee Reptarium) and positioned each in one of four corners of a 4 m × 4 m room lined with anechoic foam. We made simultaneous vocal recordings from each caged bat using four synchronized CM16 ultrasonic condenser microphones (flat ± 5 dB 10–150 kHz; Avisoft Bioacoustics, Berlin, Germany) and digitized sounds at 250 kHz and 8-bit resolution with an Avisoft UltraSoundGate 416 connected to a PC laptop running Avisoft Recorder USG software. One microphone was placed 5–20 cm in front of each bat and was directed away from the other three bats in the room. This setup allowed unambiguous assignment of calls to individuals.

We recorded calls over four nights with four different individuals each night. We recorded 134 three-minute trials, each randomly assigned to either the test or control treatments. In test trials ($n = 69$), an experimenter with a red light entered the room, moved all cages to the centre of the room, and then placed each cage into a predetermined corner as follows: one cage chosen at random was returned to its original position, and the other three cages were randomly rotated either clockwise or counterclockwise. This shuffling pattern resulted in each individual having a different conspecific to its right, left, and front after the shift.

After shuffling cage positions, the experimenter left the room and the 3 min recording trial began. In control (sham shuffle) trials ($n = 65$), an experimenter with a red light entered the room, moved all cages to the centre of the room, and then returned each cage to its original position. Care was taken to displace bats an equal distance during test and control trials. All recording took place in total darkness.

Social calls of white-winged vampire bats typically contain two continuous spectrogram elements (i.e., syllables). We used CallViewer 15 (Skowronski and Fenton 2008) to automatically count the number of antiphonal social calls using a band-pass detection filter (analysis bandwidth 10–30 kHz). In each trial, we calculated the mean number of syllables per individual (total syllables divided by four bats) and compared the number of social call syllables produced during test and control trials.

We used Avisoft SASLab Pro to validate our social call count and to determine the number of social calls that were antiphonal responses. We measured the start and end time, duration, and frequency at maximum amplitude for all social calls that were 25 dB greater than the sound floor. We used duration and frequency measurements to exclude echolocation pulses from our data set. This automated approach was previously tested and validated against hand-measured calls (Carter et al. 2008). We counted social calls as antiphonal responses when they occurred <500 ms after the onset of a call from a conspecific, but not if they overlapped or began within 8 ms of a conspecific call (i.e., if they started within the approximate sound travel time between bats in the room). We compared the number and proportion of antiphonal responses in test and control trials using nonparametric Mann–Whitney U tests and χ^2 tests in JMP version 7 (SAS Institute Inc., Cary, North Carolina) with a comparisonwise error rate of $\alpha \leq 0.05$ for all statistical tests (Zar 1984).

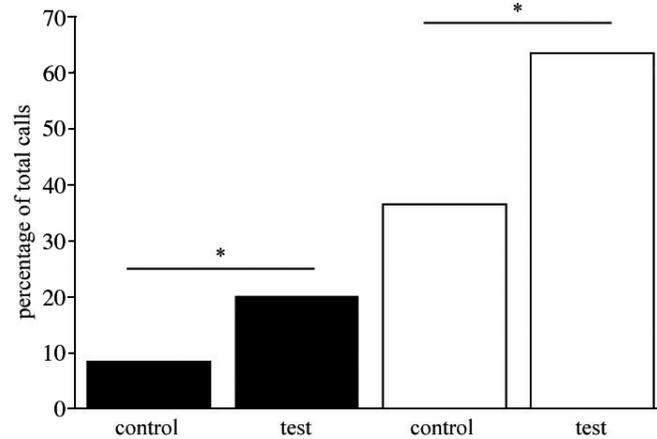
Results

White-winged vampire bats stopped calling, or dramatically reduced their calling rate, whenever the experimenter entered the room. Bats almost always resumed calling immediately after the experimenter left and shut the door.

Bats produced significantly more social calls during test trials when they were shifted to new spatial positions than during control trials when they were displaced an equal distance but then returned to their original locations (Mann–Whitney U tests; group 1: $n = 31$ trials, $U = 3.26$, $p = 0.001$; group 2: $n = 39$ trials, $U = 2.25$, $p = 0.024$; group 3: $n = 28$ trials, $U = 2.22$, $p = 0.026$; group 4: $n = 36$ trials, $U = 2.10$, $p = 0.035$; Fig. 1). Of the total social calls recorded, 63.5% occurred during the 69 test trials, while 36.5% occurred during the 65 control trials (Table 1).

