Canadian Journal of Zoology
Revue canadienne de zoologie

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Journal:	*Canadian Journal of Zoology*
Manuscript ID	cjz-2017-0188.R1
Manuscript Type:	Review
Date Submitted by the Author:	14-Oct-2017
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Keyword:	ECHOLOCATION < Discipline, bats, Tadarida brasiliensis, social calls, acoustic surveys, conservation

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In-Flight Social Calls: A Primer for Biologists and Managers Studying Echolocation[1]

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[1]This review is one of a series of papers arising from "*Learning to Listen* — Second International Symposium on Bat Echolocation Research: Tools, Techniques, and Analysis" that was held in Tucson, Arizona, USA, 26 March – 1 April 2017. Invited speakers were encouraged to submit manuscripts based on their talks, which then went through the normal *Canadian Journal of Zoology* peer-review process.

Abstract

Recent technological advances have permitted collection of immense datasets through automated recordings that are primarily aimed at capturing bat echolocation. Analyses of echolocation calls are used to identify species, relative abundance and some aspects of behaviour, such as foraging or commuting. Here we propose that social calls recorded in flight are also valuable tools for understanding bat ecology and behaviour. First, we examine how and why the acoustic structure of social calls differ from echolocation. Differences in form make social calls often, but not always easy to identify. We then use a case study on in-flight song in *Tadarida brasiliensis* (Geoffroy, 1824)*,* to show that what may appear as echolocation may instead be predominantly used for social communication. Next, we review three basic functions of in-flight social calls, include examples of each and develop a framework for testing these alternative functions using automated recordings. In a second case study, we use automated recordings of the endangered Florida bonneted bat (*Eumops floridanus* (Allen, 1932) to illustrate how behavioural information can be gleaned by examining patterns of social call production. Finally, we discuss why and how social calls provide novel information that can be crucial for conservation and management efforts.

Keywords: bats, social calls, communication, *Tadarida brasiliensis*, Brazilian free-tailed bat, *Eumops floridanus*, Florida bonneted bat, conservation, acoustic surveys

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Introduction

Since the first detailed description of echolocation by Don Griffin (Griffin 1958), biologists have been fascinated by the acoustic lives of bats. Given the nocturnal habits of bats, it is not surprising that they rely heavily on acoustic signaling for orientation, foraging, and social interactions (reviewed in Wilkinson 2003; Gillam and Fenton 2016). While bats produce both echolocation signals and social communication signals, the majority of bioacoustics research has focused on echolocation (reviewed in Schnitzler and Kalko 2001; Schnitzler et al. 2003; Fenton et al. 2016). This has led to exciting discoveries, as well as the development of sophisticated hardware and software for monitoring echolocation. These technological advances, in turn have resulted in the collection of immense quantities of acoustic data that are invaluable for research and conservation management.

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From a monitoring perspective, recording echolocation calls can be a powerful method for learning about the ecology and behaviour of bats. Depending on detectability and classification ability, passive ultrasonic recordings can potentially provide presence and relative activity of different species (Britzke et al. 2013). Additionally, echolocation calls can provide information about the type of activity and associated habitat. For example, the presence of feeding buzzes is indicative of foraging sites, whereas bat passes over short time periods at sunset and sunrise are indicative of commuting and possible nearby roosting habitat.

Bats are highly social (McCracken and Wilkinson 2000; Kerth 2008; Ortega 2016), and work in the last two decades has revealed that echolocation calls can potentially encode more socially relevant information than was originally thought. Studies have found that echolocation calls can provide information about the caller, such as sex, age, reproductive condition, and body condition (reviewed in Jones and Siemers 2011; Table 1). In some species, echolocation differs between individuals or groups, potentially providing even more detailed information about the identity of the caller (Table 1). Additionally, echolocation can provide habitat information to conspecifics such as the location of roost or foraging sites (Barclay 1982; Gillam 2007; Ruczyński et al. 2009).

Since echolocation can provide social information, one might ask: Why should bats use vocalizations specifically for social communication? Is there a difference between echolocation and social communication? And why should biologists and/or managers examine social calls, when echolocation can provide behavioural information about bats? The last question is especially pertinent because echolocation calls are much easier to record in far greater numbers than social communication signals.

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The ultimate goal of this article is to convince biologists that examining social calls recorded using automated systems can provide valuable information above and beyond what can be learned from echolocation alone. Yet, social calls are rarely if ever included in bat call libraries even though they are frequently recorded. Although ideally, social communication would be the focus of in depth research that directly observes behaviour in flight (for example Corcoran and Conner 2014), realistically this is challenging. Behavioural observations of flying animals in the wild, even with recent advances (Corcoran and Conner 2014; Theriault et al. 2014), are difficult, as they require expensive equipment (high speed video, high powered infrared lighting and a microphone array), as well as time-consuming and extensive advanced computational analyses to sync and examine audio-video data. Playback studies are a more feasible experimental method for assessing social call function of in-flight calls, yet they still require specialized equipment beyond a standard acoustic monitoring setup. In the absence of specialized technology, we argue that automated recordings of social vocalizations, if examined, could greatly contribute to our understanding of bat behaviour and even eventually be used to facilitate identification of some species.

In this paper, we begin with an examination of why and how social calls differ from echolocation based on diverse evolutionary pressures and constraints that result in distinct acoustic features. Next we use a case study to show that although social calls are often distinctive in structure, there are instances when discriminating between echolocation and social signals can be surprisingly difficult. We then review and provide examples of the different functions of social calls produced by bats in flight and develop a preliminary framework for testing social call function based solely on acoustic surveys. Throughout, we include case studies demonstrating how social calls can be incorporated into ecological and behavioural research on bats and emphasize how social calls can provide valuable information for conservation.

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Echolocation and communication signals

Evolution

Both echolocation and social calls are acoustic signaling systems in the sense that they are stimuli produced by a sender and propagated to a receiver. However, the two signals have evolved for different receivers and for different functions. Echolocation is autocommunicative; meaning the sender and receiver are the same individual, and functions to sense the environment. Echolocation facilitates orientation, navigation and prey detection. On the other hand, social communication signals (here onward referred to as “communication signals”), by definition, *evolved to influence other individuals* (Rendall et al. 2009; Bradbury and Vehrencamp 2011). Ultimately, the different receivers and functions of these two systems result in different evolutionary pressures and constraints on signal design.

Here one might note that we have shown examples of echolocation calls providing social information about the sender. Although this may appear as though echolocation calls are also social communication signals, this is not inherently the case. Echolocation calls did not evolve to influence other individuals and thus are considered *cues* rather than *signals* with respect to conspecifics. *Cues* are stimuli that have evolved for another purpose (in this case orientation) but can provide social information that is attended to by *eavesdroppers* (Danchin et al. 2004; Bradbury and Vehrencamp 2011, Fig. 1). There are two important differences between cues and signals in this context. First is that although inherent cues in echolocation signals may be elaborated upon for social functions, echolocation will be first and foremost optimized for its function in orientation, and any modifications of echolocation calls for communication will be constrained by the primary function of the signals. A second important difference between cues and signals is that in the former, the impact of the eavesdropper on the sender may be positive, negative, or nonexistent. while in the latter there must be a net benefit for both senders and receivers. In other words, in social signaling, the behaviour of the receiver will have a large impact on the evolution and maintenance of the communication system, while this impact is not required for cues used by potential eavesdroppers. Further, just because information is available to an eavesdropper does not mean that the information is used or that the receiver can even discriminate and

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appropriately respond to that information. Indeed, while a plethora of studies have shown potential social information available in echolocation calls only a handful of studies have demonstrated discrimination of such information by conspecifics (Kazial and Masters 2004; Kazial et al. 2008; Voigt-Heucke et al. 2010) and even fewer have shown that bats do so in the field (Knoernschild et al. 2012). Of note, there is little evidence to date that we can extract this information from automated recordings, making examination of social calls uniquely valuable.

