

# Frequency shifting reduces but does not eliminate acoustic interference between echolocating bats: A theoretical analysis

Melinda L. Perkins, Hannah K. Frank, John M. Pauly, and Elizabeth A. Hadly

Citation: [The Journal of the Acoustical Society of America](#) **142**, 2133 (2017); doi: 10.1121/1.5006928

View online: <http://dx.doi.org/10.1121/1.5006928>

View Table of Contents: <http://asa.scitation.org/toc/jas/142/4>

Published by the [Acoustical Society of America](#)

---

---

# Frequency shifting reduces but does not eliminate acoustic interference between echolocating bats: A theoretical analysis

Melinda L. Perkins<sup>a)</sup>

Department of Electrical Engineering, Stanford University, Stanford, California 94305, USA

Hannah K. Frank<sup>b)</sup>

Department of Biology, Stanford University, Stanford, California 94305, USA

John M. Pauly

Department of Electrical Engineering, Stanford University, Stanford, California 94305, USA

Elizabeth A. Hadly

Department of Biology, Stanford University, Stanford, California 94305, USA

(Received 10 April 2017; revised 20 September 2017; accepted 25 September 2017; published online 19 October 2017)

Bats have been observed to shift the frequency of their echolocation calls in the presence of other echolocating bats, ostensibly as a way to reduce acoustic interference. Few studies, however, have examined the theoretical efficacy of such jamming avoidance responses. The present study uses the wideband ambiguity function to analyze the effects of acoustic interference from conspecifics and congeneric heterospecifics on the target acquisition ability of *Myotis californicus* and *Myotis yumanensis*, specifically whether unilateral or bilateral frequency shifts reduce the effects of such interference. Model results suggest that in conspecific interactions, *M. yumanensis* recovers its target acquisition ability more completely and with less absolute frequency shift than does *M. californicus*, but that alternative methods of jamming avoidance may be easier to implement. The optimal strategy for reducing heterospecific interference is for *M. californicus* to downshift its call and *M. yumanensis* to upshift its call, which exaggerates a preexisting difference in mean frequency between the calls of the two species. Further empirical research would elucidate whether these species do in practice actively employ frequency shifting or other means for jamming avoidance, as well as illuminate the role of acoustic interference in niche partitioning.

© 2017 Acoustical Society of America. <https://doi.org/10.1121/1.5006928>

[JAS]

Pages: 2133–2142

## I. INTRODUCTION

Many species of bats rely on echolocation—a biological sonar system—to carry out essential survival tasks such as hunting and orienting in their nighttime environments. To function properly a sonar system must be able to discriminate an echo from background noise, rendering the system sensitive to interference that drowns out the echo or mimics it. Bats may encounter such interference in the form of calls from other bats, incidentally through proximity or deliberately as a means of food competition (Corcoran *et al.*, 2014). Understanding how bats cope with interference is key to demystifying the ecology and behavior of these species.

Studies suggest that many bat species minimize the negative effects of acoustic interference by changing their echolocation calls. A commonly reported jamming avoidance response is the frequency shift, in which an echolocating bat shifts the frequency of its call away from that of the interferer's call for the duration of the interference (Ulanovsky *et al.*, 2004; Ibañez *et al.*, 2004; Gillam *et al.*, 2007). This

jamming avoidance behavior is not limited to interfering calls from conspecifics (Warnecke *et al.*, 2015); Bates *et al.* (2008) reported that *Eptesicus fuscus* shift their calls in response to acoustic interference at constant frequencies close to the tail portion of their own frequency modulated (FM) calls, and simulated FM sounds also appear to evoke frequency shifting in *Miniopterus fuliginosus* (Hase *et al.*, 2016). Another curious source of interference is actually self-inflicted: *E. fuscus* flying amongst densely spaced obstacles have been reported to shift the frequencies of successive echolocation calls within the same sequence to avoid ambiguity in determining which echo returned from which call (Hiryu *et al.*, 2010).

There is some controversy over whether the frequency shifting response is in fact a *jamming avoidance* response. Field studies show greater variation in peak frequencies when more conspecifics are present, but these variations may reflect greater variety in individual bats' calls rather than genuine jamming avoidance behavior (Ratcliffe *et al.*, 2004). Cvikel *et al.* (2015) and Götze *et al.* (2016) argue that frequency shifting constitutes a response to objects that catch the bat's attention rather than a method of reducing acoustic interference. The discussion is further complicated by research conducted on interspecies interference that suggests bats of the same species may not consistently apply frequency shifting responses, and also that closely related species vary in whether they

<sup>a)</sup>Current address: Department of Electrical Engineering, University of CA, Berkeley, CA 94704, USA. Electronic mail: mindyjp@eecs.berkeley.edu

<sup>b)</sup>Current address: Department of Pathology, School of Medicine, Stanford University, Stanford, CA 94305, USA.

modify spectral call parameters only in the presence of conspecifics or only in the presence of congeneric heterospecifics (Bartonička *et al.*, 2007; Necknig *et al.*, 2011). To what degree frequency variation between calls reduces acoustic interference is an especially pertinent issue given that there are many alternative modifications to behavior or call design that a bat might exercise to avoid jamming, e.g., slowing pulse emission rate or ceasing to call altogether (Chiu *et al.*, 2008; Jarvis *et al.*, 2013). The same species of bat may also apply a different jamming avoidance response depending on the nature of the interference (Bates *et al.*, 2008; Chiu *et al.*, 2008; Takahashi *et al.*, 2014).

How much does frequency shifting theoretically reduce acoustic interference within and between species? The answer to this question would help elucidate the interpretation of frequency shifting responses. If interference is significantly reduced by frequency shifting, then the response may be plausibly interpreted as jamming avoidance. In addition, how much the interference is reduced depends on which species are involved and may not be the same for both individuals in a given interaction.

The present study combines sonar analysis techniques with empirical field data to develop a metric for examining acoustic interference between echolocation calls. The metric is used to evaluate the theoretical potential for frequency shifting to alleviate acoustic interference between *Myotis californicus* and *Myotis yumanensis*. Both are insectivorous vespertilionid FM bats that are found in overlapping regions in North America, including California. We characterize (a) how a bat's theoretical target acquisition ability is affected by an interfering call from another bat of the same or a different species, and (b) whether unilateral or bilateral frequency shifting reduces the effect of conspecific or heterospecific interference on a bat's target acquisition ability. Our predictions are as follows:

- (1) Conspecific and heterospecific interactions will both produce notable acoustic interference, but a bat will experience greater interference from conspecific than heterospecific calls.
- (2) Unilateral frequency shifting (in which one bat shifts its call) will reduce interference in both conspecific and heterospecific interactions, but more so for heterospecific than conspecific. The greater the magnitude of the frequency shift, the more the interference will be reduced.
- (3) Bilateral frequency shifting (in which one bat shifts its call up and the other bat shifts its call down) will reduce interference in both conspecific and heterospecific interactions. Bilateral frequency shifting will be more effective than unilateral frequency shifting, meaning that for the same magnitude of frequency shift per bat, interference will be less in the bilateral than in the unilateral case.

## II. METHODS

### A. Recordings

Recordings of free-flying *Myotis* were obtained at Jasper Ridge Biological Preserve (Stanford, CA) from 13 May 2013 to 8 August 2014. Jasper Ridge is a 481-hectare

preserve located in the eastern foothills of the Santa Cruz Mountains. Two sites were located facing over a lake with a dam at one end [lake 1:  $-122.239$  longitude (long),  $37.405$  latitude (lat); lake 2:  $-122.237$  long,  $37.406$  lat]; the other two sites were in grassy areas in the forest, which may be marshes in wet years (marsh 1:  $-122.242$  long,  $37.401$  lat; marsh 2:  $-122.242$  long,  $37.402$  lat). Recordings were captured automatically from sunset to sunrise by a BAT FR125-EXT Field Recorder paired with an AR125 Ultrasonic Receiver (Binary Acoustic Technology LLC, Tucson, AZ). The AR125 has a dynamic range of about 0–90 dB and a frequency range of 1–125 kHz with a relatively flat frequency response from 45 to 65 kHz, which straddles the mean frequency of *Myotis* calls, and a gradual drop-off from 65 to 125 kHz. Recordings were auto-species-identified and mean frequencies calculated by SonoBat™ (SonoBat™, Arcata, CA) analysis software.

