Acoustic Communication by Animals
Extended Abstracts

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Cornell University
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This symposium on Acoustic Communication by Animals is the third in a series of meetings dating back to the first meeting in 2003 at the University of Maryland and continuing with a second meeting in 2008 at Oregon State University.

These conferences have been motivated by the continued growth and interest in the evolutionary, ecological, behavioral, and functional aspects of animal acoustic communication. This increased interest has been fueled by a new generation of multi-disciplinary students and researchers. It has also been accelerated by the availability of new technologies for collecting and analyzing sounds and the applications of these technologies to previously unexplored habitats. Some examples of these new explorations include recording in a broad diversity of environments, expansions into broader spatial and temporal domains, and abilities to record data at very high sampling rates for extended periods of time. The research challenge is now clearly shifting to data analysis, management, and interpretation. Analysis now must contend with very large data sets, while interpretation pushes us to expand our thinking to spatial, temporal, and spectral scales matched to the acoustic ecologies of the systems being studied.

In addition to these mechanistic, intellectual, and conceptual challenges, the field of animal acoustic communication is now confronted with the sobering reality of the ever-increasing encroachments of human activities into animal acoustic habitats. As scientists and explorers in the natural world of biological acoustics, we are now confronted with the unavoidable responsibility of addressing the “So what?” question, and translating what we know into words and visualizations for agencies, industries, and the public. Increasingly, we must expand the kinds of questions we ask, the research we undertake, and the answers we offer so as to enable responsible, scientifically based decisions by those who are making regulatory policies or influencing the future survival of the organisms that we study and the ecosystems that sustain them. In short, we must be the scientific ambassadors and advocates for the living world that calls and sings to us from earth, sea, and sky.

As in previous meetings, this conference aims to focus the thinking of both established researchers and students by bringing together senior scholars, mid-career researchers and teachers, young investigators, and students to share ideas, data, and methods. We hope this conference stimulates, inspires, encourages, and educates those who are advancing the study of animal acoustic communication.

— Christopher W. Clark
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About this book
This book contains abstracts of oral presentations and posters presented at the third international symposium on Acoustic Communication by Animals, held at Cornell University in Ithaca, New York on 1-5 August 2011. The abstracts are in alphabetical order of the first author’s last name.

Before citing or using materials in any abstract, please contact the lead author.

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Temporal resolution and complex signal detection in the Lusitanian toadfish

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Many fishes use acoustic signals to communicate both in agonistic and reproductive contexts. In these animals it is generally agreed that the temporal structure of sounds is the main information carrier because a) the auditory system has been described as being more suited to interpret information in the temporal domain rather than the frequency domain\(^1\) and b) most acoustic signals produced by fishes are composed by series of short broad-band low frequency pulses\(^2\). This implies that the auditory system should be able to resolve the fine temporal structure of these signals, but little is known about the minimum interval between pulses that these animals are able to resolve\(^3,4\).

The Lusitanian toadfish *Halobatrachus dydactilus* (Batrachoididae) is a highly vocal teleost fish with no anatomical morphological hearing specializations. This species has an unusually large vocal repertoire with at least five different vocalizations\(^5\) and has been used in a variety of behavioral and neurophysiological studies by our research group in the past few years. Nesting toadfish emit long-distance advertising boatwhistles to attract females for mating\(^5\). Nest-holders also produce agonistic boatwhistles and grunts trains during territorial defence\(^6\). Because nests are aggregated and males often vocalize simultaneously, the arriving female might be frequently challenged to distinguish the call of one male within the chorusing male aggregation. Also males may use calls to sort out spatial relationships and for mutual assessment. Whether the auditory system of fishes is capable of accomplishing such tasks still needs to be addressed.

This study has two objectives: 1) to describe the temporal resolution of the Lusitanian toadfish hearing, using both a gap-detection paradigm and the analysis of auditory responses to playbacks of grunts with manipulated temporal structure; and 2) to determine the minimum sound amplitude difference allowing the detection of a boatwhistle over a toadfish chorus. To address these questions auditory evoked potentials (AEP) were measured to characterize the fish response to the experimental stimuli.

Our preliminary results, using the gap detection paradigm, suggest that the toadfish may detect silence gaps at least as short as 2 ms in continuous noise (Fig. 1). The analysis of the manipulated grunts indicates, however, that a correct representation of the temporal structure of the stimulus may require larger pulse periods. Moreover, a boatwhistle with an amplitude 3 dB above the ongoing background chorus appears to be represented within the auditory response. Additional work is being carried out to determine the difference in amplitude necessary for an accurate representation of the fine temporal structure of the boatwhistle.

The Lusitanian toadfish vocalizations are very complex and some temporal features of the signals may be cues for individual recognition\(^5,7\). Therefore, the evaluation of the auditory temporal resolution and of details of signal encoding in the auditory system may give hints to how these fish perform various tasks such as: individual recognition from the vocalizations, distance assessment of singing males and mate choice by females.
Fig. 1 A- Experimental stimuli (white noise low-pass filtered at 1000 Hz) with an inserted gap (arrow) used as sound stimuli. The length of the gap varied between 1-10 ms. B- AEP traces obtained from the Lusitanian toadfish using to different gap intervals. AEP traces are displayed relative to the beginning of the gap.

References


The Soundfield Around an Echolocating Atlantic Bottlenose Dolphin

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The use of remote autonomous passive acoustic recorders (PAR) to determine the distribution of dolphins at a given locations has become very popular. Some investigators are using echolocation clicks to gather information on the presence of dolphins and to identify species. However, in all of these cases, the PAR probably recorded mainly off-axis clicks, even some from behind the animals. Yet we have a very poor understanding of the beam pattern and the click waveform and spectrum from different azimuths around the animal’s body.

The beam pattern completely around an echolocating dolphin was measured at 16 different but equally spaced angles in the horizontal plane using an 8-hydrophone array in sequence. The hydrophones were B&K-8103. A schematic of the measurement geometry is shown in Fig. 1. Eight channels of data were digitized simultaneously at a sampling rate of 500 kHz and the results stored on a laptop computer.

The resulting beam patterns in both the horizontal and vertical planes are shown in Fig. 2. The beam in both planes showed a continuous drop off in sound pressure with azimuth around the animal and reached levels below -50 dB relative to the signal recorded on the beam axis. A pair of symmetrical side lobes formed at ± 45° and another smaller pair at ± 90° in the horizontal plane and the beam was relatively symmetrical. The beam in the vertical plane did not exhibit any side lobe structure.

The signals in both planes become distorted relative to the signal measured on the beam axis starting at angles of ± 22.5°. In general the center frequency decreased as the azimuth moved away from the front of the animal, however, the situation in the horizontal plane was considerably more complex than in the vertical plane. In the horizontal plane the signals began to break up into two components at angles greater than ± 45°. The two-component signals will cause the frequency spectrum to have a number of minima and maxima causing the spectrum to be very complex. The signals in the vertical plane at different aspects do not split up into multiple components, however, there are signs of multiple reflections of the signals from internal structures within the head of the dolphin. The results indicate that propagation of sounds within the dolphin’s head is a very complex and poorly understood topic.
Fig. 1. Experimental geometry showing a floating pen with a dolphin stationed on a hoop and echolocating on a spherical target 6.1 m in front of the hoop. Eight hydrophones were used in the horizontal plane in two configurations and 7 hydrophones were used in the vertical plane.

The various signal parameters as a function of angle in horizontal and vertical planes will also be discussed. These parameters are the source level, center frequency, root mean square bandwidth.

Fig. 2. The beam patterns in the horizontal and vertical planes. The number of clicks used to compute the beam patterns.
Species identification of odontocetes by analysis of whistle component shape and sequence

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Analysts who spend significant time looking at the spectrograms of odontocete whistles have developed the ability to discriminate to some extent between the whistles of different species. When asked how they tell them apart, our experience has been that the most common response is by looking at the shape of the frequency modulation. Yet with a few notable exceptions, the majority of automatic classification systems for odontocete whistles are based on statistics of whistle contours such as minimum and maximum frequency, a constant number of evenly distributed frequency measurements, number of inflection points, etc. These statistics only provide a rough approximation of the shape.

(a) Representation of a three state HMM to recognize an upsweep. Each state has a probability of transitioning to subsequent states as well as the probability distribution showing how likely it is to have the contour pass through a specific frequency while in that state. This illustration shows one possible state sequence with transitions occurring at the dashed vertical lines. b) Component recognition. A whistle component is presented to models of whistle components from varying species. The species/component associated with the best match will be used to label the call.

To exploit shape, new whistles must be aligned and compared with representations of whistles from the species to be recognized. In this work, we model whistles using Hidden Markov models (HMMs) that provide a method to align a novel whistle to a model in a nonlinear fashion, permitting speeding up or slowing down of portions of the whistle. A set of states represent different parts of a whistle using state
dependent probability distributions (Fig 1a). Models are created for each species and the species and whistle type can be derived from the model producing the highest likelihood.

Regrettably, the above procedure works well only if all possible whistle types have been observed. As a consequence, whistles are modeled at a component level with components defined by easily detected phenomena such as inflection points. Recognition of whistles is replaced with recognition of components (Fig 1b). This decreases the number of models needed, and permits recognition of whistles that were not seen in the training data but are similar to a new combination of the components.

A bigram model is created to predict the probability of seeing one type of component having just observed another. The bigram model is estimated by counting relative frequencies of component sequences in the training data, e.g. the probability of seeing component 4 from a bottlenose dolphin (*Tursiops truncatus*) following component 2 is calculated as follows:

\[
P(c_{4,T} \mid c_{2,T}) = \frac{\text{count}(c_{2,T}, c_{4,T})}{\sum_{i=1}^{n_T} \text{count}(c_{2,T}, c_{i,T})}
\]

where \(c_{i,T}\) denotes the \(i^{th}\) bottlenose dolphin component and \(\text{count}(c_{j,S}, c_{k,S})\) is the number of times that \(c_{j,S}\) was followed by \(c_{k,S}\) in the training data. Sequences that did not occur in the training data are given non-zero probabilities by the use of backoff strategies (e.g. Katz backoff). In this way, component models can be sequenced to recognize whistles that may be “characteristic” of a species, but that did not actually occur in the training data.

For each whistle, the system computes the probability that the whistle was produced by one of a set of known species using a search strategy that takes into account both the acoustic information (the component HMMs) and the component sequencing information (bigram model). The system is evaluated using about an hour of calls from four different classes: bottlenose dolphins (*Tursiops truncatus*), common dolphins (*Delphinus sp.*), melon-headed whales (*Peponocephala electra*), and spinner dolphins (*Stenella longirostris longirostris*) collected in the Southern California Bight and Palmyra Atoll. Results are reported both using analyst generated contours and automatically detected contours (*Silbid* graph-based contour extractor). The data include multiple visually confirmed sightings for each species and have a bandwidth of 96 kHz.
Beaked whale echolocation signals are mostly frequency-modulated (FM) upsweep pulses which appear to be species specific. We review and compare FM pulses of known and unknown origin from the Pacific Ocean (Aleutian Islands, southern California, Gulf of California, Pacific Islands) and Atlantic Ocean (Gulf of Mexico). Currently, we are able to identify FM pulses made by Baird’s, Blainville’s, Cuvier’s, Gervais’, Longman’s and Stejneger’s beaked whales as well as seven distinct signals of unknown origin. All of these signals are distinguishable by their spectral and temporal features. In addition to their spectral shape (Figure 1), we compared their peak frequency, center frequency, bandwidth, duration and inter-pulse interval, all of which are relevant to signal discrimination. Four of these signals from unknown species occur in the Gulf of California and offshore of southern California (Figure 1 VI, VIII, XII, and 40 kHz peak frequency - not in overview). They could represent Hubb’s, Perrin’s, Ginkgo-toothed and Pygmy beaked whale. One unknown signal occurs in the Gulf of Mexico and could originate from Sowerby’s beaked whale (Figure 1 IX). Additionally, two signals from unidentified species have been recorded and described for the Pacific Island region (Figure 1 VII & X, McDonald et al. (2009) J Acoust Societies Am 125:624-627, Baumann-Pickering et al. (2010) J Acoust Societies Am 127:3790-3799).

Evolutionary processes of niche separation may have driven differentiation of beaked whale echolocation signals used for spatial orientation and foraging similar to what is described for bats (Schnitzler et al. (2003) TREE 18:386-394). While very little is known about the differences in habitat preference and foraging behavior for all of these species, there are a few indications for trends of variation within the signals themselves. There is a linear correlation between the average adult body length and peak frequency ($R^2=0.6$; ANOVA $F_{1,9}=9.4$, $p<0.05$). Larger whales such as Baird’s beaked whales (~11 m) produce lower frequency signals (~15 kHz peak frequency) in comparison to smaller whales such as Gervais’ beaked whales (~4.5 m) with higher frequency signals (~45 kHz peak frequency). This relationship could be either due to anatomical and physiological restraints or it could be an evolutionary adaption for detection of smaller prey for smaller whales with higher resolution due to higher frequencies. Beaked whales which echolocate with higher frequency signals tend to use a higher repetition rate. The disadvantage of higher frequencies is a stronger attenuation over distance. The shorter inter-pulse interval might compensate for this. Alternatively, higher repetition rates may indicate navigation and foraging closer to the ground.

Comparison of known species at various locations suggests that despite inter-regional differences, their signal characteristics allow discrimination to species level. Evaluating the geospatial distribution, habitat preference and temporal occurrence patterns for unidentified species, and comparing those to sighting information may be useful for additional species acoustic identification. Furthermore, diel and seasonal analysis of these signals may help with planning field work for concurrent acoustic and visual species identification. Additional detailed analysis of echolocation behavior may give insight into reasons for this strong acoustic differentiation, potentially due to niche separation.
Fig. 1. Beaked whale FM pulse characteristics with known (I-V, XI) and unknown (VI-X, XII) origin from the Pacific and Atlantic Ocean, sorted by spectral values. A) Timeseries of FM pulse with inter-pulse interval in ms. B) Spectrogram of FM pulse (40 sample FFT, 98% overlap). C) Mean spectra of all FM pulses in analysis (solid line) and mean spectra of noise before pulse (dotted line), band pass filtered (10-pole Butterworth, 8-95 kHz).
The plainfin midshipman is a fish, common in estuaries along the Northeastern Pacific, which is notorious for the male’s loud, long, rasping mating call. I have studied the mating calls from three years of acoustic recordings in San Francisco Bay. The most unusual feature of this calling is a close correlation between water temperature and calling frequency. A linear fit to this variation is presented.

The plainfin midshipman (*Porichthys notatus*, or the toadfish) is a fish which depends heavily on acoustic communication in its reproduction [Bass, 1990]. This fish migrates during summer months to protected bays and estuaries in fairly shallow water, where the males tend benthic nest sites and call to attract females. Individual males may call for hours at a time, and large aggregations can be heard calling in concert at times. This calling is prominent in the North San Francisco Bay. Sound has been recorded from a monitoring station at the Romberg Tiburon Center, the SFSU marine laboratory on San Francisco Bay. A hydrophone is deployed there at the end of the monitoring pier, 200 feet from the seawall and at a depth of 40 feet, and sound is digitized continuously at 2000 samples per second. Environmental parameters, including water temperature 1 m below mean low low water level, are available from the SFBEAMS web site [Sfbeams, 2011].

Figure 1a shows a spectrogram of 15 minutes of sound, with intense midshipman calling, as well as two passing ships. Figure 1b is a spectrogram with an expanded frequency scale, showing several fish calling simultaneously. The fine structure in frequency is due to a modulation, in frequency or intensity, by the calling fish. (Beating between calls at nearly the same frequency is ruled out since this structure is present when even only a single fish is calling.)

**Figure 1.** Spectrograms of a 15-minute sound recording. (a) Frequency range 0-500 Hz (vertical), showing the midshipman fundamental near 100 Hz and many overtones. The sound from two ships passing is seen, near 90 sec and 660 sec. (b) Expanded frequency range.
The temperature near the hydrophone varies over a range of several degrees, both seasonally and over the tidal cycle, the latter due to the temperature difference between fresh water entering the estuary and sea water entering during flood tide. To study the effect of temperature on calling frequency, we determine a central fundamental calling frequency for each 15-minute recording. This is done by approximating the frequency spectrum over the range [85 Hz – 118 Hz] by a Gaussian form plus a constant background. For cases with a single caller, the central frequency is accurate to better than one Hz. With multiple callers it represents an average, favoring however callers close to the hydrophone.

Figure 2 is a scatter plot of peak frequency versus temperature, for all 15-minute sequences with a significant peak in the frequency spectrum. There is a clear approximate linear relationship. The substantial excess of points below the main distribution may be attributable to the difference in temperature, during periods of vertical stratification, between bottom water, where the fish nest, and surface water, near the temperature sensor.

References
Animals, like humans, frequently communicate using long-range acoustic signals in networks of several individuals. In socially and acoustically complex environments, however, communication is characterized by a variety of perceptual challenges that animals strive to overcome in order to interact successfully with conspecifics. These challenges are largely brought about by the accumulation of sound degradation during transmission of signals through the environment and their masking by ambient and transient background noise. In nature, all sound reaching an animal's ears, whether from biotic or abiotic sources, is also shaped by the natural environment as a result of habitat-induced degradation. Most habitats consist of reflective surfaces that cause signals to become attenuated, reverberated and masked by tails of echoes from preceding sounds. Consequently, the auditory system routinely processes sounds that are distorted, i.e. whose spectral and temporal fine structure differs considerably from that of the original sound at its source. In addition to compromising effects from background noise, these spectral and temporal alterations of the sounds likely affect the transfer of information between signalers and receivers, increasing detection thresholds and interfering with the discrimination and recognition of relevant and irrelevant sound sources.

Much recent concern has been directed toward anthropogenic noise sources and whether they affect the animals’ natural territorial and reproductive behavior and ultimately harm the survival of the species. Not much is known, however, about the potentially synergistic effects of environmentally-induced sound degradation, masking from noise and competing sound signals and what implications these interactions bear for vocally-mediated exchanges in animals. We will review some of our latest comparative studies on the perception of complex structural changes in acoustic stimuli as they become reverberated in the absence and presence of noise. All findings presented here are from psychophysical experiments with several species of small birds. In these studies we assessed the impact of reverberant multi-signaler environments and the possible species differences in auditory system adaptations to deal with and potentially utilize the associated signal alterations. We focused on reverberation as a major aspect of overall signal degradation in order to evaluate its isolated effect on biologically relevant acoustic stimuli independently from other habitat-induced acoustic changes.

Overall, our results from budgerigars, canaries and zebra finches clearly suggest that even small reverberation effects could potentially be used to gauge the properties of different acoustic environments and to locate a sound source but limit the vocally-mediated transfer of important information in social settings, especially when reverberation is paired with noise. More specifically, subtle structural changes within the signal alone (i.e. disregarding tails of echoes) can be discriminated, although this ability is somewhat dependent on both the species and, in particular, the type of signal. Discrimination of these alterations is possible with digitally reverberated artificial sounds and vocalizations as well as (to some extent) natural object-induced reverberations that are re-produced in a sound-isolated chamber with reflective objects. Such subtle changes could therefore potentially be used as a cue to distance or to the acoustic make-up of the surrounding environment. In fact, previous experiments in the field have revealed
that birds are able to use a combination of within-signal changes and tails of echoes when categorizing reverberation levels across a wide range of familiar and unfamiliar vocalizations.

Detrimental effects of reverberation, however, become obvious when birds have to discriminate similar vocalizations from different individuals. In previous studies with humans, degradation brought about by artificially created room reverberations resulted in deteriorated speech segments and decreased speech intelligibility. Similarly, own earlier sound transmission studies on sound degradation in great titmice (Parus major) indicated that similar song types, which are shared by neighbors, become yet more similar (and likely less distinguishable) when they are subject to habitat-induced degradation. Yet, our data clearly show that the ability to discriminate similar short vocalizations is significantly impaired only when both reverberation and abiotic noise levels are high, whereas it is much less affected by either of these factors alone.

Similarly, in simulated multi-signaler environments high levels of reverberation combined with biotic noise from conspecifics limit the auditory system’s ability to parse a complex acoustic scene by segregating signals from multiple individuals, indicating that reverberations contribute to the so-called Cocktail Party Effect. As in humans, animals that communicate in groups are faced with the problem of acoustic interference from multiple sound sources as well as the scattering of sound waves in the environment. The listener receives a composite waveform that has to be parsed by the auditory system into separate, perceptually coherent sound components that represent different sound sources. Discrimination can therefore also be affected when longer vocalizations of one individual or species cannot be separated from those of others in the form of a separate auditory object. In our study, the birds’ ability to selectively attend to a specific sequence of sounds in its entirety was particularly compromised when very high reverberation levels coincided with many birds singing in the background. In contrast, many signalers or high reverberation levels alone did not have an effect of similar severity. This suggests that at low to moderate reverberation levels receivers can ‘hear out’ and distinguish longer sequences of sounds from multiple individuals despite degraded auditory grouping cues. More severe reverberation, however, may limit this ability considerably.

In all experiments, the auditory system of budgerigars seemed to be a step ahead in solving the perceptual problem of listening in noisy, reverberant habitats. This may be reflective of the species’ advanced cognitive flexibility or capacity that also enables the birds to learn large numbers of new vocalizations throughout life. Therefore, a rich social environment (as in the flock-living budgerigar) combined with the retained capacity to learn new songs may help equip the auditory system with a perceptual flexibility that is necessary for the advanced task of communicating in social groups and sound degrading environments. Our studies strongly imply that in order to fully understand the potentials and constraints of communicating in social networks, one must consider not only the acoustic properties of the signals and the masking noise, but also the physical make-up of the environment in which those signals are transmitted. Clearly, high levels of reverberation pose a special problem to all receivers, particularly because their effect on communication strongly interacts with other factors such as overall levels of biotic and abiotic background noise.
Despite a great deal of research, the evolution of mammalian vocal complexity, particularly human speech remains poorly understood and controversial. Birdsong is a prominent model for language because of its complexity and flexibility - it has variable syntax, hierarchical organization and is vocally learned. This is in part because most mammals, other than humans, produce relatively invariant, innate vocalizations that do not require auditory feedback or incorporate different types of sounds in specific orders (syntax). Consequently, virtually nothing is known about the function, evolution, or production of mammalian vocal syntax. Here we present an exciting new mammalian model, Brazilian free-tailed bats (Tadarida brasiliensis) that use hierarchically structured songs that parallel those of birds and cetaceans (Fig. 1). Here, we qualitatively and quantitatively describe the songs of free-tailed bats and behaviors associated with singing. Next, we examine song perception and test whether individuals can discriminate among different males’ songs. Finally, we examine the behavioral contexts of song production using playbacks in captivity and in the field.

Fig. 1-Song of T. brasiliensis. A. All individuals use the same three types of phrases: chirps, buzzes and trills. The spectrogram displays changes in frequency (i.e. pitch, y-axis) over time (x-axis). B. Spectrogram of a portion of the chirp phrase showing the two types of chirp syllables “A” and “B”. C. Transition model for the order of phrases within songs. Songs are constructed highly non-randomly. Darker and thicker arrows denote higher frequencies of transitions, “+” and “– “ denote deviations from expected Markov model frequencies.
We have examined and quantified songs for multiple individuals (N > 40) from a captive colony in Austin, a natural colony at Kyle Field at Texas A&M, and our captive colony at Texas A&M. All songs follow a specific hierarchical structure. All are composed of the same four types of syllables that are combined to form three types of phrases (Fig. 1A and 1B). Both syllable and phrase types are distinct, discrete and easily identified across individuals. Furthermore, songs can be categorized into “song types” based on the order of phrases. Although songs can vary from 1 to over 20 phrases in length, phrase order follows a few specific rules and particular phrase combinations are preferred over others (Fig. 1C). The most compelling feature of this system however is song flexibility. Even though song construction and phrase order follow basic rules, the number and order of syllables and phrases in songs varies immensely within and among individuals. Thus, males dynamically vary syntactical features while simultaneously adhering to syntactical rules. This type of vocal signal in particular—hierarchical, structured, yet flexible—is exceedingly rare in non-human mammals, making this a compelling system for exploring how and why complexity and flexibility, fundamental requisites for language, arose in a mammalian system.

Using habituation-discrimination experiments in the laboratory we tested whether five individuals could discriminate among males’ songs. Five different songs from one male (Male A) were played in random order and subjects’ responses were scored by whether or not they turned towards or moved their pinnae in response to songs. Once subjects had habituated, either a random sequence of five different songs was played from a second male (Male B, test trial) or a random sequence from the original male (Male A) was played (control trial). We found that across ten pairs of songs, subjects responded more in test trials than control trials, indicating discrimination among different males’ songs. Using an identical design we then tested whether the syllables with the highest degree of repeatability, Chirp Type B syllables, were sufficient to allow discrimination. For this experiment, test trial stimuli were songs from one male (Male A) whose Chirp Type B syllables were replaced by Chirp Type B syllables from a second male (Male B). We found no difference in responses between test and control trials indicating that Chirp Type B syllables alone are not sufficient to allow for discrimination.

Using infrared video recordings and playback experiments, we examined the social contexts in which males sang. First, in captivity we show that singing is associated with territorial confrontations, by introducing males into the territories of singing males. Next we show that males in our captive colony respond with song whenever males fly past their territories. We hypothesized that males used the echolocation signals of conspecifics to assess proximity. To test this hypothesis we played echolocation passes to territorial males in captivity and in the field. We found an almost ubiquitous immediate (within 1 to 2 s) response to echolocation passes across different males both in captivity and in the field (N = 10). Males also responded repeatedly across days (N = 3 days). This is an excellent example of passive listening unintended cues and one of the most robust vocal responses to acoustic playbacks observed in mammals. In conclusion, T. brasiliensis is a widespread and abundant mammal that uses flexible vocal syntax, adapts well to captivity and responds well to playbacks and psychoacoustic experiments. The results shown here indicate that this species has the potential to provide a unique opportunity for exploring the evolution and neurobiology of complex vocal behaviors in mammals.
When is it too late? Echolocation and flight adaptations to last minute prey movements in the trawling bat *Myotis daubentonii*

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Echolocating bats adjust their sonar calls to their prey capture behavior and show characteristic changes in the call time-frequency structure as they approach targets. For a typical aerial insectivorous bat a pursuit can be divided into search, approach and terminal (buzz) phases (Griffin, 1958). Search phase calls are characterized by shallow frequency modulation, slow repetition rate (~10 Hz) and relatively long durations. Once the bat detects and selects a prey item, it produces approach phase calls with increased repetition rate, steeper frequency modulation and reduced duration. In the final capture phase, terminal buzz calls shorten further and are produced at very high repetition rates (up to 200 Hz; Griffin, 1958).

Some bat species trawl for insects or fish protruding from water surfaces and produce acoustic pursuit sequences very similar to aerial insectivores, including terminal buzzes prior to prey capture. The ubiquitous occurrence of sonar buzzes in trawling and aerial captures point to their importance for high sampling update of prey position, and serve to illustrate the bat’s adaptive control over acoustic information flow.

Despite its obvious importance, no experiment has so far focused on the significance of the buzz sequence for the final phase of prey pursuit. What is the processing time? How fast can the bat react to sudden changes in prey position and thus acoustic flow of information? Is there a “point of no return” where the bat completes the behavioral and acoustic sequence even if the prey is no longer there?

Here, we used Daubenton’s bats (*Myotis daubentonii*) to study the significance of the buzz-sequence. Final buzzes of *M. daubentonii* contain two sequences, buzz I and buzz II, separated by a short pause in call emission. Buzz II pulses are further characterized by a distinct drop in terminal frequency. During buzz I, *M. daubentonii* reduces pulse interval to 5.5 ms, whereas in buzz II, pulse interval is consistently at a minimum of 5 ms (Kalko & Schnitzler, 1989).