Treatment type also influenced the relative proportions of antiphonal and independent social calls. Test trials contained a significantly higher percentage of antiphonal responses than control trials (Pearson χ^2 tests; group 1: $n = 5378$ calls, $\chi^2 = 50.92$, $p < 0.001$; group 2: $n = 3182$ calls, $\chi^2 = 9.81$, $p = 0.002$; group 3: $n = 857$ calls, $\chi^2 = 4.08$, $p = 0.043$; group 4: $n = 353$ calls, $\chi^2 = 19.45$ calls, $p < 0.001$; Fig. 1). During all test trials, 32% of social calls were antiphonal responses, whereas during all control trials, 23% of social calls were antiphonal responses (Table 1).

Fig. 1. Percentage of total social calls shown for antiphonal responses only (solid bars) and all social calls (open bars) during test trials when the spatial position of caged white-winged vampire bats (*Diaemus youngi*) were shuffled, and during control trials when the cages were “sham shuffled” (i.e., returned to their original spatial position). Significant differences indicated by an asterisk were found for each of the four groups (see text).



Discussion

All four groups of bats produced more social calls when we shuffled the relative positions of individual bats than when we sham shuffled them, by displacing individuals the same distance and then returning them back to their original positions. In other words, bats called more after disturbance events that shuffled conspecific positions than after disturbance events that did not. The reaction of the bats suggests they can remember and match previous identities of conspecifics with new spatial locations. Therefore, these results also support our earlier report that white-winged vampire bats can vocally discriminate individuals using social calls (Carter et al. 2008). Thus, white-winged vampire bats can use social calls to both discriminate between, and monitor the positions of, conspecifics. Such vocalizations have been reported from a wide variety of social birds and mammals, and are often known as “contact calls”. Past studies have shown correlations between contact calling rate and distance to conspecifics (Boinski 1991) or habitat visibility (Koda et al. 2008). Here, we controlled for distance to show that shifting the spatial positions of conspecifics can also increase the rate of contact calling.

In test trials, bats not only increased the total number of calls but also increased the proportion of antiphonal vocal responses. This suggests that temporal precision plays a role in tracking conspecific locations. Evidence that antiphonal responses enhance contact maintenance also comes from studies of pairs of black-bellied wrens (*Thryothorus fasciatoventris* Lafresnaye, 1845) (Logue 2007) and affiliated female African elephants (*Loxodonta africana* (Blumenbach, 1797)) (Leighty et al. 2008), where antiphonal responses increased the likelihood that two focal individuals would subsequently move closer to each other.

We cannot exclude the possibility that bats were responding to a change in absolute location in the world rather than to a relative change in the position of conspecifics. There is evidence that some bats can detect the earth’s magnetic field

Table 1. Number of antiphonal responses and independent social calls produced by white-winged vampire bats (*Diaemus youngi*) during test and control trials.

	Social calls		
	Antiphonal	Independent	Total
Test (shuffle)	1961	4244	6205
Control (sham shuffle)	828	2737	3565
Total	2789	6981	9770

Note: Social calls were scored as antiphonal responses when they occurred between 8 and 500 ms following a social call from a conspecific (Carter et al. 2008).

for use in homing and long-distance migration (Holland et al. 2006) through a polarity-based magnetic compass (Wang et al. 2007). Therefore, theoretically an increase in social calling by white-winged vampire bats could have resulted if bats were responding to a change in their absolute location (“map” sense) or the direction of conspecifics (magnetic “compass” sense). It is also possible that bats detected a change in their location through room acoustics. Regardless, a change in absolute location by itself does not lead to increased social calling in other contexts (Carter et al. 2008).

We conducted our study with 16 captive white-winged vampire bats of unknown relatedness that have been living together for at least 5 years. We do not fully understand how and when social calls are used by free-ranging white-winged vampire bats because there are no published reports on social behaviour in the wild. Based on the contexts in which social calls are produced, they seem not to function primarily as alarm, mating, or food advertisement signals because they are produced in the absence of human disturbance, by both sexes and to both sexes, in the absence of food, and by bats as young as 4 months. Indeed, the most reliable way to record social calls from white-winged vampire bats is to physically isolate individuals but allow them to remain in acoustic contact with each other (Carter et al. 2008).

Contact calls in other bats

Several anecdotal reports and a few detailed studies provide evidence of contact calls in other bat species (reviewed by Fenton 1985, 2003). So far, researchers have described four basic types of contact calls in bats. (1) Adult female greater spear-nosed bats (*Phyllostomus hastatus* (Pallas, 1767)) produce “screech calls”, which are socially learned, group-specific contact calls (Boughman 1998; Boughman and Wilkinson 1998). Evidence from free-ranging greater spear-nosed bats suggests that the harsh, atonal, and broadband screech calls are used to coordinate group movements and foraging (Wilkinson and Boughman 1998). (2) Pups of every bat species examined produce “isolation calls” that facilitate recognition by and reunions with mothers (Wilkinson 2003; Bohn et al. 2006). Unlike screech calls, isolation calls are tonal, frequency-modulated sweeps that are usually individually distinct (Wilkinson 2003; Bohn et al. 2007) and often have two elements (i.e., double-notes: Gould et al. 1973). (3) Adult bats of some species respond to pups with distinctive tonal “directive calls” (e.g., Brown et al. 1983; Balcombe and McCracken 1992) or echolocation-structured pulses (e.g., Matsumura 1981). And as in adult white-winged vampires, mothers and pups of some bat