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Having oneself versus another animal as a receiver has multiple effects on signal evolution. First, when an animal is both the sender and the receiver there is no conflict of interest (Fig.1). As long as the benefit of echolocating outweighs the costs, echolocation systems will persist. Alternatively, if communication signals fail to elicit responses or result in negative responses by receivers, the signaling system will break down, as signal production by the sender will be selected against. These differences may seem subtle but can have large ramifications. Second, in communication systems, ambiguity about the location of possible receivers and their perceptual abilities often drive signal design to maximize detection distance; that is, to hedge one’s bets by broadcasting loud, often conspicuous signals (Bradbury and Vehrencamp 2011). Alternatively, in echolocation the sender has precise information about the location and perceptual abilities of the receiver (oneself) and the active range is generally the immediate environment in which the animal is navigating. Although there can be some overlap, such as for species that forage exclusively in open environments, echolocation is often used over shorter distances than social communication. The maximum detection range of echolocation is also potentially hindered by the production of echoes from background clutter, such as vegetation. If a bat is hunting in anything other than a completely open environment, a longer echolocation detection range will lead to an increase in the number of non-target echoes from clutter, which can greatly reduce the bat's ability to discriminate prey targets. Thus, a significant design difference between the two types of signals is the effective range over which they operate (see Signal Design below).

The types of information encoded in echolocation versus social communication also drive divergent signal design. In echolocation, the primary information obtained from signaling includes the size, shape, velocity and distance of objects in the surrounding environment. This information is extracted, in large part by comparing outgoing calls and incoming echoes; this requirement likely serves to constrain signal design to at least some degree. In social communication, on the other hand, signal design often reflects information about the senders themselves, such as identity, "quality" or intention, and thus varies with context and the sender's internal state. These two distinctive types of information – external environment versus potentially variable sender condition, state or context will result in divergence in optimal signal design. Indeed, recent research has supported a tradeoff between echolocation and social communication functions in signal design (Finger et al. 2017).

Signal Design

To provide a framework for comparing signal design for echolocation and social communication we will simplify acoustic variation into three components: shape, frequency, and duration. We group signals into three basic spectro-temporal shapes (Fig. 2): constant frequency (CF), downward linear frequency modulated (dFM), and

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non-linear frequency modulated (variable frequency modulated or vFM). In general for the majority of bat species, echolocation call shape can be described as linear FM or CF; signals vary substantially between species, with slopes or bandwidths that range from flat (low bandwidth, CF) to steep (large bandwidth, dFM). Other shapes, including even upward FM are used in some molossid species (Guillén-Servent and Ibáñez 2007; Jung et al. 2014), however, here we focus on dFM signals. For bats using dFM signals, range is estimated using time delays to specific frequencies in the FM sweep (Schnitzler and Kalko 2001). Multiple time points in the signal with the same frequency (*i.e.* U-shaped calls) would cause ambiguity in determining the time delay between specific points within the call and those points in returning echoes. In high duty cycle CF bats, frequency modulation, bandwidth and shape are constrained by strong pressure to focus energy at the frequency of the acoustic fovea of the individual (Neuweiler et al. 1980; Schnitzler and Denzinger 2011). Conceptually, one can think of these shapes then being shifted in frequency (for high versus low frequency signals) or stretched and compressed in time (for long versus short signals, Fig. 2). Although this description of echolocation is highly simplified, it is useful in the context of comparing echolocation with social communication calls.

Echolocation calls are generally high frequency signals; as a reference, there are more than 1 200 species of echolocating bats, but only a handful of those produce echolocation calls in which the loudest, or peak, frequencies are within the audible range of humans (0.02 – 20 kHz). For insectivorous bats in particular, high call frequencies are adaptations for detecting small insect targets (Barclay and Brigham 1991). This is because for targets to produce significant echoes, the wavelength of the

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signal (which is the inverse of the frequency) must be at *most* equal to the size of the target. For example, a 10 kHz signal has a wavelength of approximately 3.4 cm (using 340 m/s as the speed of sound), much larger than small insects. Echolocation calls with peak frequencies below 20 kHz (wavelengths greater than approximately 1.7 cm) are much less efficient at detecting small targets (Möhl 1988). Interestingly, Waters et al. (1995) found that for echolocation calls with peak frequencies of 20 to 100 kHz, the ability to detect insect prey was comparable, indicating that a lower threshold exists for detecting small insects. As a result, calls above this spectral threshold may not increase the diversity of prey items detected, although prey perception depends on more than echo strength alone.

In the temporal domain, echolocation is primarily constrained by the need to avoid overlap between the outgoing pulse and the returning echo. This overlap is referred to as “forward masking” (Schnitzler and Kalko 2001), and is primarily a function of the outgoing pulse being much louder than the weak, returning echo. While some bat species are tolerant of pulse-echo overlap due to specializations of the acoustic fovea (Neuweiler 1990), most echolocating bats cannot effectively process echoes if such temporal overlap occurs. As a result, effective use of echolocation requires a silent period, the interval between pulses in which the bat is listening for returning echoes. This constrains maximum signal duration, as longer calls that suffer forward masking will not efficiently provide information for orientation or prey detection. Overall, echolocation calls, particularly for bats that use dFM signals, are constrained to higher frequencies and shorter durations for effectively detecting small objects in the surrounding environment. Optimal echolocation call design is further impacted by a

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variety of other factors, such as foraging habitat (open vs. cluttered; Neuweiler 1989; Schnitzler and Kalko 2001; Schnitzler et al. 2003), the presence of conspecifics (Gillam et al. 2007; Cvikel et al. 2015), and potentially local climactic conditions.

While optimization of echolocation includes high frequencies, short durations, and dFM (or CF) shapes, optimization of social communication signals should result in very different signal design. First, social calls can potentially have any shape with high degrees of overlapping frequencies *e.g.* sinusoids, U shapes, or upside-down U shapes (*e.g.* Fig. 3f). Second, although there can be some range overlap, social calls will often be selected to operate over a longer range than echolocation, which will drive the use of lower frequency, longer duration signals. For example, if the same echolocation pulse discussed above at 20 kHz were used for social communication it would attenuate quickly in the environment, resulting in a range of only 100's of meters to a conspecific; a 50 kHz pulse would attenuate below detection level at less than 50 m (Lawrence and Simmons 1982; also see Hoffmann et al. 2007; Jones and Siemers 2011). Those estimates assume that the receiver is in an ideal position to hear the signal, which is an overestimate for a bat flying at 5 – 30 meters per second. Additionally, signals are often produced for *potential* receivers, that is, to attract conspecifics from a distance, in which case even larger ranges would increase the probability of responses. Signal detectability also likely drives the finding that social calls are much longer than echolocation pulses through the use of longer syllables and/or producing multisyllabic calls (*e.g.* songs, Fig 3a - d). Frequency modulations generally transmit better over long distances than amplitude modulated signals (Wiley and Richards 1978) and if a great number of different signals are required for a signature system this can result in highly

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variable signal shapes (vFM, Fig. 2, Fig. 3f, Table 1 and see below). In conclusion, compared to echolocation calls, communication signals are generally expected to be lower frequency, contain longer duration syllables or sequences of syllables, and have more highly variable FM shapes. An important practical aspect of divergent call design between echolocation and social communication is that social calls can frequently be easily distinguished in automated recordings, facilitating analyses of social call use and function (see below, Table 2).

Case Study 1: *Tadarida brasiliensis* (Geoffroy, 1824) song

Throughout this review we have highlighted how social calls are structurally and functionally different from echolocation calls. This is to emphasize that social communication and echolocation are not necessarily a smooth continuum of signals. However, here we present a case study on social calls produced in flight that incorporate echolocation-like pulses.