We trained 4 bats to capture prey while trawling over a small pool in the lab and studied their acoustic and flight capture behavior as we removed (submerged) the prey at different phases of the pursuit. We used a trigger-synchronized setup combining a 4-microphone array for acoustic recordings, a high-speed video camera and a custom-built prey-remover device. We conducted randomized series of trial sets, based on the following three trial types: 1) mealworm floating on surface, 2) mealworm attached to prey remover wire without removal and 3) mealworm removed below water surface as the bat approached. Figure 1 illustrates a type 3 capture sequence, where the worm was pulled under water (screenshot b-d) just before capture.

Preliminary analyses of high-speed video and pulse interval (time between start of two consecutive calls) data from one *M. daubentonii* showed that there is a “point of no return” somewhere in or just prior to the buzz I phase, even if prey is removed. Contrarily, at pulse intervals down to ~17 ms, the buzz (I+II) could still be completely aborted if prey suddenly disappeared. If the prey was removed at pulse intervals of 12 ms, buzz II could still be completely aborted, while down to 9 ms buzz II could be shortened. Finally, at pulse intervals below 7 ms the bat was no longer able to interrupt buzz II and proceeded with the buzz even if prey was removed. Congruent results were found for the bat’s flight behavior.
We have yet to analyze data from 3 additional *M. daubentonii* to confirm whether these restrictions on acoustic and flight behavior are similar between individuals. Based on our results we discuss the importance of terminal buzzes and information processing time in bats.

Fig. 1. Screenshots from a highspeed video recording of a trawling Daubenton's bat (*Myotis daubentonii*) closing in on a mealworm attached to a small wire protruding from the water surface. In our experiment, the mealworm was pulled under water (b-d) at different times before and during the final buzz to examine to what extent the bat still can still adjust echolocation emissions to last minute changes in prey position.

References
Barn-talk: Increased equine vocalization in a restricted environment

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At pasture, horses rely primarily on visual identification of friend or foe, desiring to evaluate any intrusion from a distance to allow time to escape if needed. In a barn, however, the conditions they encounter are significantly different; mobility is severely restricted, typically to a box stall, visibility to the outside of such a stall is limited, while the adjacent corridor makes close access by all possible. In addition, the barn acoustic environment can be noisy and unsettling, both from animal and man-made sounds, which the horse may neither see or initially understand. We find horses try to compensate by increased vocalizations, some of which have not been observed outside, such as upon hearing the sound of an approaching feed cart, a familiar rider, or a horse passing nearby in the corridor. In addition to a background of tonals, a whinny has a strong frequency variable component resulting in its characteristic sound and offering the possibility, if they can control this component, of at least a primitive form of emotional expression. A previous analysis has shown the frequency structure of whinnies under stressful conditions, such as mare-foal separation, is significantly different than under an assumed happy condition, for example arrival of the feed cart. We are now just starting to determine if we can quantify the frequency variations observed in this increased range of vocalizations to determine on the simplest level any expression of emotion.
Developing a Portable and Persistent Autonomous Real-Time Marine Mammal Acoustic Monitor

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Marine mammal monitoring (MMM) methods for mitigating the potential disruption of acoustic habitat, such as from military exercises or seismic surveys, traditionally rely on one of two technologies: archival recorders or towed hydrophone arrays. Both have significant disadvantages, as archival recordings are analyzed long after the acoustic events of interest, while towed hydrophone arrays suffer from the noise of the ship towing the array and require dedicated on-ship computers and human reviewers to acquire and process the data. Even more recent approaches such as the Auto-Buoy system,¹ which transmits suspected detections of marine mammal vocalizations as audio clips, does not provide for archival data storage and can only operate in "near real-time" with delays on the order of 20 to 30 minutes.

To overcome the disadvantages of these existing technologies, we are integrating archival recorder hardware and established detection, classification, and localization (DCL) algorithms into a Wave-Powered Glider Persistent Autonomous Vehicle (Liquid Robotics "WaveGlider" – see Figure 1) combined with a broadband satellite communications system (SAIC “Satcom”), to develop an autonomous MMM system capable of transmitting DCL data in near real-time to an on-ship or on-shore receiver. Such a system would be capable of persistent, autonomous, real-time monitoring of marine mammals in areas that would otherwise not be surveyed, as it will not require a local ship for its deployment, its retrieval, or reception of data for human review.
The current goal is demonstrating the feasibility of the integrated system with a towed four-element hydrophone array, for capturing and transmitting acoustic data to an on-ship data collection system. Results of the initial bench-tests for feasibility will be presented and discussed, including (a) mechanical integration of the recording and Satcom electronics into the WaveGlider payload areas (Figure 1); (b) power consumption measures of the combined electronics as compared to the WaveGlider’s solar power capability; and (c) hydrophone array data acquisition testing.

References

Invited Speaker

Communication Masking: The Influence of Ship Noise on Marine Mammal Acoustic Habitats

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There is now considerable evidence documenting the rising level of ocean noise in the marine environment. The anthropogenic components of this increase and their potential impacts on whales (cetaceans) are topics of substantial interest and concern, and the Marine Mammal Protection Act specifically imparts cetaceans with legal standing on this issue. Human activities in marine environments often overlap spatially and temporally with the habitats or seasonal occurrences of many whale species. Some species in certain contexts are known to respond to and in a few cases be impacted by anthropogenic noises, but the mechanisms and scales of actual or inferred impacts, at both individual and population levels, remain unclear.

Whales rely on the production and reception of sound for carrying out basic life functions. Acoustic signals are essential for critical activities such as communicating, foraging and navigating, and disruptions to any of these can impact survival and fecundity. Acoustic productions within the cetacean group span a frequency range of at least 10^4 - 10^5 Hz, a signal duration range of approximately 10^-5 - 10^1 sec, and a spatial range of at least 10^1 - 10^5 m. Here we refer to the acoustic behavior of an animal (or population) within the context of its ecological and acoustic environment as its acoustical-behavioral ecology, and to the spatial-temporal-frequency space within which an animal (or population) carries out basic life functions as its acoustic habitat. It is the acoustic habitat that is influenced by anthropogenic sound sources, and it is the acoustic ecology of an individual or population that is impacted by those sources. Therefore, baseline acoustic behaviors of whales are required in order to evaluate the impacts and that baseline needs to extend over spatial and temporal scales that match the spatio-temporal scales of a species’ acoustic ecology.

We present an acoustical-behavioral-ecological paradigm for evaluating and interpreting the influences of anthropogenic sound generating activities on individuals of selected whale species based on considerations of the acoustic habitats and communication contexts in which the animals produce and perceive their sounds. This work is driven by the need for scientifically-based understandings of baseline behavioral ecology to enable protective and defensible policies and regulations. Historically, the approach
for evaluating and regulating short-term, anthropogenic effects on the individual have been based on dB exposure level (e.g., a dose response as estimated by the RMS dB received level), while longer-term, population level or cumulative effects have been left almost entirely to speculation. It is now increasingly recognized that in many cases RL is not a good predictor of either behavioral response or biological risk, and empirical evidence shows that “context” has a significant influence on an animal’s response to anthropogenic sound exposure. This underscores the critical need to include considerations of behavioral ecology to properly interpret and understand the influences of anthropogenic noise on an animal’s or a population’s acoustic habitat.

Here we use results from a number of studies representing different cetacean species in different behavioral and ecological contexts to illustrate the spatio-temporal-spectral influences of cumulative anthropogenic noise sources on acoustic habitat. This includes humpback whales in the Glacier Bay National Park in Southeast Alaska during the summer feeding period when cruise ships enter the bay, North Atlantic right whales off New England during their winter-spring feeding period (e.g., Figure 1), and Southern Resident killer whales off Vancouver Island, British Columbia during summer. We apply an analytical algorithm to quantify the influence of ship noise on modeled populations of sending or receiving animals. Results reveal the ecologically spatial and temporal scales over which acoustic habitat is lost and lead to questions concerning the cost of this habitat loss for species that are highly dependent on the acoustic modality for basic life functions.

Figure 1. Comparative examples of humpback whale acoustic communication space in Glacier Bay National Park with (left) only weather noise and with (right) weather noise and vessel noise (10-minute sample, humpback frequency band). In this example each individual humpback’s communication space and each vessel’s noise “footprint” is represented as a higher intensity point source with decreasing intensity at increasing distance from the source. In the right panel, the cumulative influence of vessel noise masking on humpback communication is illustrated by a decrease (in some cases disappearance) of each individual humpback’s communication space beneath the vessel noise footprint.
Vocal cues reveal intruder nestlings: Evidence for an acoustical host-parasite arms race that starts inside the egg

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Recognition is a critical mechanism of any discriminatory behaviour. Yet recognition is not error proof, as evidenced from studies on parent-offspring recognition and host-parasite discrimination. The evolutionary puzzle of why hosts of cuckoos often eject mimetic foreign eggs but accept acoustically and visually non-mimetic cuckoo chicks arises, in theory, because of error in learned discrimination. Indeed, the cost of mistakenly rejecting one’s own young (especially young that are larger and beg more intensively, and hence, appear the healthiest) is extremely high.

Nevertheless, hosts of some brood parasites are able to detect and reject parasitic young. For example, superb fairy-wrens (Malurus cyaneus), an endemic Australian songbird, recognize the acoustically and visually mimetic horsfield’s bronze-cuckoos (Chalcites basalis) and abandon them to start a new breeding attempt. It has been suggested that the female fairy-wren discriminates cuckoo nestlings with reference to an acoustic recognition template; but the developmental and perceptual mechanism guiding the behavioural rejection mechanism was unknown.

Here, we show that (1) female superb fairy-wrens make a previously undescribed incubation call when in the nest with their unhatched eggs, (2) the female incubation calls have a distinct signature element; and (3) the mother’s signature element is present in the subsequent begging call of her nestlings. Playback experiments of nestling begging calls (own, neighbour, cuckoo) showed that adults (males and females) responded differently to the stranger calls (neighbouring nestlings, cuckoos) with lower feeding, higher vigilance, and more alarm calls. Interestingly, the response intensity was comparable for the stranger calls, suggesting that adults did not recognise the cuckoo per se, but differentiated “own” versus “other”.

We suspect that we have uncovered the vocal cue that serves as a parent-offspring specific password for females and males to recognize their own genetic young and thus detect the presence of an intruding cuckoo nestling. Such a password is transferred by the mother to her young to produce in their begging calls, so it can be recognized using self-referent phenotype matching between the incubation calls and the offspring begging calls.
Trill performance and trill consistency do not affect male responses to playback in house wrens

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Handicap and indicator signals of male quality are of interest because they have clear costs maintaining signal reliability. Two components of bird song, trill performance and trill consistency, are potential costly or constrained signals of male quality that researchers recently began to investigate. Trills are parts of songs in which a note or series of notes is repeated consecutively. Trill performance is a measure of the speed of sound frequency modulation, measured as deviation from the maximal combination of fast syllable repetition rate and broad syllable frequency bandwidth. Trill consistency is a measure of how precisely notes are repeated, measured using spectrogram cross-correlation. Mechanistic arguments suggest that it is physically difficult to produce high performance and/or high consistency trills, creating an intuitively appealing explanation for the constraint on signal production. Virtually all published studies on these signals find support for their role in communication, either via correlations with male quality measures or via differential receiver responses to different signals. In this study, we tested whether male house wrens (Troglodytes aedon) responded differently to songs with different trill performance and consistency characteristics.

In two separate playback studies, we exposed individual territorial males to three different trill performance levels (low, medium, and high) at a single consistency level (low or high). We measured responses as song rate, rate of flights above the speaker, and approaches toward the speaker. Order of presentations was balanced, and no stimulus song was included more than once, to avoid pseudoreplication.

We found no differences in male responses to songs with different performance and consistency characteristics, despite good sample size and ample variation in males' responses to playback (Fig. 1). Statistically controlling for focal male characteristics did not uncover any effects of playback treatment. This study is one of the first to not find an effect of trill performance and consistency, suggesting that these signals may not be as widely used across passerines as had been previously assumed. Alternatively, unique aspects of house wren song structure may make these trill components less useful signals, either by altering the costs of producing high performance/high consistency trills or by altering the ease of evaluating trill performance/consistency.
Fig. 1. Mean ± SE responses to playback of high (H), medium (M), and low (L) performance songs, averaged across males for Experiment 1 (left side) and Experiment 2 (right side). Males exposed to consistent playback stimuli are in white bars, while males exposed to inconsistent songs are in grey bars.
Griffin Was Right: Language Reveals an Animal’s Thoughts

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Decades earlier, Donald Griffin shocked the scientific community contending, “… communication among animals can serve as a ‘window’ into what animals think and feel, just as human speech and nonverbal communication tell us most of what we know about the thoughts and feelings of other people.” He challenged widely accepted conventional ideas about animal communication and animal consciousness. At the time, few animals in language experiments had attained sufficient linguistic fluency to express more than primitive concepts.

Previous reports described experiments with trained dolphins, dogs, great apes, and parrots showing their ability to learn the rudiments of language. Studying volunteered statements spoken by an educated, but untrained, talking bird demonstrates advanced linguistic capabilities not revealed by earlier experiments.

This paper introduces Passive Speech Research as a means to evaluate declarations by a free-speaking macaw. No human is present while recording the bird’s volunteered speech.

Bird trainers and some researchers teach parrots to speak using vocal cues and praise. The training procedure also triggers recognition for the parrot’s speech in the listener’s mind. If the trainer’s statements are removed from recorded speech sequences, listeners generally fail to perceive single words and untutored sentences spoken by the parrot.

Experienced listeners learn to understand a bird’s isolated speech by focusing on decoding phrases and skillfully identifying phonemes and syllables of words. Neophyte listeners need to develop aural acuity for avian speech to evaluate isolated statements. Repeated audition of English spoken with a strong parrot dialect is one way to learn to discriminate words spoken by a parrot better. The challenge is to transcribe unfamiliar and unanticipated thoughts expressed in monologs and dialogs by free-speaking parrots.

The research findings outlined in this work demonstrate a talking bird’s ability: (1) to learn cognitive speech lacking a specific model, (2) to transfer meaning for words to new situations, (3) to use synonyms without specific training, (4) to learn to substitute pronouns appropriately, (5) to pose and answer a question, (6) to attribute characteristics to others, and (7) to improvise related sequences of statements about a single topic. The evidence in this report derives from recordings, which, when transcribed and evaluated, shows that parrots are capable of learning language and expressing complex thoughts. Consequently, “Language Reveals an Animal’s Thoughts” is a corollary for Griffin’s often quoted contention.
The Effects of Polychlorinated Biphenyls (PCBs) on the song of Black-capped Chickadees (Poecile atricapillus)

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Song is a vital aspect of bird communication and subsequent reproductive success. Many female songbirds (Passeriformes) use the costly display of song as an honest indicator of male quality. In the Black-capped Chickadee (Poecile atricapillus), males sing the familiar fee-bee song. This song is typically sung in a territorial context, and used to attract and arouse females during the breeding season. The interval ratio (the frequency of the end of the fee note divided by the frequency of the beginning of the bee note) is a well-conserved characteristic of the Black-capped Chickadee song; it has been shown to vary less than 2% across the entire Chickadee range (northern North America). The interval ratio appears to be the most difficult feature of the fee-bee song for male Chickadees to learn, while female Chickadees use the consistency of the ratio as an indicator of male quality during mate choice. Therefore, any alteration of song characteristics, such as the interval ratio, may affect the establishment and defense of territories, mate attraction, pair bond maintenance, and ultimately, reproductive success.

During the last century, polychlorinated biphenyls (PCBs) have emerged as a harmful, worldwide chemical pollutant, and dozens of federally mandated Superfund Sites are on the National Priorities List due to PCB contamination. Currently, most research on the biological effects of PCBs emphasizes the critical effects of PCBs, such as embryo and juvenile mortality, survival, and growth, and concentrates on presence/absence data. Furthermore, most research on PCBs necessitates destructive sampling by measuring PCBs in tissues. The goal of this research is to address these deficiencies in our knowledge by examining the sublethal consequences of PCB exposure. Due to the chemical structure and physiological effects of PCBs, one sublethal consequence should be alterations to animal behaviors; however few studies have investigated this. Behaviors are the end point of sensitive neurological processes and an abnormal behavior may indicate disrupted nervous system pathways caused by sublethal PCB levels.

Bird song is likely to be a highly effective behavioral indicator of bioavailable PCBs in the environment for two reasons. First, the brain areas that produce song in birds are complex and highly vulnerable to environmental stressors. Both internal (i.e. developmental stress) and external (i.e. habitat fragmentation and parasitism) factors influence song. Second, the brain areas associated with song in songbirds are extremely well studied, and compelling evidence shows that key areas in the learning and production pathways in the avian brain song system decrease in size when young birds are exposed to PCBs.

During the breeding seasons (April-June) of 2006-2009 we studied Black-capped Chickadees residing along the Hudson River, in northeastern New York. According to the 1991 Environmental Protection Agency (EPA) Report, General Electric (GE) plants on the Hudson River illegally discharged up to 1.3 million pounds of PCBs into the river between 1914 and 1977, resulting in the Hudson River being listed as a National Priorities List Superfund Site in 1984. Adult chickadees living in riparian areas forage for aquatic insect larvae, which accumulate PCBs in contaminated regions. Not only are these larvae used to provision young; the larvae are also the primary prey of adults during the breeding season. Male Black-capped Chickadees have territories that border the water’s edge, and are either year-round...
residents or have high between-year site fidelity, and short natal dispersal distances. Therefore, birds hatched in areas with high levels of PCBs are likely to be ingesting them their entire lives.

The goal of this study was to determine whether PCB exposure causes a song change in Black-capped Chickadees. Using a Tascam HD-P2 Solid State Recorder, a 24-inch Telinga Universal Pro Parabola, and Seinnheiser ME62 Omni Microphone, recordings were made directly onto a 4GB flash card. All recordings were analyzed with RavenPro (Bioacoustics Research Program, Cornell University) and JMP8. Black-capped Chickadees were also captured using mist nests (USFWS permit: André A. Dhondt) at the recording locations in 2008 and 2009. Approximately 100 µL of whole blood was taken from the right arterial vein, and the 2\textsuperscript{nd}, 4\textsuperscript{th}, and 6\textsuperscript{th} primaries and 2 outer tail feathers were collected and stored in paper envelopes for PCB analysis. PCBs will be extracted from the blood and feather samples according to established protocols after addition of a mix of stable isotope-labeled $^{13}$C$_{12}$-PCBs as an internal standard. After Solid Phase Extraction (SPE) cleanup and evaporative concentration of the final extracts to 20 µL the samples will be analyzed by gas chromatography-mass spectrometry. We will correlate the song data with the PCB concentrations found in the blood and feather samples of male Black-capped Chickadees from the same regions to demonstrate a direct link between PCB exposure and song development in Black-capped Chickadees.

Our results show that along a PCB gradient on the Hudson River, key characteristics of the interval ratio, such as its variation, vary significantly. These results support the importance of sublethal PCB levels on both the learning and production of birdsong. Furthermore, the results indicate that low levels of PCB in the environment can change a vital component of communication and reproductive success, birdsong.
How Much of a Bird’s Call or Song is Required for Recognition?

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For animals to effectively communicate, the transmitted message must be heard appropriately by the receiver. Under noisy conditions, effective communication becomes more difficult because pieces of acoustic signals may be obscured. Fortunately, many animal signals contain redundancies which aid in recognition and discrimination. Animals may exploit those redundancies, as well as invoke different listening strategies, to identify a caller’s identity, status, intentions, and important discoveries (e.g., Bradbury and Vehrencamp, 1998). Studies on acoustic communication in birds have shown that vocal signals, including both calls and songs, are easily discriminated, localized, and identified under many circumstances. What remains largely unknown, however, is whether or not certain locations within a call or a song are more important than others for these tasks. The current study sought to determine how much of a call or song is necessary for categorization and whether information at the beginning, middle, or end of the song or call is more beneficial for this task.

Eight budgerigars were trained using operant conditioning procedures to categorize either two zebra finch songs (Exp 1, n = 4) or two budgerigar contact calls (Exp 2, n = 4). Once the birds reached a criterion performance of 85% correct on the training stimuli, they were moved on to the testing phase. During testing, 85% of the presented stimuli were the training endpoints and the other 15% of the trials consisted of probe stimuli. The probes were always rewarded, as long as the subjects chose one of the two categories. For both experiments, the testing stimuli were either small portions of the whole stimuli or combinations of those small portions. For Experiment 1, the zebra finch songs were presented in individual syllables (1-6) and in syllable combinations (e.g., 1+2, 1+2+3, 5+6). For Experiment 2, the budgerigar contact calls were split into quarters and presented individually (1-4) and in quarter combinations (e.g., 1+2, 1+2+3, 3+4). The birds were required to categorize these probe stimuli as either belonging to the left or right category, and percent correct responding was measured. Once the birds completed 20 trials of each probe type, the experiment was repeated using two new endpoint stimuli, and then again using an additional two endpoint stimuli so that each bird was trained and tested on a total of six stimuli.

Results for classifying very small portions of the stimuli in both experiments are shown in Fig. 1 (left panels). The budgerigars were poor at categorizing both zebra finch songs and budgerigar calls when presented with only one syllable or one quarter of the stimulus, respectively. For all conditions, performance was near chance. These results are similar to those from Guillette et al. (2010), who showed that chickadees suffered in their ability to discriminate song when only one song note was presented, and from Knudsen et al. (2010), who showed that European starlings had difficulty classifying song when only one motif was presented. Budgerigars cannot identify a zebra finch song based on just one syllable and cannot identify a budgerigar contact call when presented with only a quarter of the call.
Fig. 1. Mean percent correct discrimination of zebra finch songs (top) and budgerigar contact calls (bottom) as a function of stimulus type. For the zebra finch songs, categorization of individual syllables 1-6 are shown in the left panel and categorization of syllable combinations are shown in the right panel. For the budgerigar calls, categorization of call quarters 1-4 are shown in the left panel and categorization of quarter combinations are shown in the right panel. Chance performance is 50% and is represented by the dashed line.

Results for classifying larger portions of the stimuli in both experiments are shown in Fig. 1 (right panels). The budgerigars’ performance improved when a greater percentage of the stimulus was presented. Interestingly, the birds were better able to categorize the stimuli when the content was combined in the forward direction compared to the reverse direction. These differences were significant for both stimulus types ($p < 0.05$).

The asymmetrical performance of the budgerigars in categorizing budgerigar contact calls and zebra finch songs suggests that the beginnings of vocal signals contain more information than the ends. These results are similar to spoken word recognition findings with human speech (e.g., Salasoo and Pisoni, 1985), and highlight another similarity between vocal communication in humans and animals.

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Vocalizations of a Nocturnal Lemur: 
_Avahi peyrierasi_, a Data Deficient Species

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Woolly lemurs (_Avahi sp._) are folivorous, nocturnal, and pair bonded. There are eight species of woolly lemurs identified. The calls of of _Avahi peyrierasi_, a recently defined species listed as data-deficient on the IUCN Red List, have not yet been described. During a three month study in the rainforests of Madagascar, I followed seven groups of _A. peyrierasi_ during the night to document their calls. Previous studies on other non-human primates have demonstrated that vocalizations tend to be context specific. For example, in tamarins (_Saguinus fuscicollis_) certain calls are associated with mobbing, group cohesion, alarm, or the discovery of food. In indris (_Indri indri_) certain calls are associated with territorial defense and mate location. The role of vocalizations in social interactions of woolly lemurs has not received much attention. In 1979 Petter and Charles-Dominique gave a comprehensive description of the calls of _Avahi laniger_ with speculations on their function. The following vocalizations were described: grunting sounds, weak snorting, resonant snorting sounds, whistle calls, “ava-hi” calls, and infant calls (“plaintive whistle like noises”). More recent studies focusing on various aspects of the behavior and ecology of other species of woolly lemurs also report whistles and “ava-hi” calls.

The study sites are located in Ranomafana National Park (RNP), a protected southeastern rainforest, and Ambatolahy Dimy a non-protected forest fragment a few kilometers from RNP. During the month of July and October evening walks were taken in RNP and woolly lemurs were identified using flashlights and followed for 15min-1hr. In November two males were radio collared, one in each study site, and behavioral data was obtained during 6hr follows until December. Vocalizations were recorded using a NAGRA ARES BB+ and a Sennheiser MKH 70. Calls were analyzed using Raven Software v1.4.

A total of 68 sound files of woolly lemur vocalizations were obtained and 24 of these, from seven groups, were of high enough quality (minimal background noise) to analyze. Five types of calls are identifiable: grunts, whistles, ‘ava-hi’ calls, chatter-like calls, and whistle-like calls. A total of 34 individual grunts from one male were analyzed. These have an average length of 0.37s and range in frequency from 1-20 kHz. Grunts are low calls that would be difficult to hear in the field. These calls were only recorded during the physical examination of the radio-collared males. Whistles seem to come in three forms: a high volume long distance whistle (LDW) with 1-3 long notes, a low volume whistle with 2-3 short notes (LW), and lastly a high volume short whistle (SW) containing several short notes (3-5). Recordings are of four groups. The notes of 45 LDWs, 19 SWs, and 3 LWs were analyzed from four, two, and one night respectively. These calls have a frequency range of 3-5 kHz. The distances at which each of these calls can be heard was not measured but are estimated as follows: LDW >15m, LW <5m, SW >15m. Whistles are often emitted together (ex: SW followed by a LDW). A LDW caller is generally answered with LDWs and then joined by another individual (likely the one who responded). Low whistles are followed by more LW from a nearby individual, suggesting a group cohesion function.

‘Ava-hi’ calls recorded on two evenings (out of six) were used for analysis. A total of 11 ‘ava-hi’ calls recorded from three groups were analyzed. “Ava-hi” calls have an average length of 0.60s and a high frequency of 9 kHz. These calls are sometimes preceded or followed by LDW calls or LW calls.
Individuals were seen moving towards another individual emitting ‘ava-hi’ calls suggesting a group cohesion or territorial function. The chatter call was emitted by five groups. This call is a low volume call that was only heard when the animals were 5-10 meters above the observer on quiet evenings with very little background noise. Individuals were observed to fixate on a stationary observer while emitting the call and shortly thereafter move away from the observer, suggesting a group cohesion or alarm function. Only one recording of the chatter call could be detected on a sonogram. This call has an average length of 0.64s, a low frequency of 4 kHz and a high frequency of 5 kHz. The whistle-like calls were recorded from one group on two nights. It could not be determined whether the dependent infant (riding dorsally) emitted these calls or the adult. These could possibly be infant calls, calls generally reserved for infants or calls of such low volume that they could not be detected in other cases. Eleven whistle-like calls were analyzed. These have a frequency range of 2-5 kHz, a length of 0.01-0.20 seconds and were composed of several shorter notes.

This project is one of the first documentation of the vocalizations of *A. peyrierasi*. It provides valuable preliminary information on the role of vocalizations in social interactions. Several of the calls described by Petter and Charles-Dominique in 1979 for *Avahi laniger* are also emitted by *A. peyrierasi*. The information presented in this study will support the transformation of a data deficient species into one with conservation status. Published results will increase awareness of this species and also allow for between-species comparisons. These results can furthermore be used when devising conservation management strategies.
A Database of Insect Acoustic Signals

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Insect sound is an understudied element of acoustic environments. Where calling insects occur, their signals surround us both day and night yet most people would be hard pressed to identify the organisms from which these signals originate.

I am building a database of these insect calls for several geographic regions throughout the United States, including Texas, Louisiana, New York, Ohio, and Montana. To accomplish this, I am collecting insect specimens from these areas, taking detailed macro photographs of relevant taxonomic features and recording their calls at several different temperatures. The insect voucher specimens will be pinned, cross-referenced with the audio collection, and archived along with a sample of DNA for a genetic record. GPS data, date of collection, behavior notes, and a description of basic habitat will also be collected.