### B. Pulse modeling

Bats exhibit great flexibility in call design depending on the environment and activity in which they are engaged (e.g., honing in on insect prey). Changes to call design would be expected to change the level of interference experienced by the animals. We focused our analysis on single search-phase pulses, a flying bat's "default" pulse used to scan surroundings for obstacles or objects of interest. The recordings we referenced originated at the edge of a calm lake bordered by foliage. We decided to study simulated instead of recorded pulses in order to (a) remove all noise from the pulse shapes, as these might have deleterious effects on the ambiguity function calculation; and (b) simplify the process of modifying pulse parameters.

Pulse parameters for *Myotis* exhibit slight variation by region. In the Jasper Ridge dataset, the pulses swept from approximately 90 kHz to 40 kHz for both *M. californicus* and *M. yumanensis*. Across 68 813 call sequences, *M. californicus* had an average mean frequency of 49.64 kHz ( $\sigma^2 = 1.49$  kHz) and mean pulse duration 3.54 ms ( $\sigma^2 = 0.73$  ms); across 56 173 call sequences, *M. yumanensis* had an average mean frequency 50.91 kHz ( $\sigma^2 = 1.89$  kHz) and mean pulse duration 4.38 ms ( $\sigma^2 = 0.62$  ms), similar to published values (Thomas *et al.*, 1987).

We observed the end of a low-amplitude harmonic (minimum frequency 100 kHz) in pulses from both species, although the majority of the harmonic fell outside the maximum frequency we could record with our equipment (125 kHz from a sampling rate of 250 kHz). We could not find precise measurements of harmonic amplitude in the literature, although Fenton and Bell (1979) suggest that *M. californicus* may suppress its second harmonic in certain situations, and *M. yumanensis* appears to have no reported harmonics at all (Thomas *et al.*, 1987). Neither study cited harmonics higher than the second, and it remains unclear how frequency shifting affects the amplitude of harmonics. Although the work of Simmons and Stein (1980) suggests that harmonics tend to distance sidelobes from peaks, as well as reduce sidelobe height when frequency modulated, in our study incorporating a harmonic as loud as the fundamental produced results that

were nearly identical to those without a harmonic (see supplementary material A<sup>1</sup>); therefore, we present here results for which the harmonic is disregarded.

We based the final mathematical models of search-phase echolocation pulses on spectrograms of select calls from the Jasper Ridge dataset. Reference recordings were identified with high confidence by both SonoBat™ (SonoBat™, Arcata, CA) and Kaleidoscope (Wildlife Acoustics, Inc., Maynard, MA) and were visually distinct from noise or other sounds in a spectrogram. We assumed that only one frequency was present at a time and that amplitude was fixed. We used piecewise functions of polynomials and exponentials to estimate the instantaneous frequency of each pulse based on observation of the spectrogram. We chose parameter values such that the duration, frequency range (maximum frequency minus minimum frequency), and frequency at visible inflection points in the model pulse matched those of the reference pulse (see Fig. 1). We further adjusted the parameters to ensure a closer resemblance between the spectrograms and auto-ambiguity functions of the model and reference pulses.

Mathematical models of pulses ultimately provide the basis for generating frequency shifted versions that maintain the same shape as the original but are centered at a higher or lower frequency. These generated pulses are used to carry out subsequent analysis.

### C. Frequency shifting

A unilateral frequency shifting jamming avoidance response occurs when one bat at a time shifts the frequency of its call. There are four possible caller/interferer pairs: the two conspecific pairs, *M. californicus* (shifting)/*M. californicus* (non-shifting) and *M. yumanensis* (shifting)/*M. yumanensis* (non-shifting); and the two heterospecific pairs, *M. californicus* (shifting)/*M. yumanensis* (non-shifting) and *M. yumanensis* (shifting)/*M. californicus* (non-shifting).

We decided to analyze frequency shifts ranging from  $-10$  kHz to  $+10$  kHz. Unpublished data from Jasper Ridge Biological Preserve suggest that the maximum biologically relevant frequency shift is about  $+10$  kHz from the mean for *M. californicus* and  $+13$  kHz from the mean for *M. yumanensis*, but seeing as only about 0.0001% (7 out of 56 173) of the recorded *M. yumanensis* calls were in the range greater than  $+10$  kHz from the mean, a maximum frequency shift of  $+10$  kHz for both species maintains consistency in the analysis. A minimum frequency shift of  $-10$  kHz preserves symmetry in the results, although the minimum biologically relevant frequency shift for either species is about  $-5$  kHz.

A bilateral frequency shifting jamming avoidance response occurs when both bats shift the frequency of their calls. Of particular interest are symmetric bilateral frequency shifts in which both bats shift their calls away from the mean by equal and opposite amounts; for example, one bat shifts its call by  $+1$  kHz and the other shifts its call by  $-1$  kHz. Symmetric bilateral frequency shifts have previously been reported for *Tadarida teniotis* (Ulanovsky *et al.*, 2004). Again, there are four possible caller/interferer pairs: the two conspecific pairs, *M. californicus* (upshifting)/*M. californicus* (downshifting) and *M. yumanensis* (upshifting)/*M.*

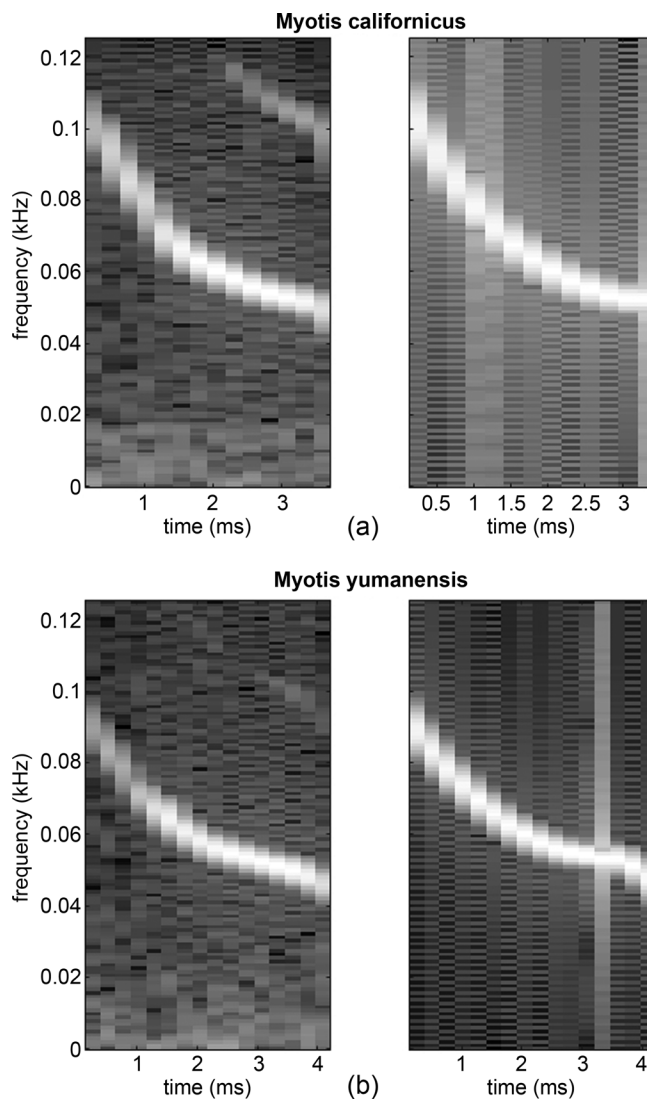


FIG. 1. Spectrograms of reference pulse (left) and synthesized pulse (right) for (a) *Myotis californicus* and (b) *Myotis yumanensis*. Plots were made with a 256-point fast Fourier transform (FFT), Hamming window size 128, overlap 64. Lighter shading indicates higher amplitude. The spectrograms of recorded calls reveal gradual amplitude changes and quiet first harmonic components that are not included in the synthesized pulses. The vertical bands in the spectrograms of the synthesized pulses are artifacts of discontinuities in the instantaneous frequency (see supplementary material A<sup>1</sup>).