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Over the past decade, Bohn et al. have extensively investigated the elaborate songs used by Brazilian free-tailed bats at roost sites (Bohn et al. 2008; Bohn et al. 2009; Bohn et al. 2012, Fig. 3a and 3b). Songs are produced at high levels during the mating season by males that defend territories at roost sites where reproductive females reside (Bohn et al. 2008). Songs are composed of multiple syllables that are hierarchically combined into distinct phrases. Two syllable types appear similar to components of echolocation. First, “*Chirp A*” syllables are downward FM sweeps that resemble steep echolocation calls. Second, *T. brasiliensis* songs often include “buzz” phrases that are nearly identical to feeding buzzes even though they are produced while bats are roosting. These buzzes are also used during agonistic encounters over food in captivity, while bats are not flying and are nearly identical to foraging buzzes produced on the wing (Schwartz et al. 2007). Thus, in this species echolocation-like pulses appear to be used in purely social contexts. However, these echolocation-like pulses are never produced singly; instead they are embedded into longer multisyllabic calls (see Bohn et al. 2008).

Recently, while conducting acoustic surveys in Florida, it was discovered that *T. brasiliensis* also produce songs in flight (Fig. 3c and 3d). While our extensive experience recording over 1 000 songs at roosts across the southern US and Mexico facilitated confident recognition of these vocalizations as songs, a naïve observer would likely classify these signals as echolocation “approach” and “buzz” phase calls mixed with some social calls (compare Fig. 3d and 3e). One question to ask is whether these social vocalizations, such as *Chirp A* syllables, are in fact echolocation calls. If so, the basic syllable features and, most importantly, the interval between syllables, should not differ from typical echolocation passes at the same location.

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To test the similarity of echolocation and echolocation-like syllables, we compared the characteristics of *Chirp A* song syllables with echolocation pulses from bat passes recorded within 10 s of each song. To balance analyses and control for environmental differences, we randomly selected echolocation pulses to match the number of *Chirp A* syllables at each location and used location as a random block in analyses. Location is crucial here because echolocation calls can vary considerably with environment, as they should be adapted to maximize efficiency in a given habitat particularly with respect to the amount of clutter and especially in *T. brasiliensis* (Gillam and McCracken 2007). We recorded 27 songs at five sites in the Miami area for a total of 251 *Chirp A* syllables and 251 echolocation pulses. For each syllable, the duration and inter-syllable interval was measured from oscillograms and peak frequency and bandwidth at -10 dB peak were measured from power spectrums (SASLAB, Avisoft Bioacoustics).

We found highly significant differences between *Chirp A* syllables and echolocation pulses in duration ($F_{1, 496}$=525.0, $p < 0.0001$), bandwidth ($F_{1, 496}$=180.4, $p < 0.0001$), and inter-syllable interval ($F_{1, 496}$=550.6, $p < 0.0001$), although not in peak frequency ($F_{1, 496}$=0.27, $p = 0.98$). Although there is considerable overlap in the distributions, *Chirp As* were generally shorter (4.4 ± 2.5 versus 10.7 ± 3.6 ms; ± SD) and steeper (22.9 ± 12.9 versus 10.4 ± 9.4 kHz) than echolocation pulses. The inter-syllable interval was the most divergent between the two signals, with average intervals seven times shorter for *Chirp As* (*Chirp As*: 34.6 ± 19.1 ms versus echolocation: 246.2 ± 137.7). Such short duration, rapid pulse trains align most closely with the features of approach phase echolocation calls, when pulse bandwidth is the greatest and duration and interpulse intervals are the shortest. To test the similarity between *Chirp A* syllables and approach phase echolocation, we measured 57 approach phase pulses from across the region (there were not sufficient data to match locations). On average, the interpulse interval of approach phase echolocation calls was still four times greater than the intervals between *Chirp A* syllables (149.8 ± 64.2 ms). Interpulse interval can be translated directly to the active range of echolocation, as echoes should be received prior to emission of consecutive calls. Using 340 m/s as an estimate of the speed of sound, this translates into an active range of typical echolocation intervals of approximately 40 m (246 ms from above multiplied by the speed of sound and divided by two to account for two-way sound travel), while there is only a 6 m range for *Chirp As* (35 ms). This does

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not account for the bat’s travel during production and sound reception. For example, during the 35 ms interval for *Chirp As,* the bat will have traveled between 1.5 and 3 m if flying at 5 – 10 m/s. These analyses suggest that while some *Chirp A* syllables could technically be used for orientation, most of them are not appropriately structured for efficient echo use, supporting a social function of these sounds.

A second important question relating to the social calls of *T. brasiliensis* is whether flight songs are different from roost songs. We compared *Chirp A* syllables from flight songs with songs that were recorded at roost sites in the region (N = 15 songs, 154 *A* syllables). We found no differences in duration, interval, peak frequency or bandwidth between roost songs and flight songs (all $t_{403} < |1.9|$, $p > 0.05$), supporting a social function of *Chirp A* syllables and the hypothesis that these entire sequences in flight are one long social vocalization.

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This case study highlights two important points. First, what appear to be echolocation pulses or buzzes may, in fact, be social calls. This can impact estimates of foraging activity, particularly in *T. brasiliensis*. Second, identifying the unit of a vocalization type, that is what actually is a *call*, is crucial when performing acoustic analyses of social communication (see Bohn et al. 2008). Is the call a single syllable or is it a multisyllabic sequence, or even an elaborate song? Vocalization units can be identified through comparisons across recordings to identify stereotypical patterns surrounding obvious social syllables. Note that this is only crucial if in depth acoustic analyses are being conducted on echolocation or social communication signals - presence / absence analyses of social communication calls can be easily conducted without extensive comparative analysis (see *Eumops Case Study* below).

In Flight Social Calls

In bats, the majority of in-flight social calls studied have one of three potential functions: social integration, conflict resolution, and courtship/territoriality establishment. The last two categories sometimes overlap, because territorial calls are a form of conflict resolution, but often also function in mate attraction. Below, we discuss each of these categories of function and provide examples from studies of bats.

Social Integration

Communication calls that integrate conspecific behaviours for a common goal are considered social integration signals. A key feature of social integration signals is that they facilitate recognition at either the individual or group level Bradbury and Vehrencamp 2011. Frequently, this “signature” information is encoded through vFM shapes (Beecher 1989; Bradbury and Vehrencamp 2011, Table 1). The most common types of social integration signals in bats function in parent-offspring communication or group cohesion. Most, if not all, bat species produce individually distinctive vFM infant isolation calls in roost sites for parent-offspring recognition (Gould et al. 1973; Wilkinson 2003; Bohn et al. 2007; Gillam and Fenton 2016 reviewed in in Wilkinson 2003; Gillam and Fenton 2016). It would not be surprising if parent-offspring communication occurred in flight or if modified isolation calls were used in affiliative contexts (for example see calls by *Eptesicus fuscus (*Palisot de Beauvois, 1796*)*; Wright et al. 2013). Support for this could be easily deduced from automated recordings that show an increased frequency of vFM calls during the first weeks that pups become volant.