The resulting data could be relevant for several interesting questions, including but not limited to the following: (1) Does the relationship between dominant frequency and body size hold true within or between different taxa? (2) Are communities acoustically structured relative to the insects that compose that community? In other words, are calls more dispersed than we would find randomly? and (3) Does habitat type influence acoustic parameters in insects? For example, do pitch or frequency vary consistently with habitat type? This database will also be valuable as a baseline for future research tracking changes in calls and community structure over time.
Kiwi acoustic communication

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Fig. 1. A little spotted kiwi (Apteryx owenii)

New Zealand kiwi (Apteryx spp.) have been the subject of few acoustic analyses, yet as nocturnal birds with very limited visual ability, vocalizations are a principal form of communication for these iconic species. We are using kiwi calls to yield insight into their behavioral and population ecology, and to provide vital conservation monitoring tools for these cryptic and threatened birds.

Although physiologically and behaviorally very different from other birds, kiwi repertoires contain many features that are common in many animals, such as territory calls and duets. Comprehending how the ecologically unique kiwi employ these vocalizations will yield insights into their use in other species. More generally, as primitive, ground-dwelling ratites, kiwi can provide a platform for robust tests of hypotheses of avian signal divergence.

We present the first acoustic study of little spotted kiwi (Apteryx owenii), the smallest and second rarest kiwi species. We are also using a population of North Island brown kiwi (Apteryx mantelli) with unusual breeding biology to further understand how kiwi use calls for social interaction and territory defense.

We show that calls can be used to identify individuals and provide evidence of two-voicing in little spotted kiwi. Dialects are used to compare translocated island populations of little spotted kiwi that have suffered genetic bottlenecking. We also demonstrate the application of autonomous monitoring, automatic call recognition and wireless microphone arrays for monitoring kiwi, and hence for other similar cryptic, nocturnal vocal communicators. We have recorded calls of hybrid kiwi species, which we relate to their progenitor species, and consider as a means of searching for these extremely rare birds that are potentially very important for kiwi conservation and understanding of kiwi evolution.
Fig. 2. Spectrogram of a little spotted kiwi duet.
Using automated species recognition software to assess frugivore activity in a tropical forest

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Automated Species Recognition Software (ASRS) is a prototypical tool that may be used to identify animal species based on audio signal structure and frequency range. ASRS may help answer fundamental ecological questions by relaxing a number of logistical constraints. Two main advantages of this emergent technology are (i) simultaneous sampling across multiple locations and (ii) temporally intensive sampling.

More than 80% of tropical forest trees are thought to have their seeds dispersed by vertebrate frugivores. As a result, spatial and temporal variation in frugivore activity has implications for community dynamics and regeneration of tropical forests. Understanding the spatial and temporal scales at which frugivores respond to patterns of resource availability has been a persistent question in ecology.

We conducted an intensive acoustic study at the Luquillo Forest Dynamic Plot (LFDP), a 16-ha mapped forest plot located in the mountains of northeastern Puerto Rico. We characterized activity patterns of the Bananaquit (Coereba flaveola), one of the most locally abundant birds during a one-month period. The LFDP provides an ideal system in which to apply ASRS to this question because of the availability of fruit production data collected across the plot at 2-week intervals and information on the spatial location and size of adult trees. We used ASRS in this system to address two primary research questions: (1) Is activity of C. flaveola related to estimated fruit availability in tree neighborhoods? and (2) How do activity patterns of C. flaveola change depending on temporal scale of observation?

We placed a Song Meter SM2 recorder (Wildlife Acoustics, Inc.) adjacent to each of 10 seed traps located throughout the 16-ha LFDP. To maximize the links between acoustic data and fruit phenology, recorders were collected adjacent to fruit collection baskets. We recorded nine minutes of acoustic data per hour between 5am and 7pm for 35 days from December 9, 2010 through January 8, 2011, resulting in more than 1,100 total hours of recordings. Using Song Scope 3.4 software (Wildlife Acoustics, Inc.), we identified and counted C. flaveola vocalizations during each nine-minute sample period. Using this software, known calls are first assembled to create a “recognizer” (Fig. 1) for the focal species, which is then used to scan the field data for matched calls. Our current recognizer for C. flaveola is based on 86 known calls. Matched calls were then checked manually to quantify and eliminate false positives. We then used random testing of subsets of audio field data to account for the presence of false negatives.

We demonstrate how ASRS can be used with long-term field data to address fundamental ecological questions that would previously be considered financially or logistically prohibitive. In addition, we add to the accumulation of a permanent database of “recognizers” to be applied across different systems. Future work would expand our study to include more frugivorous species (including both birds and bats) to gain a better understanding of how the frugivore community responds to spatial and temporal variability in fruit availability.
Fig. 1. An audio recognizer of a Bananquit (*Coereba flaveola*) generated in Song Scope 3.4 (Wildlife Acoustics, Inc.). The upper spectrogram is the signal detection of a single *C. flaveola* call on a log scale. The lower spectrogram is the same call on a log frequency scale.
Sound transmission across an urban development gradient: consequences of bird song adjustment in cities

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Numerous studies have described differences in bird song frequency characteristics between urban and rural environments, most assuming that these differences are adaptive and allow for better signal transmission. Although the changes observed (increases in minimum frequency in noisy environments and decreases in maximum frequency in urban environments) are consistent with those predicted by acoustics theory, no previous study to date has directly examined: 1) how animal signals degrade as they transmit through environments with different noise and structural characteristics, including urban habitat and 2) whether the changes observed in bird song in loud and/or urban areas lead to better transmission in those areas.

We investigated sound degradation across a gradient of urbanization and canopy cover, quantifying sound transmission properties of areas that are forested, rural, suburban and urban. We also tested the hypothesis that the spectral adjustments observed in bird songs in cities lead to better song transmission, which would support the idea that these adjustments represent an adaptation that facilitates communication in urban environments. We investigated transmission with respect to: 1) masking from noise and 2) sound degradation and distortion from the physical environment.

To describe transmission properties generally, we synthesized a single-frequency tonal sound and transmitted that sound at 62 sites that varied continuously in their noise and urban development characteristics. To test for transmission benefits to avian spectral adjustment in cities, we synthesized several bird-like songs that varied independently in their spectral characteristics (maximum, minimum and dominant frequency) and transmitted these songs at all 62 sites.

We quantified degradation of all transmitted sounds using a cross-correlation comparison with a model sound that was recorded in an anechoic chamber. We measured three characteristics of the transmitted sounds: 1) Signal-to-noise ratio (both total and within certain frequency ranges), which measures the energy of the signal given the energy of background noise, 2) blur ratio, which measures time distortion in the transmitted signal, and 3) tail-to-signal ratio, which measures energy of the echoed tail of the signal compared with energy of the signal.

If the spectral adjustments observed in natural bird songs (increase in minimum frequency in noisy environments and decrease in maximum frequency in urban environments) are indeed adaptive, then we expect songs that are experimentally adjusted in a similar fashion to transmit better in these environments. Specifically, we expect songs with an increased minimum frequency to experience less masking by noise in noisy environments (i.e. higher signal-to-noise ratio) and songs with a decreased maximum frequency to experience less degradation and distortion (i.e. reduced blur ratio and tail-to-signal ratio) in urban environments.
Comparison of Sonar Behavior During Landing in Laryngeal and Lingual Echolocating Bats, *Eptesicus fuscus* and *Rousettus aegyptiacus*

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Echolocating bats use sonar for navigation, localization, and identification. They actively modulate the timing and frequency content of their sonar pulses in a task dependent way (Moss and Surlykke, 2010). Bats also actively control the directional characteristics of their vocalizations with respect to objects in the environment. *Eptesicus fuscus*, the big brown bat, a species which produces sounds using the larynx and uses a frequency-modulated call structure, has been shown to aim the maximum intensity of its sonar vocalizations at insect prey as it prepares to intercept a target (Ghose and Moss, 2003). This finding comes from microphone array recordings that were bandpass filtered (center frequency, 35 kHz; 3 dB down, 28 and 42 kHz) and enveloped, yielding the intensity of the sound within that frequency band. However, this microphone array did not allow for analysis of the sonar beam outside this set of frequencies. *Rousettus aegyptiacus* produce very short (50-100 µs) tongue clicks in pairs. In a landing task investigated with the same microphone array, *Rousettus* placed the maximum slope of intensity of each click towards the landing target during the approach and landing (Yovel et al., 2010). By placing each click on either side of the target, the mean direction of the two clicks fell on the target. The placement of maximum slope of each click on the landing target yields the maximum localization information (Fisher information). The frequencies analyzed with the microphone array match the frequencies used by *Rousettus*, but unlike *Rousettus*, *Eptesicus* modulates the frequencies it uses for sonar in a task dependent manner, such that as the beam width changes at different frequencies (Hartley and Suthers, 1989), the spatial position of maximum slope, and maximum intensity also change.

Using a newly designed microphone array which allowed recording the sonar signals at high sample rates with no enveloping, we recorded the wide-bandwidth signal of the vocalizations of *Eptesicus fuscus* during landing behavior. This allowed for the characterization of the changing beam width with frequency during approach to a landing platform (Fig. 1). We examine the differences in beam directing behavior between *Rousettus* and *Eptesicus* during the same landing task, to investigate whether *Eptesicus* positions the slope of its sonar vocalizations at different spatial locations at frequencies different from those measured with the original microphone array.

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Fig. 1. Top view of the big brown bat’s trajectory towards the landing target and microphone array for the same trial and vocalization. The bat’s sonar vocalization received at each microphone is plotted as a vector, with intensity normalized for each frequency band. The measurements are made at different frequency bands (labeled) and show changing beam shape with frequency.

References


Relative comparisons enable auditory grouping in frogs

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Auditory object formation is the process of sorting, grouping and assigning sounds to their correct sources. Object formation is complicated by the fact that sounds from different sources combine linearly and arrive at a receiver as a single complex wave. As a single stimulus, the complex wave is not source specific and thus, groups and source assignment must be “deduced”. This means that during acoustic communication, perception of information and identification of its sender are inherently linked to how receivers make such deductions. The auditory system often accomplishes this by deconstructing the complex wave into its individual components, a result of processing so called “primitive” (e.g., temporal, spectral, spatial; and amplitude parameters) and “schema-based” (e.g., stored information) acoustic cues. Correct grouping and source assignment result from the ability to compare within and between these cues, a process made more difficult when there are multiple sources producing similar sounds. Indeed, under conditions in which multiple cues overlap, absolute perceptual boundaries may not explain all perceptual grouping, as listeners may employ a relative strategy in which objects are formed by grouping stimuli with the most similar acoustic parameters and excluding those more distinct. Using a phonotaxis assay modeled after experiments designed for humans, this study determines how mate-searching female frogs use relative comparisons to deduce the source of complex male signals in breeding aggregations on the rain forest floor.

In multi-male choruses male túngara frogs (Physalaemus pustulosus) produce complex calls consisting of two components: the frequency modulated “whine”, which is necessary and sufficient to elicit phonotaxis; followed by 0-7 broadband “chucks”. Chucks are never produced alone, creating a spatial cue for whine-chuck grouping. Also, chucks can only follow a whine due to male vocal anatomy, creating a sequence or schema-based grouping cue. Our previous papers showed that these two call components are perceptually distinct, as the whine is used in both “what and where” decisions, and the chuck is only used in “where” decisions. Important to this study is that phonotaxis to a chuck is contingent on the presentation of a whine. This combination sensitivity, in part, reveals auditory grouping of the whine and chuck. Previous tests of whine-chuck grouping have shown that absolute spatial and temporal differences have a limited effect (e.g., grouping up to 135° whine-chuck separation and for non-natural whine-chuck sequences) and predict that in a dense male chorus whines and chucks from different sources could be incorrectly grouped. The stimuli in previous tests, however, used only two call components, a single whine and a single chuck. In contrast, we show here that for presentation of >2 call components grouping is more likely for the two components with the smallest relative differences in call parameters, including relative spatial separation (a primitive acoustic cue) and relative similarity to the species-specific call sequence (a schema-based cue). The data also reveal that grouping is categorical (calls are either excluded or included), as grouping responses are directed to only one chuck in a pair, with no evidence for averaging the position of the two. Furthermore, by presenting spatially separated noise bursts with a whine and chuck we show that spatial acuity for grouping is not explained by the acuity for spatial unmasking. Thus, like humans, the cognitive rules for the perception of auditory groups amidst multiple sound sources include the use of relative comparisons, a flexible strategy for dynamic acoustic environments.
Effects of Mozart-Music on the Rat’s Learning Capacity and Short-Term Action Catalogue - Preliminary Study

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There are anecdotal reports that indicate that continuous and consistent background sounds help laboratory animals overcome the negative effects of inevitable intermittent noises (cleaning, feeding, experimental procedures, air conditioning, air filtration engines etc.). The so-called “Mozart effect” (Rauscher, 1993) indicated that, in the case of humans, a musical environment might improve the learning capacity and spatial intelligence. In that work the energizing “Sonata for Two Pianos in D Major, K 448” by Mozart was effective. Results related to animals are contradictory. Our basic goal was to determine if there are any measurable effects of the human music on laboratory animal behavior, and if so, to find relaxing music for use in animal facilities to prevent or alleviate distress or discomfort of the animals. Environmental enrichment is widely considered to be an important part of refinement: represented by the third of the “Three R’s” of humane and ethical animal experimentation.

**Trial 1**

In the first trial, after 1 week adaptation and 1 week acquisition period 12 male rats were exposed once daily to a 8.5-min-long arrangement of Mozart K 448: “Sonata for Two Pianos in D Major”. The animals' spatial learning and memory ability was tested in an 8-arm radial maze (Columbus Instruments, Ohio, USA)(Figure). Week 1: In the first week of treatment (adaptation), all animals had a 10-minute training twice a day, adapting them to find food pellets in the maze arm ends. Perfect performance of this task required entering each arm only once. Week 2 (acquisition of the task). During the 2nd week, with one training per day, the rats were first individually trained to learn the general cues of the task, that is, entering each one of the 8 arms only once in a given session, with no more than one error per session in 6 consecutive days. Acquisition errors consisted of revisiting an arm previously visited in the same session. This way, the rats were forced to learn a win-shift food search strategy (Beatty and Shavalia, 1982). The percent rate of correct responses was counted as: (correct responses - acquisition errors) x 100, and was taken as performance indicator. All animals achieved a run performance of over 75%. Successful solution of the maze task requires the rats to recall the arms already visited, mainly when the performance is interrupted (Olton et al., 1977).

Week 3 and 5: They were done in the 3rd and 5th treatment weeks, that is, after successful acquisition. The rats (all 12 per group) were one by one put for 10 min maximum in the center of the maze, but were allowed to enter only 4 of the 8 open and baited arms (at their own random selection); this was the “event-to-be-remembered”. After visiting the four arms, the animal was returned to its cage and kept there for 2 (week 3) or 4 hours (week 5). The rats were then put again in the maze center and allowed to complete arm choices 5-8 to obtain rewards in the 4 baited arms not visited before. In the working memory (WM) tests, WM errors meant re-entry into any of the arms visited in the first run. Working memory performance was thus counted as (correct responses - WM errors) x 100. Week 4: It was tested in the 4th treatment week with 12 rats per group. Here, food reward was (Preference test) put only in the 4 arms preferred by the individual rats. Entering an unabated (empty) arm constituted a reference memory error, from which performance was calculated as above. Week 6 and 7 (Resting Period): the animals were kept in the housing room, were exposed to the music once a day, but did not have any testing and were not exposed to new information. Week 8, 9 and 10 (Long-Term Working Memory Test): The long-term WM was tested in the 8-10th treatment weeks and, repeatedly. In the 8th
treatment week (Recall), memory return was observed and in the 9th and 10th treatment week, 2- and 4-hours WM, respectively.

The rats’ spontaneous motor behavior was assessed, using a fixed subset of each group, in the 5th and 10th week of treatment phase test was performed always once in the given weeks, following the maze-learning session in an open-field (OF) box (ACTIFRAME, Gerb Electronic, Berlin, Germany). The animals were placed into the center of the box and their spontaneous horizontal (running), vertical (rearing) and local (predominantly grooming) activity was scored during a 10 min session. Movement scores were computed on the basis of beam interruptions.

For statistical analyses the *Kolmogorov–Smirnov* has been used. a PC software having present conditions to discriminate between forms of movement.

**Results.** Rats, exposed to the acoustic exposure (Mozart music), tested by maze-learning capacity and memory performance, showed significant improvement of the short-term reference (55.3±0.57 vs 75.3±0.39%, df=7, t=5.00915, p=0.00155), in the recall after the resting period (83.5±0.33 vs 89.4±0.25%, df=8, t=2.91994, p=0.01929), and 4-hour-interruval long-term WM (60.0±0.29 vs 65.9±0.24%, df=8, t=3.20159, p=0.01258), compared to the control. The spontaneous locomotor activity of the control and music-exposed animals during the open-field test did not show significant differences. The defecation activity during these mobility tests on weeks 5 and 10 did not indicate any important difference between the emotional state of the control and music-treated rats.

**Trial 2**

Ten weaned male rats were exposed to the same Mozart piece of music as in Trial 1 but 10-times accelerated (and therefore at 10 times the frequency). The quality was according to the CD-standard (44.1 kHz and 16 bit resolution). For the repeatability, a variant with the dominant “d1” measuring voice of 293.665 Hz was also prepared, the by an attenuation of – 6 dB. The Sound Pressure Level (SPL) during the music exposure was 70 dB. The experimental design was self-controlled, and the interval between recording the basal OF activity and that just after having listened the music lasted 60 to 70 minutes. Changes of the short-term (300-second-long) action catalog (washing, watching, drinking, walking, sniffle, rearing, standing jump, self-grooming, litter digging. after each rat the box was cleaned with a neutral detergent. The OF investigation was performed from 9.00 to 12.00 A.M. After the OF test the rats were returned to their conventional home environment.

Results suggest some influence of the accelerated music relative to the basal values: the average walking, sniffling, raising and grooming time dropped by 30-50%, respectively. The grooming, previously 22% of the whole ethogram, at some animals, totally disappeared. On the contrary, the originally very rare (6, 12, 18 and 24 sec at four rats) immobility became general and overwhelming with an average of 180 second-long duration. Owing to the great individual variations, the differences are not statistically significant.

**Conclusions**

This particular music in human hearing range (was appropriate for improving learning capacity, but the spontaneous free-running movement did not change significantly. The human and rat audiograms, measured between 60 to 70 dB SPL are different: 50 to 15-20,000 Hz versus 500 to 30,000 Hz (Heffner et al. 1994, 1998), or up to 80-90,000 ! According to Steele (2006), rats are not able to hear 33 to 57% of the used Mozart sonata. At the same time, in the present experiment is proved to be efficient to improve some memory types without influencing the open-field results..

On the contrary, using the accelerated, higher frequency version of the same music, there was a strong tendency amongst the rats to become startled and immobilized, neglected the previously practiced other activities, like walking, sniffling, raising and grooming. The individual variation of the animals’ reaction is considerable.

Considering the animal welfare issue, and the fact, that the background noise level in animal facilities is indicated as 40-50 dB, we currently are testing calming and relaxing music (a selection from Bach’s: Goldberg Variations), both as composed for humans and in a rodentized, 10-times faster version and a higher range, to find a tool to prevent or alleviate the discomfort of laboratory animals.
Sound Analysis for Respiratory Health Monitoring in Commercial Piggeries

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Respiratory pathologies have a high prevalence in intensive pig farming and cough is their principal symptom. It is well-known that, under intensive breeding conditions, it is very unlikely for a pig to reach the slaughter weight without having shown any kind of respiratory infection. Follow-up and treatment of these diseases are often related to expensive veterinarian intervention costs. They are also related to high mortality and a drop in production due to reduced feed conversion and growth rate. This economic side of the problem is particularly relevant for farmers. To overcome this, they treat diseases by administering large spectrum antibiotics to all the animals that, in long term, results in antibiotic resistance in both animals and meat consumers. In today's intensive livestock farming the high density of bred animals helps a rapid spread of the disease that cannot be followed by punctual observation of animals. Cough is a clear marker in case of respiratory disease warning related to the health status. It is common practice by veterinarians to assess cough sounds, by audio monitoring, in pig houses for diagnostic purposes. A limitation to this technique stands in the short observational period in both time and space. To achieve this goal, there have been attempts to identify the characteristics of coughing in animals (Van Hirtum and Berckmans, 2002, 2002; Ferrari et al., 2008, 2009, 2010) and automatically identify and localize cough sounds in field recordings (Aerts et al., 2005; Van Hirtum and Berckmans, 2001, 2003, 2003, Exadaktylos et al., 2009, Silva et al., 2008, 2009). This paper wants to show an overview on the highlights of these ten years research in the field of sound analysis for health monitoring in piggeries focusing especially on the last two years results.

In a first study, in laboratory conditions, algorithms have been developed to recognize pig cough sounds; they were applied to a sound-database of 5319 individual sounds including animal vocalizations, background-noises and 2034 coughs. This resulted in a positive cough-recognition of 92%. Later studies focused on the acoustic characterization of coughs according to the type of infection (dry cough, moist cough, upper or lower respiratory tract), experiments were conducted both in laboratory and field conditions and more than 500 Gb of coughs sounds have been labeled and analyzed in terms of Peak frequency, fundamental frequency, RMS and duration in order to understand which acoustic parameter was more significant as a discriminant. In the last two years, the experiments were focusing on the development of real time coughs warning systems coupling cough recognition with sound localization. Respiratory disease was strictly investigated along several production cycles in swine piggeries. Biotic and abiotic factors have been also investigated like airborne bacteria and viruses, dust, ammonia and climate parameters to understand their role in the outburst of respiratory diseases and in the type of cough. Cough recognition was based on both frequency and time domains and the duration of the signal. This technique evaluates fuzzy c-means clustering to parts of the training signals (pre-labeled coughs) and provides a frequency content reference that mirrors the characteristics of sick pig cough. Sound fragments that are closer than 100 ms to each other be considered as a single sound. Furthermore, the length of each sound contains information that can be used in classification. Screams and grunts, for example, are longer sounds and can last for up to a few seconds. Coughs on the other hand are sharp sounds that usually last from 200 ms up to 600 ms. Sounds that are longer than 600 ms or shorter than 200 ms are therefore considered as non-cough sounds and ignored from the rest of the process. Based on such an estimation of the actual sound signal, an attempt to form a classifier is made. In this regard, it is observed that the positions of the AR parameters in a 3D space for the pre-labeled sounds can serve as an adequate and
computationally efficient classifier. It is suggested that when plotting the AR parameters on the space, those that result from sick coughs form a well-defined cluster. 88% of the sick coughs are correctly identified (12% false negatives), achieving a 92% of correct overall classification rate (with 6.8% false positive classifications).

For cough localization the time difference in arrival time of a sound signal between multiple microphones was used. To assess the accuracy of the method, estimated positions of a reference sound were compared with real positions in various microphone configurations. All the configurations showed good position estimation, with mean error between 1.5 and 0m, and a maximum SEM of 0.4 m. After mapping the locations in the stable, three hazard zones could be identified. This information can be used for visualizing the spread of respiratory diseases and eventually contribute to the reduction of the use of antibiotics by means of selective and early treatment of single pens instead of the whole compartment.

Figure 1: a) Time–signal (left column) and frequency content (right column) for a sick cough (top row), a grunt (middle row) and a scream (bottom row); b) Mapped cough attacks during a field experiment (the number of stars indicates the number of cough attacks recorded in that pen, the circles indicate the position of the microphones)

The combination between cough sound automatic recognition and localization together with sanitary and environmental parameters brings information in relation to the respiratory disease that is present in a pig compartment and helps us develop real-time applications that would speed up the diagnosis and treatment process and improve animal welfare in pig houses. In particular, the ability of detecting and localizing cough sounds and the increasing importance of animal welfare and monitoring has in the final part of this research brought to an automatic monitoring system that will help both farmers and veterinarians to achieve continuous feedback on the pigs’ condition by automatic on-line monitoring and hopefully contribute to the reduction of the use of antibiotics by means of selective and early treatment of single pens instead of the whole compartment.

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The use of Red Deers vocalization for population census

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Red deer populations have increased both in North America and Europe, in the last 50 years probably as a consequence of the general improvement of habitat quality, shorter hunting seasons, food supply, reintroductions and restocking. This growth intensity and distribution of red deer populations has brought benefits to hunters but also damages to forestry and agriculture. Considering these aspects, deers management should gain a sort of balance between harvesting and conservation. Different strategies should be adopted to adjust population density according to different habitats and ecosystems. The first action to take is the population census. Traditional methods are the visual and roaring census. Counting roaring stags during the rut has been proposed as a mean to assess deer population size and trends but few, if any, attempts have been made to evaluate the reliability of this technique.

In this research 7 roaring stags were recorded during mating season from late August to October 2010 in five areas located in the Alps in north Italy and in the northern Appennines in central Italy. Animals were both confined in farm corrals or in natural parks and recordings were made in specific check points at least 50 m distance from the animals. For the audio collection of vocalizations a long gun directional microphone (Sennheiser ME 67) was used. The sensor was connected to the external microphone input of a handheld digital recorder (Marantz PMD 620) and sounds were recorded, as uncompressed WAV files 24-bit and 44.1 kHz sample rate, on a SD flash media. Audio playbacks were processed using Adobe® Audition® 3 to label vocalizations. A total of 150 sounds were then analysed both in Praat (5.2.22) and in Matlab® 2009b (Fig1).

Fig 1. Labeling and visual inspection of sound’s spectra in Praat.

Average Power Spectrum of each signal has been calculated (Hanning window, frequency resolution of 173.9Hz, FFT size 253). The transform generated 24 variables (F1 and F2 up to F24 ranging
from 50 to 4000 Hz) which represent sound distribution over the duration of the signal for each of the 24 intervals. These variables average the distribution of energy in the frequency domain over the total length of the signal (Fig.2). Variability between ASP in the different subjects has been calculated by Anova analysis (SAS 9.2). The variation among the 24 variables in each sound of each subject has been also calculated by Anova.

The Anova results showed that variables like F1 and F7 up to F24 varied significantly (P < 0.001) among animals whereas roars within the same stag were homogeneous in all the F (P < 0.001). Plotted spectrum profiles showed great variability among subjects underlying the efficacy of this analysis in single stags individuation cues (Fig.2).

![Average power spectrum profiles of seven roaring stags.](image)

Acoustic signals can encode and transmit a variety of biologically significant information such as individual identity, age, size, physical condition, competitive ability and mating success. Individual morphology of their vocal apparatus directly influences spectral features of acoustic signals which are pre-requisite for individual recognition. Improvement of acoustics roaring census looks a promising reliable tool to supervise the native deer’s populations and it might also be combined to other technologies like GPS, Tags or RIFD for a fully automatic wild animals monitoring.

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Sound Analysis toward heat stress assessment in swine farming

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Heat stress is widely recognized as a stressful condition that affects most livestock populations among several latitudes and in Europe especially during the summer months where high intensity hot weather patterns are referred to as heat waves. In intensive swine farms this stressful condition affect animal behaviour, welfare and production quality. Generally pigs respond to high ambient temperature by nutritional and physiological adaptation to maintain homoeostasis: a decrease of the average daily feed intake to limit heat production and an increase of respiratory rate to remove excess heat. Beside, behavioural reactions to distress exist including animal vocalizations. This research will observe and record several animal vocalizations from piglets bred in standard intensive conditions coupling them with environmental and physiological parameters. Animal vocalizations were recorded in group of seven weaned piglets, bred in standard intensive conditions, exposed to increased temperature.