species exchange social calls in an antiphonal pattern (Matsumura 1981; Brown et al. 1983; Knörnschild and von Helversen 2008). (4) Finally, some social calls appear to be directed at other adults while foraging (Fenton 2003; Pfalzer and Kusch 2003), but in these contexts, their functions are unclear and may be inconsistent across species. Barlow and Jones (1997) found that playback of the tonal social calls of the aerial hawking insectivorous common pipistrelle (*Pipistrellus pipistrellus* (Schreber, 1774)) repelled conspecifics. Similarly, Lemke (1984) observed that Pallas's long-tongued bats (*Glossophaga soricina* (Pallas, 1766)) produced social calls only when chasing competitors away from flowers. Therefore, we suggest that group-foraging bats that feed on dense patches of food (e.g., vertebrate blood, trees with ripe fruit) might use social calls to alert and attract conspecifics to a concentrated food resource, perhaps for cooperative group defense (Wilkinson and Boughman 1998). Alternatively, for bat species where individuals forage independently, bats may produce social calls to regulate spacing between competitors (e.g. Radford and Ridley 2008).

Antiphonal responses as cooperation

In several social birds and mammals, individuals precisely “answer” the calls of conspecifics. Examples include vocal duetting in 200+ species of birds (Hall 2004; Logue 2007), whistle matching in bottlenose dolphins (*Tursiops truncatus* (Montagu, 1821)) (Janik and Slater 1998; Janik 2000), antiphonal long calls of cotton-top tamarins (*Saguinus oedipus* (L., 1758)) (defined as a reply within a 5 s latency; Weiss et al. 2001), and the antiphonal rumble vocalizations of African elephants (defined as a reply within a 30 s latency; Soltis et al. 2005). Contact maintenance is a secondary function of song duets in avian pairs (Logue 2007), but it is considered the primary function of more simple antiphonal exchanges. Antiphonal contact calls are common in several species that travel or forage in groups (e.g., Lamprecht et al. 1985; Biben et al. 1986; Sugiura 1993; Janik and Slater 1998; Janik 2000; Weiss et al. 2001; Miller et al. 2004; Soltis et al. 2005; Yosida et al. 2007). Yet, in most cases of contact calling, isolated individuals vocalize independently rather than in precise antiphonal sequences. What then might be the benefit of precise antiphonal responses over independent calling?

We suggest that most antiphonal responses to contact calls are cooperative (sensu West et al. 2007), and hence provide fitness benefits to the receiver of the response, such as signaling who is where (e.g., Miller et al. 2004) and reducing the waiting time for a response (Lamprecht et al. 1985). In some cases, antiphonal responses might be selfish if, for instance, responses are used to attract a passing conspecific to an unrelated, unfamiliar lost caller; however, this cannot provide a general explanation for the evolution of antiphonal calling because signaling honest information, such as caller identity and location, normally benefits a receiver. If antiphonal responses are cooperative, then they might arise from kin altruism if the callers are related, or through mutual benefit (sensu West et al. 2007) if the responder also instantly benefits from having conspecifics know its identity and location. In these cases, the direct or indirect fitness benefits of responding would outweigh the benefits of only listening to such calls. Alternatively, the benefits of responding might be

less than those of only listening. In other words, there is no immediate incentive for any individual to respond. Antiphonal contact calling might still evolve under these conditions if the following additional conditions were met: (i) the benefits of hearing and responding are greater than the benefits of no calling from either bat, (ii) the benefits of no calling from either bat are greater than the benefits of calling with no response from a conspecific, and (iii) the chance of interacting with the same bat again exceeds the cost to benefit ratio of responding (Axelrod and Hamilton 1981; Nowak 2006). In this scenario, which resembles the “iterated prisoner’s dilemma”, the classic stable strategy, “tit for tat”, equates to calling initially and then responding thereafter (i.e., antiphonal exchanges). This vocal reciprocity could result from a genetic predisposition (evolutionary stable strategy) or from a socially mediated form of operant conditioning (developmentally stable strategy; Dawkins 1980).

We plan to investigate explanations for antiphonal calling through further analyses of the conditions that promote or reduce antiphonal exchanges. Future experiments on white-winged vampire bats will examine the effects of prior vocal interactions and the relatedness of signalers and receivers on the probability of responding antiphonally.

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