In flight, the most studied social integration calls are those used to maintain group cohesion and coordinate movement, *i.e.* “contact calls”. Contact calls have been

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documented in a wide suite of vertebrate taxa (*e.g.* Snowdon and Cleveland 1980; Boinski 1991; Wright 1996; Maurello et al. 2000; Koda et al. 2008; Guillette et al. 2010). In bats and other taxa, calls can provide individual (Maurello et al. 2000; Oda 2002; Gillam and Chaverri 2012) and/or group-level identity information (Boughman 1997; Weilgart and Whitehead 1997; Keen et al. 2013). For example, *Phyllostomus hastatus* (Pallas, 1767) produce group-specific screech calls upon emergence that permit relocation of group members before departing the area surrounding the cave (Boughman and Wilkinson 1998; Wilkinson and Boughman 1998). Given that up to one thousand bats regularly emerge from the cave at dusk, these loud communication calls likely serve to reform groups when this would otherwise be a very difficult task. These calls are also produced at foraging sites, far from roosting locations, and serve to attract group mates who appear to defend resources from other social groups (Wilkinson and Boughman 1998). Other species produce contact calls at dawn before selecting a day roost site. For example, pallid bats, *Antrozous pallidus* (LeConte, 1856), produce contact calls while circling crevice roosts after foraging (Arnold and Wilkinson 2011, Fig. 4a). These individual-specific calls presumably facilitate formation of social groups before entering the roost. This idea is supported by the finding that pallid bats preferentially respond to the contact calls of familiar versus unfamiliar individuals (Arnold and Wilkinson 2011). Interestingly, contact calls have also been observed during apparent teaching behaviour in captivity (Bunkley and Barber 2014).Vampire bats - *Desmodus rotundus* (Geoffroy 1810), *Diaemus youngi* (Jentink, 1893), and *Diphylla ecaudata* (Spix, 1823), (Carter et al. 2012), and may also produce these signals in flight at feeding sites (Carter, pers. comm.).

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An interesting case study of contact calling in bats comes from Spix's disc-winged bat, *Thyroptera tricolor* (Spix, 1823). These small insectivores native to Central America primarily use immature, furled leaves of *Heliconia* plants as their roosts (Findley and Wilson 1974). These leaves are highly ephemeral, unfurling and becoming unsuitable roosts in ~5-60 hours (Vonhof and Fenton 2004). As a result, groups of *T. tricolor* must relocate to a new roost within their ~0.2 ha home range almost every day (Vonhof et al. 2004; Chaverri and Kunz 2011). Despite this frequent movement, social groups are relatively stable with the same individuals comprising a social group for as long as 22 months (Chaverri 2010). Studies have found that group cohesion is maintained through the use of at least one contact calling system. Chaverri et al. (2010) documented a two-call system that bats use when separated. A flying individual in search of a roost produces an "inquiry" call, which is often rapidly answered by a bat in a nearby roost via production of a "response" call. Both call types have individual signatures (Gillam and Chaverri 2012) and bats preferentially enter roosts from which response calls of familiar individuals are being emitted (Chaverri et al. 2013). When these bats are recorded flying throughout their home range at night (Montero and Gillam 2015), two types of social calls are commonly produced - inquiry calls and a newly described signal type, "long upward modulated" (LUM) calls. Montero and Gillam (2015) hypothesize that inquiry calls may be used for maintaining contact with group members over short distances, while the loud, vFM, LUM calls may be used for communication over longer distances.

Conflict Resolution

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Conflict resolution signals arise in disagreements over limited resources, such as food, territories or mates. The function of these signals is for each opponent to predict the probability of success. Two key types of information are often encoded in conflict resolution signals: fighting ability or resource-holding potential (RHP) and motivation ("intent", Table 2). In a wide range of species, RHP is positively correlated with body size, which is often negatively correlated with frequency (Bradbury and Vehrencamp 2011). Motivation or "intent" is the degree to which an individual is willing to fight for a resource. Conflict resolution signals across many vertebrate taxa are lower in frequency (indicating larger size) and noisy (broadband) following Morton's motivational-structural rules (Morton 1977; for extensive review see Bradbury and Vehrencamp 2011). In roost sites, aggressive vocalizations in the form of low frequency "squawk-like" calls (Pfalzer and Kusch 2003; Bohn et al. 2008; Knörnschild et al. 2014) and "buzzes" are extremely common. However, in flight, low-frequency broadband calls are rare (although see *P. hastatus* foraging calls) while buzzes are quite common (Pfalzer and Kusch 2003, see *Tadarida* case study above).

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Multiple species have been shown to use social calls in food patch territoriality, food "claiming" and direct interference. Low-frequency social calls in conjunction with chases at feeding sites have long been observed in free-flying vespertilionid species (Miller and Degn 1981; Rydell 1986). In *Pipistrellus* species, social calls are produced at foraging sites and playbacks demonstrate that calls repel conspecifics as predicted for a food patch defense function in *P. pipistrellus* (Schreber, 1774), *P. pygmaeus* (Leach, 1825), *P. kuhlii* (Kuhl, 1817) (Fig. 4b) and *P. maderensis* (Dobson, 1878) (Barlow and Jones 1997*b*; Russo et al. 2009). These calls also function in courtship and territorial defense at roost sites (see below). More recently, high-speed video and audio have elucidated the rapid interactions that accompany social calls during prey capture (Corcoran and Conner 2014; Wright et al. 2014). Experiments in captivity show that *E. fuscus* use bouts of short vFM syllables in flight to claim food; bats that produced calls were more likely to successfully capture a prey item (Wright et al. 2014, Fig. 4c). *T. brasiliensis* directly interfere with prey capture by jamming bats during feeding buzzes with long sinusoidally FM calls (Corcoran and Conner 2014).

Courtship

Courtship vocalizations are used to attract mates but often also commonly serve in territorial defense of either resources or mates. Courtship signals will be driven by female preference, which in turn should be correlated with male fitness (“quality”, Table 2). This can overlap with RHP signaling in territoriality when greater RHP is correlated with greater mate quality. For example, in some *Pipistrelle* species the same vocalizations used to defend foraging territories are also used at breeding territories near roost sites during the mating season (Barlow and Jones 1997*a*; Russo and Jones 1999; Russo et al. 2009). Interestingly, other *Pipistrelle* species use different calls (Georgiakakis and Russo 2012) or elaborate songs (Russ and Racey 2007; Jahelkova et al. 2008) exclusively during mating season.

One feature of courtship vocalizations is that they are often the most complex vocalizations in an animal’s repertoire, being composed of more numerous and diverse elements (syllables). This may be due to female preference for song complexity (Catchpole 1980; Searcy and Marler 1981; Mountjoy and Lemon 1996; Reid et al. 2004), and/or the multiple types of messages encoded in these types of signals

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(Jahelkova et al. 2008). Multiple bat species have been shown to produce elaborate courtship songs at roost sites (*i.e. T. brasiliensis*, Bohn et al. 2009; *Saccopteryx bilineata* (Temminck, 1838*),* Behr and von Helversen 2004; Davidson and Wilkinson 2004; for a review of bat song see Smotherman et al. 2016) and less commonly in flight (here for *T. brasiliensis*; Jahelkova et al. 2008). Another feature of courtship songs is that they often contain signature information. An excellent example is the use of *Chirp B* syllables in *T. brasiliensis*. These syllables are embedded in phrases, demonstrate high interindividual variation in shape yet are highly stereotyped within individuals and how they are incorporated into songs (Fig. 3f).

What can be learned from automated recordings of social calls?

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One potential, but relatively unexplored, value of social calls is as a tool for species identification. In some ways, social calls are superior signals for species identification compared to echolocation calls. Russo et al. (this issue) and Barclay (1999) point out that echolocation is very different from bird song, which has a communicative function and has often been selected for high stereotypy to convey specialized messages between conspecifics. Alternatively, social calls of bats are much more similar to bird song than echolocation; hence, it is likely that species-specific social signals could be more effectively used for species ID than echolocation (see Russo and Jones 2000).

In addition to species ID, one can glean valuable information about the biology of a species by attending to social calls, especially those in which call function is known. For example, agonistic encounters during foraging sites indicate that food is a limiting resource. Social integration signals, particularly at the group level have large ramifications for the minimum viable population size and the effects of disturbing roost sites in a given area. Most importantly, if the function and form of in-flight social calls are determined for a species, future recordings can then glean valuable information based solely on recordings, such as whether a bat is male or if mating is actively occurring (courtship signals present). For this to occur, investigators need to document and describe social communication calls produced on the wing.