Heat stress trials have been performed at the experimental farm of the Milan Veterinary. The average initial live weight of animals was 4.92±0.35 kg. Piglets were housed in a mechanically ventilated building. Room temperature was adjusted for thermal comfort zone of weaned piglets ranging from 32.2°C, to 25.2°C in the last week of the trials. Relative humidity ranged from 20 to 30% and ventilation rate was 3 m³h⁻¹.

Two or three piglets were assigned to high temperature tests (29°C up to 41°C for 1 hour), in order to stimulate specific related behaviours and vocalizations. During the trial, the piglets were placed in a test crate on top of which two infrared lamps (150W) were hung 50 cm above the animal. Temperature inside the crate was measured at time 0 (t₀) and after 20 (t₁), 40 (t₂) and 60 (t₃) minutes using a standard mercury glass thermometer. Rectal temperature was measured at t₀ and t₃ from a commercial digital pocket thermometer. Respiration rates were determined by counting flank movements and recorded as frequency per minute at t₁, t₂ and t₃. Vocalizations were recorded for one hour during every trial with a long gun directional microphone placed on the top of the crate 50 cm above the animals. The sensor was connected to the external microphone input of a handheld digital recorder and sounds were recorded, as uncompressed WAV files 24-bit and 44.1 kHz sample rate, on a SD flash media. Normal activity sounds (e.g. games) were also recorded. Audio playbacks were processed using Adobe® Audition® 3 to label vocalizations from piglets before and during the trials. Sounds were manually divided in two main groups Heat Stress (HS) and Non Stress (NS) and analysed for peak frequency (fig.1). Climate and acoustic data were coupled using the Pearson Correlation procedure of SAS 9.2. Pig weight, room temperature (T) and relative humidity (RH), test temperatures: t₀, t₁, t₂, t₃, respiratory rate (RR) at t₁, t₂, t₃, rectal temperature (RT) at t₀, t₃ and number of heat stress vocalizations were considered in the model. One-way Anova was also performed over the peak frequency calculated on HS and the NS sounds to examine the effect of high temperature exposure on the acoustic quality of vocalizations to search a discriminant for an automatic sound classification. Rectal temperature measured at t₀ and t₃, of the HS trial, showed a smooth increase 0.41°C from 39.3°C to 39.71°C positively associated (P<0.05) to the increase of air temperature from t₀ to t₃ (µΔt= 5± 3°C) and with the RR (P<0.05). The latter increased from t₁ to t₃ (34 to 116 bpm). RR and increased Δt were correlated for 91% (P<0.001) during HS. RR was also correlated (P<0.05) with animal
weight and animal growth (52%; P<0.05). During these HS tests 991 sounds were collected while 442 vocalizations came from normal group situations recordings. Peak frequency analysis allowed distinction between two types of sounds according to their energy content. Most sounds analysed (89%) had peak frequency lower than 1 kHz both for HS and NS and they were classified as “grunts”. Sounds that exceed the 1 kHz were significantly less frequent and due to their high frequency were classified as “screams”. HS grunts were positively related with RT and rising temperature in the test crate (P<0.001). HS screams occurred the most during the central 20 minutes period and were negatively correlated (P<0.001, -78%) with the room temperature. Screams didn’t show any relevant correlation with climate parameters involved in HS. The comparison between peak frequencies of all HS and NS sounds demonstrated relevant difference (P<0.001). During this trial the increase of RT was directly associated with higher temperature in the trial crate and with RR showing the efficacy of this method to induce heat stress in the piglets for these, we can assume the vocalization recorded during the trial are typical of HS and that animals in distress emit great amount of specific sounds (991 HS vs 442 NS). The comparison of the peak frequency showed acoustic differences between HS and NS which is crucial for the development of an intelligent algorithm to count and classify heat distress sounds.

Understanding negative animal responses and observing and recognizing animals in distress is a key skill to implement appropriate practices in order to reduce the stress effects. A possibility toward this goal is applying sound analysis, in livestock farming compartments, as a tool for early detection of disease and distress from continuous recording and automatic processing of animal sounds. Vocalisation must be considered as good indicator to assess heat stress as well as physiologic parameters, climate or feed intake are widely. Nowadays intensive sustainable livestock farming require advanced planning of production management systems which may adapt dynamically to the animals conditions.

![Fig 1. Smoothed AR spectrum estimated for each sound to measure frequency with the highest value Matlab® 2009b.](image)

Aknowledgment: this work is part of a research project called “Integrazione di Sistemi Tecnologici Innovativi per il Monitoraggio a Distanza di Animali” financed by PRIN MIUR 2008, area 07, prot. 20088YWZ28.
Invited Speaker

Estimating the scope of noise masking in National Parks

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Acoustical monitoring throughout the system of U.S. National Park units has documented the pervasive presence of noise. A dominant source is transportation noise, which is increasing much more rapidly than population. Numerous studies have documented changes in animal communication in response to noise: shifts in frequency away from the noisy part of the spectrum, diel shifts away from the noisy parts of the day. Accordingly, NPS is seeking estimates of the intensity and spatial and spectral extents of noise masking in park units.

As in urban environments, there is a pronounced diel pattern to noise exposure in National Parks. Analysis of data from 71 sites in 14 park units is summarized by the percent time that noise is audible, as evaluated by expert human listeners.

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Most sites, including remote sites in wilderness areas, have substantial increases in low frequency background sound levels for more than an third of most hours between 6am and 7pm.

Although there is increasing evidence that the decreases in wildlife diversity and density near road corridors and energy developments is substantially mediated by noise, analogous studies of aircraft noise have not been conducted. Other important issues are also unresolved. How important are low frequency components of adventitious sounds as auditory cues? What are the effects of transportation noise on perception of sounds above 1 kHz? What are the costs of compensating for loss aural awareness? Are the costs of habituation similar to the costs of masking, in terms of lost awareness?

Transportation systems are vital to our society, so restrictive management based on plausible worst-case impact assessments is not an option. Additional research into fundamental aspects of acoustical ecology and the effects of noise on wildlife is needed to support efficient and effective approaches to preserving National Park resources unimpaired for the enjoyment of future generations.
Initial Quantification of the Ocean Basin Scale Low Frequency Masking Potential of a Seismic Survey

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The efficiency with which sound travels through water highlights the fact that anthropogenic noise sources can potentially have impacts over vast areas of the ocean. Relatively recently, there has been a greater focus on the potential for anthropogenic noise to mask the communication of marine mammals, in particular the low frequency specializing baleen whales. Here, we present an initial attempt at quantifying the communication masking potential of a distant seismic survey that occurred off the coast of Australia.

From March 25th to May 30th, 2006, the Aragorn 3D Seismic Survey was conducting operations utilizing 2 x 3090 cubic inch airgun arrays in the western edge of the Bass Strait off the north-west coast of King Island. During this time period, 3 long term acoustic loggers were deployed between just southwest of Tasmania, down to the Antarctic continent (Fig. 1), at distance of approximately 450, 1500, and 2800kms from the survey site. Loggers were deployed at depths of between 1100-1900m, had at a sampling rate of 4kHz, and recorded 13 minutes every hour for the full deployment of up to a year.

The 5 day period from April 26 through April 31st, when seismic airgun pulses were recorded on a large percentage of the sound files, was examined. The calibrated power spectral density was calculated over the 5 day dataset leading to spectral density values for each individual 1s sample in the recordings. Sound pressure level (SPL) for each second was integrated over the 20-50Hz bandwidth for comparison between recording sites, and times with and without seismic surveys present. Visual inspection of spectrograms for each sound file was conducted to separate files with and without airgun signals present.

Of the 120 sound files examined from each logger, approximately 38% had airgun signals present. A comparison of average SPL for 1s samples in files with versus without airguns, shows during ‘seismic’ periods, average SPL was increased by 4.2dB at the closest logger, 3.5dB at the central logger, and 3.0dB at the logger furthest south. While this broadly illustrates the increased mean sound levels present, they are averaged over times both during and between shots and therefore do not effectively demonstrate the intermittent nature of shots from a seismic survey.

To illustrate this, we can assume that the mean SPL from samples recorded in files without seismic activity present is representative of the ‘true’ background sound level. And the degree to which a distant seismic survey raises sound levels and how they vary over time can be quantified relative to this level. These percentage increases in background noise during seismic periods can be compared with natural variability in sound levels during non-seismic periods (Fig. 2).

On logger 1, located approximately 450km from the survey site, noise levels were increased by between 6-15dB for 32% of the time when airgun shots were recorded, compared to less than 1% of the time during non-seismic periods. On the central logger, 1500km away, levels were increased by 6+ dB for 22% of the time during seismic periods, as compared to just 2% during non-seismic periods. And finally, on the southern-most logger 2500km distant, levels were elevated by at least 3dB for 50% of the time during seismic, compared to 19% during non-seismic periods.

The increases in background noise levels illustrated here would impact species that vocalize in the lowest frequency ranges (e.g. blue and fin whale vocalizations in the 20-50 Hz bandwidth), decreasing the detection range of biological signals or making signals more difficult to detect at reasonable ranges from a
source. Considering the distances over which these increased levels were measured, the potential for masking of communication to varying degrees can extend the entire width of ocean basins.

Fig. 1: Locations of acoustic loggers (black stars) and presumed location of the seismic survey recorded (white box near north-west corner of Tasmania). Loggers are labelled from 1 to 3, from North to South.

Fig. 2: Decibels above or below mean background level (mean SPL of samples from ‘non-seismic’ data files) for all 1s samples in seismic and ‘non-seismic’ files. Percentages of occurrence in 3 dB bins are shown.
Neural mechanisms for individual vocal recognition in songbirds

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In the face of limited neural resources, vertebrate nervous systems have adapted to enhance the detection and recognition of signals that carry behaviorally relevant information. These selection biases are achieved through the hierarchical representation of increasingly high-dimensional stimulus features, and the learning-dependent association of these features with behavioral goals. For songbirds, this means learning the acoustic features of the songs produced by neighboring conspecifics. The necessity that learning acts to modify hierarchical representations of natural signals is likely shared by most vertebrates, including humans, yet surprisingly little is known about these processes at either the circuit or cellular level in the auditory system. I will review our recent work on the coding of natural vocalizations across multiple auditory forebrain regions in a species of songbird, European starlings. I will emphasize the role of learning in modifying both the excitatory and inhibitory responses of single neurons, tied at multiple anatomical levels to representations of increasingly complex acoustic features. At the highest levels in the system, these features correlate directly with learned individual vocal recognition in each animal.
Adjusted phonotactic reactions towards sound intensity and fine temporal traits mediate territorial defense in the poison frog *Oophaga histrionica*.

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A central question in communication is how much information animal signals convey. Auditory signals contain information that might allow receivers to estimate the distance to the sound source, as well as the size or the aggressive or motivational state of the sender. Proper differential reactions by receivers in aggressive contexts might be important for territorial species, because they allow behavioral adjustments towards intruders according to the perceived risk of losing a territory.

Males of the poison frog *Oophaga histrionica* are territorial and respond aggressively towards conspecific male intruders. To know whether signals convey information on male body size, first we investigated the relationships between advertisement-call traits and body size of males. Then, we used playback experiments to understand the auditory coding scheme of this species. By manipulating sound pressure level, gross (inter-call intervals) and fine temporal (number of pulses) structure of the synthetic signals, we simulated near and far intruders with potentially variable sizes or motivational states.

Our results suggest that call traits do not communicate information about body size. Moreover, sound intensity and temporal traits do not predict whether or not a resident will attack an opponent. However, males recognize and use the variations of sound intensity and number of pulses per call, to adjust its behavioral reaction accordingly. Therefore, we distinguish the fine temporal trait as a functionally important cue for territorial defense. This finding demonstrates that, under field conditions, males use sound intensity and fine temporal traits as source of information useful to adjust an aggressive reaction. We discuss the possible role of the fine temporal traits of calls on the transmission of information about the motivation to fight. Simultaneous and independent recognition of both distance and fine temporal traits might improve the efficiency of males during territorial defense.

![Box plot](image)

**Fig. 1.** Males who did not attack the loudspeaker reduced the number of pulses emitted per call. In contrast, those who approached the sound source increased the number of pulses per call. Numbers at the top denotes significant correlation; numbers at the bottom indicate the number of males tested.
Fig. 2. *Left panel*: Sound Level (dB) manipulation of stimuli call increased the number of (a) orientations and (b) pulses per call performed by males of O. histrionica. *Right panel*: The manipulation of the number of pulses of stimulus call increased the number of movements of males of *O. histrionica*. The Change in the number of (a) orientations and (b) walks performed by males differed between levels of low, average and high number of pulses of the stimulus call. Numbers at the bottom of each panel denotes the number of males tested. Statistical significance between levels is highlighted after post hoc procedures.
Acoustic Ecology Of Predator-Prey Interactions: Distant Early Warning Systems In Communication Networks

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Predators are a major source of mortality for many animals. This is especially true for smaller birds and mammals, in which more than 75% of mortality can be from predators. Biologists have known for a long time that animals produce many alarm signals in response to predators. Recent studies suggest that alarm signals may be much more complex and sophisticated than previously suspected: animals may encode a great deal of information in their alarm signals, such as the type and behavior of a predator (predator on the ground, perched raptor versus flying raptor), the general threat level posed by the predator, and even the “hunting motivation” of flying raptors. In addition, many species of unrelated birds and mammals may decode information contained in the alarm signals of many other species and respond appropriately. In some cases, waves of information about predators can sweep through environments astonishingly quickly and travel far. These complex networks of interacting species may act as distant early warning systems that can alter the behavior of many species long before the potential predator arrives in an area. However, we know exceedingly little about the acoustic ecology of these important behavioral interactions.

Many species of birds and mammals produce acoustically very similar alarm calls in response to the same sort of danger. In response to aerial danger, such as flying hawks, many birds (especially passerines) and some mammals tend to produce “seet calls” (Fig. 1, a-f). These alarm calls tend to be short duration, low to medium amplitude, relatively high frequency (typically 5-9 kHz), relatively pure tone, and difficult to localize. In contrast, the mobbing calls given in response to perched raptors (Fig.1, g and h) are loud and harsh (broadband with often complex overtone structure), repeated often (high duty cycle), and extremely easy to localize.

Fig. 3. Seet calls recorded in response to models of flying raptor: (a) seets of six red squirrels, (b) Lazuli Bunting, (c) Black-capped Chickadee, (d) Dark-eyed Junco, (e) Ruby-crowned Kinglet, and (f) American Robin. Harsher, broad-band mobbing calls produced in response to perched raptor: (g) Red Squirrel, and (h) American Robin. Figure modified from Greene and Meagher (1998) and additional recordings by Greene.
Seet alarm calls and mobbing signals tend to elicit very different behavioral responses from animals that hear them. When birds and mammals hear seet calls, they typically stop what they were doing, immediately look up, and usually seek shelter. In contrast, mobbing calls tend to attract other nearby animals, which typically results in a large group of animals harassing the perched raptor, often forcing it to fly out of the area.

It is becoming clear that animals can encode a surprising amount of information about predators in their mobbing calls. Variation in acoustic characteristics of mobbing calls has been shown to vary with predator type or threat level. We know much less about whether seet calls encode information about predators, but a couple of studies suggest that they do. For example, Black-capped chickadees appear to produce higher-pitched seet calls in response to models of more dangerous species of accipiter hawks.

The general dogma about seet alarm calls is also that they do not travel very far. I present the results of playback experiments that show that seet alarm signals can travel astonishingly fast and far under some conditions. These distant early warning systems are normally “on standby” and not passing along information, but they can be “turned on” extremely quickly in response to a very subtle signal. Information about flying raptors can be conveyed by many different species of birds and mammals. This wave of information can travel up to 60 m/s (130 mph), much faster than a flying raptor. These waves of information about approaching raptors can spread rapidly at least 300 m.

Ecologists are making exciting advances in understanding the acoustical ecology of the complex interactions between prey and predators. We will soon be able to characterize predator alarm “infoscapes” for much better. The results will be of broad importance to behavioral ecology, landscape ecology and conservation biology.
Integrating underwater noise within coastal and marine spatial planning frameworks: lessons from the Stellwagen Bank National Marine Sanctuary

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Despite over 30 years of implementing cumulative impact regulations in the U.S. and other countries, the health of global marine ecosystems is in serious decline due to impacts from multiple stressors, including overfishing, pollution, invasive species, coastal development and climate change. These declines have spurred the recent development of coastal and marine spatial planning (CMSP) frameworks designed to comprehensively manage human uses in both near shore and offshore waters. Nearly all emerging CMSP efforts assert the goal of protecting marine ecosystem health; however, integration of information regarding the ecological implications of human activities continues to lag behind efforts to reduce overlap among different human uses. Mismatches between the scales of research, monitoring and management and the scales of impacts are impeding the consideration of wide-ranging, chronic stressors like low-frequency underwater noise within more comprehensive planning frameworks.

Here, we present results from a study that sought to address this mismatch by quantifying the loss of acoustic habitat or “communication space” available to calling baleen whales due to the obscuring of their signals by low-frequency anthropogenic noise sources over long enough time periods and large enough areas to be biologically relevant, including accurate representation of natural and human-induced noise contributions at those scales. Specifically, this study characterized the influence of communication masking on calling North Atlantic right whales (Eubalaena glacialis or NARW) within a ~10,000 km$^2$ area surrounding and including the Stellwagen Bank National Marine Sanctuary (SBNMS or Sanctuary). The Sanctuary is a federally-designated marine protected area that represents important feeding and nursery ground for several species of endangered baleen whales, with approximately one-third of the remaining NARW population predictably utilizing its waters in late spring and early winter. In addition, the area is bisected by heavily-transited commercial shipping lanes to and from the port of Boston and hosts a high volume of coastal traffic. As a result, this Sanctuary was an ideal study site in which to investigate the potential influence of chronic noise on a vulnerable population.

Between December 2007 and May 2010, arrays of Marine Autonomous Recording Units (MARUs) were used to gather low-frequency acoustic data (< 1000 Hz) within the Sanctuary. MARU data were used to calculate the spatial and temporal variability of noise fields and to detect and localize calling NARWs. Methodologies were developed to combine MARU data with commercial ship track data from the U. S. Coast Guard’s Automatic Identification System (AIS) to calculate the noise contributions from vessels within and outside the Sanctuary. Data from regional oceanographic buoys were related to MARU data to estimate present-day ambient noise conditions and approximate historical (mid 20th century) ambient noise levels, providing a necessary reference point for comparison of current vs. past communication capabilities.
Integrative tools applied to these noise fields estimated that signal excess for contact calling right whales averaged ~0 decibels under present-day noise conditions, and was negative during periods when discrete noise sources (ships) were abundant. When compared to communication space available under approximated historical noise conditions, today’s calling right whales were estimated to have lost, on average, over 60% of their communication space. Maps of received levels associated with calling right whales relative to discrete noise from ships visually depict loss of communication space during periods with less versus more commercial ship traffic (Figure 1). Finally, a comparison between assessments of noise impacts derived from current exposure-threshold-based “acoustic harassment” metrics versus communication-space quantifications highlighted limitations of threshold-based approaches for adequately characterizing chronic and widespread impacts.

More complete integration of communication masking on marine mammals and other animals within CMSP frameworks will require the development of methodologies for translating the implications of lost communication capabilities on “ecosystem services”. Baleen whales have legally-coded intrinsic cultural value in U. S. waters, support whale watching industries and play a variety of roles in ecosystem dynamics that support commercial and recreational fisheries. Metrics of noise impacts that relate directly to functional consequences for whales can thus be integrated within models that evaluate tradeoffs between services. Current efforts to facilitate such modeling across all U.S. waters will rely on high-resolution datasets like those generated in this study to ground-truth assumptions, perform sensitivity analyses and guide future data collection efforts.

Fig. 1. 10-minute snap shots of received sound levels (71-224 Hz, dB re 1µPa, scale far right) in Massachusetts Bay during a time with one distant (left) versus three central (right) AIS-tracked commercial ships. Black outline represents the boundaries of the SBNMS.
Metabolic rates of sound production in bottlenose dolphins (*Tursiops truncatus*) and evaluating costs of noise-induced vocal compensation

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Animals often modify their acoustic communication signals in response to fluctuations in background noise. For example, some birds and marine mammals increase the amplitude, duration, repetition rate, and/or shift frequencies of their vocalizations as noise levels increase. Such behavioral flexibility on the part of the sender is particularly advantageous in acoustic environments that are highly dynamic since it reduces the probability that masking will occur at the position of the receiver. However, very little empirical data on the energetic costs of sound production in animals exist, particularly in mammals. The objective of this study was to measure the metabolic costs of sound production in dolphins to assess impacts of vocal compensation as an anti-masking strategy.

The subjects of this study were two male Atlantic bottlenose dolphins housed at the University of California Long Marine Laboratory in Santa Cruz, California. These individuals were trained to produce sounds on command while stationed under a metabolic hood to measure oxygen consumption. One of the subjects of the current study produced whistles while the other produced pulsed squeak or quack-like sounds during trials (see Fig 1). These sounds are representative of those described as communicative sounds of wild, free-ranging bottlenose dolphins.

Only one trial per dolphin per day was conducted and trials were run first thing in the morning. The dolphins were fasted overnight before trials to eliminate the potential for the metabolic cost of digestion to confound oxygen consumption measurements. Only one subject was run at a time and remained at the water surface under a metabolic hood for the entire trial period. Each experimental trial consisted of a 10-minute period of rest to determine baseline metabolic rate, followed by a two minute vocalization period, and concluded with another rest period to measure recovery (of at least 10 minutes, or until oxygen consumption values return to resting values). During all trials, the subject was acoustically monitored in real-time and sounds were recorded for further analysis. Respirations were also recorded during trials to compare respiration rates among baseline, vocalization, and recovery periods.

The rate of oxygen consumption was determined as follows: air was drawn into the hood at a flow rate of 300 L min$^{-1}$. The flow rate was maintained such that the content of oxygen in the hood remained above 20%. Water and CO$_2$ from subsamples of excurrent air from the hood were absorbed using Drierite and Baralyme, respectively, prior to entering the oxygen analyzer. The percentage of oxygen in the sample line was monitored continuously (FC-1B O$_2$ Analyzer, Sable Systems International) and recorded by a laptop computer every second during the experimental trial. Oxygen consumption rates during baseline, vocalization, and the recovery periods of each trial were calculated from the percentage oxygen data using respirometry software (Expedata data acquisition and analysis software, Sable Systems International).

The acoustic recording equipment included a calibrated Reson hydrophone (TC 4033) that was connected to a preamplifier with a bandpass filter (Reson VP 2000). The signal was then digitized at a
sampling rate of 96 kHz, and recorded and monitored in real-time in the time and frequency domain. Calibration was checked on a regular basis with a pistonphone connected to a custom adaptor (42AA with RA78, GRAS Sound & Vibration). Hydrophone placement was the same during all periods (baseline, vocalization, and recovery) of each experimental trial.

Preliminary results from a limited number of trials analyzed thus far indicate that when dolphins produced sounds in nominal conditions, both types of vocalizations increased oxygen consumption rates while respiration rates did not change relative to baseline levels. These results indicate that increased oxygen consumption was due to increased metabolic demand related to sound production rather than to changes in breathing patterns. In some cases, it took 5-10 minutes for dolphins to recover to baseline oxygen consumption rates following the vocalization period. Phase two of this study will repeat measurements during trials when the dolphins produce sounds at different amplitudes to assess energetic costs of vocal compensation in response to increased masking noise by free-ranging animals.

Fig. 1. Spectrograms showing 8 second examples of the whistles of one dolphin (top panel) and the pulsed squeaks of the other dolphin (bottom panel) recorded during trials.
The potential communication value of species specific terminal frequencies in European pipistrelle bats

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Bats are well adapted to their nocturnal life by using echolocation for orientation in space and food acquisition. The strongest constraint on the design of the echolocation signals is exerted by the echolocation task a bat has to solve. However, there is evidence that echolocation calls are also used for communication. If communication is an important function of echolocation signals, it should exert a selection pressure on the signal design leading to the selection of species specific traits. We assume that the terminal frequency is a main trait which discriminates species and allow species identification. For a safe communication the terminal frequencies should be separated in species specific communication channels. To test the communication hypothesis we determined the position and the width of the frequency channels in different species. In situations where channels overlap sympatric species should show character displacement. We recorded the echolocation signals of sympatric and allopatric pipistrelle bats, Pipistrellus pygmaeus, P. maderensis P. pipistrellus, P. nathusii and P. kuhlii at appropriate locations in Europe and measured terminal frequencies. Since terminal frequency depends on signal duration we plotted frequency against duration and calculated linear regressions for each species. We defined channel width as standard deviation of the residuals and the position of the channel as the mean frequency value of signals with a duration of 5 ms. This method has the advantage that the defined frequency channel for a given species is independent of signal duration. A species is sufficiently described by the slope of the regression line, the channel width and its position. We also calculated channels for initial frequency and peak frequency but terminal frequency proofed to be the most reliable species specific signature.

Terminal frequency channels were clearly separated in species that have most likely been living sympatrically for a long time in the past, i.e. in France between P. pipistrellus and P. kuhlii, in Germany between P. pygmaeus, P. pipistrellus and P. nathusii, and in Switzerland between P. pipistrellus and P. nathusii and between P. pipistrellus and P. kuhlii. The solitary P. maderensis occupies the same acoustic niche as P. pipistrellus on mainland Europe. No acoustic separation was found between P. nathusii and P. kuhlii in Switzerland. Both species have only been found in area of sympathy for three decades and possibly species specific frequency channels have not yet been established. However, selective pressure for character displacement should be highest in this area of sympathy.

The within-species comparisons revealed that in all pipistrelle species channel position and channel width did not depend on species composition. Minor differences were within the range of variance between single colonies of a recording site. In Norway where only P. pygmaeus occurs the channel did not differ from the channel of P. pygmaeus living sympatrically with P. pipistrellus. One possible explanation is the maintenance of an already achieved acoustic separation due to former sympatric spreading.

In all species channel width was between 0.08 -0.15 octaves, independent of species composition, which may indicate the maximum tolerance of variance for species identification.

Our results support the hypothesis that echolocation signals have a communication function.
Directionality of echolocation calls from two species of sheath-tailed bats (Emballonuridae), Saccopteryx bilineata and Cormura brevirostris.

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Bats are the second most species rich order of mammals with more than 1200 species occurring all over the world. The enormous success of bats has been ascribed to their ability to exploit the night sky. This foraging niche is accessible to bats due to their ability to fly and echolocate i.e. position objects in their immediate surroundings by emitting short high frequency sound pulses and listening for the returning echoes. The directionality of the echolocation pulses defines the acoustic field of “view” and therefore plays a crucial role in how the world is perceived by bats. Vespertilionid bats can adjust the directionality of their echolocation signals to the context. They adjust directionality to the surroundings emitting a narrower beam in the field compared to the lab. They also adjust directionality on a short time scale during a pursuit to broaden the beam in the last phase of insect pursuit (Surlykke et al., 2009; Jakobsen & Surlykke 2010).

Emballonurid bats are an ancient lineage having evolved more than 45 mil years ago and they produce short multiharmonic shallowly modulated calls presumed to resemble those of the first echolocating bats, whereas Vespertilionids are considered more advanced echolocators (Schnitzler et al., 2004). Thus, comparisons of vespertilionids and emballonurid echolocation adjustments in comparable behavioral situations, e.g. insect capture, will facilitate identification of crucial acoustic constraints for perception through echolocation and help us understand the evolution of echolocation.

Fig 1. Echolocation calls emitted by C.brevirostris and S.bilineata when navigating a large flight cage. The short call emitted by C.brevirostris is consistently emitted when the bats are close to the microphone array.
Hence, we focused on the directionality of the sonar beam and studied if and how the two emballonurid bat species, *Saccopteryx bilineata* and *Cormura brevirostris* adjust directionality to a given context or environment.