*yumanensis* (downshifting); and the two heterospecific pairs, *M. californicus* (upshifting)/*M. yumanensis* (downshifting) and *M. yumanensis* (upshifting)/*M. californicus* (downshifting). We chose to examine frequency shifts ranging in magnitude from 0 to 10 kHz per bat, which is equivalent to a frequency separation between calls of 0 to 20 kHz.

### D. Target acquisition ability

Although bats may ultimately possess signal processing capabilities that are more sophisticated than conventional engineering analysis methods (e.g., Saillant *et al.*, 1993; Simmons, 2012), previous research using the ambiguity function has proved enlightening for developing intuition about the function of bat echolocation and pulse shape (e.g., Altes, 1970; Simmons and Stein, 1980). Therefore, we chose

to assess target acquisition ability using the cross-ambiguity function, a measure of the correlation between a signal  $u(t)$  (the emitted pulse) and another signal  $w(t)$  distorted by the Doppler effect (the return pulse plus an interfering pulse). For wideband signals such as the echolocation calls of FM bats, it takes the normalized form

$$\chi(\tau, \alpha) = \sqrt{\alpha} \int_{-\infty}^{\infty} u(t)w^*(\alpha t - \tau) dt, \quad (1)$$

where  $\tau$  is the time delay and  $\alpha$  is the ‘‘Doppler stretch factor,’’ defined as

$$\alpha = \frac{c - v}{c + v} \quad (2)$$

for a constant pulse propagation velocity  $c$  (i.e., the speed of sound), with a constant relative radial velocity  $v$  between target and transmitter (where positive  $v$  corresponds to transmitter and target moving away from each other). We defined the biologically relevant range as the parameter region bounded by the situations where two bats fly directly toward each other and two bats fly directly away from each other for a flight speed of 5 m/s per bat (Hayward *et al.*, 1964) and a speed of sound in air of 340 m/s. (A more detailed discussion of the ambiguity function can be found in supplementary material B.<sup>1</sup>)

The wideband cross-ambiguity function is calculated between a baseline pulse from one species (the ‘‘caller’’) and a sum of that species’ pulse with a frequency-shifted pulse from the same or a different species (the ‘‘interferer’’) within the biologically relevant range. This arrangement simulates the situation in which a ‘‘caller’’ sends out a pulse and hears a perfect echo of that pulse simultaneously with a pulse from the ‘‘interferer’’ (for various relative speeds between the two). If we let  $u(t)$  represent the caller’s pulse,  $w(t)$  the interferer’s pulse, and  $k$  a constant adjusting the amplitude of the received echo, the wideband cross-ambiguity function is given by

$$\begin{aligned} \chi(\tau, \alpha) &= \sqrt{\alpha} \int_{-\infty}^{\infty} u(t)[ku^*(\alpha t - \tau) + w^*(\alpha t - \tau)]dt \\ &= \sqrt{\alpha}k \int_{-\infty}^{\infty} u(t)u^*(\alpha t - \tau)dt \\ &\quad + \sqrt{\alpha} \int_{-\infty}^{\infty} u(t)w^*(\alpha t - \tau)dt. \end{aligned} \quad (3)$$

Note that the first term in Eq. (3) is just the auto-ambiguity function for the caller’s pulse scaled by  $k$ . To assess interference we chose to emphasize the effect of intrinsic pulse shape rather than echo amplitude, and therefore set the amplitude of the echo and interfering pulse equal to each other ( $k = 1$ ), with the knowledge that different echo amplitudes can be compensated for by adding or subtracting scaled versions of the caller’s auto-ambiguity function to the calculated cross-ambiguity function. The case of equal amplitudes can be thought of as the situation in which caller and interferer call simultaneously, and the caller hears an echo from a 100% reflective target located half as far from the caller as the two bats are from each other.

There are at least two basic ways in which a bat may fail to locate a target owing to acoustic interference. It may

hone in on an object other than its desired target—referred to herein as ‘‘incorrect target acquisition’’—or it may be less capable of pinpointing the exact location of a correct target. Incorrect target acquisition is analyzed via the peak-to-side-lobe ratio (PSR) of the ambiguity function within the biologically relevant range. The PSR serves as a measure of how loud of an echo an object located at the highest sidelobe would have to return relative to the amplitude of an echo returned by a target of interest in order for a bat to mistake the object for the target of interest. The lower the threshold for an object to be mistaken for the ‘‘correct’’ target, the higher the probability that any given object in an acoustic scene returns an echo above that threshold. Hence, the PSR acts as a proxy for how likely a bat would be to mistake an appropriately placed extraneous object as the ‘‘correct’’ target.

The highest peak in an ambiguity function is assumed to correspond to the ‘‘correct’’ target. A single ambiguity function represents an echo returning from one target; an area with multiple targets results in a superposition of ambiguity functions each centered at the location of the respective target and scaled by the amplitude of the return echo for each target. Therefore, if undesired target B is located at point P in a sidelobe of desired target A, then the height of the ambiguity function at P is a sum of A’s sidelobe height and B’s peak height. B’s peak height depends on the amplitude of the echo, with weaker echoes returning lower peaks, so the higher A’s sidelobe, the weaker an echo B must return in order for the height at P to exceed the height at desired target A, i.e., even a weak target can masquerade as the ‘‘correct’’ one. Hence, to reduce the chance that a small undesired target located on a sidelobe is falsely identified as the desired target, sidelobes should be as short as possible relative to the height of the peak.

The potential for incorrect target acquisition for each caller/interferer pair is considered from the perspective of both bats in the pair. The PSR for each species is normalized to the PSR value for a conspecific interaction at no frequency shift (the autocorrelation of the pulse), which represents the target acquisition ability of a species when no interference is present. Therefore, percent target acquisition is calculated as the PSR divided by the conspecific PSR at no frequency shift. Interference is designated ‘‘critical’’ if the percent target acquisition is  $\leq 50\%$ , or equivalently the normalized PSR is  $\leq 2$ , meaning the tallest sidelobe is over half the height of the peak. This choice of threshold is roughly analogous to the conventional ‘‘half-power point’’ or ‘‘half maximum’’ that is invoked to identify or localize peaks in a signal, as in quantifying spatial resolution or cutoff frequency.

Changes to the relative phase between the simulated pulses of caller and interferer manifest as ‘‘noise’’ in the PSR calculation. The plots shown here have been smoothed to emphasize qualitative trends.

For all interacting pairs from either point of view, an interfering sidelobe becomes more distant from the peak with greater absolute frequency shift (see Fig. 2). If the shift is too small (the black region in Figs. 3 and 4), the tallest sidelobe is merged with the peak and cannot be differentiated from it. Interference in this region manifests as a reduction in the bat’s ability to accurately locate a target rather than an

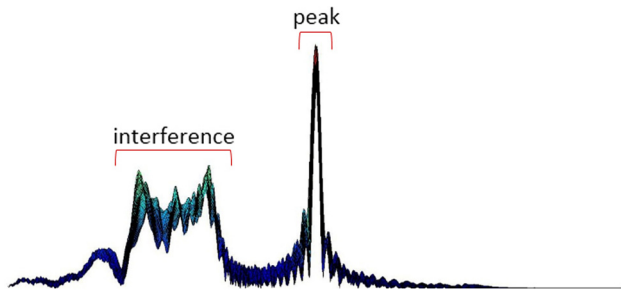


FIG. 2. (Color online) Peak and sidelobe of a cross-ambiguity function calculation. Cross-ambiguity function for *M. californicus* (shifting)/*M. yumanensis* (non-shifting) for frequency shift of +10 kHz. Note that the peak is higher and sharper than the interference sidelobe. The highest point in the interference sidelobe would be taken in the calculation of the peak-to-side-lobe ratio (PSR).

increased probability of incorrect target acquisition. As the PSR is not the appropriate method to analyze interference in this region, these values are disregarded.