With recent advances in the technology and affordability of passive ultrasonic recordings, a plethora of bat acoustic data are being gathered. Included in those data are social vocalizations. As we have shown, visual confirmation of the presence of social calls is extremely simple using spectrograms (Fig. 4). Here, we highlight when you are most likely to record signals of a given function; simply identifying the presence of such social signals can inform you about the behavioural state of your study animals (Table 2). Social integration signals could potentially be produced at any time, but often are most common during times of emergence from, and return to, a roost. Production of in-flight social integration calls should also be independent of the presence of food and whether it is the mating season. Alternatively, conflict resolution signals are predicted to become more common with increasing bat activity and may be associated with foraging (presence of feeding buzzes). To test between integration and conflict resolution, one can examine the number of echolocation passes immediately before and after a social call to determine whether the social call attracts or repels conspecifics (Table 2). Finally, although courtship signals can vary immensely in structure and function, but one main prediction is that they should be produced in a highly seasonal manner that is dependent on mating season.

Can Social Calls Be Informative for Conservation Efforts?

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It has long been recognized that social communication signals play a critical role in a variety of behavioural processes related to fitness. Indeed, without fitness benefits social calls would not be produced. Hence, it is logical that monitoring for such signals can give insight into the health of populations and provide early warning signs that a species requires conservation attention, potentially before declines even begin (Laiolo 2010). One of the clearest cases in which examining social call activity in bats can provide conservation-relevant data is using agonistic food calls to assess the severity of food competition. While accurately determining the density of insects that bats regularly eat is an involved process requiring specialized knowledge of insect identification, attending to social calls that are primarily produced when animals are competing heavily for limited food resources is much more straightforward. For example, several *Pipistrelle* species are known to produce agonistic calls related to defending a foraging territory; the occurrence of these calls is highest when insect densities are lowest (Barlow and Jones 1997*a*; Russo and Jones 1999; Russo et al. 2009). Tracking the occurrence of these sounds over time can reveal if, and how, the quality of foraging sites is changing.

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Tracking changes in mating activity via monitoring for social calls can also be valuable from a conservation perspective. For many species, especially Molossids and Vespertilionids very little is known about mating, including where or when mating occurs. While we often think of habitat loss and emerging infectious disease as the main factors causing declines in bats, once populations fall below a certain threshold size, other impacts related to social behaviour can become significant. For example, there may be minimal population sizes for mating to occur, as was believed to be the case with the passenger pigeon, *Ectopistes migratorius* (L., 1766) (Bolen and Robinson 2003). Identifying and confirming in-flight mating calls whenever possible can facilitate determining where and when mating occurs in other populations or closely related species. For example, once mating calls have been described, monitoring for in-flight mating songs near known roosts could provide an early warning about disruption of reproduction due to low population size or other factors.

Finally, bats as a taxon are generally extremely social, living in aggregations, groups or even societies (see Kerth 2008). Social communication likely facilitates information transfer on crucial resources like foraging and roosting sites. In fact, research suggests that information transfer is a key factor in the evolution of male sociality in temperate (Safi and Kerth 2007) and may also occur in tropical insectivorous bats (Dechmann et al. 2010). Small population sizes can disrupt information transfer and have large effects on survival. Roosts have been shown to be an important location for exchange of information about food resources (Wilkinson 1992) and at least some species have been shown to forage in groups after emerging from roost sites (Wilkinson and Boughman 1998; Dechmann et al. 2010). While it is not clear how this information transfer occurs, it is plausible that disruption of such an “information centre” (Nunney and Campbell 1993) due to reduced colony size could impact the foraging success of individuals. Future research understanding the role of social calls, both in flight and within the roost, for information transfer about limited resources would be valuable. Next we use a case study to illustrate how examining social calls in automated recordings can provide insight into the behaviour of species for which little is known.

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Case Study 2: *Eumops floridanus* (Allen 1932)

E. floridanus is one of the rarest and most enigmatic species in North America. Although historically considered a subspecies of the widespread neotropical *Eumops glaucinus*, morphometric analyses support separate species classification for *E. floridanus* (Timm and Genoways 2004). *E. floridanus* was listed as endangered by the US Fish and Wildlife Service in 2013 and there are currently no data on the actual population size of this species (estimates are as low as only 500 individuals). With respect to conservation, *E. floridanus* is unique for multiple reasons. First, in the United States the majority of bats and endangered bat species, are vespertilionids, whereas *E. floridanus* is a molossid. Species in these families have very different ecologies, seasonal patterns (molossids do not hibernate), echolocation and behaviour. Second, *E. floridanus* is essentially a Caribbean species that is limited to the most tropical region of the United States. The closest related overlapping species to *E. floridanus* is *T. brasiliensis*, but they too are extraordinarily different. *T. brasiliensis* is one-third the body size of *E. floridanus* and lives in colonies of up to millions of individuals while *E. floridanus* roosts are exceptionally small (10 – 30 individuals; KMB pers. observ.). Combined with small population sizes, small colony sizes of this species make them difficult to locate. Further, their tendency to fly high make them extremely hard to catch which has resulted in little published information on the species (but see Braun De Torrez et al. 2017 and below). Given these difficulties, and the fact that this species uses low frequency audible echolocation (12 – 16 kHz) that propagates over long distances, one of the best ways to collecting information on *E. floridanus* is through automated ultrasonic recordings. The echolocation calls and low frequency social calls

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(8 – 10 kHz) of these bats can be frequently heard at a golf course in Coral Gables, Florida (Fig 5a and 5b); hence, we placed an automated ultrasonic recorder (SM2, Wildlife Acoustics) at a fixed location at the site for one year (June 2014 to May 2015, with the exception of December and April when equipment was required for other projects). Given the distinctiveness of social calls in frequency (lower) and duration (longer), we were able to easily and rapidly train researchers and volunteers to determine whether files contained *E. floridanus* echolocation, social calls and/or feeding buzzes. Here we present preliminary analyses of these data as an example of how simple examinations can provide insight into a bat species' behaviour.

Our survey resulted in over 77 000 files with *E. floridanus* echolocation calls including approximately 11 000 files with social calls. This level of social communication (14 % of files) is remarkably high and indicates that sociality is a key component of these bats' lives. Based on the predictions in Table 2, we examined the potential function of social calls in *E. floridanus*. When examining social call presence and abundance from automated recordings, the number of files with social calls must be divided by the number of files with bat activity (here we refer to these as "passes") because there is an inherent correlation between bat presence and social call presence. The resulting frequency variable, "*relative social call activity*", can be calculated per night and compared over time and with respect to the total amount of bat activity. We found that nightly relative social call activity varied considerably from month to month (N = 152, $F_{9,142}$= 4.8, p < 0.0001, zero activity nights removed from analyses, arcsine square root transformed data to meet normality) but this variability was not isolated to a single season as expected for vocalizations used exclusively for courtship (Fig. 5c).

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Second we examined if social call use increased immensely with bat activity, as predicted for conflict resolution signals. This prediction was not supported, as there was only a minor trend in the effect of overall bat activity on social call activity (N = 152 nights, regression, $F_{1,152}$= 3.6, p = 0.07) which disappears entirely when extremely low activity nights are removed (Fig. 5d, cluster of points in lower left corner). Furthermore, we had the highest relative social call activity on one of our least active nights (52 passes, 16 of which contained social calls, relative call activity = 0.30) and there were many low activity nights with high frequencies of social calls (Fig. 5d). Finally, we noted that this area was not typically a foraging area as on average less than 2% of bat passes contained buzzes (mean = 1.9% ± 2% SD).