The study revealed the first measurements of echolocation call-directionality for emballonurid bats. Our results show that directionality is comparable to that of aerial hawking vespertilionid bats navigating a similar environment. *S. bilineata* exhibited little or no adjustment of their call directionality, while *C. brevirostris*, when flying close to obstacles in the cage, modified the frequency content of their calls increasing the peak frequency, thus increasing the directionality of their calls quite substantially. Hence, *C. brevirostris* emitted a substantially more directional signal when flying close to objects than did *S. bilineata*. The study thus implies that the ability to modify the directionality of emitted calls is a crucial part of the echolocation system for any bat.

**References**


Delphinid sound production: Tonal sounds of toothed whales are produced by continuously vibrating the left pair of phonic lips

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Toothed whales are highly social animals that depend on acoustic signals for echolocation and for communicating with conspecifics. Toothed whales produce sounds pneumatically by pressurizing air in the nasal passages. During echolocation, this pressurized air accelerates a pair of connective tissue structures (the phonic lips) to generate a transient, high-amplitude biosonar click. Whistles, on the other hand, have been thought to result from either vibration of nasal tissue structures or from resonances in vestibular air sacs that are associated with the nasal passages, and it is poorly understood whether the nasal air spaces may function to filter tonal sounds as the vocal tract in terrestrial mammals filter glottal pulses.

Here we investigate the tonal sound production of toothed whales by analyzing the frequency-modulated whistles produced by a bottlenose dolphin breathing a mixture of 80% helium and 20% oxygen (heliox) and comparing to the whistles produced while breathing regular air. Due to the lighter density of helium, the resonance frequency of internal air structures filled with heliox will be 70% higher than similar air structures filled with air. If sounds are produced as an aerodynamic whistle, by stabilizing air vortices according to the resonance of associated air spaces, the fundamental frequency would therefore be expected to increase with a factor of 1.7 in a heliox atmosphere. In contrast to this prediction, we show that the fundamental frequency of bottlenose dolphin whistles is unaffected by the elevated resonance frequency of internal air structures when breathing heliox, demonstrating that the fundamental frequency of whistles arise as a result of vibrating tissue structures, such as the left pair of phonic lips.

By quantifying the acoustic energy within individual harmonics, we further show that whistles produced while breathing heliox has significantly less energy in the fundamental frequency compared to the second and third harmonic. This shows that air spaces filter the produced tonal sounds just as the vocal tract of terrestrial mammals and birds filter the glottal pulses, but with a much wider frequency response. This loose coupling is likely an adaptation to a diving lifestyle, where the size (and resonance frequency) of air sacs depends on the depth of the animal and on the temporally changing location of air within the enclosed nasal sound production system. Bottlenose dolphins encode individual identity within the fundamental time-frequency contour of their whistles, so a mode of sound production that is insensitive to pressure changes is essential for successful communication throughout a dive.
Fig. 1. Examples of bottlenose dolphin whistles produced in air (A) and in a heliox mixture consisting of 80% helium and 20% oxygen (B). While the fundamental frequency does not show significant changes, the distribution of energy within harmonics is slightly altered in the heliox atmosphere. This implies a mode of tonal sound production in toothed whales that is analogous to the vibration of vocal cords or syringeal labia in terrestrial mammals and birds respectively.
INTRODUCTION Fish call diversity includes variation in amplitude, frequency, temporal traits across species and waveform differences within species (Amorim 2006; Amorim et al. 2008). Marshall (1962) observed that fish sound mechanism morphology was taxon specific and hypothesized that variation could be responsible for call specificity across taxa, particularly frequency components. The actual presence of diverticula on the swimbladder mechanism of sciaenids was observed by Dufosse (1874, translated in Sorenson 1894-5) to influence intensity of calls. Sorenson (1894-5) observed a similar phenomenon in a tropical doradid species that had complex diverticula. Calls produced by the swimbladder mechanism of catfishes vary greatly in tone and quality to an observer (Kaatz 1999). We conducted a preliminary test of this hypothesis by mapping characteristics of disturbance call diversity onto a genus level cladogram for a super family of vocal catfishes. Our hypothesis was that taxa with diverticula present on the swimbladder would have call characteristics that differ from taxa that lack them.

METHODS Sampled taxa included 20 species in 15 genera of the Doradidae, and 5 species in 5 genera in the Auchenipteridae, with comparison to three out group families. We examined the following call characteristics: waveform and spectrogram patterns, repertoire size and audibility. Sound recordings of disturbance sounds were elicited from individuals by holding them underwater next to a hydrophone in the field (Cornell Biological Field Station, Lake Oneida). SIGNAL analysis was used to graph waveforms and spectrograms. Each adult individual was recorded under the same field conditions from 1992 to 1998. The number of individuals recorded per species ranged from 1-15 (mean 4 ± 3 SD). Sounds sampled per individual ranged from 1-337 (maximum per species mean 69 ± 68 SD). Morphological specimens were obtained from natural mortality of maintained populations. Diverticula for this comparative study are defined as out-pocketing of the swimbladder and may include the reduced posterior division of the swimbladder (Birindelli and Sabaj 2009). A phylogeny was constructed for the individuals whose swimbladder morphology had been dissected and whose sounds had been recorded.

RESULTS Call diversity in doradoid swimbladder sounds released during disturbance recordings included: 1) nonpulsatile or continuous (consecutive pulses lacking interpulses) with harmonics; 2) fixed interval pulsed series. All doradoid species produced continuous calls at irregular sound intervals during disturbance. One doradid and two auchenipterid species additionally produced temporally fixed series of short repeated pulses. Repertoire size (# of spectrographic and waveform distinct sounds) based on disturbance sound samples ranged from one to two per species. Only one genus of auchenipterid produced sounds that could be considered high amplitude or audible to a human observer without a hydrophone next to the sound producing fish, all other species produced low amplitude sounds. Diverticula were present in Agamyxis, Platydoras, Orinocodoras, Pterodoras, Megalodoras, Oxydoras, Hemidoras and Nemadoras. The number and lengths of diverticula were species specific and varied greatly from diverticula less than several mm in length to greater than 1 cm in length. Phylogenetic patterns indicate that continuous sounds with harmonics are basal for the clade. Pulsed sounds, high amplitude sounds and the presence of swimbladder diverticula are all derived conditions but none correlated with each other.
DISCUSSION The swimbladder mechanism of doradoids has evolved independently and involves vocal muscles attaching to bony elements that insert on the swimbladder (Ladich and Bass 1997; Parmentier and Diogo 2006), but little is known about how morphology might influence interspecific call variation. How did the calls of doradoid species differ? The majority of species produced continuous sounds consisting of multiple oscillation maxima patterns, suggestive of multiple pulses in series without interpulses (functional analysis is necessary to determine individual pulse durations). The highest amplitude sounds were audible to a human observer outside of an aquarium at least 30 feet away. Underwater low amplitude sounds tested could be detected at a distance of at least 3 feet. The most intense callers’ swimbladders lacked diverticula. None of the limited call variation we examined correlated with diverticula presence on the swimbladder. Whether disturbance call patterns represent the full repertoire of a species requires further investigation. Long-term direct behavioral observations (both non-reproductive and reproductive seasons) have only been conducted for a very small number of taxa in this speciose clade (Kaatz 1999). Further studies should examine differences between species by additionally considering: frequency, statistical comparisons of waveform (oscillation maxima patterns, pulse period), duration, sound pressure level and functional morphological analysis of the basis for call variation.
Syntactic structure in the vocalizations of the rock hyrax

(*Procavia capensis*)

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Few mammalian species produce richly structured vocalizations comparable to bird songs, and this greatly restricts the capacity for information transferal. Such syntactically complex vocalizations have previously been studied only in a few mammalian taxa, such as primates and cetaceans. We provide the first evidence of complex syntactic vocalizations in a small mammalian species, the rock hyrax (*Procavia capensis*: Hyracoidea).

Previous research has used frequency-domain analysis to show geographic variation in the vocalizations of a small number of mammal species. However, such acoustic analyses fail to take into account the significance of the syntax, or order, of elements in a vocalization. If information is encoded in the order of different notes, motifs or other syntactic elements, frequency-domain analysis alone cannot identify or extract such information.

The hyrax is a small (~3kg), social terrestrial mammal that lives in groups of 10-50 individuals. Male hyraxes produce long and complex vocalizations that can be heard for several hundreds of metres. The role of these vocalizations is not yet clear, although it has been shown that they encode multiple information about the singer (size, social status, etc). These vocalizations consist of a string of characteristic notes, or “syllables” drawn from a limited repertoire (Figure 1). Sequential vocalizations of a single individual are similar to each other, but rarely identical.

We used algorithms taken from genetic sequence analysis and information theory to examine the order of syllables in hyrax calls. We examined how the distance between hyrax sites affected the difference in call syntax; as indicated by the quantitative difference between pairs of vocalizations (using the Needleman-Wunsch algorithm; Figure 2), and the information theoretical difference between vocalization assemblies (relative entropy).

We found that call syntax is significantly different between different regions in the country, raising the possibility that call dialects exist. In addition, calls from locations less than 10km apart are more similar to each other than those separated by more than 10km. This suggests a mechanism of information transmission limited to the approximate range of movement of the animal. This is the first evidence of rich syntactic structure in the vocalizations of a mammalian species not previously thought to have strong cognitive abilities.
Fig. 1. Spectrogram of rock hyrax (*Procavia capensis*) showing four different syllable types: (W) ‘wail’ is long, tonal, and frequency modulated (descending), (C) ‘chuck’ is a series of pulses, (Q) ‘squeak’ is short, tonal and frequency modulated, and (S) ‘snort’ is non-tonal.

Fig. 2. Sequence alignment of two sample calls using the Needleman-Wunsch algorithm. The calls differ at four locations, one insertion (blue) and three replacements (black). The Needleman-Wunsch algorithm finds the minimal cost of converting one string to another, given a user-supplied cost matrix for each replacement and insertion operation.
Morphology and Viscoelastic Properties of Panthera Vocal Folds

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To carry loads, geometries and material composition of biological structures have evolved over long periods of time. It is believed that laryngeal anatomy is uniquely designed for a species’ vocal repertoire. Causal links between vocal fold structure and function, however, are not developed. Here we investigated the design of Panthera vocal folds normally used to produce loud and very high-amplitude sounds. Relative to human voice production, restoration of damaged or diseased vocal folds continues to be a difficult challenge. Medical and engineering solutions remain less than adequate, but investigating other species provides insight and alternatives. We asked whether histological features and biomechanical measures of lion and tiger vocal folds were predictive of the characteristic low pitched and very loud roaring sounds. These vocalizations are a result of air flow from the lungs being shuttered by self-sustained vocal fold oscillation due to fluid-tissue interaction. Previous studies revealed that a Panthera vocal fold contained fat, but the distribution of the fat among other extracellular components (e.g., elastin and collagen) and its relationship to vocalization had not been described.

The key finding from our investigation was that the Panthera vocal fold possessed a deep concentrated fatty region and a medial non-fatty fibrous region (Fig. 1) yet viscoelastic properties were similar and low throughout (Fig. 2). The structural and mechanical distribution suggests an alternative design for human vocal fold reconstruction. Integration of fibrillar proteins into amorphous materials such as fat in both the deep and medial portion of the human vocal folds should be considered for retaining structure (without resorption) while promoting good vibratory characteristics.

Evidence of the key finding was based on histology, elongational stress/strain ergometry, and oscillatory shear rheometry of six lion and tiger vocal fold specimens. Connections to function were made by using these data to calculate fundamental frequencies and phonation threshold pressures (minimum lung pressure needed to induce vocal fold vibration) from well-established constitutive models. Calculations predicted frequencies of 40 – 300 Hz, a range measured from captive and free-ranging animals and recently measured in the laboratory using excised tiger larynges in a separate study. Predicted phonation threshold pressures were very low compared to other species.

Our data provide, for the first time, a comprehensive and integrative approach to study the relationship between mechanical properties, predicted vocal output and anatomy. It advances our understanding of the vocal folds as a load-bearing and sound-producing device; and increases our understanding of behavior of an endangered species, Panthera tigris, where raising awareness is a critical component of protecting wildlife.
Fig. 1. Elastica-van-Gieson stain of a lion vocal fold. A: Overview of a midmembranous section. Bar indicates a 5mm distance. Larger magnifications indicated by four squares in the overview are shown in B-E. The black dots in B are cross sections of elastic fibers. They indicate that most of the elastic fibers are oriented dorso-ventrally. More laterally (C, D and E), fibers are cut along as well as perpendicular to their longitudinal axis suggesting that fibers are more variably oriented. Bars in B-E indicate a 100µm distance. TA: thyroarytenoid muscle; BV: blood vessel; FC: fat cells; EP: epithelium.

Fig. 2. Shear elastic modulus (top) and viscous modulus (bottom) of Lion, Siberian Tiger, and Sumatra Tiger vocal fold tissue as a function of frequency.
Communication on the wing: pronounced individual- and sex-specific signatures in echolocation calls of the greater sac-winged bat

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Bat echolocation not only allows precise navigation in complete darkness but also holds great potential for social communication, a research field that is still largely unstudied. Several studies have used various mathematical approaches to detect vocal signatures in bat echolocation calls but the experimental validation of statistical findings is still lacking in most cases. Our experimental study shows that echolocation calls of the greater sac-winged bat, Saccopteryx bilineata, feature pronounced individual- and sex-specific signatures and demonstrates, for the first time, that sex-specific echolocation calls prompt bats to produce complex social vocalizations in the appropriate respective social context.

Saccopteryx bilineata is a highly social Neotropical bat exhibiting resource-defense polygyny. Males become territorial as they mature and vigorously defend small areas of suitable roosting space in the day-roost against other males. During territorial defense, males produce several types of aggressive vocalizations, the most remarkable of which is called “territorial song”. Males also produce complex courtship songs to attract females for roosting in their territory and joining their harem. Day-roost colonies may contain up to twelve different harem territories. The echolocation calls of S. bilineata are multiharmonic and consist of a central, narrowband component accompanied mostly by two short frequency-modulated sweeps, one each at the start and at the end of a call. During search flight S. bilineata often alternates call frequencies, resulting in call duplets of a low call followed by a high call.

We analyzed 206 echolocation call duplets from 27 free-flying bats (13 males, 14 females) at three locations in Costa Rica. Individual bats were released after capture and recorded while circling the capture site. We measured 14 call parameters for both low and high calls including duration, peak frequency, start and end frequency, and three principal components describing call curvature. The parameters were corrected for body size because female S. bilineata are larger than males and because both sexes varied in size between locations. We subsequently used the corrected call parameters in a DFA which revealed a strong individual signature in echolocation calls (71.4% correct classification of individuals) that was significantly better than random (Wilcoxon test: Z=-4.483, n=27, p<0.0001). In order to assess sex- and location-specific differences in echolocation calls, we used the Mahanalobis distances between individual bats in the signal space defined by the DFA. The closer individuals clustered together in signal space, the more similar were their echolocation calls. Individual bats from the same location were significantly closer together in signal space than individuals from different locations (paired t-test; t_{26}=-3.581, p=0.001). Moreover, at a given location individuals clustered significantly closer with members of the same sex than with members of the other sex (paired t-test; t_{26}=-2.465, p=0.021). Correspondingly, a multivariate model with echolocation call parameters as variables revealed significant effects of the factors sex and location as well as their interaction (GLM with sex and location as fixed factors; sex: F_{14,8}=6.481, P=0.006, partial \eta^2=0.919; location: F_{28,16}=2.850, P=0.016, partial \eta^2=0.833; sex*location: F_{28,16}=2.202, P=0.050, partial \eta^2=0.794). These results indicate pronounced sex- and location-specific signatures in echolocation calls of S. bilineata that were not caused by mere differences.
in body size. Individual signatures were mainly due to differences in call curvature and duration, sex-
specific signatures due to differences in call duration. In order to experimentally verify the sex-specific
signature in echolocation calls of *S. bilineata*, we tested the ability of males to sex conspecifics solely
based on their echolocation calls. We conducted experiments at three locations in Costa Rica in which we
released bats of both sexes one by one under controlled circumstances in the vicinity of their colony and
recorded the subsequent vocal responses of resident males to the echolocation calls of the released
conspecifics. Male vocal responses were further analyzed when they complied with strict criteria: Firstly,
the vocal response was uttered when the approaching bat was still at least 5m away from the colony,
ensuring that only echolocation calls, not scent, behavior or visual appearance, could be used to sex
conspecifics. Secondly, simultaneous behavioral observations of all individuals in the colony ensured that
the vocal response was actually directed at the approaching bat and not at other colony members. Thirdly,
the vocal response either interrupted the echolocation series or, if the approaching bat ceased
echolocating, succeeded the last echolocation call with an interval of less than 500ms. We analyzed the
vocal responses of eight males to the echolocation calls of 20 released conspecifics (twelve females, eight
males). All males produced aggressive vocalizations (barks and territorial songs) in response to
approaching males whereas they exclusively uttered courtship songs in response to approaching females
(Fisher’s exact test; n=8, p<0.0001; Fig. 1). Our results demonstrate that male *S. bilineata* could sex
conspecifics based on echolocation calls alone. To our knowledge, this is the first time that the
experimental presentation of echolocation calls in a natural environment prompted bats to produce
complex social vocalizations in response.

Fig. 1. Oszillograms and spectrograms depicting vocalizations of roosting *S. bilineata* harem males in response to
the echolocation calls of conspecifics approaching the roost. Echolocation calls of males always triggered
aggressive or territorial vocalizations (a), whereas echolocation calls of females triggered courtship vocalizations
(b), demonstrating that harem males were able to sex conspecifics solely based on echolocation call properties.
Tonal whistles or burst pulses? How models of sound production mechanisms and wavelet analysis may provide insights into the classification of toothed whale sounds

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The sounds produced by toothed whales are traditionally classified into three categories: whistles, burst pulses, and echolocation clicks. Except for the well defined acoustic features and clear functional definition of echolocation clicks, the classification of the first two categories, commonly performed through visual inspection of spectrograms, has been somewhat arbitrary and subjective. Furthermore, when there is an abrupt or gradual transition from ‘pulse-like’ or ‘nonlinear/chaotic’ into ‘tonal’ features within a single call (Fig. 1), the distinction between these two categories becomes artificial.

Recent studies reveal that the tonal sounds of toothed whales are likely produced by pneumatically-induced tissue vibration in a manner that is analogous to the operation of vocal folds in terrestrial mammals and the syringeal labia of songbirds. By drawing from our understanding of the sound production mechanisms of terrestrial mammals and songbirds, this study aims to construct a framework capable of describing the differences in toothed whale signals quantitatively through the production mechanism. More specifically, the sound production mechanism of toothed whales may be characterized by combining physical models of the sound source(s) and the spectral filtering effect of the upper respiratory tract and associated air spaces. Spectrally-simple ‘tonal whistles’ and spectrally-rich ‘burst-pulses’, ‘nonlinear’ or ‘chaotic’ sounds may be generated by varying critical parameters in the sound source dynamics, such as the nasal pressure or phonic lip tension.

Recognizing the transient nature of toothed whale vocalizations and their pulse-driven sound production system, this study also explores the use of wavelet analysis to represent various types of sounds produced by toothed whales. Wavelet analysis represents a signal through the superposition of a set of wavelets, which are dilated, shifted, and scaled versions of a fixed, time-limited function (the mother wavelet). Since these wavelets are finite in time, as opposed to the sinusoids that stretch to infinity in Fourier analysis, the wavelet analysis is well-suited for analyzing transient signals. Compared to the smear in the spectrogram resulting from the time/frequency resolution trade-off in short-time Fourier analysis, wavelet analysis is capable of providing both temporally and spectrally local information within a signal, and has the potential to facilitate automatic classification of different signal types (Fig.2).
Fig. 1. Spectrogram of a pilot whale vocalization. There is a transition from ‘pulse-like’ into ‘tonal’ features around 0.18 sec. The spectrogram was produced with 50% overlapping hanning windows with a window size of 512 sample points. The signal was sampled at 60 kHz.

Fig. 2. Spectrogram (upper row) and wavelet transform (lower row) of a “burst-pulse” (left column) and a “rasp” signal (right column). Vertical lines on the spectrogram indicate the sections used in the wavelet transform. The wavelet transform provides spectral information with much finer temporal resolution for the burst-pulse. It also reveals the spectral difference between these two signals without sacrificing the temporal resolution. The spectrogram was produced with 25% overlapping hanning windows with a window size of 256 sample points. The wavelet transform used Daubechies wavelet of order 4. Both signals were sampled at 196 kHz.
Auditory Brainstem Response in a harbor porpoise (Phocoena phocoena) performing an echolocation task

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The auditory system analyzes the information carried by the sound. Toothed whales that rely on echolocation for orientation and feeding are dependent on extracting the relevant information from a highly complex acoustical environment. While earlier investigations of the hearing capabilities have been carried out mostly using psychophysical techniques, the introduction of noninvasive electrophysiological measurements to study hearing has tremendously enhanced the knowledge about the hearing process of aquatic mammals during the last couple of decades. To understand echolocation it is of particular importance to study the hearing while the animal is actually echolocating. Until now this has only been done successfully for two delphinids, the false killer whale and the bottlenose dolphin.

During 2009/10 we successfully trained a male harbor porpoise at the Fjord & Bælt, Denmark, to perform an echolocation detection task. The experimental set-up and procedure were kept as similar as possible to the delphinid studies to make results directly comparable. The porpoise was trained to position itself in a hoop 80 cm below surface while suction cup electrodes were attached to its body surface to monitor the neural activity. A visual screen at 30 cm distance from the porpoise prevented the animal from using visual cues and echolocation viewing time (5 sec at a time) was controlled by an acoustical shield (-30 dB). An aluminum cylinder was presented at 2, 4 or 8 m distance at the same depth as the hoop and the animal reported whether it detected the cylinder or not.

A total of 600 (200 trials in 10 sessions at each distance) were conducted with a hollow aluminum cylinder being present 50% of the trials in a random order obtained from a Gellermann table. The animal performed the task with a false alarm rate of 3.0%. Auditory brainstem response recordings (ABR) showed a clear response to the outgoing echolocation clicks and the returning echoes from the cylinder (see Figure 1). For the three tested distances the amplitudes of ABRs varied according to echolocation distance and energy from the cylinder echo. The animal reduced the source level and also showed a lower hearing sensitivity with decreasing echolocation distance. The results demonstrate that this harbor porpoise adjusts its hearing sensitivity to the difficulty of the task probably to reduce forward masking for shorter echolocation ranges.

The results for the harbor porpoise are in general comparable to the findings from the delphinids with smaller differences that probably result from the much lower energy levels of the echolocation clicks used by the harbor porpoise. From an ecological point of view it may be an advantage for the harbor porpoise to use lower level signals as it lives in shallow, coastal waters and needs to extract the relevant information from a larger amount of clutter noise.
Fig. 1. Auditory Brainstem Response (ABR) of a harbor porpoise (*Phocoena Phocoena*) echolocating at an aluminum cylinder at a distance of 8 m, recorded in the facilities of Fjord & Bælt, Denmark. The ABR consists of several oscillations that, resulting from neural activity at different centers in the hearing pathway is plotted in relation to sound production at time zero. The first ABR is to the echolocation click and the second, smaller ABR is to the weaker echo of the cylinder. The spacing of time between the two events correlates to an echolocation distance of 8 m.
The use and possible function of multiple song classes in a novel song system: the grasshopper sparrow (*Ammodramus savannarum*)

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Unlike many emberizids, grasshopper sparrows produce two distinct classes of song. The type I or territorial song, also known as the “buzz song,” is the principal advertisement song. Buzz songs consist of 3 or 4 introductory notes and conclude with a sustained, high-pitched “buzz,” that comprises a series of rapid frequency- and amplitude-modulated notes, followed by a final note (Fig. 1, left column). Songs exhibit little geographic variation in overall form – all are composed of the same general components or element types across a broad geographic range.

The function of the secondary or type II song class, the “warble song,” remains unclear. Warble song is less commonly produced than the buzz song. This song class is made up of a series of frequency-modulated tones, also at very high frequencies, with less stereotyped overall structure from male to male (Fig. 1, right column). Less is known about variation within and between males, as well as between populations, in the warble song. Each male grasshopper sparrow sings a single, unique buzz song, and a single, unique warble song.

Males produce buzz song immediately upon arrival on the breeding grounds in late April, and it can be heard throughout the summer until early-mid August. Every territorial male sings this song, and it is typical for males to begin a breeding cycle singing buzz song exclusively. Within a week to 10 days, if paired, males begin appending their warble song to the end of the buzz song, producing a double song (in these double songs, buzz always precedes warble, never the reverse). By the latter part of each month-long breeding cycle, assuming nests are not depredated, males often switch to singing the warble song by itself.

As an initial approach to quantifying song use and functional distinctions between the song classes, we measured song output at the population level using semiweekly transects through a large population (50 – 80 breeding pairs) at the Chester River Field Research Center, Chestertown, Maryland. Buzz song was more common initially, but warble song was heard more commonly than buzz midway through the first breeding cycle. Thereafter song use fluctuated as breeding cycles within the population became asynchronous due to nest predation, and buzz song was heard more commonly than warble song. We measured the song output of individual males directly using long-term automated song monitoring recorders (Wildlife Acoustics, SM2 terrestrial acoustic package) placed in the approximate center of a male’s territory. Because the songs of individual sparrows are unique, songs of neighboring non-target males were easily differentiated from those of the target male. Males generally followed a typical pattern through their breeding cycles, initially singing the buzz song, then appending warble to the end of this song, and finally producing warble song exclusively, at least for extended singing periods later in the breeding cycle. The timing and ubiquity with which the buzz song was produced early in each breeding cycle, especially early in the season, suggest that the buzz song is the principal class of song used in intersexual interactions during pair formation.
Fig. 1. Sound spectrograms of buzz and warble songs of two male grasshopper sparrows (color band codes RYGX and RKGX) from the Chester River Field Research Center (CRFRC) population in eastern Maryland. Songs are unique to a specific male and can be differentiated visually on spectrograms and, with practice, acoustically in the field.

In order to examine potential intrasexual functions of the two song classes we performed a song playback experiment with targeted males known to be singing either the buzz song, or double/warble song. Males singing the buzz song responded to playbacks of both buzz song and warble song exclusively with the buzz song class. Responses by males singing double or warble song to playbacks of either of the two song classes were mixed, but these males responded to both song classes with buzz song at greater levels than chance. These results suggest that the buzz song is also the principal class of song used in interactions between territorial males.

As it does not seem subserve the major functions associated with song, territory defense and mate attraction during pairing, warble song remains enigmatic. One possibility is that warble song functions in male-female social cohesion and/or reproductive synchrony after pairing. Indirect evidence for this potential function comes from the observation that warble song is never produced by males that are unpaired. Another intriguing possibility stems from the high rates of extra-pair paternity measured in this population. In a given year, up to 40% of all nestlings may be extra-pair young. It is possible, that extra-pair matings may be a consequence, at least in part, of female choice based on the warble song rather than buzz song. Future tests will examine possible associations between the timing of extra-pair mating with specific neighbors, and the song class those neighbors are singing when extra-pair mating occurs.
Our research proposes the hypothesis that heterospecific territorial songbirds, living in the same community, coordinate their songs to manifest a cooperative behaviour.

By analysing the pattern of songs of a bird community inhabiting an environment at low fragmentation level (i.e. with a low internal turnover of species and individuals), we observed that heterospecific territorial songbirds tend to sing at the same time without masking reciprocal signals (i.e. without overlapping frequencies), at least during part of the day.