In Figs. 3 and 4, the hatched background designates the non-biologically relevant range for which the mean frequency of the shifted call would fall beneath the minimum mean

frequency found in the recordings. The analysis henceforth focuses on the biologically relevant range (non-hatched regions in Figs. 3 and 4).

### III. RESULTS

The PSR is one measure for the interference a bat may experience due to acoustic interference, with a lower PSR corresponding to a higher probability of incorrect target acquisition (greater interference). Percent target acquisition (normalized PSR) is calculated as the ratio of the PSR to the PSR in the absence of interference (equivalent to the conspecific PSR at 0 frequency shift). Comparing percent target acquisition from the point of view of each bat in a shifting/non-shifting or upshifting/downshifting pair reveals differences in the severity of interference experienced by two interfering bats in a given pair. In a given interaction, frequency shifting is more “effective” if a lower magnitude of frequency shift produces a greater reduction in interference (greater recovery in target acquisition ability). In Secs. III A–III D, we address the conclusions pertaining to each prediction in turn.

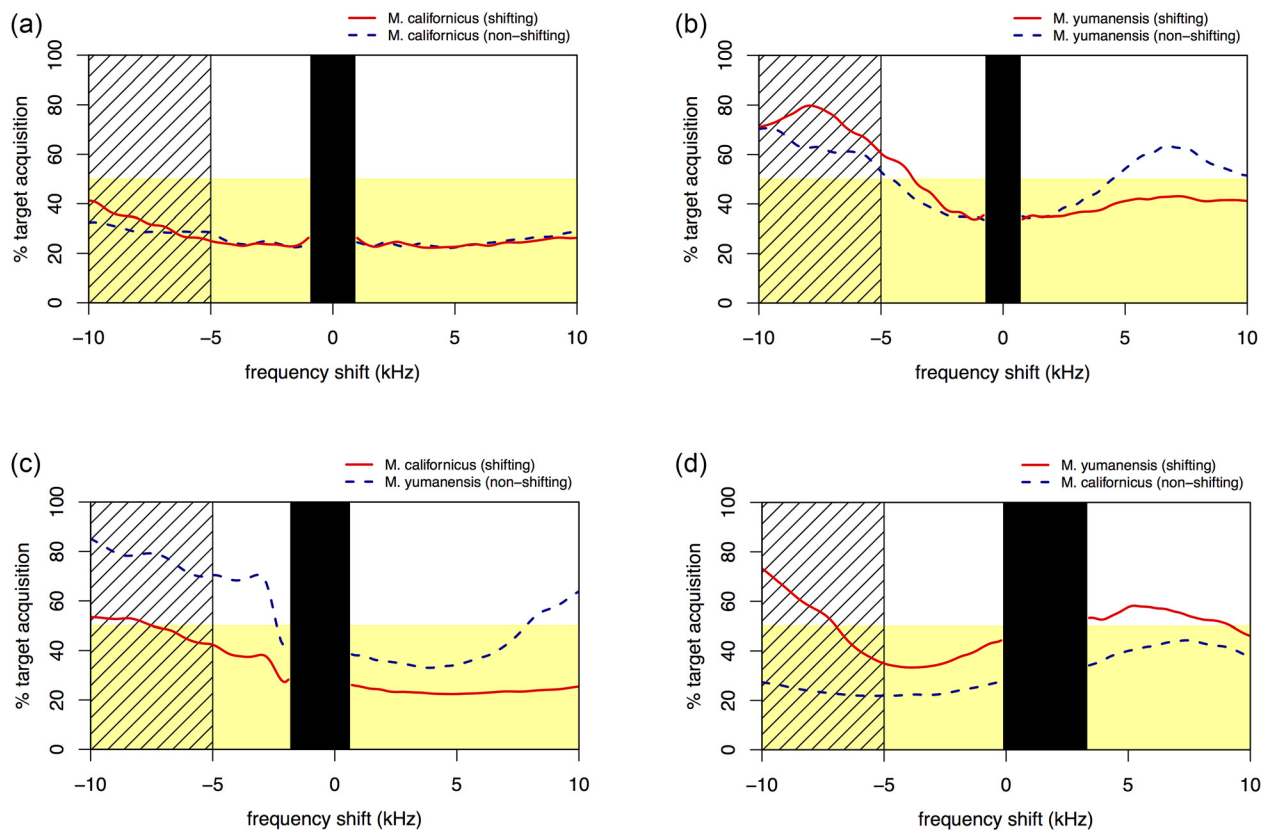


FIG. 3. (Color online) Unilateral frequency shifts reduce interference for conspecific *M. yumanensis* and in heterospecific interactions where *M. californicus* downshifts or *M. yumanensis* upshifts, contrary to prediction (2). Results from simulation. (a) Both *M. californicus* in a conspecific interaction experience critical interference across all examined frequency shifts. (b) Both *M. yumanensis* in a conspecific interaction experience reductions to interference with greater frequency shift, and the bat with the lower-frequency call benefits more. (c),(d) In a heterospecific interaction unilateral frequency shifting is most effective when *M. californicus* downshifts. Percent target acquisition [PSR/(conspecific PSR at 0 frequency shift)] measures a bat’s theoretical ability to appropriately identify a target relative to the situation with no interference. Dashed line is from the point of view of the non-shifting bat; solid line is from the point of view of the shifting bat. The hatched background on the left designates the non-biologically relevant range for which the mean frequency of the shifted call would fall beneath the minimum mean frequency found in the recordings. The shaded background on the bottom designates the region where interference is critical (% target acquisition < 50%). The center black box denotes the region where the peak and interference sidelobe merge, and where interference manifests as a reduction in the bat’s ability to accurately locate a target rather than an increased probability of incorrect target acquisition. As the PSR is not the appropriate method to analyze interference in this region, the values are disregarded.