Our preliminary data indicate that *E. floridanus* are likely using calls for social integration rather than agonistic interactions. One potential context of these calls is group foraging, which has been observed in other molossid species (Dechmann et al. 2010). We observed the highest incidence of social calls immediately after sunset when bats emerge from nearby roosts (Bohn, pers. observ., analyses in prep.) The calls themselves are vFM and can be complex, which supports the potential for signature information commonly used in social integration or courtship signals. Indeed, recently these social calls have been used as acoustic lures to attract *E. floridanus* to mistnets. (Braun De Torrez et al. 2017). However, Since we have not classified calls by their features it is possible that some of these calls serve different functions, particularly in courtship. Future analyses that compare the structure of calls across seasons may shed light on courtship, however currently no information is available on the timing of reproduction to base comparisons. Our current and future analyses are focusing on

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whether calls appear to attract or repel conspecifics (by comparing bat activity before and after a social call is produced), which would better differentiate between social integration and potential courtship calls (Bohn, in prep).

Conclusions

The goal of this article was to highlight for biologists and managers that there is more to the acoustic lives of bats than echolocation. Currently, social calls recorded during long-term passive acoustic monitoring are primarily ignored, as there is not an established framework for analyzing these signals or inferring behavioural states from their presence/structure. Yet, attending to such social calls can be highly informative and provide new information about the ecology and behaviour of bats that cannot be deduced from echolocation alone. Finally, in some species, like *E. floridanus* social calls can directly translate to methodology in the form of “acoustic lures” (Braun De Torrez et al. 2017).

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Even in automated recordings, researchers can test multiple hypotheses regarding the function of social calls. Although social call shape, frequency and/or duration are usually distinctive from echolocation, in some cases, social calls can contain elements that are structurally similar to echolocation calls. Documenting and cataloging social calls in addition to echolocation calls for known species could build a framework for understanding social signals and can facilitate future species identification. Eventually for some species, social calls could be incorporated into automated identification since they often have distinct structures and frequencies. For example, *T. brasiliensis* are notoriously difficult to identify because of their highly variable echolocation that can overlap with various species; however, their songs are unique to the species. Future research analyzing communication calls in large (primarily echolocation) datasets will be of value for further elucidating the types of information that can be learned from social signals and the potential value of such information to conservation efforts.

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Table 1. Compilation of peer-reviewed literature examining if personal information is encoded into the echolocation calls of bats. This includes information related to sex, age, reproductive condition, body size/condition, group identity, and individual identity.

Species	**Frequency Difference?**	**References**
SEX		
Asellia tridens	Yes (F>M)	Jones et al. 1993
Cardioderma cor	Yes (M<F)	Smarsh and Smotherman 2015
Eptesicus fuscus	Yes, No	Masters et al. 1995; Kazial et al. 2001; Kazial and Masters 2004; Grilliot et al. 2009; Grilliot et al. 2014
Hipposideros caffer	No	Jones et al. 1993
Hipposideros commersoni	Yes (M>F)	Ramasindrazana et al. 2015
Hipposideros fulvus	No	Jones et al. 1994
Hipposideros ruber	No, Yes (M>F)	Jones et al. 1993; Guillén et al. 2000
Hipposideros pratti	Yes (M>F)	Fu et al. 2015
Hipposideros speoris	Yes (M>F)	Jones et al. 1994; Guillén et al. 2000
Myotis daubentonii	No	Jones and Kokurewicz 1994
Myotis lucifugus	No	Kazial et al. 2008

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Pteronotus parnellii	Yes (F>M)	Suga et al. 1987
Rhinolophus blasii	No, Yes (F>M)	Heller and Helversen 1989; Siemers et al. 2005
Rhinolophus clivosus	No (dur only)	Finger et al. 2017
Rhinolophus euryale	No	Heller and Helversen 1989; Russo et al. 2001
Rhinolophus ferrumequinum	No	Heller and von Helversen 1989
Rhinolophus hipposideros	No, Yes (F>M)	Heller and Helversen 1989; Jones et al. 1992
Rhinolophus mehelyi	No	Heller and Helversen 1989; Russo et al. 2001; Schuchmann et al. 2012
Rhinolophus monoceros	Yes (F>M)	Chen et al. 2009; Schuchmann et al. 2012
Rhinolophus pumilus	Yes (F>M)	Yoshino et al. 2006
Rhinolophus rouxi	Yes (F>M)	Neuweiler et al. 1987
Saccopteryx bilineata	Yes (F>M)	Knornschild et al. 2012
AGE		
Asellia tridens	Yes (A>J)	Jones et al. 1993
Eptesicus fuscus	Yes (A<J)	Masters et al. 1995, Kazial et al. 2001
Myotis daubentonii	Yes (A>J)	Jones and Kokurewicz 1994
Myotis lucifugus	Yes (A>J)	Pearl and Fenton 1996; Moss et al. 1997; Kazial et al. 2008

Draft

Pteronotus parnellii	Yes (A>J)	Vater et al. 2003
Rhinolophus blasii	Yes (A>J)	Siemers et al. 2005
Rhinolophus euryale	Yes (A>J)	Russo et al. 2001
Rhinolophus ferrumequinum	Yes (A>J)	Jones and Ransome 1993; Liu et al. 2007
Rhinolophus hipposideros	Yes (A>J)	Jones et al. 1992
Rhinolophus mehelyi	Yes (A>J)	Russo et al. 2001
Rhinolophus monoceros	Yes (A>J)	Chen et al. 2009
REPRODUCTIVE STATE		
Eptesicus fuscus	Yes	Grilliot et al. 2014
Myotis lucifugus	Yes	Kazial et al. 2008a
BODY SIZE/CONDITION		
Asellia tridens	Yes	Jones et al. 1993
Myotis daubentonii	Yes	Jones and Kokurewicz 1994
Hipposideros fulvus	Yes	Jones et al. 1994
Hipposideros ruber	Yes	Guillen et al. 2000
Rhinolophus ferrumequinum	Yes	Jiang et al. 2017

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Rhinolophus mehelyli	Yes	Siemers et al. 2005
GROUP		
Eptesicus fuscus	Yes (Family)	Masters et al. 1995
Hipposideros larvatus	Yes (Colony)	Jiang et al. 2010
Hipposideros terasensis	Yes (Colony)	Hiryu et al. 2006
Myotis lucifugus	Yes (Colony)	Pearl and Fenton 1996; Jameson and Hare 2009
Noctilio albiventris	Yes (Social Grp)	
Rhinolophus ferrumequinum	Yes (Social Grp)	Mohres 1967
INDIVIDUAL		
Cardioderma cor	No	Smarsh and Smotherman 2015
Eptesicus fuscus	Yes	Brigham and Cebek 1989; Masters et al. 1991; Masters et al. 1995; Burnett et al. 2001; Kazial et al. 2001
Euderma maculatum	Yes	Obrist 1995
Rhinolophus clivosus	Yes	Finger et al. 2017
Lasiurus borealis	Yes	Brigham et al. 1989, Obrist 1995
Lasiurus cinereus	Yes	Obrist 1995

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Myotis bechsteinii	Yes	Siemers and Kerth 2006
Myotis lucifugus	Yes	Kazial et al. 2008*a,b*
Myotis myotis	Yes	Yovel et al. 2009
Otomops martiensseni	Yes	Fenton 2003; Fenton et al. 2004
Pteronotus parnellii	Yes	Suga et al. 1987

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Table 2. Function, type of information, acoustic features and predictions for three types of social calls. Some signals can function in territoriality (conflict resolution) and courtship.