We recorded the acoustic emissions of the bird community at dusk in three different days. From each recording, we sampled the eight consecutive minutes richest in songs. Time and frequency coordinates were extracted for 1084 songs, emitted by 13 species. For each sample, temporal overlap among songs was verified at a short temporal scale (3 secs) with an overlap niche analysis (Pianka index). Songs overlapping both temporally and by frequency were compared with songs overlapping only in time, using ANOVA statistical method. Collected data were tested against randomly computed association data using Monte-Carlo methods (30.000 and 5.000 simulations respectively). We found both temporal niche overlap, and a significant tendency to avoid spectral overlap when vocalizations are temporally overlapping (Fig 1).

Reciprocal influence in the timing of songs implies an interaction among performers. Temporal overlap is thought to be an aggressive signal, as it led to spectral overlap and thus signal masking. To avoid masking effect when singing at the same time, requires a complex short-time timing behaviour. Being apparently not functional, it requires an explanation in evolutionary terms.

![Spectrogram of vocalizations of a bird community recorded in Manziana wood, Central Italy. Heterospecific territorial songbirds tend to sing at the same time without masking reciprocal signals (i.e. without overlapping frequencies).](image)

We interpret the pattern of coordination among songs in this community as an expedient through which heterospecific cooperation is manifested. To sustain our hypothesis, we need to call on several mechanisms, as acoustic manifestations of birds are part of a complex net of intra and heterospecific communication:
- Heterospecific cooperation: different species aggregating in cooperative groups often need similar resources and thus act for a common purpose, with a lower rate of intra-group competition than for monospecific groups (Terborgh 1990, Goodale et al 2010);

- Communication networks and social information: from eavesdropping on interactions, an individual can draw inferences on reciprocal relations among individuals (McGregor & Dabelsteen 1996), or the presence of a suitable habitat (Danchin et al 2004);

- Dear Enemies effect (Fischer 1954): territorial species inhabiting the same environment for a sufficient period of time, often organize in neighbourhoods, whose components show no reciprocal aggressive behaviour and defend reciprocal territories;

- Functions of duets between conspecifics birds: the more a duet is coordinated, the higher is the emerging fitness and mates cohesion, and the more threatening the duet functions against intruders (Thorpe 1967, Seibt & Wickler 1977, Wickler 1980, Smith 1994). Coordinated duets require a long period of practice, which is costly in energetic terms.

On these basis, we sustain that coordinated songs among heterospecifics territorial neighbours could gain the same functions as duets between conspecifics (joint resource defence, signalling fitness, maintaining group cohesion). By attracting and/or repelling eavesdropping individuals, in the form of public information (Valone 1989), coordinated songs can influence the community structure. Indeed, composition of communities is driven more by cooperative than competitive interactions among species (Stensland et al 2003).

The same analysis performed on recordings of a community inhabiting an environment at a high fragmentation level (i.e. with a high internal turnover of species and individuals), showed a random or segregated pattern for the distribution of songs in time, confirming that coordinated choruses are achieved only in stable neighbourhoods. Cooperative Dear Enemies relationships and coordinated choruses can indeed be achieved only after a long period of negotiation and practice, respectively.

More experiments are needed to verify the proposed hypothesis, but it appears as a plausible explanation of the pattern observed, with strong theoretical basis. This study is the first exploring the acoustic structure of a bird community in a temperate region, and one of the few exploring it in the world.
Fishes display a stunning array of adaptations for acoustic communication in both mechanisms of sound production as well as mechanisms of sound reception. Fish detect sounds with otolith organs, which are directionally sensitive accelerometers. Some species that have gas filled air-bladders located in close proximity to the ear also detect acoustic pressure. Fish, such as toadfish and croakers, produce sounds by rapidly contracting muscles attached to their swimbladders (Fig. 1). Other species, such as catfishes, produce sounds by stridulating bones. These sound production mechanisms generally limit fish sounds to relatively simple pulsed or tonal sounds. While the focus of this talk is on acoustic communication, it is important to remember that there are other important modalities of communication including chemical, visual, electric, and mechanosensory. Indeed, it is likely that many forms of communication are integrated by both sender and receiver. One good example is the damselfish courtship dip where the fish integrates an exaggerated swimming motion with sound production.

Acoustic communication ranges estimated from hearing thresholds and source levels of individual fish sounds suggest that most fish communication occurs over relatively short ranges (<100 m). Some species, notably the croakers and drums, call simultaneously and thus can produce a loud chorus of sounds (Fig 2). How fish communicate within a chorus and whether they use the sound of a chorus for orientation is not known. A fish chorus recorded with a pressure-sensitive hydrophone sounds like a cacophony of overlapping, indiscriminable sounds. However, the way fish perceive a chorus could be different if they also use their otolith organs to detect acoustic particle acceleration in three dimensions. Another possible exception to short-range acoustic communication is in the deep-sea, where background noise levels are significantly lower than in coastal oceans where most studies of fish acoustic communication have occurred. We still do not have a confirmed identification of a fish sound-production in the deep ocean.

In addition to understanding acoustic communication in the context of the appropriate sense (particle motion and/or pressure), there is a great need for fundamental natural history studies of fish sound production to identify what sounds are produced by different species. There are over 30,000 species of fishes. While not all are soniferous, many do produce sound. The pioneering work of Fish and Mowbray laid the groundwork for a library of fish sounds. With the development of autonomous recorders, we are finding that we do not know the identity of most sound producers. While we are able to map the distribution and occurrence of sounds in great detail, we are unable to easily identify the sound source. New approaches, in addition to traditional captive recordings and video recordings are needed to identify the sounds produced by fishes. One tool may be embedded recording tags with hydrophones or accelerometers, which can be implanted in potentially soniferous fishes. These tags would not only help build our library of fish sounds, they would also be useful in understanding the context of acoustic communication in fishes by measuring fish movement simultaneously with sound production.
Fig. 1. Sound production by silver perch (*Bairdiella chrysoura*) and spotted seatrout (*Cynoscion nebulosus*). Silver perch produce wide-band (up to ~4,000 Hz) pulses calls. Spotted seatrout produce a grading pulsed-tonal call up to about 800 Hz.

Fig. 2. Composite spectrogram of sound production recorded every 10 minutes in Charlotte Harbor, FL showing an intense, sustained nighttime chorus beginning around 1900 hours with spotted seatrout, with silver perch joining in around 2100 hours.
The importance of referential alarm calling in rodents: Do ground squirrels differentiate between species?

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Alarm calls are vocalizations produced by many species when threatened or startled by a predator or other significant disturbance. Some species (including primates, birds and rodents) vary the alarm call to include information about the type of predator. The observations that some animals use predator-specific alarm calls and that signal perceivers respond with distinct, adaptive antipredator behaviors, have led to the hypothesis that alarm calls function to designate different classes of external danger. This type of antipredator behavior has been termed referential specificity. Although a number of species use referential communication to incorporate information about predator class (e.g., aerial vs. terrestrial), the extent to which some incorporate information about different species within a predator class is unclear. Our study aims to shed light on whether California ground squirrels (Otospermophilus beecheyi) use different alarm calls to distinguish between two predator species (human or dog) within the same predator class (viz., terrestrial mammal), thereby indicating whether rodent signals contain more information than previously thought.

Predators of California ground squirrels have been traditionally categorized as aerial (raptors), terrestrial (e.g., coyotes and bobcats), and reptilian (e.g., rattlesnakes). California ground squirrels use predator-specific alarm calls and escape responses to snakes, terrestrial mammals, and aerial predators — responses which differ significantly among ground squirrel species — indicating some degree of referential specificity.

Although species-level predator recognition has been suggested in prairie dogs, such has not been investigated in ground squirrels. We predicted if similar levels of referential specificity exist in California ground squirrels, then apparent dog-specific and human-specific alarm calls should be manifested by significantly different temporal and spectral acoustic parameters. We trapped 50 California ground squirrels at Lake Solano Park, Winters, California during the summer of 2010. Upon capture, each squirrel was approached by both a dog and a human in random order. Audio and video recordings were made of the squirrels’ responses, and the squirrels were released after individuals were tagged for later identification. We performed preliminary acoustic analysis on a subset of these recordings, the results of which will be discussed. If the acoustic structure of alarm calls given to these two predators is different, this will indicate that California ground squirrels recognize them as two distinct predator species within one predator class (terrestrial mammal). Finding this distinction is important because differences in danger that predators pose to prey has been hypothesized to underlie the evolution of distinct forms of antipredator behavior, including the structure of the vocalizations used to escape these predators. These data provide further insight and understanding of how predator behavior shapes prey acoustic behavior.
Fig. 1. Spectrogram of California Ground Squirrel (*Otospermophilus beecheyi*) dog-specific alarm calls recorded in Winters, California.
This object of this work was to create a microphone specifically designed for use in the recording of overflying passerines. Of particular interest were several species of thrush of the family Turdidae. The microphones in question had to be able to withstand a variety of weather conditions ranging from rain and snow to extreme dry air, and a variety of temperatures from -20-40 °C. The specification for the microphones also included that they be able to capture approximately 60° of the sky in a conical field of view while excluding ground noise from insects and amphibians. Finally, the other requirement was that each unit be built out of <$200 worth of components.

Fig. 1. Prototype "barrel" microphones developed for the above application
Several different prototypes were conceived and built. All of these were tested systematically, first in an anechoic chamber, where their polar and frequency responses were characterized, and later in actual outdoor testing. The outdoor testing involved putting a signal source in the air above the microphones by ~80 m, about the lowest height that passerines of interest would be flying. The resultant data was recorded and analyzed, with the eventual winning prototype coming out with a 3 dB better SNR than any others.
A method for detecting chirps, whistles, moans, and other tonal sounds

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Automatic detection of animal vocalizations is used for analyzing sound signals in real time during surveys (e.g., Leaper et al. 2000, Clark et al. 2010), for analyzing large recorded data sets (e.g., Mellinger et al. 2004), for real-time warning systems to mitigate the impact of human activities on wildlife (e.g., Clark et al. 2007), estimating population or population density (e.g., Küsel et al. 2011), and other purposes. A common vocalization type is a frequency contour—a sound comprising one or more tonal harmonic components that are not impulsive but instead last over some duration. Such sounds include whistles of dolphins and other odontocete cetaceans, chirps of birds, moans of baleen whales, squeaks of rodents, and many other animal and non-animal sounds.

Here we present an algorithm for detecting such sounds. The algorithm operates using a spectrogram normalized and flattened (whitened) to remove long-duration background noise. In each time slice (each equalized spectrum) in the spectrogram, and within the user-specified frequency bounds, the algorithm finds any local peaks in the spectrum—that is, any values sufficiently far above the median spectrum value, and also larger than any other peaks within the frequency bounds. Actually it does not necessarily use the median; a user-specified parameter controls which percentile is used. Each such peak it finds becomes a candidate frequency contour, and multiple candidates (multiple hypotheses) are assessed. In successive time slices in the spectrogram, the algorithm attempts to find a spectral peak that is the continuation of each current contour. Initially it examines the frequency of the peak in the previous time slice. But as soon as two or more spectral peaks are present in successive time slices, it calculates a best-fit line, or later a quadratic curve, through them and then uses that line or curve to estimate the frequency of the next peak—the target frequency for this frequency contour. The peak must be within a certain distance (in frequency) of the target frequency. This allows independent crossing contours to be tracked successfully (Fig. 1).

Candidate contours must persist for a certain minimum amount of time to be registered as detected contours. This prevents the numerous small blips of noise typically seen in spectrograms from being registered as thousands of very short frequency contours. Candidate contours must also be a certain distance apart in frequency from existing contours to be valid independent contours. This practice is enforced because a sound can have secondary components associated with it that are no more than small bits of noise in the spectrogram on the side of the main sound.

This procedure uses nine parameters, including the ones needed for spectrogram calculation and normalization. Finding optimal values for all of these parameters simultaneously requires a search of
parameter space, and a grid search technique is described. The frequency contour detection method and parameter optimization technique are applied to the problem of detecting “boing” sounds of minke whales (*Balaenoptera acutorostrata*) offshore Kauai, Hawaii. The test data set contained many humpback whale (*Megaptera novaeangliae*) sounds in the frequency range of interest. Detection performance is quantified, and the method is found to work well at detecting boings, with a false-detection rate of 3% for the target missed-call rate of 25%.

![Frequency contour detection method](image)

Fig. 1. An example showing the algorithm tracking two crossing frequency contours.

Examples are also shown for a number of other marine mammal sounds, including whistles of dolphins and killer whales and songs of humpback and bowhead whales, as well as whistled songs from a variety of bird species. The algorithm works on non-animal tonal sounds as well, including machinery noise. The algorithm has been implemented in the software package *Ishmael* (Mellinger 2001) to make it available in a user-friendly form.

**References**


Humans have pondered the sounds of whales for hundreds of years, but scientists had little to say about the sounds of large whales until about forty years ago when two papers describing recordings of vocalizing humpback whales revealed that humpbacks were producing predictably structured sound sequences, comparable in certain respects to birdsongs (Payne & McVay, 1971; Winn, Perkins, & Poulter, 1970). Since that time, numerous researchers have analyzed these sequences, and leading to the following conclusions: (1) the sounds that humpbacks produce are sufficiently intense that they can be heard several kilometers away; (2) individual sounds are produced in predictable patterns (called phrases) that whales often successively repeat; (3) when whales switch from repeating one pattern to repeating a different one, the sequence is highly predictable (i.e., sets of repeated patterns – themes – are produced in a stereotypical sequence); (4) the sequenced patterns that whales produce change progressively within and across years; (5) whales in a particular geographical region produce the same sequence of patterns, whereas whales in other regions produce a different sequence; (6) sounds are produced at a regular tempo; (7) sound production within groups of whales is not coordinated across individuals; and (8) sound sequences are communicative displays (songs) that provide information to other whales about the location and fitness of a vocalizing male.

Most of the observations and interpretations listed above are contingent on the methods that researchers traditionally have used to analyze recordings of whales. Briefly, past analyses have involved measuring acoustic features of individual recorded sounds, categorizing individual sounds into various types, and analyzing patterns within sequences of classified sounds. This approach is systematic and utilizes standard bioacoustic techniques that have proven useful in many studies of animal vocalizations. Nevertheless, several assumptions underlie this approach that are not empirically based, raising questions about its usefulness for understanding the nature of humpback whale songs. For example, this labeling approach assumes that the acoustic features most salient to human listeners or to researchers visually inspecting time-frequency representations are the most useful/relevant features for characterizing variations in produced sounds. It also assumes that perceptual categorization of sounds into different types by human observers based on aural, visual, or measured features provide an appropriate taxonomy of recorded sounds. Similarly, patterns within sound sequences that are most easily detected either aurally or visually by humans provide the standard for identifying what counts as a repeated pattern. By using human perceptual biases as the standard, past analyses of sound sequences produced by humpback whales potentially discount or ignore features of sound sequences that may be important for understanding their structure. The dangers of such assumptions are illustrated by the historically recent discovery of echolocation in bats. Scientists studying bats initially argued that vocalizations were irrelevant to aerial navigation by bats based in part on subjective observations that flying bats were not producing sounds.

Recent analyses suggest that the “songs” produced by humpback whales contain acoustic and sequential structures that are quite different from those presumed to be important in past analyses (Branstetter & Mercado, 2006; Green et al., 2011; Mercado et al., 2008; 2010). These newer analyses suggest that, contrary to past reports: (1) the sounds that humpbacks produce vary substantially in the
distances that they travel; (2) patterns of sounds often occur independently of the salient acoustic features of the sounds within those patterns; (3) transitions between sets of repeated patterns do not always involve switches between discrete themes, and may not involve any switch in content, despite differences in the acoustic properties of constituent sounds; (4) whales produce several patterns consistently across years and populations; (5) whales in a particular geographical region produce widely varying sequences, some components of which are quite similar to those produced in remote populations; and (6) sounds considered to be different types in past studies represent points along a continuum rather than acoustically discrete units, raising questions about the validity of patterns defined by sorting sounds into these types.

These new findings were revealed through microscopic and macroscopic analyses of recordings that took into account how humpback whales produce, transmit, and receive sound sequences. Such analyses can reveal acoustic structure that is unlikely to be discovered through subjective, “anthroposcopic” analysis techniques. For instance, biomimetic reception-based analyses highlight spectrotemporal components of sounds that are likely to register in a whale’s cochlea, while minimizing other acoustic details that are less likely to be resolved (Branstetter et al., 2007). Similarly, production-based analyses can provide clues about the acoustic features that whales are able to modulate through vocal control versus those that are at the mercy of propagation-related distortion (Mercado et al., 2010). Analyses that take into account the likely temporal windows within which whales can integrate and compare variations in sound properties provide an alternative way to assess the role of repetition and rhythm in the structure of whale songs. Techniques that dispense with categorical labeling of individual sounds and selective processing of idiosyncratic structural features reveal continuity within and across songs that has effectively been hidden in all past analyses of songs.

Overall, these recent findings suggest that current approaches to analyzing humpback whale songs (and the conclusions derived from those analyses) should be reevaluated. The issue is not whether the resolution and reliability of existing measurement tools are adequate, but whether these tools are actually measuring functionally relevant properties of humpback whale sound sequences. Many researchers currently studying humpback whale songs implicitly or explicitly assume that repeating sound patterns (or cycles of patterns) are the communicative/informative elements of songs. Consequently, several recent studies have focused on refining measurements of these elements (e.g., automating sound and pattern recognition algorithms and quantifying the information content of repeated patterns in terms of entropy measures). If subjectively identifiable patterns within songs are epiphenomenal, or if currently identified patterns do not correspond to the information bearing patterns that whales are generating, then all inferences drawn from such analyses are questionable. Now that scientists are fully aware that humpback whales are producing structured sound sequences, it is important that this awareness not be misconstrued as understanding, and that multiple avenues for identifying the nature and content of that structure be explored. If researchers can discover structured vocal behavior beneath the ocean surface, where they did not previously suspect it, then they should not be surprised by (or resistant to) the idea that the structure that they have discovered may not adequately reflect the structure that is actually present, and that there may yet be secrets lying just below the surface.

The ribbon seal is an aquatic-mating species endemic to the North Pacific. These animals rely heavily on ice for breeding and molting during the winter and spring. Compared to some other aquatic-mating pinnipeds in polar regions, relatively little is known about the mating system, foraging, or vocal behavior of ribbon seals (Van Parjis, 2003; Van Opzeeland et al., 2010). This is most likely due to their pelagic and ice-edge associated existence which makes direct observation by capture or tagging difficult, unsafe, and logistically challenging. Passive acoustic monitoring offers a non-invasive alternative to direct observation of animal presence and behavior when traditional observation methods are not possible.

The seasonal presence of ribbon seals on the central and southeastern Bering Sea shelf was determined from vocalizations recorded with a Passive Aquatic Listening (PAL) recorder at two sites along the 70m isobath from 2007-2010. Ribbon seal vocalizations were identified as intense downsweeps, roars, and grunts. Acoustic detection was seasonal with peak acoustic activity occurring in April at the southeastern site and May at the central shelf location. Ribbon seal acoustic presence was tightly coupled to sea ice presence, and onset of detection was associated with thicker, more extensive ice cover compared to the other Arctic pinnipeds (bearded seals and walrus) detected in the region. Ribbon seal vocalizations were detected only when ice cover in the area exceeded 80%, indicating that this species has a habitat preference or requirement for a more stable ice platform for some activities during the winter breeding season.
Fig. 1. Spectrograms of ribbon seal A) downsweep, B) grunt, and C) roar. Spectrograms were made from 100 kHz recordings downsampled to 44.1 kHz. (1024 point FFT, 50% overlap).

References
Small Ears and Hearing Aid Microphones

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The development of novel directional microphones for hearing aids is described. The mechanisms underlying the design of these unusual microphones were inspired by our earlier study of the ears of the parasitoid fly *Ormia ochracea*. The structure of *Ormia*’s ears inspired new approaches to the design of directional microphones that are more sensitive and have lower thermal noise than existing miniature microphones. The microphones have been fabricated out of silicon employing either capacitive sensing or optical sensing to convert the diaphragm motion into an electronic signal. Measured results indicate that the directivity of these microphones is very similar to that of an ideal first-order differential microphone. The low noise floor of these microphones has been achieved by minimizing sources of viscous damping. Since light damping adversely affects the response of microphones, an electronic damping scheme has been incorporated that does not adversely affect the microphone’s noise floor.
Echolocating bats foraging in groups, whether they are cooperating or competing for food, must coordinate their acoustic behaviors. As bats fly in close spatial proximity, they face the challenge of sorting their own signals and echo returns from those of nearby conspecifics [1, 2, 3]. They must also rely on dynamic echo information to adapt flight trajectories with conspecifics to avoid collision and track prey [4]. Furthermore, individual bats may acquire information about food sources from the echolocation behavior of nearby conspecifics [5]. This talk will summarize research findings from laboratory studies that reveal how echolocation signals produced by individual big brown bats, *Eptesicus fuscus*, can directly influence the behavior of nearby conspecifics.

A series of experiments were conducted in which pairs of free-flying bats were given access to a single food source, a tethered mealworm, positioned randomly in a large, carpeted flight room (6 x 7 x 2.5 m). Acoustic foam lined the walls and ceiling of the room, and low level, long wavelength lighting (> 650 nm) permitted IR video recording with 2 high speed (250 frames/second) video cameras (Photron), which were used to reconstruct 3D bat flight paths. A linear microphone array was used to reconstruct the bat’s sonar beam pattern, and ultrasound microphones on the floor recorded full bandwidth sonar calls. Video and sound recordings were synchronized with a common trigger. The video position data and arrival time of calls at the floor microphones permitted accurate assignment of calls to each vocalizing bat.

Studies of adaptive sonar and flight behaviors were conducted with seven different pairs of adult bats, both experienced in taking tethered mealworms. A single prey item was presented, and the animals’ flight and vocal behavior were recorded and analyzed off line. Paired bats engaged most frequently in following flight behavior [4]. The trailing bat was often the one that succeeded in taking the prey. In these experiments, bats made adjustments in call frequency structure and directional aim in response to the presence of another bat. The magnitude of these adjustments depended on the baseline similarity of calls produced by individuals in a pair, and the spatial separation of the bats throughout a trial [3]. In this competitive prey capture situation, silent behavior (no vocalizations over a period of at least 200 msec) was observed an average of 40% of analyzed trial time when bats flew less than one meter apart. The prevalence of silent behavior also depended on baseline similarity of individual bats in a pair, with the most silent behavior occurring in pairs with similar call design [1, 2].

Studies of social learning of a novel foraging task were conducted with individual bats, paired either with an adult bat that was experienced in taking tethered mealworms (experimental group) or naïve to the task (control group). Both juvenile and adult bats were assigned to experimental and control treatment groups. Only individual bats exposed to the experienced adult learned the novel foraging task. Following flight behavior was observed more often in bats prior to learning the task [5].

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Figure 1. Overhead schematic view of behavioral test room, with microphone array along the walls. A segment of the flight paths of two bats is shown, along with the sonar beam pattern of a single sound. The sticks placed along the flight paths illustrate the directional aim of the beam axes of each call produced by the individual bats. Note that one bat points the beam axis sequentially at the prey and its conspecific (right panel). Bats generally point their sonar beam axes away from each other when their flight paths converged.

Figure 2. Overhead display of following flight paths of two bats competing for a single prey item. Each circle along the flight path denotes the bat’s position when it vocalized. An absence of circles denotes silent behavior (see bat flight path adjacent to red arrow). Pulse interval (PI), duration and start/end frequencies of the two bats’ FM calls are plotted separately in red and blue.
Comparative Ambient Noise Levels Across the Coastal Western North Atlantic Ocean: Implications for Changes in Cetacean Acoustic Ecology and Communication Space

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Noise throughout the world’s oceans has increased due to growing anthropogenic activities. Changes in physical characteristics among ocean environments, and varying degrees of anthropogenic input have resulted in varying levels of ambient noise and sound propagation at different locations. As a result, cetaceans migrating over large areas are now exposed to a myriad of altered acoustic environments, within which they must navigate, feed and reproduce. With these increases in anthropogenic noise, the resultant masking of communication and naturally occurring sounds may stress cetaceans already facing other forms of habitat degradation. Additionally, there is concern over the potential for changes in hearing threshold resulting from high amplitude sound exposure. A great deal of inquiry has focused on acute instances of high amplitude noise, as it has been demonstrated to temporarily displace several cetacean species from their preferred areas or disrupt their behavior. However, the possible adverse effects of chronic exposure to increased ambient noise over ecologically relevant spatial and temporal scales remains poorly understood. Such exposure may not induce an immediately noticeable behavioral response, but rather cause a low key chronic obstacle to behaviors that rely on effective communication. To identify trends of this nature, analysis must occur over spatial and temporal scales large enough and long enough to be significant to an entire population.

As a critical first step to understanding the acoustics of key marine ecosystems, we examined long-term acoustic data from ten sites along the Western North Atlantic coast that are either known critical habitats or located along migratory corridors of the highly endangered North Atlantic right whale (NARW; Eubalaena glacialis) and several other cetacean species. The data was gathered using arrays of hydrophones positioned at depth to capture communication sounds and background noise occurring in specific areas. NARWs were acoustically detected at all of the sites examined, while fin whales (Balaenoptera physalus), sei whales (Balaenoptera borealis), minke whales (Balaenoptera acutorostrata), blue whales (Balaenoptera musculus) and humpback whales (Megaptera novaeangliae) were detected at several of the sites. High-amplitude noise occurred at both major and non-major shipping ports located in or near the areas of study. The majority of this noise occupied low frequency bandwidths, including the 50-350 Hz communication range utilized by vocalizing baleen whales.

While chronic, pervasive noise did not occur at consistent levels in all areas, the spatio-temporal variability of anthropogenic noise can be viewed as a form of habitat fragmentation, where inundations of noise mask key sounds, resulting in a loss of “acoustic space” (the frequency bandwidth over time relative to that of the whale’s vocalizations), which could otherwise be occupied by vocalizations and other acoustic cues utilized by cetaceans. This loss of acoustic space could potentially degrading habitat suitability by reducing the geographic distance across which individuals acoustically communicate, and ultimately disrupt aspects of their behavior and ecology. Because communication plays a vital role in the life history of cetacean species, understanding temporal and geographical differences in ambient noise as part of cetacean ecology and habitat may elucidate future conservation strategies.
Building on Darwin’s Legacy: Environmental Influences on the Evolution of Communication Systems

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Many species of animals, including man, face the formidable task of communicating in naturally noisy environments. From his travels in South America, Darwin was acutely aware of the musical quality of frog vocalizations, as well as their importance in communication in naturally noisy environments.

In this talk, I shall review the evidence for the remarkable ability of amphibians to shift their call timing in response to both high-level interfering tones or to small intensity shifts in the background noise. We have explored communication behavior in a wide variety of taxa that in many cases appears to have evolved specifically to tailor and sculpt intraspecific communication signals to their environment. To illustrate, I shall discuss two distantly related organisms: the concave-eared torrent frog (*Odorrana tormota*), calling near fast-flowing mountain streams of Anhui Province, Central China, and the endemic Bornean frog, *Huia cavitympanum*, living in a very similar riverine habitat in Sarawak, Malaysia. In addition to the high-pitched audible components, both of these species’ calls contain previously unreported ultrasonic harmonics. Until recently, amphibians were believed to be able to detect sound frequencies no higher than 5-8 kHz, possibly because the link between the tympanic membrane and the oval window consists of a single ossicle with cartilagenous extensions that should absorb high frequencies. Our studies of these two Asian frogs revealed that they communicate acoustically using ultrasound and that their remarkable auditory systems are sensitive up to 34-38 kHz. This extraordinary frequency shift into the ultrasonic range of both the harmonic content of the advertisement calls and the frogs’ hearing sensitivity are likely to have coevolved as an adaptation that prevents signals from being completely masked by the intense broadband background noise from local streams.