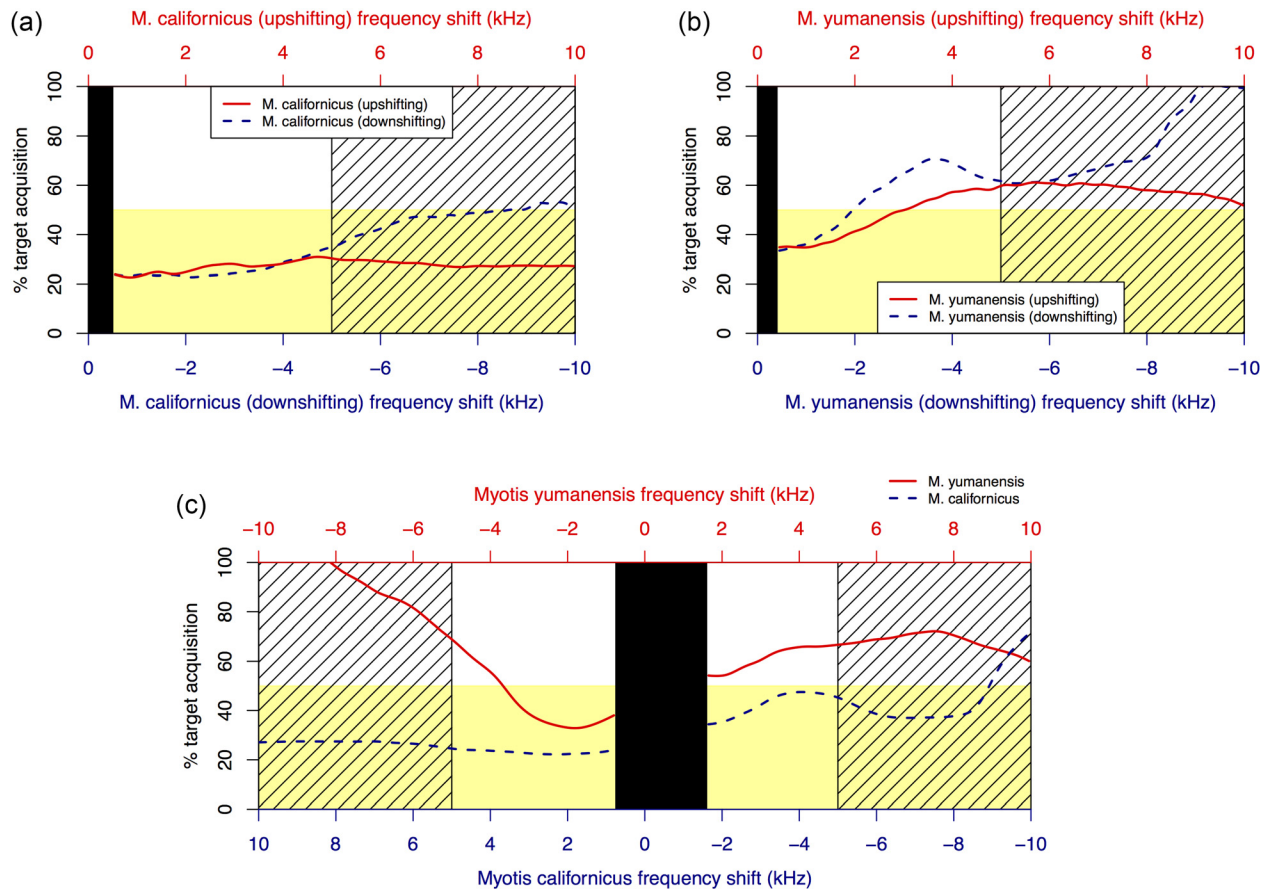


FIG. 4. (Color online) Bilateral frequency shifts are more effective than unilateral frequency shifts, especially in heterospecific interactions, in line with prediction (3). Results from simulation. (a),(b) In conspecific interactions bilateral frequency shifting is more effective for *M. yumanensis* than for *M. californicus*. For either species, the downshifting bat benefits more. (c) The optimal method for reducing heterospecific interference is for *M. yumanensis* to upshift and *M. californicus* to downshift. Percent target acquisition [PSR/(conspecific PSR at 0 frequency shift)] measures a bat's theoretical ability to appropriately identify a target relative to the situation with no interference. In (a) and (b), the solid line is from the point of view of the upshifting bat with frequency shift given by the top axis, and the dashed line is from the point of view of the downshifting bat with frequency shift given by the bottom axis. In (c), the solid line is from the point of view of *M. yumanensis* with frequency shift given by the top axis, and the dashed line is from the point of view of *M. californicus* with frequency shift given by the bottom axis. Hatched and shaded areas are as in Fig. 3. Note that *M. californicus* experiences a greater reduction in percent target acquisition ability due to the fact that it has a greater PSR at 0 frequency shift than does *M. yumanensis*, although both species exhibit similar absolute PSRs.

### A. Prediction (1): Conspecific interactions produce more interference than heterospecific interactions across a range of frequency shifts

As we predicted, both conspecific and heterospecific interactions produce considerable amounts of interference, but conspecific interactions produce more interference than heterospecific interactions consistently across a range of frequency shifts. *M. californicus* experiences critical or near-critical interference levels in all interactions for all values of frequency shift considered in the study [Figs. 3(a)–3(d)]. In heterospecific interactions, *M. yumanensis* experiences less disruption to its target acquisition ability than does *M. californicus*, especially at greater frequency shift [Figs. 3(c) and 3(d)].

### B. Prediction (2): Unilateral frequency shifts reduce conspecific interference for *M. yumanensis* and heterospecific interference when *M. californicus* downshifts or *M. yumanensis* upshifts

Contrary to our predictions, unilateral frequency shifts do not always reduce interference. In conspecific interactions, *M.*

*yumanensis* may reduce interference with shifts in either direction, while *M. californicus* is unable to recover target acquisition ability by any appreciable amount for shifts within the biologically relevant range. In heterospecific interactions, unilateral shifting within the biologically relevant range only reduces interference when *M. californicus* downshifts or *M. yumanensis* upshifts. Interference is actually exacerbated when *M. yumanensis* downshifts its call by at least  $-2.5$  kHz with maximum interference at  $-5.0$  kHz, which results in a mean frequency for *M. yumanensis* that is lower than the minimum mean frequency for this species found in the Jasper Ridge dataset. In a heterospecific interaction where only one bat shifts its call, the optimal strategy to reduce interference for both bats is for *M. californicus* to shift its call downward by  $\geq 3.0$  kHz [ideally, at least 5.9 kHz; Fig. 3(c)].

### C. Prediction (3): Bilateral frequency shifts are more effective than unilateral frequency shifts, especially in heterospecific interactions

Bilateral frequency shifts reduce interference in both conspecific and heterospecific interactions, more effectively

in heterospecific than conspecific, and more effectively than unilateral frequency shifts of the same magnitude per bat. Although *M. californicus* does not recover much target acquisition ability within the biologically relevant range [Figs. 4(a) and 4(c)], outside that range the reduction in interference is better than observed for a unilateral shift of equivalent magnitude. *M. yumanensis* in a conspecific interaction may exit the zone of critical interference with about 2.8 kHz of frequency shift per bat [Fig. 4(b)]. In a heterospecific interaction with a downshifting *M. californicus*, an upshifting *M. yumanensis* never experiences critical interference outside the inaccuracy zone, which ends at about a 1.6-kHz shift per bat [Fig. 4(c)]. If both bats shift their calls, the optimal strategy to reduce interference for both bats would be for *M. californicus* to shift its call downward and *M. yumanensis* to shift its call upward.

#### D. Summary: Interference level and the effectiveness of frequency shifting depend on individual and interaction

The level of interference experienced by a caller depends both on its species and on the species of the interferer, as well as whether the mean frequency of the caller's call is lower or higher than that of the interferer.

In conspecific interactions with unilateral or bilateral frequency shifts, *M. californicus* experiences considerable interference across all biologically relevant frequency shifts, while both *M. yumanensis* can exit the critical zone of interference for some frequency separation within the biologically relevant range. When both conspecifics shift their calls, the bat with the lower-frequency call recovers target acquisition ability at a smaller frequency separation between calls than the bat with the higher-frequency call.

In heterospecific interactions, *M. yumanensis* experiences less disruption to its target acquisition ability than does *M. californicus* and recovers the most target acquisition ability with the least absolute frequency shift when its call has a mean frequency higher than that of *M. californicus*, with more recovery for greater frequency separation. Although in the latter case *M. californicus* does not exit the critical interference zone within the biologically relevant range (except for a few isolated points), it also experiences less reduction in target acquisition ability relative to the situation in which its call has a mean frequency higher than that of *M. yumanensis*. Across all the options explored in this theoretical analysis, the optimal method for reducing heterospecific interference is for *M. californicus* to shift its call downward and *M. yumanensis* to shift its call upward.