Function	Information	Features	Predictions from automated recordings
Social Integration	Identity	dur ↑, vFM	• Calls produced when few or no other bats present. • Bat passes before call < after call. • Calls produced during early pup volancy (parent-offspring communication). • Calls produced at sunset (group foraging) or sunrise (roost localization).
Conflict Resolution/ _Territoriality*_	Intent RHP *Identity*	buzzes or broadband elements kHz ↓ *vFM*	• Calls only produced when other bats present, social calls per pass rapidly increase with passes per unit time. • Bat passes before call > after call. • Call production correlated with feeding activity (foraging competition).
Courtship/ *Territoriality*	Identity Quality	vFM, dur ↑ or multiple elements kHz ↓, multiple elements,	• Calls produced most frequently during mating season.

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		elaboration
	Intent	*buzzes or broadband elements*
	RHP	*kHz*↓

[*] Features associated with territoriality in *italics*.

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Fig. 1. Diagram of echolocation (a) and communication (b) signals. In echolocation systems, the sender and the receiver are the same individual. Signal echoes provide information like object size, velocity or distance. Social information can be available in echolocation calls, which are *cues* to eavesdroppers. Eavesdroppers in turn can have a negative, positive or no effect on sender for cues to be used since echolocation calls have a separate primary function. In communication systems, signals evolve to influence another individual, the receiver. Senders frequently provide information about themselves like identity, quality and intent. Signals must have a net positive effect on both the sender and receiver to evolve.

Fig. 2. Illustration of signal design characteristics. Signals can be described by three features: duration (dur), frequency (khz) and shape. All signals in this illustration have the same durations and are centered at the same frequency (dotted line). They are broadly categorized into three shape groups: constant frequency (CF), downward frequency modulated (dFM) and variable frequency-modulated (vFM).

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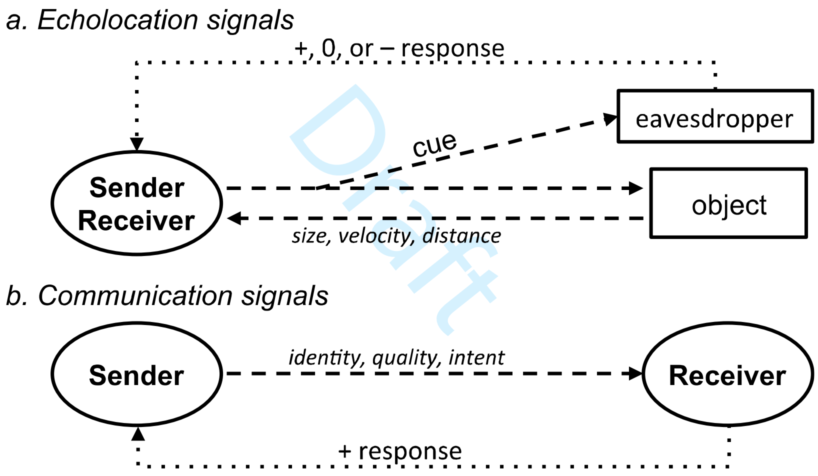
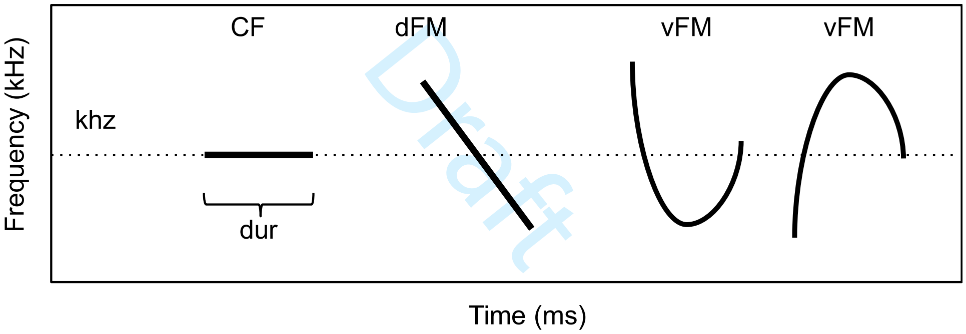
Fig. 3. Songs of *T. brasiliensis*. Typical songs recorded in roost sites (a and b), illustrating chirp, trill and buzz phrases and Chirp *A* and *B* syllables. Note the stereotypy of B syllables within bats (each song). Song recorded in flight (c and d) and an echolocation sequence (e). *B* syllables recorded in flight at different locations (f).

Fig, 4. Spectrograms of echolocation and in flight social calls (highlighted boxes) from three species. (a) *A. pallidus* social integration calls (provided by B. Arnold, note sample rate was 96 kHz whereas all others were recorded at 250 kHz or greater). (b) Food-related agonistic calls in *P. kuhlii* (provided by D. Russo). (c) Food claiming calls of *E. fuscus* (provided by G.S. Wright).

Fig. 5. Spectrograms of echolocation (a), in flight social calls (a) and relative social call activity (d and e) in *E. floridanus*.(d) Box plots of nightly relative social call activity (number of social calls divided by number of passes) across months. (e) There was no relationship between relative social call activity and bat activity across nights.


a. Echolocation signals
+, 0, or – response
eavesdropper
cue
Sender
Receiver
object
size, velocity, distance
b. Communication signals
Sender
identity, quality, intent
Receiver
+ response