The study of hearing in Asian frogs is not only demanding a reevaluation of the spectral limits of non-mammalian middle ears, but it also has revealed a novel mechanism of behavioral middle ear tuning in vertebrates. These two case studies provide strong evidence that a coordinated approach to the physiological mechanisms underlying natural behavior can be a fruitful avenue for elucidating the selective forces acting on the evolution of animal communication systems.

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Female and Male Mice Vocalize in Response to Auditory Playbacks of Mouse Ultrasonic Vocalizations

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Previous studies have found that both male and female mice produce ultrasonic vocalizations (USVs) under a variety of circumstances, yet the function of these USVs remains unclear. A male mouse will readily produce USVs when in the presence of a female mouse or when placed in female-soiled cage shavings (Sales, 1972b; Whitney & Nyby, 1979). Female mice in diestrus are also known to vocalize to other females (Sales, 1972b). These studies suggest that these USVs may be important for social and sexual acoustic communication. It is not known, however, if either male or female mice emit ultrasonic vocalizations in response to auditory playbacks alone, as is found in many other animals.

In the present study, solitary caged male and female CBA/CaJ mice were placed into a sound-deadened chamber approximately three hours after lights off. The mice were kept in their own cage and bedding to avoid introducing any novel olfactory stimuli. The estrous cycle for each female was determined visually using three distinct estrous markers (Chaplin et al., 1973). Two experimenters checked each vagina daily for discoloration, swelling, and discharge, indicative of estrus. Each female was tested twice, once while in estrus and once while in diestrus. To keep the number of playback sessions constant for all of the animals, the males were tested in two, three-minute sessions. Previously recorded USVs from male and female conspecifics were played back to the mice through an ultrasonic speaker on a continuous loop, separated by several seconds of silence. The stimulus recordings used for the playbacks were taken from males and from females in estrus and diestrus. These recordings were edited so that each contained the same number of calls (12 per three-second interval). A microphone was placed over the mouse’s cage and recorded any vocalizations emitted by the subjects in response to these playbacks.

Results for the playback recordings are shown in Figure 1. Females called significantly more to the playback calls than males ($p < .01$). Also, females in diestrus, but not females in estrus, called significantly more than males recorded the first or second time ($p < .01$). These results suggest that females vocalize more in response to auditory stimuli than males do, and that it is important to examine the function of female vocalizations in the future.

Additionally, when we compare responses across call type (Figure 1, bottom), we see that females called significantly more than the males in response to the “female estrus to female estrus” call (Fisher LSD, $p < .05$). No other comparisons were significant across call types. We also see a large amount of variability in calling rates between males and females. Some animals called a lot and some animals called very little.

In summary, both males and females called to these mouse recordings without any additional visual or olfactory cues, demonstrating that USVs can be elicited solely by auditory cues. These results suggest that USVs are important in mouse interactions, possibly even facilitating reproductive and social behavior. Further research is being conducted to analyze the calls that were emitted to see if the parameters vary systematically between females and males across call types.
Mean number of USVs across conditions

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Fig. 1. Mean numbers of USVs produced by estrous females, diestrous females, and males recorded twice across all call types, along with mean total numbers of calls from the females and males (top). Mean responses by these four groups to the different call stimuli (bottom). Error bars in each graph represent between subjects standard errors.

References


Vocalizations of Risso’s Dolphins, *Grampus griseus*, in Relation to Behavioural Context in the Canary Islands.

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The classification of animal sounds is the first step to understanding an animal’s communication system. While many different parameters can be chosen for classification, it is important to select the ones that lead to a biologically meaningful classification that reflects how the animal itself would categorize sounds. One way of testing the biological validity of sound categories is to investigate whether categories are context specific. Sometimes, the behavioural data necessary for such a test are difficult to obtain, specially in deep diving cetacean species. Therefore, descriptions of the vocal repertoire and its context are not as common as should be expected for such a highly vocal taxon.

Here, we describe vocalizations of a poorly known cetacean: Risso’s dolphin, off the island of Gran Canaria, Canary Islands (Spain), and investigate how they relate to behavioural context. Risso’s dolphins were recorded on 30 occasions from 2008 to 2011 with 45 hours of sound recordings analyzed. Sound recordings were obtained with a square 4-hydrophone array used during focal group follows.

Three main types of sounds were found: click trains, whistles and isolated high frequency burst-pulses. The number of each type of vocalization was modeled against water depth, behaviour group patterns (socializing, foraging, resting and traveling), and group size.

We found that individual Risso’s dolphins produced most whistles per minute while socializing, followed by foraging, then resting and at last travelling. However, whistle production in this species was very low which suggests that other types of sounds must also have a communicative function. The most likely candidate for this appeared to be the burst-pulse sound. Risso’s dolphins produced more isolated burst pulses during socializing and foraging than during any other behaviour pattern. Individual production of click trains was highest during foraging, followed by socializing, then travelling and at last resting. This was to be expected, as click trains are important to detect and capture food. Finally, group size only affected the production of isolated burst pulses. Individuals in smaller groups produced less isolated burst pulses per minute. This also suggests a primary role in communication. The production of all three types of vocalization by individual decreased in shallow water, where animals spent more time traveling and resting leading to a general decrease in vocal production.

Our study was the first to investigate the relationship between behavior and vocalizations in Risso’s dolphins. Unlike many other whistling delphinids, Risso’s dolphins have minimized the use of whistles and use burst-pulses more widely to communicate. Like killer whales, they form an intermediate strategy between animals that use whistles a lot (such as bottlenose dolphins) and those that do not whistle at all. Further studies should investigate the role of whistles in such species and try to identify the possible reasons for this strategy.
Increase in Peak Fin Whale Calling Levels Observed in the Mid-Atlantic Ocean

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Recent research has confirmed that low-frequency (< 1 kHz) human sources of noise pollution have increased dramatically over the last 50 years. Of growing concern is the effect these increasing levels of low-frequency noise have on protected species, such as baleen whales, that use low-frequency sound for communication, orientation and navigation, or prey-finding (Richardson et al. 1995; Clark et al. 2009). Right whales have been observed to increase the frequency of their calls in noisy areas (Parks et al. 2007), blue whales increased their rate of calling in response to airgun sounds (Di Iorio and Clark 2009), killer whales increase the amplitude of their vocalizations in response to increased levels of background noise (Holt et al. 2008), and fin whales changed multiple call characteristics in high noise conditions (Castellote et al. 2008). Such changes in calling behavior have the potential to significantly affect these acoustically active species.

In a previous study of a multi-year acoustic data set collected from mid-Atlantic, we observed high levels of anthropogenic noise, especially from the sounds associated with seismic airgun surveys, despite the remote location of the experiment. We also recorded the low-frequency sounds of baleen whales, including the fin whale (Balaenoptera physalus) “20 Hz pulse”. One striking observation was that when data were available for multiple years, the peak levels of our calculated fin index, a relative measure of fin whale calling levels, often increased over time (Figure 1), a trend opposite that observed by Charif and Clark (2009) to the northeast of our study.

![Figure 1](image_url)

Fig. 1. Histogram of percent days per month with airgun sounds (black bars) and fin whale index levels (circles) recorded on an autonomous hydrophone moored at 32° N, 35° W. The fin whale index was calculated from long-term spectrogram data and is used here as a relative estimate of fin whale calling.
The purpose of this study was to further investigate this observed increase in peak levels of fin whale calling activity. Numerous explanations are possible for these observed changes; some of these explanations are potentially linked to increased ambient noise levels. Like other vocal animals, fin whales can compensate for increased ambient noise levels and avoid masking by vocalizing more often, changing the timing or frequency of vocalizations, or increasing the source level of the sounds they produce. All of these changes could affect the fin index. We examined data from the hydrophone at 32° N 35° W, a location for which data were available over a ten-year period. Analysis of both discrete fin whale calls and aggregated sounds of distant fin whales are described and are examined in relation to noise levels recorded throughout the study.

References:


The minke whale (Balaenoptera acutorostrata) is a small, elusive baleen whale that is rarely sighted in tropical waters of the North Pacific Ocean. Because of this, almost nothing is known about their spatial distribution and habitat preferences. During winter and spring, minke whales produce complex sounds called ‘boings’ in sub-tropical waters around the Hawaiian, Northern Mariana and other Pacific Islands (Fig. 1). The objectives of this study include characterizing the acoustic behavior and ecology of vocalizing minke whales in these areas. We will present our findings on the differences among boing characteristics in three large-scale geographic regions in the sub-tropical North Pacific. We will also present preliminary data on distribution trends and habitat preferences of minke whales around the Hawaiian and Mariana Islands. Finally, we will discuss these results in relation to population structure, the possible function of calls, and the spatial patterns of calling minke whales in these areas. These findings will provide insights into the biology, behavior and ecology of this visually elusive species in the sub-tropical waters of the North Pacific.

We conducted passive acoustic monitoring of minke whales at four sites between 2006 and 2010:

1) The Northern Mariana Islands in the Western North Pacific.
2) The Pacific Missile Range Facility (PMRF) off the island of Kauai, Hawaii.
3) Ladd Seamount, off Midway Island, in the Northwestern Hawaiian Island chain, and;
4) Wake Island, located in between the Hawaiian Islands and the Mariana Islands.

Acoustic data were collected using towed hydrophone arrays deployed during opportunistic and line transect surveys of study sites 1 & 2, a cabled seafloor hydrophone array at study site 2, and autonomous High-frequency Acoustic Recording Packages (HARPs) deployed in deep water on the seafloor at sites 3 & 4.

Minke whale ‘boings’ recorded at all four study sites are being analyzed to investigate whether specific features in the calls can be used to identify the geographic location of animals. Our previous work indicated that boings from Kauai and the Northern Mariana Islands could be categorized to their respective locations using Classification and Regression Tree (CART) analysis. We will expand on this analysis by comparing boings from all four areas sampled using Random Forest analysis. This analysis involves a collection of decision trees that are grown using binary partitioning of the data based on the value of one variable at each branch, or node. To extract acoustic features from boings, we measured 15 acoustic variables (e.g. upper/lower frequency, median frequency, pulse repetition rate) using OSPREY, a Matlab-based signal analysis program. Results of these analyses will indicate how accurately boings can be classified to their respective geographic study site and identify which variables (i.e. features) are important to the classification process. These findings might then be used to better define stock structure using remotely collected acoustic data.
A preliminary spatial analysis was conducted on locations of calling minke whales determined using acoustic line-transect data collected in 2007 from a large 170,000 nm² (585,800 km²) area of the Mariana Island study site. This analysis indicates a dispersed (uniform) distribution within the region. However, animals appear to show an affinity for deep waters with a clustered bi-modal distribution at two distinct depth ranges. Minke whale distribution in this area will be discussed in relation to geographic variables. These data will be compared to data collected at the Kauai study site in 2010. Implications of differences and similarities in relation to habitat preferences will be discussed.

The acoustic behaviors of minke whales are poorly understood. We will provide examples of counter-calling recorded using towed and fixed hydrophones at the Kauai study site. In addition, we will present examples of possible acoustic behavioral responses to vessel noise by animals that were passively tracked using the seafloor hydrophone array. The effects of noise from the research vessel on call rates were quantitatively examined by comparing call rates during consecutive 10 min periods with low and high noise conditions using paired t-tests. Preliminary results indicate a complex response to vessel noise. These results will be discussed in relation to implications for vessel-based line-transect surveys, mitigation, and monitoring of this vocally active but elusive species.

The results of these analyses are providing a better understanding of the acoustic ecology and behavior of minke whales in areas of the North Pacific, which are presumed to be low-latitude breeding areas. We hope that our results will provide important and useful information that can be used by resource managers and policy makers to improve the conservation and management of this poorly understood but common species of baleen whale.

Fig. 1. Spectrogram of North Pacific minke whale (*Balaenoptera acutorostrata*) ‘boing’ vocalization. The complex nature of amplitude modulation is apparent from the banding pattern which is directly related to the pulse repetition rate (i.e. the distance between each band is approximately 115 Hz).
Variation in the Signaling between Mares and Foals (*Equus caballus*); Implications for the Function of Communication for Mother and Offspring

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Despite extensive research, debate still exists over the function of the juvenile stage in mammals. Namely, do the behaviors exhibited by young mammals serve as “practice”, not conferring benefits until adulthood, or do they serve a more immediate purpose, enabling individuals to survive an inherently dangerous period? To address these questions, researchers have traditionally focused on the play behavior expressed by juveniles. In most species, however, the mother’s behavior is integral to the survival of the offspring. Therefore, a complete investigation of the juvenile stage’s function must take maternal behavior into account. Mother-infant communication reveals important measures of both cooperation and conflict; as such, it offers an excellent proxy with which to investigate this question.

We studied 37 mares and their multiple foals, totaling 87 wild horses living on Shackleford Banks, North Carolina, USA, to determine patterns of mare-foal communication. Subjects were followed for 30-plus months, totaling more than 3,000 hours of observation. Mares and foals (aged 0-6 weeks) differed in their communicative strategy.

Mares were more likely to initiate communication when in closer proximity to their foals (*P* < 0.0001) using snorts, while foals were more likely to do so at greater distances, using whinnies (*P* < 0.0001, see Fig. 1). Mares and foals also differed in the degree to which they alter signaling according to habitat type. Mares do not alter their choice of signal according to habitat (*P* = 0.53). Foals, however, vary their choice of signal, whinnying more often in habitats where the distance to their mothers tends to be greater (*P* = 0.01). The outcomes of mare versus foal-initiated communication bouts also varied, with mare-initiated bouts more often leading to no change in the animals’ activities or proximity and foal-initiated bouts more often leading to suckling or to changes in mare-foal proximity (*P* = 0.01).

These results indicate differences in the reasons why mares and foals initiate communication and that the function of communication differs for mother and offspring. In addition, the results reveal a flexibility in both maternal and offspring behavior consistent with a juvenile stage that offers more immediate benefits to young mammals.
Fig. 1. Signaling differences with increasing distance between mare and foal (*Equus caballus*).
Ancestral state reconstruction and life history traits associated with duetting in the New World blackbirds

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A diverse array of animals produce coordinated vocal duets between mates. On closer inspection, however, these taxa represent only a subset of the species in which both males and females vocalize. This leads to the intriguing question: why do only a select number of species produce these complex, coordinated acoustic displays? Interest in duets has led to a lot of research on the function of duets, particularly in birds, but few studies have investigated the evolutionary patterns or potential life history correlates of these elaborate vocal displays. Our goal was to use ancestral state reconstruction to evaluate the prevalence and patterns of duetting in a family of birds, the New World blackbirds. We also compared patterns of occurrence of duets to the occurrence of female song, and several other life history traits, to explore potential causes for duetting in the New World blackbirds.

We used life-history accounts for the New World blackbirds in Jaramillo and Burke (1999) to score duets as present or absent. We also scored the presence or absence of female song and four other life-history traits: tropical breeding, sexual monochromatism, social monogamy, and solitary nesting. We overlaid occurrence of duets, female song, and these life-history traits on a well-supported molecular phylogeny of 65 icteridae by Lanyon and Barker (2007). We reconstructed duetting using both unordered parsimony and a Markov k-state one parameter maximum-likelihood model. We then used Pagel’s discrete correlations to compare parsimony trees of duets to the four life-history traits. These methods emulate protocol of ancestral state reconstruction of female song by Price et al. (2009).

Both parsimony and maximum-likelihood reconstructions revealed several independent gains of duetting in a small number of lineages. Duetting occurred in only 11 of the 25 New World blackbird species known to have frequent female song (Fig.1). Duets were loosely correlated with tropical breeding, sexual monochromatism, and social monogamy. Patterns of solitary nesting behavior most closely matched patterns of duetting we observed in the New World blackbirds.

Our results indicate that duetting is linked to general life history traits typical of tropical species (i.e. monogamy and elaborate male and female coloration), but our results alone do not explain why only a subset of these tropical species duet. In the future, we plan to address whether other finer-scale life history traits better explain the evolution of duets. The troupials (Icterus icterus, I. croconotus, and I. jamacaii) and their sister taxa (spot-breasted and yellow-tailed orioles, I. pectoralis and I. mesomelas, respectively) represent a small clade of blackbirds with diverse duetting behavior. In a comparative field study of these closely related species, we hope to assess whether precise behavioral and life-history differences, such as territory size, territoriality, and pair cohesiveness better explain the existence of coordinated duetting behavior in New World blackbirds.
Fig. 1. Parsimony ancestral state reconstruction of female song (A) versus duets (B) reveals that duets are much less common than female song and are the result of several independent gains of combined male and female song.

References


Integrative Biology of Acoustic Communication in Neotropical Singing Mice (*Scotinomys*)

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Neotropical singing mice (*Scotinomys*) are diurnal, insectivorous rodents distributed throughout the mountains of Central America. Alston’s singing mouse (*S. teguina*; 9-12 g) is a widespread species inhabiting mid- to high-altitude cloud forest, forest edge, and abandoned pastures from southeastern México to western Panamá (1000-2900 m), whereas the Chiriquí singing mouse (*S. xerampelinus*; 13-15 g) is restricted to the highest forested summits and páramo of Costa Rica and Panamá (2200-3300 m).

Males of both species commonly sing species-specific trills that are modulated by androgens and used in mate attraction and male-male aggression (Fig. 1). Vocalizations of *S. teguina* are long (4-7 s), decelerating trills of moderate power (54 dB SPL at 1 m) and high dominant frequencies (22-26 kHz), whereas *S. xerampelinus* trills are shorter (1-2 s), louder (63 dB SPL at 1 m), and lower in frequency (16-20 kHz; Fig. 2). We have been investigating the biology of vocal communication in *Scotinomys* for the past 5 years, including vocal ontogeny, the influence of androgens on song, individual variation and female preference, geographic variation, interspecific communication, the neurobiology of song perception, and sound transmission. In our poster, we feature findings from each project. Highlights include the importance of genetic drift in shaping population differentiation in song, the role androgens in modulating the performance of physically challenging displays, and how interspecific communication reflects underlying dominance interactions and contributes to altitudinal zonation of ecologically similar congeners. Neotropical singing mice are emerging as an important model that enables us to draw parallels to vocal communication systems in traditionally more tractable species.

Fig. 1. Photograph of a male Alston’s singing mouse (*Scotinomys teguina*) vocalizing at Cerros La Carpintera, Cartago Province, Costa Rica.
Fig. 2. Spectrograms of trills produced by a male Alston’s singing mouse (*S. teguina*; top) and Chiriqui singing mouse (*S. xerampelinus*; bottom).
Do painted gobies sing their quality out loud?

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Female mate choice based on variability in one or more male attribute is key to the sexual selection theory (Andersson, 1994). Acoustic signals are good examples of sexually selected traits predominantly used by females of several taxa to identify, locate and choose between potential mates (Andersson, 1994; Bradbury and Vehrencamp, 1998). Many vertebrates including teleosts rely on acoustic signals for communication (Lindström and Lugli, 2000). Benthic, burrow digging fish such as sand gobies (Pomatoschistus) are known to communicate acoustically (Lugli and Torricelli, 1999). Sound production has been documented in four species of sand gobies (Pomatoschistus). Males of P. minutus, P. marmoratus and P. canestrini produce drumming sounds when the female enters the nest (Lugli and Torricelli, 1999; Lindström and Lugli, 2000). Painted goby males (P. pictus) have also been described to produce similar drums and also thumps to attract females to their nest (Amorim and Neves, 2007). The aim of this study was to test the hypothesis that acoustic courtship signals advertise male quality such as male size and condition using the painted goby as a study model.

Fish were collected from shallow water using hand nets in Parede (38° 41'N, 009° 21'W), Portugal, during the breeding season (January to June 2010 and January to March 2011). Males and females were kept in separate stock aquaria (ca. 18.4l) with sand and shell shelters, at 18 ±1°C with a natural photoperiod. Fish were fed triturated mussels daily. Experimental aquaria (ca. 35l) were divided with two acrylic partitions in three distinct compartments. Lateral compartments were provided with shelters (5.5x3x7cm). Each shelter had a small PVC chimney (that covered a 2cm hole) to allow for a hydrophone to be placed inside. A single male was placed in each lateral compartment while one gravid female occupied the middle compartment. Territorial males showed nuptial colouration and covered the nest with sand. Experimental males were subjected to the same photoperiod as the stock aquariums and kept at a temperature of 16°C with a range of ±1°C.

Sounds were recorded to a laptop via a USB audio capture device Edirol UA25 (16 bit, 44 kHz acquisition rate), controlled by Adobe audition 2.0, with two hydrophones: one High Tech (94 SSQ, sensitivity –165 dB re. 1 V/1Pa) and one Brüel & Kjaer type 8104 (sensitivity -250dB re. 1μPa) conditioned by a sound level meter (Brüel & Kjaer 2238 Mediator). The High Tech hydrophone was placed 4 cm above the substrate and located close to the partition (in the female compartment). The Brüel & Kjaer hydrophone was placed within the nest chimney. The aeration was stopped 10 min prior to the sound recordings. At the beginning of the twenty minute recording session one partition was removed allowing the gravid female to interact with the territorial male.

Drums were analysed using Raven 1.2.1 and Adobe Audition 2.0 for sound pressure level (measured as the RMS total power ), sound duration (ms), number of pulses, pulse period (measured as the average peak to peak interval between pulses, ms) and peak frequency (measured at the maximum...
sound energy, Hz). In addition, drum, thump and total sound rate (nº of sound min⁻¹) were also tallied for one recording session for each male.

Preliminary data analysis showed that drum features differed significantly among males (Table 1). Sound duration and number of pulses showed the highest within-male variability (CVw) whereas sound pressure level and pulse period showed the smallest CVw. Drum duration and number of pulses were significantly correlated with male condition factor (Spearman correlation, r = 0.5, P < 0.05) suggesting that these sound features can signal male quality. Body lipid content, the degree of nest cover with sand, and visual courtship rate are presently being analysed as other measures of male quality (Svensson and Kvarnemo 2005). Sand goby females are known to use cues such as male size and courtship in mate choice (Svensson and Kvarnemo 2005) but whether females use acoustic cues for mate choice remains unknown. We suggest that courtship acoustic signals can advertise male quality in the painted gobies and could be used by females to choose their mates.

Table 1. Descriptive statistics for courtship drums produced by 18 *Pomatoschistus pictus* males, including the within-male variability (CVw) and the between-male variability (CVb). Results of Kruskal–Wallis tests (DF = 17, n = 168) comparing differences between males for each acoustic feature are also given, showing differences among males for all variables. An average of 9.3 sounds (6-10) were analysed per male.

<table>
<thead>
<tr>
<th>Acoustic variables</th>
<th>Mean</th>
<th>SD</th>
<th>Range</th>
<th>CVw</th>
<th>CVb</th>
<th>CVb/CVw</th>
<th>H⁰</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sound pressure level (dB)</td>
<td>-29.6</td>
<td>13.1</td>
<td>-53.9- -9.8</td>
<td>0.07</td>
<td>-0.44</td>
<td></td>
<td>6.47</td>
<td>159.4</td>
</tr>
<tr>
<td>Sound duration (ms)</td>
<td>659.6</td>
<td>343.3</td>
<td>160.8-1403.9</td>
<td>0.49</td>
<td>0.52</td>
<td>1.07</td>
<td>96.2</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Nº of pulses</td>
<td>25.5</td>
<td>11.4</td>
<td>7.8-49.5</td>
<td>0.45</td>
<td>0.45</td>
<td>1.00</td>
<td>90.3</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Pulse period (ms)</td>
<td>23.2</td>
<td>3.1</td>
<td>17.8-29.4</td>
<td>0.09</td>
<td>0.14</td>
<td>1.48</td>
<td>111.2</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Pulse rate (Hz)</td>
<td>40.9</td>
<td>5.8</td>
<td>33.5-50.9</td>
<td>0.12</td>
<td>0.14</td>
<td>1.23</td>
<td>103.5</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Peak frequency (Hz)</td>
<td>180.6</td>
<td>59.7</td>
<td>62.6-281.2</td>
<td>0.15</td>
<td>0.33</td>
<td>2.27</td>
<td>130.9</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

References


Stress-induced vocalizations in male Zebra Finches: clues of expression of emotional state?

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Vocalizations play a prominent role in the communication of many species. While it is now well established that vocalizations carry information about the emitter such as its species, its sex or its identity, few studies are interested in how vocalizations could hold information about the emotional state of the sender. Nevertheless, some recent studies in mammals revealed that a physiological stress is often associated with modified vocalizations, implying that an emotion of stress could be expressed through vocalizations.

We focused our study on a gregarious bird, the Zebra Finch that forms monogamous pair bond. Although they use acoustic communication during social interactions, little is known to date on how birds encode emotional and physiological states like stress in their vocalizations and how receivers of these signals might use the information. Because it has been demonstrated that isolation is a strong stressor in many species, we supposed that isolation would provoke a raise of stress hormone and/or a change in behaviour such as emission of stress-induced vocalizations.

We investigated call rate and acoustic structure of calls used by domestic males in response to the playback of female calls of varied saliences (familiar versus stranger) in two situations: social isolation and social housing. Social isolation provoked a raise of plasmatic corticosterone, abolished vocal preference for stranger stimuli, and evoked calls with longer duration and higher pitch (Fig. 1). To verify the implication of corticosterone in these modifications, we investigated whether oral administration of exogenous corticosterone could mimic the effects of isolation in socially housed subjects. Our treatment induced isolation-like higher pitched calls (Fig. 1). Thus, social isolation caused a physiological stress that provoked modulation of acoustic features of male calls.

To investigate whether the stress-induced calls’ modifications are relevant to other birds, domestic female zebra finches were temporarily isolated from their pair mate and exposed to four conditions: unstressed calls from the mate, stressed calls from the mate, calls from a familiar male, or no auditory stimuli. Levels of plasmatic corticosterone were monitored after one hour in each treatment. We hypothesized that the vocalizations could attenuate the physiological stress response that is induced in zebra finches by separating them from their social partner. We predicted that the magnitude of this “vocal buffering” would differ depending on the nature of the acoustic stimulus used.
Fig. 1. Spectrogram of distance calls of male Zebra finches. Stressed birds emit higher-pitched calls as they do in social isolation. (NO CORT: control context. Birds were socially housed during the experiment. CORT: birds were socially housed but received an oral dose of exogenous corticosterone before the experiment. ISOLATION: birds were isolated during the experiment).
Behavioral Discrimination of Ultrasonic Vocalizations in CBA/CaJ Mice

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Previous studies have shown that both male and female mice produce ultrasonic vocalizations (USVs) under a variety of circumstances, but the function of these USVs remains unclear. In addition to emitting many calls, these mice also produce a wide array of call types, hinting that unique information is conveyed to listeners with each call. These different call types have been suggested as a means of social communication between members of this species. At this time, however, it is not clear whether mice can actually discriminate amongst these different call types. Most studies attempting to categorize mouse USVs have done so by using call categories constructed by human visual estimation. However, these categories are based on intuition, usually involving similarities in spectral shapes. Although these categories seem reasonable to humans, we do not know if these categories hold true from the perspective of the mouse. This study was conducted to see if mice can discriminate between human-classified categories of USVs, and to determine the acoustic cues most salient to the mice when discriminating among a variety of mouse vocalizations.

Twelve different ultrasonic vocalizations (USVs) were used in this experiment. These twelve stimuli were categorized into four different call types: frequency modulation, jump, complex and narrow sweep. The frequency modulated calls were classified as bands of energy that varied in frequency over time. The jump calls were classified as a band of energy followed by a large change in frequency within a very short time span. The complex calls were categorized as calls that contained multiple non-harmonic frequencies over a continuous time span. Finally, the narrow sweep calls were those that spanned a large frequency range over a very short amount of time. Additionally, three call types were isolated based on gender and sex state: male, female in estrus, and female in diestrus. In addition to these twelve categorical stimuli, each call was also manipulated in several ways. The calls were reversed, silent gaps were inserted within each call, the duration of the calls was doubled, and synthetic calls were created that mimicked the structure and frequency of each call type.