## IV. DISCUSSION

### A. Do bats need to avoid acoustic interference?

As hypothesized, the theoretical analysis indicates that bats would experience notable acoustic interference in both conspecific and heterospecific interactions. Although acoustic interference may be theoretically problematic, bats may not have to actively avoid it if they do not encounter it; for example, if they spatially or temporally segregate themselves from other bats. For these particular species, such situational

avoidance is not always possible, especially during roosting. Conspecifics aggregate in large nursery colonies during the summer, with *M. yumanensis* forming colonies of up to 2000 individuals in buildings, 5000 in mines, and as many as 10000 individuals in the Davis Dam at the Colorado River (Kruttsch, 1954; Adams, 2003). Even small colonies may have high potential for conspecific interference: One study found that roost trees averaging less than 60 cm in diameter at breast height housed a mean of just under 14 *M. californicus* and, in one case, as high as 52 individuals (Brigham *et al.*, 1997). *M. yumanensis* that hunted nightly at Jasper Ridge were also reported to roost together in trees, although the authors did not count the number of individuals within each (Evelyn *et al.*, 2004). *M. californicus* and *M. yumanensis* have also been found roosting together and with other congeners, especially in manmade structures (Dalquest 1947; Braun *et al.*, 2015).

How frequently might these bats encounter interference while hunting? Multiple studies have found that bats (including *M. yumanensis*) are attracted to feeding buzzes from conspecifics, which would tend to increase the density of bats at a feeding site (e.g., Barclay, 1982; Balcombe *et al.*, 1988; Gillam, 2007). Although our recording methods were insufficient to distinguish between individual conspecifics, for heterospecifics we were able to conduct ballpark estimates for simultaneous foraging activity at the four surveyed sites. The peak activity of *M. californicus* preceded that of *M. yumanensis* by about an hour each night, with substantial overlap in between. Heterospecifics at the lake sites passed through the same location within a minute of each other in about a tenth of all recorded passes, rising to between a fifth and a fourth for arrivals up to two minutes apart (Table I). Although these results provide only a rough estimate of the bats' actual proximity to each other, they do demonstrate that the bats hunt simultaneously within the relatively small area recorded by the microphone. Together with the observation that roosts often house a high density of bats, these observations suggest that some form of jamming avoidance would be beneficial for *Myotis*.

### B. Does frequency shifting significantly reduce interference?

In the event that bats find themselves in the vicinity of other echolocation bats, is frequency shifting a reasonable

TABLE I. Heterospecifics occupied the same location within two minutes of each other in a nonnegligible fraction of recorded passes. Below is shown the percentage of recorded calls of a single species that occurred within one or two minutes of a recorded call of the other species. For example, at lake 1, 7.64% of all recorded *M. californicus* call sequences occurred within a minute of a call from *M. yumanensis*. With the exception of the lake 2 site, *M. yumanensis* is more likely to pass a site occupied within the previous two minutes by *M. californicus* than vice versa, probably due to the fact that we obtained fewer recordings of *M. yumanensis* than *M. californicus*. The lake 2 site overlooks open water, a hunting habitat that *M. yumanensis* are known to prefer.

	Lake 1		Lake 2		Marsh 1		Marsh 2	
	1 min	2 min	1 min	2 min	1 min	2 min	1 min	2 min
% of <i>M. californicus</i> calls	7.64	16.6	13.1	26.1	4.93	9.94	4.72	6.76
% of <i>M. yumanensis</i> calls	8.95	19.4	10.3	20.4	17.3	34.9	42.6	60.9



response to reduce interference? Our results indicate that frequency shifting does not equally benefit callers and interferers and is not equally effective for all caller/interferer pairs. The inconsistency in benefit to the bats, as well as the practical difficulties in coordinating frequency shifts, do not rule out frequency shifting as a jamming avoidance response, but do suggest limitations on its overall efficacy.

Theoretical analysis indicates that, in general, bilateral frequency shifting is superior to unilateral frequency shifting for reducing interference with regard to target acquisition ability. Specifically, to reduce interference by the same amount, bilateral frequency shifting requires less frequency shift per bat than does unilateral frequency shifting, especially if the bilateral shift enlarges preexisting separation in mean frequency of calls. Whether unilateral or bilateral, frequency shifts must have greater magnitude to reduce interference in conspecific interactions relative to heterospecific ones, also in line with our predictions.

Studies have indicated that frequency-shifting FM bats aim to avoid interference in the flutter, terminal-phase, low-frequency components of their calls (Bates *et al.*, 2008; Takahashi *et al.*, 2014; Hase *et al.*, 2016). In conspecific interactions, a bat with a lower-frequency call recovers more target acquisition ability on average than its higher-frequency counterpart for a given frequency separation. No frequencies in the higher-frequency bat's call will overlap with the terminal frequency (TF) of the lower-frequency bat's call, but frequencies in the lower-frequency bat's call will overlap with the TF of the higher-frequency bat's call. This fact suggests that the lower-frequency bat's relatively better target acquisition ability might be attributed to the lack of overlap in the TF component. That two interfering conspecifics may experience overlap across the same absolute frequency range but the bat with no TF overlap perceives less interference provides theoretical justification for bats' observed frequency-shifting behavior to avoid spectral overlap in the TF component specifically.

In conspecific interactions, the effects of frequency shifting only marginally benefit *M. californicus* within the biologically relevant range; *M. yumanensis* reaps a greater benefit but still requires a shift of at least  $\sim 2.8$  kHz in the bilateral case to recover 50% of its intrinsic target acquisition ability. Furthermore, bilateral frequency shifts require cooperation: If the interferer does not shift, then the shifter may not benefit. A unilateral frequency shift that favors the non-shifting bat is unlikely to occur in nature, as the bat making the active adjustment would not receive the benefit. Thus, without guarantee of the interferer's cooperation, *M. yumanensis* should not shift up. In a unilateral or bilateral case, however, *M. yumanensis* could benefit from downshifting provided that the conspecific did not also shift down. This introduces a dilemma: If both bats downshift, neither benefits; if one bat downshifts, it benefits a little; if one bat upshifts, the other benefits; if one upshifts and one downshifts, both benefit. Without altruism, communication, or a consistent rule for deciding which bat exercises which shift (e.g., the bat with the lower call always downshifts), no individual *M. yumanensis* maximizes its benefits by upshifting, which lowers the probability that a bilateral frequency shift would occur by individual action on the part of both bats. The difficulty in

coordinating bilateral frequency shifting, combined with the magnitude of frequency shift required to reduce conspecific interference, strongly suggests that *Myotis* rely on alternative methods to frequency shifting to mitigate or obviate conspecific jamming effects.

In heterospecific interactions, *M. californicus* always benefits from downshifting, provided that *M. yumanensis* either does not shift or shifts equally upward. Similarly, *M. yumanensis* always benefits from upshifting, provided that *M. californicus* either does not shift or shifts equally downward. Hence, assuming no other jamming avoidance techniques are employed, the optimal strategy to reduce heterospecific interference for *M. californicus* is to shift lower and for *M. yumanensis* is to shift higher, regardless of the behavior of the interferer. Functionally, this strategy enlarges the preexisting separation in mean frequency between heterospecific calls: On average, the mean frequency of *M. californicus* calls is lower than that of *M. yumanensis* by 1.27 kHz. This fact hints at an intriguing evolutionary question: Could the potential for acoustic interference between heterospecific calls contribute to phenotypic divergence in mean call frequency and pulse shape? Further research would be necessary to investigate this possibility.

For both conspecific and heterospecific interactions, *M. yumanensis* recovers its target acquisition ability more completely and with less absolute frequency shift than does *M. californicus*. The discrepancy in the two species' potential to recover target acquisition ability may reflect ecological differences in foraging activity: *M. yumanensis* feeds almost exclusively over open water (Adams, 2003; Braun *et al.*, 2015), while *M. californicus* hunts in a variety of locations, including forest margins and tree canopies (Kruttsch, 1954; Fenton and Bell, 1979; Adams, 2003). Without the clutter introduced by foliage, *M. yumanensis* may be more likely to encounter conspecific or heterospecific calls, including those reflected off the water's surface, and thus may have greater need to alleviate interference from other bat calls. Alternatively, *M. californicus* may be inherently less susceptible to acquiring incorrect targets as an adaptation to the foliage in its habitat, which constitutes a substantial source of physical and, thus, acoustic clutter (Schnitzler and Kalko, 1998). Clutter is analogous to interference in that it can be considered to increase the probability that an object is located at a sidelobe and, therefore, the probability that a bat hones in on an object other than its intended target (incorrect target acquisition). Indeed, *M. californicus* has a higher PSR at no frequency shift than does *M. yumanensis* (4.6 vs 3.1), possibly indicating that its call has a greater intrinsic robustness to interference. Future work would be required to illuminate the inherent clutter detection abilities of *Myotis*.