Draft



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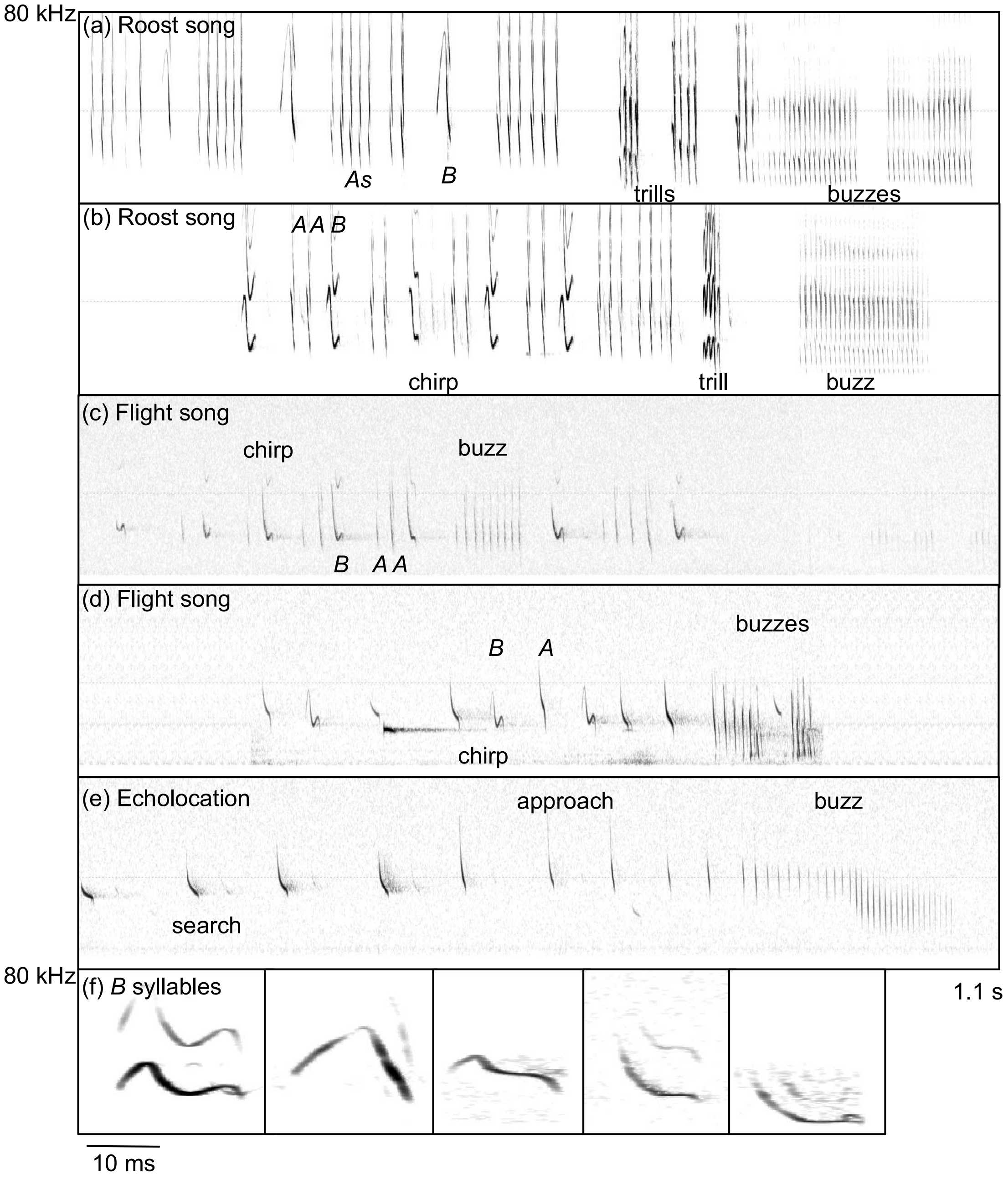
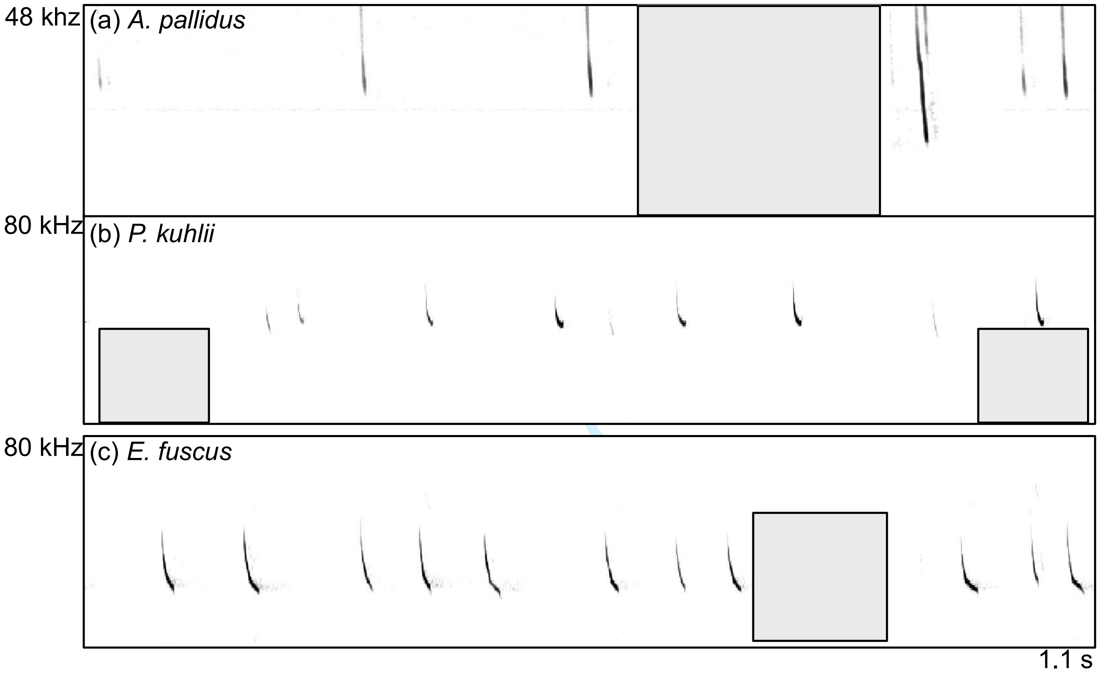
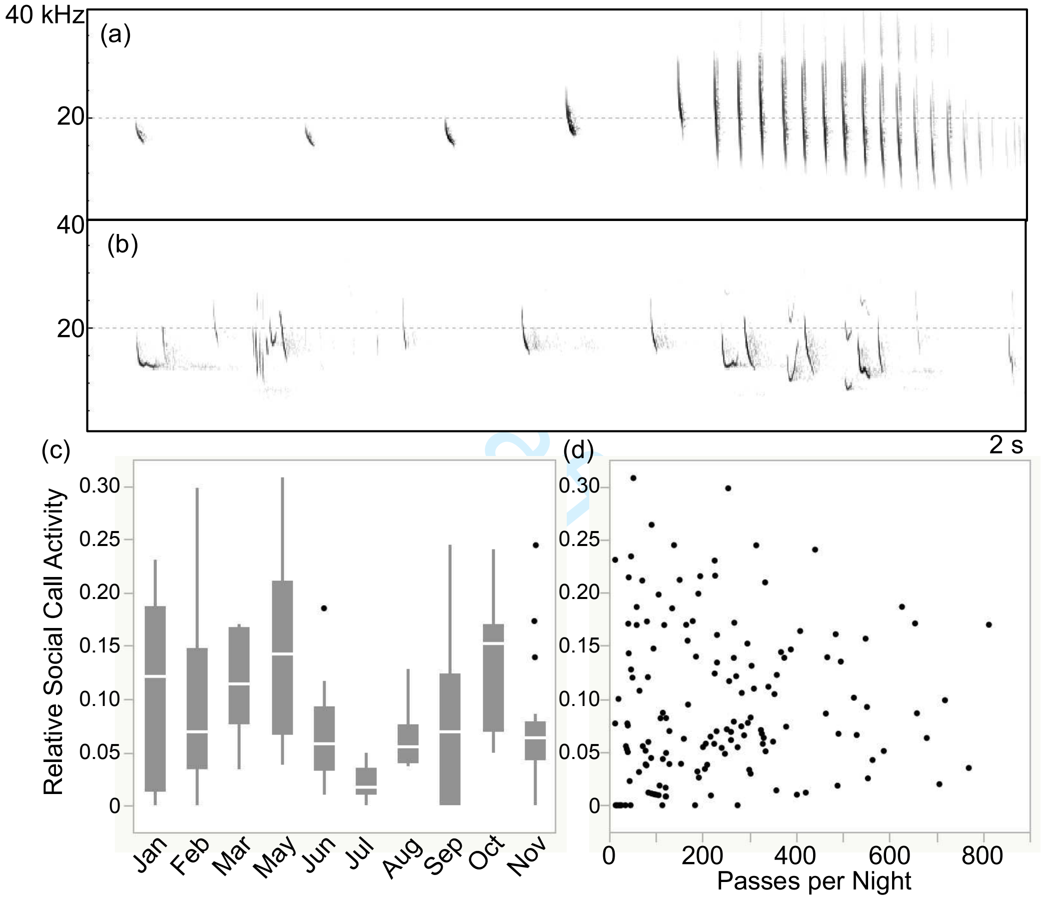

80 kHz
(a) Roost song
As
B
trills
buzzes
(b) Roost song
A A B
chirp
trill
buzz
(c) Flight song
chirp
buzz
B
A A
(d) Flight song
buzzes
B
A
chirp
(e) Echolocation
approach
buzz
search
80 kHz
(f) B syllables
1.1 s
10 ms


48 khz
(a) *A. pallidus*
80 kHz
(b) *P. kuhlii*
80 kHz
(c) *E. fuscus*
1.1 s


40 kHz
(a)
20
40
(b)
20
2 s
(c)
Relative Social Call Activity
0.30
0.25
0.20
0.15
0.10
0.05
0
Jan
Feb
Mar
May
Jun
Jul
Aug
Sep
Oct
Nov
(d)
0.30
0.25
0.20
0.15
0.10
0.05
0
0
200
400
600
800
Passes per Night