### C. Jamming avoidance alternatives to frequency shifting

While frequency shifting does reduce interference in select situations, the lack of consistent effectiveness as well as the difficulty in implementation strongly suggest that interfering bats employ alternative methods of jamming avoidance.

Several passive mechanisms may exist to mitigate possible interference. The duty cycle of echolocation plays a role in the likelihood that interference is encountered: If a bat emits fewer pulses per unit time, then a randomly timed interfering pulse is less likely to overlap with an emitted pulse or echo. Genera such as *Myotis* with low duty cycle echolocation may simply be less likely to encounter interference in the first place, obviating the need for an active compensatory mechanism (Surlykke *et al.*, 2015). Interference may also be avoided by inter-individual variation: Bats could identify other individuals by unique characteristics in their calls (Obriest, 1995; Yovel *et al.*, 2009; Voigt-Heucke *et al.*, 2010), or avoid confusion simply by chance differences between their calls and those of a conspecific. For example, using recordings from onboard microphones, Cvikel *et al.* (2015) determined that *Rhinopoma microphyllum* exhibits no frequency-shifting response, and further concluded that individual variation in the peak frequency of calls is sufficient for a bat to distinguish its own signal from that of a conspecific in nearly three-quarters of interactions.

While such a mechanism might reduce interference for narrowband-calling bats such as *R. microphyllum*, it is less likely that intrinsic variation in peak frequency would be sufficient to eliminate interference in *Myotis*. Calls from *R. microphyllum* sweep a frequency range of less than 10 kHz. In contrast, *M. californicus* and *M. yumanensis* each have a frequency range greater than 50 kHz. Assuming that a difference in 500 Hz between peak frequencies is sufficient for *R. microphyllum* to distinguish its call from that of a conspecific, then with a frequency range of 10 kHz, *R. microphyllum* tolerates 95% overlap in call frequencies. For two *Myotis*, a difference in 500 Hz between peak frequencies would produce an overlap in call frequencies of 99%. To achieve a 95% overlap, the *Myotis* calls would have to differ by 2.5 kHz.

The standard deviations in mean frequency for calls from *M. californicus* (1.49 kHz) and *M. yumanensis* (1.87 kHz) in our study suggest that an overlap of  $\geq 95\%$  would occur in the majority of interactions. As our data do not distinguish between individuals, inter-individual variation in mean frequency is potentially greater than the standard deviation of all the recorded calls. Nevertheless, FM bats likely deal with interference differently than narrowband bats, and further investigation of broadband bats would be necessary to generalize the results from Cvikel *et al.* (2015).

If passive interference avoidance mechanisms fail, then active jamming avoidance behavior may be required. The behavior could involve physical adjustments—for example, to the direction of the sonar beam (Chiu *et al.*, 2010), flight path/spacing between bats (Warnecke *et al.*, 2015), head position, or ear position—and/or modifications to call parameters, such as intensity or interpulse interval (Chiu *et al.*, 2008; Jarvis *et al.*, 2013; Amichai *et al.*, 2015).

Actual interference may be stronger than inferred because the calls of both the caller and interferer were given equal volume (amplitude), when in practice a caller's echo may be quieter (smaller amplitude) than the call of the interferer and would be expected to differ in spectral content from the original call. Owing to bats' highly directional sonar beams, however, interfering calls may also have reduced

amplitude if the caller and interferer are not directly facing each other (Surlykke *et al.*, 2009). Hunting bats likely also rely on non-auditory cues, including vision, knowledge of their own flight speed, and the expected distance or velocity of environmental objects, to enhance their target acquisition ability (Falk *et al.*, 2014). Further empirical studies would be necessary to determine whether and to what extent jamming affects prey capture success.

## D. Conclusion: Putting insights from theory into practice

While exact values derived from theoretical examinations should be treated with caution, the results provide a valuable framework for assessing the variety and severity of problems faced by echolocating bats. Unilateral frequency-shifting jamming avoidance responses are unlikely to reduce acoustic interference from the calls of conspecifics and heterospecifics for bats with broadband echolocation calls; bilateral frequency shifts, however, may reasonably reduce interference from heterospecific calls provided that the shifts exaggerate preexisting differences in mean frequency between the calls of the two species. These results suggest that, in heterospecific interactions, a bat that shifts its call away from an interferer's may greatly recover target acquisition ability if the interferer also shifts its call. In contrast, in conspecific interactions, broadband bats may more reliably mitigate jamming through alternative call modifications or avoidance behaviors.

In any application of theory one must make a tradeoff between complexity and clarity. We chose to concern ourselves with a simple test case for the frequency shifting jamming avoidance response (i.e., sympatric species with similar echolocation calls during the typical search phase near open water). In doing so, we have left much territory unexplored. It is our belief that the metric we have developed to analyze acoustic interference may apply to a much broader range of problems in echolocation call design, and may offer insight into evolutionary divergence and niche partitioning. Overall, this study reiterates the power of theoretical analyses to deliver insight into biological systems. Through our work we hope to inspire further application of engineering techniques to investigate the natural world.

## ACKNOWLEDGMENTS

The authors would like to thank the staff and docents at Jasper Ridge Biological Preserve—especially Trevor Hebert, Tom Malloy, Philippe Cohen, and Nona Chiariello—for supplying the dataset of bat calls. The authors would also like to thank Dr. M. Brock Fenton and an anonymous reviewer for their helpful comments, which greatly strengthened the manuscript. The equipment for acoustic monitoring was funded through a donation from the family of Henry Thomas “Tom” Mudd. Additional funding for this project was partially provided by Stanford Undergraduate Advising and Research, a division of the Office of the Vice Provost for Undergraduate Education.

<sup>1</sup>See supplementary material at <http://dx.doi.org/10.1121/1.5006928> for more detailed explanations of (A) pulse modeling and (B) the ambiguity function.

- Adams, R. A. (2003). *Bats of the Rocky Mountain West: Natural History, Ecology, and Conservation* (University Press of Colorado, Boulder, CO), pp. 170–173, 202–205.
- Altes, R. A., and Titlebaum, E. L. (1970). “Bat signals as optimally Doppler tolerant waveforms,” *J. Acoust. Soc. Am.* **48**(4), 1014–1020.
- Amichai, E., Blumrosen, G., and Yovel, Y. (2015). “Calling louder and longer: How bats use biosonar under severe acoustic interference from other bats,” *Proc. R. Soc. B* **282**, 20152064.
- Balcombe, J. P., and Fenton, M. B. (1988). “Eavesdropping by bats: The influence of echolocation call design and foraging strategy,” *Ethology* **79**(2), 158–166.
- Barclay, R. M. R. (1982). “Interindividual use of echolocation calls: Eavesdropping by bats,” *Behav. Ecol. Sociobiol.* **10**(4), 271–275.
- Bartonička, T., Reháč, Z., and Gasiler, J. (2007). “Can *Pipistrellus pipistrellus* (Schreber, 1774) and *Pipistrellus pygmaeus* (Leach, 1825) foraging in a group, change parameters of their signals?,” *J. Zool.* **272**(2), 194–201.
- Bates, M. E., Stamper, S. A., and Simmons, J. A. (2008). “Jamming avoidance response of big brown bats in target acquisition,” *J. Exp. Biol.* **211**, 106–113.
- Braun, J. K., Yang, B., González-Pérez, S. B., and Mares, M. A. (2015). “*Myotis yumanensis* (Chiroptera: Vespertilionidae),” *Mammal. Species* **47**(918), 1–14.
- Brigham, R. M., Vonhof, M. J., Barclay, R. M. R., and Gwilliam, J. C. (1997). “Roosting behavior and roost-site preferences of forest-dwelling California bats (*Myotis californicus*),” *J. Mammal.* **78**(4), 1231–1239.
- Chiu, C., and Moss, C. F. (2008). “When echolocating bats do not echolocate,” *Commun. Integr. Biol.* **1**(2), 161–162.
- Chiu, C., Viswanadha, P. R., Xian, W., Krishnaprasad, P. S., and Moss, C. F. (2010). “Effects of competitive prey capture on flight behavior and sonar beam pattern in paired big brown bats, *Eptesicus fuscus*,” *J. Exp. Biol.* **213**, 3348–3356.
- Corcoran, A. J., and Conner, W. E. (2014). “Bats jamming bats: Food competition through sonar interference,” *Science* **346**(6210), 745–747.
- Cvikel, N., Levin, E., Hurme, E., Borissov, I., Boonman, A., Amichai, E., and Yovel, Y. (2015). “On-board recordings reveal no jamming avoidance in wild bats,” *Proc. R. Soc. B* **282**, 20142274.
- Dalquest, W. W. (1947). “Notes on the natural history of the bat, *Myotis yumanensis*, in California, with a description of a new race,” *Am. Midl. Nat.* **38**(1), 224–247.
- Evelyn, M. J., Stiles, D. A., and Young, R. A. (2004). “Conservation of bats in suburban landscapes: Roost selection by *Myotis yumanensis* in a residential area in California,” *Biol. Cons.* **115**(3), 463–473.
- Falk, B., Jakobsen, L., Surlykke, A., and Moss, C. F. (2014). “Bats coordinate sonar and flight behavior as they forage in open and cluttered environments,” *J. Exp. Biol.* **217**, 4356–4364.
- Fenton, M. B., and Bell, G. P. (1979). “Echolocation and feeding behaviour in four species of *Myotis* (Chiroptera),” *Can. J. Zool.* **57**, 1271–1277.
- Gillam, E. H. (2007). “Eavesdropping by bats on the feeding buzzes of conspecifics,” *Can. J. Zool.* **85**(7), 795–801.
- Gillam, E. H., Ulanovsky, N., and McCracken, G. F. (2007). “Rapid jamming avoidance in biosonar,” *Proc. R. Soc. B* **274**, 651–660.
- Götze, S., Koblitz, J. C., Denzinger, A., and Schnitzler, H.-U. (2016). “No evidence for spectral jamming avoidance in echolocation behavior of foraging pipistrelle bats,” *Sci. Rep.* **6**, 30978.
- Hase, K., Miyamoto, T., Kobayashi, K. I., and Hiryu, S. (2016). “Rapid frequency control of sonar sounds by the FM bat, *Miniopterus fuliginosus*, in response to spectral overlap,” *Behav. Proc.* **128**, 126–133.
- Hayward, B., and Davis, R. (1964). “Flight speeds in Western bats,” *J. Mammal.* **45**(2), 236–242.
- Hiryu, S., Bates, M. E., Simmons, J. A., and Riquimaroux, H. (2010). “FM echolocating bats shift frequencies to avoid broadcast-echo ambiguity in clutter,” *Proc. Natl. Acad. Sci.* **107**(15), 7048–7053.
- Ibañez, C., Juste, J., Lopez-Wilchis, R., and Nuñez-Garduño, A. (2004). “Habitat variation and jamming avoidance in echolocation calls of the savinged bat (*Balantiopteryx plicata*),” *J. Mammal.* **85**(1), 38–42.
- Jarvis, J., Jackson, W., and Smotherman, M. (2013). “Groups of bats improve sonar efficiency through mutual suppression of pulse emissions,” *Front. Physiol.* **4**(140), 1–9.
- Krutzsch, P. H. (1954). “Notes on the habits of the bat, *Myotis californicus*,” *J. Mammal.* **35**(4), 539–545.
- Necknig, V., and Zahn, A. (2011). “Between-species jamming avoidance in *Pipistrelles*?,” *J. Comp. Physiol. A* **197**(5), 469–473.
- Obrist, M. K. (1995). “Flexible bat echolocation: The influence of individual, habitat and conspecifics on sonar signal design,” *Behav. Ecol. Sociobiol.* **36**, 207–219.
- Ratcliffe, J. M., ter Hofstede, H. M., Avila-Flores, R., Fenton, M. B., McCracken, G. F., Biscardi, S., Blasko, J., Gillam, E., Orprecio, J., and Spanjer, G. (2004). “Conspecific influence call design in the Brazilian free-tailed bat, *Tadarida brasiliensis*,” *Can. J. Zool.* **82**, 966–971.
- Saillant, P. A., Simmons, J. A., and Dear, S. P. (1993). “A computational model of echo processing and acoustic imaging in frequency-modulated echolocating bats: The spectrogram correlation and transformation receiver,” *J. Acoust. Soc. Am.* **94**, 2691–2712.
- Schnitzler, H.-U., and Kalko, E. K. V. (1998). “How echolocating bats search and find food,” in *Bat Biology and Conservation*, edited by T. H. Kunz and P. A. Racey (Smithsonian Institution, Washington, DC), pp. 193–196.
- Simmons, J. A. (2012). “Bats use a neuronally implemented computational acoustic model to form sonar images,” *Curr. Opin. Neurobiol.* **22**, 311–319.
- Simmons, J. A., and Stein, R. A. (1980). “Acoustic imaging in bat sonar: Echolocation signals and the evolution of echolocation,” *J. Comp. Physiol.* **135**, 61–84.
- Surlykke, A., Olsen, M. N., and Mol, C. (2015). “Listening through the ears of echolocating *Myotis daubentonii* bats hunting in groups,” *J. Acoust. Soc. Am.* **137**, 2250.
- Surlykke, A., Pedersen, S. B., and Jakobsen, L. (2009). “Echolocating bats emit a highly directional sonar beam in the field,” *Proc. R. Soc. B* **276**, 853–860.
- Takahashi, E., Hyomoto, K., Riquimaroux, H., Watanabe, Y., Ohta, T., and Hiryu, S. (2014). “Adaptive changes in echolocation sounds by *Pipistrellus abramus* in response to artificial jamming sounds,” *J. Exp. Biol.* **217**, 2885–2891.
- Thomas, D. W., Bell, G. P., and Fenton, M. B. (1987). “Variation in echolocation call frequencies recorded from North American vespertilionid bats: A cautionary note,” *J. Mammal.* **68**(4), 842–847.
- Ulanovsky, N., Fenton, M. B., Tsoar, A., and Korine, C. (2004). “Dynamics of jamming avoidance in echolocating bats,” *Proc. R. Soc. B* **271**, 1467–1475.
- Voigt-Heucke, S. L., Taborsky, M., and Dechmann, D. K. N. (2010). “A dual function of echolocation: Bats use echolocation calls to identify familiar and unfamiliar individuals,” *Animal Behav.* **80**(1), 59–67.
- Warnecke, M., Chiu, C., Engelberg, J., and Moss, C. F. (2015). “Active listening in a bat cocktail party: Adaptive echolocation and flight behaviors of big brown bats, *Eptesicus fuscus*, foraging in a cluttered acoustic environment,” *Brain Behav. Evol.* **86**(1), 6–16.
- Yovel, Y., Melcon, M. L., Franz, M. O., Denzinger, A., and Schnitzler, H.-U. (2009). “The voice of bats: How greater mouse-eared bats recognize individuals based on their echolocation calls,” *PLoS Comput. Biol.* **5**(6), e100040.