The twelve stimuli were then used in a discrimination experiment. Each stimulus served as the background with the other eleven stimuli serving as targets, and all combinations were tested in a random order. The manipulated calls were also used as targets. Using an operant conditioning paradigm, the mouse had to poke its nose to a left hole to initiate a trial. Upon initiating a trial, the background stimuli alternated with one of the randomly selected target stimuli. The mouse was reinforced with access to water for correctly discriminating between the two stimuli by poking the right hole. Approximately 30% of all trials were catch trials. If the mouse responded by poking to the right hole during a catch trial, indicating a difference between the two identical stimuli, a timeout was given. The mouse’s false alarm response was considered when analyzing the results and any session where the false alarm rate was above 25% was discarded. Two male and two female CBA/CaJ mice were tested.
Fig. 1. Spectrograms of eight of the mouse ultrasonic vocalizations used in the discrimination experiment.

The discrimination results suggest that the mice are capable of distinguishing between different call types. Certain calls, such as the male, estrus, and frequency modulated calls, were more difficult to discriminate against most other call types, whereas other call types, such as the complex, jump, and narrow sweep calls, were easily discriminated against. The synthetically modified calls were not easily distinguished from the originals. Future studies will be needed to determine which acoustic cues the mice use when discriminating one call from another.
Parental and alloparental behaviour in a strongly vocal fish

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Parental care has evolved when benefits of offspring maintenance outweighs the costs (Farmer & Alonzo, 2008) and is often given by females, as in mammals, but may also be exhibited by males. Paternal care is common in fish as males often need to defend a territory/nest to attract females to mate with and continue this process while guarding the nest, thus not suffering significantly increased costs. Another poorly understood behaviour, however, is alloparental care (i.e. directed to others’ offspring), where benefits to the attendant male appear unlikely.

Batrachoididae males (toadfish and midshipmen) defend their nests in the reproductive season, use acoustic signals to attract mates, and provide parental care to the offspring during c. 30 days (Brantley & Bass, 1994). Nest-holding Lusitanian toadfish males (Halobatrachus didactylus) defend their nests with sound emissions (agonistic boatwhistles), frequently resulting in the expulsion of the intruder (Vasconcelos et al., 2010). However, as the competition for nests increase during the breeding season (Amorim et al., 2010) it is probable that territorial intrusions and subsequent nest takeovers occur (Vasconcelos et al., 2010), leading to situations where males care for foster eggs. Our aim was to study the existence of alloparental care in Lusitanian toadfish, by comparing nest defense during territorial intrusions, egg survival and physiological differences (androgen levels) between parental and alloparental males. We predicted, if males do not show alloparental care, that (1) parental males would defend their nests more aggressively and therefore would perform less display behaviour, including acoustic signaling, than alloparental males, and that (2) parental males would show higher offspring survival.

Fish were randomly assigned to three different treatments; (1) parental males in nests with eggs from another male (AP), (2) parental males in nests with their own eggs (PWE), (3) parental males in nests without eggs (PNE). We also used a control group with nests with eggs but without males (ENM). To test these different groups, we made territorial intrusions in 2.5 m tanks with 2 resident males and 2 intruders, and observed all the acoustic and visual behaviours during one hour. These intrusions were done in 3 different days (1st, 5th and 10th day after a 48h acclimation period) with the same residents but different intruders. We photographed the nests on the first and last day and counted the eggs to calculate egg survival. Blood samples to measure testosterone (T) and 11 keto-testosterone (11KT) circulating levels were collected after the third intrusion and compared between males from the three treatments and a set of unmanipulated males sampled directly from estuary nests.

There were no differences in acoustic and visual behaviour between treatments and along intrusions (ANOVA, P>0.05), but egg survival was significantly higher in nests with males (AP and PWE) than in control nests without a male (ENM) (Fig. 1). These results suggest the existence of alloparental care but we cannot exclude the hypothesis that egg survival increased by the simple presence of a male and not due to active care. In fact, fish may possess compounds in the epidermal mucus that might have prevented fungus infection and this could have increased egg survival (Knouft et al., 2003).
Fig. 1 – Egg survival (mean ± SD) in the different groups. (AP) parental males in nests with eggs from another male, (PWE) parental males in nests with their own eggs, (ENM) nests with eggs but without males. Egg survival in nests without a male was significantly smaller than in AP and PWE nests (pairwise LSD tests, P<0.05). Groups that are significantly different (P<0.05) are indicated by different letters.

Territorial defense behaviour, including vocalizations, did not reveal significant differences among males, despite a recent study where parental males with eggs were found to be more aggressive than males without eggs (Vasconcelos et al., 2010). However, in the work of Vasconcelos et al. (2010), some males were already guarding embryos, what may explain the discrepancy with our study.

Androgen circulating levels (T and 11KT) exhibited significant differences among male groups (AP, PWE, PNE), with the alloparental males presenting higher circulating levels. Experimental fish had lower T levels (Mann-Whitney test, U=44.0, P<0.01) but similar concentrations of 11KT (Mann-Whitney test, U=124.0, P>0.05) than males sampled directly from estuary nests suggesting that experimental procedures did not affect the main teleost androgen (11KT).

References
Vocal Signatures of Male Northern Elephant Seals and Differential Responses to Playbacks Predicted by Hierarchical Status

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Northern elephant seals (Mirounga angustirostris) are large, highly polygynous mammals that have a breeding system based on the defense of female harems by dominant males. Female reproductive cycles are synchronous and seals gather in large numbers on natal beaches each year to give birth and breed prior to departing for long foraging migrations at sea. Competition among sexually mature males is intense, with only a small fraction of adult males likely to successfully gain access to receptive females. Males establish reliable dominance hierarchies early in the breeding season after which their interactions are mediated primarily by stereotyped vocal signaling and only occasional physical fights. The aim of this study was to examine the acoustic characteristics and functional significance of these male calls in order to improve understanding of communicative behavior and the potential role of associative learning in maintaining social structure.

More than 50 adult male elephant seals were studied throughout the breeding season over two consecutive annual seasons at the Año Nuevo breeding colony in San Mateo County, California. Comprehensive observations of acoustic signaling, behavioral interactions, physical characteristics, and spatial movement patterns were obtained from individually marked and identified males. Male vocal displays were digitally recorded from <20 m and analyzed for spectral, temporal, and sound pressure level characteristics. Dyadic behavioral interactions between identified males were scored and used to determine quantitative ELO dominance rankings. The mass and size of individual males was derived from repeated photometric measurements, and movement patterns and spatial relationships to other males on the rookery were determined by daily GPS sampling. Two field playback experiments (based on Holt et al., 2010) were conducted using calls recorded from individuals of known size, rank, and familiarity directed toward dominant or subordinate associates. Responses were scored as movement relative to the speaker and vocal displays during 2 minute matched baseline and playback exposure periods.

The threat display calls of males comprised repeated units of pulsed transients or modulated guttural pulse trains emitted at highly regular rates (as described by Le Boeuf and Peterson, 1969) and extremely loud levels (120-130 dB peak re 1uPa peak @ 1m). The calls of different males were individually reliable and easily discernable with acoustic features that were not obviously correlated to size or dominance status. Vocal signaling occurred in the majority (78%) of male-male competitive interactions (n=1177), while physical contact between males was rare (6% of interactions) and typically followed repeated vocal exchanges of calls from both individuals. More commonly, conflicts were settled by negative phototaxis from the receiver at distances of several body lengths, thus avoiding costly fights.

To determine if calls alone would elicit the same behavior responses observed during actual interactions between marked individuals, playback experiments tested responses to the calls of individuals with known ELO rank, size, and spatial relationships. The results show strong and predictable differential phonotaxis and calling behavior based on hierarchical status of the receiver relative to the playback (Fig.
Therefore, these unique signals are not likely to be honest indicators of resource holding potential, but rather serve to convey information about individuals that is managed through complex associative learning.

Fig. 1. Phonotaxis observed in male elephant seals during two playback conditions. In Playback 1, 10 males were presented with two playback conditions: calls of a known subordinate individual and a similar set of calls from a known dominant individual. In Playback 2, 20 individuals were tested in 10 reciprocal pairs, with each individual receiving the calls of a known rival. In both plots, mean distance moved in response to the playback are shown with standard deviations. The sample size for each bar is 10 individuals, and a subset of individuals were tested in both Playback 1 and 2. Both plots show significant movement patterns in the direction predicted by previously observed behavioral interactions between the callers and listeners, while no movement occurred during the baseline period prior to playbacks. Vocal responses during playbacks showed similar trends, with listeners calling more often when the playback track was subordinate to the focal animal.

This work was supported in part by award N00014-06-1-0295-11 from ONR. The research was conducted under NMFS marine mammal research permit 14636 with the permission of Año Nuevo State Reserve and the Institutional Animal Care and Use Committee at UC Santa Cruz. We thank Selene Fregosi, Dan Costa, and Patricia Morris for their important contributions to this research.

References
Understanding the Dynamics and Interactions of the Nearshore Marine Acoustic Community

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Like many biological communities, nearshore coastal ecosystems are filled with a wide variety of taxa which all rely on acoustic communication as an integral component of their life history. However, in most previous analyses of spatial and temporal periodicity, patterns of vocalization are usually examined at a species- or population-level, but rarely take interspecific overlap or interactions. This single-species approach overlooks the fact that these organisms are not vocalizing in isolation of one another. Previous community-level analyses examples of acoustic behaviors from frogs and birds have developed a paradigm of an “acoustic community,” but this concept has still largely been examined among still relatively closely related taxa at a genus or family order. Such a community level interpretation of vocalization patterns raises the question of if and how phylogenetically distant taxa may acoustically interact. We examine patterns of vocalization between two distantly related groups of acoustic taxa whose sounds dominate the coastal soundscape: whales and fishes. While examining eavesdropping and any behavioral effects requires a rigorous experimental approach, examining spatial and temporal patterns of vocalizations of these taxa can serve as a first indication for whether there is any evidence of acoustic interaction. A basic understanding of the bioacoustic properties of calls from these groups combined with estimations of their auditory physiology suggests that individuals from these groups can likely hear one another.

Here, we use representative passive acoustic data from several different nearshore ecosystems (the Western North Atlantic Ocean and Gulf of Mexico) to evaluate if and how the vocalizations of members of these ecosystems overlap in time and space. Calls from North Atlantic right whales and different fish species (such as red drum, black drum, silver perch) overlap in both time, space and frequency bandwidth, and are all detectable on the same recording unit, demonstrating that organisms producing these sounds are clearly exposed to sounds from other taxa. In examining these patterns, we have found that a long-term multi-species acoustic assessment of habitats also presents a number of technical challenges, including automated signal detection, system integration and data management.

However, the conceptual development, implementation and expansion of this “community acoustic” approach can further shape the computational requirements for further exploration of these ideas.

By looking at the possible interactions of acoustic organisms, we extend the basic ecological concept of the biological community to a bioacoustics-centered perspective and attempt to expand the development of the concept of the acoustic community within a broad taxonomic framework. Additionally, by incorporating this acoustic community perspective with physical parameters from the environment which impact these bioacoustic signals, we attempt to develop the concept of the “acoustic ecosystem” as a new paradigm by which to understand and evaluate the behavior and ecology of acoustic organisms in their habitat.
Minke whale vocalizations in the Stellwagen Bank National Marine Sanctuary, USA

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Better knowledge of large whale vocalizations is important for using increasingly efficient passive acoustic monitoring methods to determine distribution patterns and estimate animal abundance over large spatial and temporal scales. These data can be instrumental in conserving rare or declining species and highlight conservation needs. However, large data gaps exist in our knowledge of baleen whale vocalizations. For example, apart from few descriptions and opportunistic observations, very little is known about minke whale (Balaenoptera acuturostrata) vocalizations, their seasonality or behavioral context in the North Atlantic. This study used data from a long-term monitoring project (2006-2009) in the Stellwagen Bank National Marine Sanctuary, to (1) investigate their seasonal distribution and diel trends off the coast of Massachusetts and (2) further describe minke whale vocalizations recorded in the Western North Atlantic.

Data were collected using several arrays of Marine Autonomous Recording units (MARUs). Recorders were set to sample at a rate of 2 kHz. To investigate the seasonality of minke whale pulse trains, one channel of each array deployed in 2006 was scanned with an automated energy detector in XBAT. Detection probability was 0.92 and detection results were hand-browsed to remove false positive detections. Data collection was continuous throughout all of 2006 except for the month of June. Minke whale vocal activity was strongly seasonal, with pulse trains detected between February and November. Detection rates were low during spring and peaked in late summer with detections on over 80% of all recording days in August and September. Detection rates decreased again in autumn, and no detections were recorded in December and January. This strong seasonality mirrors the scarce visual data that exists for minke whales in this area. Largely absent during the winter, visual sighting records show a distinct peak from July to September. In addition, a clear diel pattern in minke whale vocal activity was apparent. Detection rates were generally low during the day and peaked in the early evening.

Since August, September and October were peak months of minke whale vocal activity; the data were sub-sampled such that every fifth day was selected for detailed acoustic analysis. The objectives of these analyses were to determine the frequency of occurrence of different types of pulse trains, measure basic descriptive sound parameters and estimate source levels, when calls were of sufficient quality to be localized. Recorded pulse trains displayed variability in duration, frequency content and inter-pulse-interval (IPI). Based on changes in IPI, three different types of pulse trains could be identified. While only 3 % of all good quality calls showed regular spacing of individual pulses (“regular type”), 12 % showed a decrease in IPI (“speed-up type”) and 85% were characterized by an increase of IPI over time (“slow-down type”). The dominantly recorded “slow-down” pulse trains (see Fig. 1) had a mean duration of 34.4 ± 10.1 sec, a mean IPI of 0.4 ± 0.06 sec and consisted of 14 – 138 individual pulses (mean=77.4 ± 23.6). Individual pulses were 0.1 ± 0.01 sec in length and had a mean peak frequency of 118.5 ± 12.0. Peak frequency as well as IPI changed throughout the duration of a pulse train. Estimated source levels for minke whale pulses averaged 163.1 ± 3.9 dB RMS re 1µPa.
More research is needed to interpret these results with respect to minke whale behavior. However, detailed descriptions of species-specific vocalizations, their seasonality and geographic extent are a necessary first step in order to begin to ask questions about their ecological significance in a species’ life-cycle.

Fig. 1. Example of minke whale pulse train of the “slow-down type”. Note the change in IPI half way through the call.
Auditory biomechanics in microscale hearing organs

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The auditory organs of insects are very small, as they often span no more than one millimeter. Despite, or perhaps because of, their small size, insect ears perform all the elementary tasks of acoustic detection [1, 2]. To hear, insects have evolved at least two fundamental forms of detectors, tympanal ears and flagellar ears. The most studied is the tympanal form, a system superficially similar to that found in vertebrates. Tympanal ears display a vast diversity of forms and functions across the insects, and can be found in locust, moth, cricket, katydid, parasitoid fly, mantis, and cicada. Flagellar ears are taxonomically the most common form across insects, yet they have not been studied in similar depth and breadth. As 98% of insect species have antennae with a mechanoreceptive organ at its base. Somewhat speculatively, flagellar ears might even be very common among arthropods, as they may be more generally found in spiders and crustaceans. Sensitive to the particle velocity component of the sound wave, flagellar ear can also take different forms, but usually have an elongated structure that serves the capture of sound energy through viscous coupling to the medium. Such ears typically consist of a hair-like structure protruding from the body surface or a pair of antennae set on the head. Mechanical vibrations are invariably sensed by a mechanoreceptive organ situated at the base of the flagellar structure; the sensory receptors proper are the typical scolopidia that comprise one or several ciliated mechanoreceptive neurons. Most notably found in mosquitoes and fruit flies, these ears have been dubbed "near-field" detectors because they sense particle velocity, the form of acoustic energy that is dominant near the sound source. Yet owing to their extreme sensitivity [3] their range of operation can extend past the acoustic near-field. By contrast, tympanal ears are used for the long-range detection of the pressure component of the propagating sound field. Examples of both flagellar and tympanal ears will be presented, in particular, the mechanical response of the locust ear will be illustrated (Fig. 1).

The mechanical response of the locust ears is interesting as it presents an unsuspected case of sophistication in the way an auditory system performs frequency discrimination [4]. Understanding the exact biophysical mechanism for frequency discrimination requires more exact knowledge of the physical characteristics of the propagating waves, and the overall and local material properties of the membrane itself. To this effect, atomic force microscopy is used to determine local mechanical properties, in conjunction with dual beam focused ion beam technology to modify the mechanical membrane properties in a controlled way. The complex structure of the tympanum is revealed, shedding some light on the structural organization supporting its mechanical response (Fig.1)

Most notably, as the vibrational wave travels across the membrane, the magnitude of deflection increases gradually. The peak magnitude is similar for different driving frequencies, yet its location and sharpness differ. In effect, this is at the attachment site of the high frequency neural receptors (PV, Fig. 1A) that ultrasonic stimulus frequencies find their maximum peak wave magnitude. Upon approaching the PV location, the velocity of propagation of the travelling wave decreases gradually, reaching zero at the PV. Wave velocity varies from ca. 10 to 30 m/s for low and high frequencies, respectively. The wave's transit time across the membrane at 15kHz is about 70-80µs. This frequency dependence of wave velocity is likely to be related to the mechanical behavior of a stiff plate rather than a thin film. The
outcome of this travelling wave is a concentration of kinetic energy around the PV, enhancing the efficiency of energy capture at the location where it is to be transduced by mechanosensory receptors.

Fig. 1. The locust ear. A. SEM of the tympanal membrane, perimeter delimiting the tympanal membrane, FB: folded body, the attachment site of the low frequency receptors. PV: pyriform vesicle, site for high frequency receptors. B. Microscanning laser Doppler vibrometry radial lattice centered on PV location. C. Vibrational response across a radial transect showing membrane deflection velocity at PV and FB locations (11.8 kHz). Grey lines show deflection shapes through a stimulus cycle every 20° phase angle, building up the deflection envelope across the membrane (x-axis). D. Deflection shapes in response to four cycles of acoustic pressure at 15.0kHz. Different phase angles are shown, starting at 0° (dot on sinusoid inset), showing in sequence the membrane deflection across one cycle. Note the concentric traveling wave which culminates at the center of the scanning mesh at 180°, the position of the PV. The wave travels no further, and dissipates.

References
Assessing the distribution of bottlenose dolphins (*Tursiops truncatus*) in the New River, NC using passive acoustic and visual monitoring

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Passive acoustics offer a more effective means of monitoring the occurrence and distribution of vocalizing marine mammals than visual surveys alone, which can be limited by periods of darkness and poor weather. We used passive acoustic monitoring and concurrent visual surveys to monitor the distribution of bottlenose dolphins in the New River, North Carolina, which forms part of the U.S. Marine Corps Camp Lejeune. We deployed four echolocation click detectors (C-PODs) at four sites in the New River (Inlet, Stone Bay, Farnell Bay, and Morgan Bay). C-PODs in the Inlet and Stone Bay were deployed on 20 November 2010; the C-POD in Farnell Bay was deployed on 30 January 2011; and the C-POD in Morgan Bay was deployed on 6 April 2011. These devices continuously record the presence of echolocation clicks between 20-160 kHz. We used click trains as a proxy for the occurrence of dolphins near each C-POD.

An analysis of thousands of dolphin click trains from the C-PODs indicates that dolphins occurred frequently at the Inlet, Stone Bay and Farnell Bay sites (Figure 1). C-POD acoustic recordings from the Morgan Bay site have not yet been analyzed, although dolphins were sighted near this deployment site on 6 April 2011. Further analyses of these data will provide information on the diurnal and tidal patterns of dolphin occurrence in the New River.

To ground-truth the C-PODs, we deployed an acoustic recorder (DMON) 30 meters from the C-POD located in Stone Bay (Figure 2). The DMON recorded continuously at a sampling rate of 100 kHz from 6 to 10 February 2011. Analysis of acoustic recordings from the DMON indicated that the C-POD recorded most click trains and produced few false detections (93% true positive detection rate).

![Fig. 1. Mean hourly presence of bottlenose dolphin (*Tursiops truncatus*) echolocation click trains recorded on C-PODs at three sites in the New River, North Carolina. Bottlenose dolphin click trains were detected throughout day and night time hours at each site.](image-url)
Fig. 2. Acoustic recordings from Stone Bay on 7 February 2011 displaying bottlenose dolphin echolocation clicks recorded on (A) a C-POD and (B) a spectrogram from a DMON.

Deployments of the four C-PODs and a DMON, and visual surveys will continue throughout 2011, providing a seasonal picture of bottlenose dolphin occurrence in the New River. These acoustic and visual data provide important insights into spatial and temporal patterns of bottlenose dolphin distribution and abundance in the New River. The U.S. Marine Corps Camp Lejeune funded this research.
Sound Production in Freshwater Invertebrates: Documentation and Applications in Biomonitoring

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Sound plays an important role in the communication of many well known terrestrial insects such as cicadas, grasshoppers, and katydids. But, little is known about auditory communication in aquatic invertebrates, though several studies have documented as both quite plausible and probable. Adult stoneflies communicate acoustically across logs on land to find mates, and predacious stoneflies can sense mechanical vibration in prey items to determine which is more desirable. Water Striders signal to one another using vibrations across the water’s surface. Nevertheless, communication between freshwater macroinvertebrates has never been documented underwater.

We are currently using a hydrophone and field recorder to listen to aquatic invertebrates under both laboratory and field conditions. Several specimens have yielded extensive vocalizations across a wide range of frequencies. These highly vocal invertebrates have the capability of creating multiple distinct sounds. Calls are typically repetitions and combinations of short sounds, each lasting less than one second. Water Scavenger Beetles (Hydrophilidae) (Fig. 1), Backswimmers (Notonectidae), and Whirligig Beetles (Gyrinidae) all produce definite vocalizations that can be differentiated by ear. Predacious Diving Beetle adults of the genus Cybister produce extensive rattles, grating, and popping sounds. Video recording and observation suggests that these vocalizations are primarily used as intraspecies communication and alarm signaling.

This is the first time aquatic invertebrates have been documented calling under the water’s surface and we hope to describe these sounds, behaviors, and the mechanisms by which they are produced. We also are very interested in exploring new ways these vocalizations could be used in the biomonitoring of our freshwater ecosystems.

Fig. 1. Spectral frequency of Water Scavenger Beetle (Hydrophilidae) vocalization.
Cultural breakdown of learned avian alarm calls: implications to management and conservation

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Mobbing is a common response of prey birds to aggressively displace potential predatory birds. This response transcends lineages and empirical evidence indicates that auditory cues from one species elicit mobbing responses in the same and different species. The Black-capped Chickadee (BCCH; Poecile atricapillus) varies the number and amplitude of D notes in the “chick-a-dee” mobbing call to denote information about the level of threat a potential predator poses and there are approximately 50 heterospecifics known to eavesdrop and respond to these alarm calls. However, culturally transmitted vocalizations are known to quickly diminish in populations of other songbird species that become isolated or are small in size due to habitat fragmentation, potentially exacerbating their decline. Isolation is an important force in sound variation, particularly when cultural evolution shapes animal communication. Whereas the BCCH and associated mixed flock members are common, we use this system as a model to study the cultural transmission of information important to prey survivorship, including potential cultural breakdown in populations that are threatened primarily by isolation via habitat fragmentation.

This project was replicated in areas containing persistent populations of Eastern Screech Owls (ESOW; Megascops asio) and in those historically lacking them to assess whether BCCH alarm calls for ESOWs have a site-specific learned cultural component. The ESOW is a large predatory threat to BCCHs throughout their eastern range but is patchily distributed and as such, may culturally isolate local BCCH populations. Regional dialects are not hard-wired but learned in many songbirds, and locale-specific calls may uniquely convey information to members of the same mixed flock. If this is the case, BCCH alarm call structure and the corresponding mobbing responses should differ among locales, depending on whether they co-occur with ESOWs.

We found a difference in the structure of the “chick-a-dee” warning call and it predictably changed as a function of ESOW presence. In particular, where BCCH co-occurred with ESOWs, the average number of “D” notes was 4.25 but in areas historically lacking an ESOW population, the average number of D notes was only 2.05. This indicates a breakdown in learned alarm calls and suggests cultural transmission of vocalizations is relatively limited in BCCHs. As such, we contend that management which increases the connectivity of otherwise isolated populations can be of strong conservation value to many songbirds in decline, particularly by preserving culture important to individual survivorship.
Fig. 1. Spectrogram recorded at Ford Nature Center in Youngstown, OH, is of a “chick-a-dee” warning call given in response to an ESOW in an area absent of ESOWs.

Fig. 2. Spectrogram recorded at Beaver Creek State Park in East Liverpool, OH, is also in response to an ESOW, but in an area with ESOWs.
High frequency whistles produced by killer whales (*Orcinus orca*) and its variation in Northeast Atlantic populations

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Identifying the sound repertoire of animal species is essential for vocal behavior comparisons between species and different populations. Killer whales off Iceland and Norway are herring-feeders and are most vocally active during feeding producing pulsed calls, whistles and clicks. Despite suggestions that these populations had contact in a recent past and similarities in feeding ecology and behavior, no movement between the two populations has been reported to date. There is also little evidence of call type sharing between Iceland and Norway, although call type sharing occurs between groups within each population.

In addition to producing clicks, pulsed calls and lower frequency whistles as previously described for the species, killer whales in Iceland and Norway also produce high frequency whistles. Nevertheless, these were not detected in two populations from the Northeast Pacific indicating substantial intraspecific variation in whistle production in killer whales. High frequency whistles are defined as whistles with fundamental frequency contours entirely above 17 kHz, although most have entirely ultrasonic (>20 kHz) frequency contours. Here, we investigated the high frequency whistle repertoires of killer whales from the Northeast Atlantic.

We compared the repertoire of high frequency whistles produced by killer whales in Iceland and Norway using a combination of classification and non-classification based approaches. Non-classification methods included comparison of parameters extracted from the fundamental frequency contour (minimum, maximum and mid frequency, frequency range and duration) between locations using non-parametric Wilcoxon rank sum tests. These parameters were then input into a discriminant function analysis. Classification was conducted using visual classification and an automated method combining dynamic time warping with an adaptive resonance theory neural network.

A total of 827 high frequency whistles were recorded (N\text{Iceland} = 570; N\text{Norway} = 257). Unlike the previously reported low frequency whistles from other locations, high frequency whistles were short and had simple contours (Fig. 1). Most whistles (98%) had one or no inflection points and the majority (60%) were upsweeps. High frequency whistles produced by killer whales in Iceland and Norway were similar both in overall measured parameters and in whistle type repertoire (Fig. 1). The only significant differences between Iceland and Norway were in maximum frequency and frequency range. Whistles from Iceland had slightly higher maximum frequency and frequency range than those from Norway. Norwegian killer whales also produced proportionately more descending-ascending whistles than did Icelandic killer whales. Both the discriminant function analysis and the automated classification method were not able to consistently distinguish between whistles from different locations. Additionally, visual observers regularly grouped whistles from both locations in the same categories.

These results suggested that despite the apparently substantial intraspecific variation in whistle repertoires across ocean basins, within the Northeast Atlantic the repertoires of high frequency whistles were very similar. The function of the slight differences in maximum frequency, frequency range and whistle type use remain unclear. The fact that most whistles were upsweeps and the similarity between populations suggests these whistles do not act as individual, group or population identifiers. Upsweep
whistles are an important component of the whistle repertoire of other delphinid species and appear to be used particularly during socializing, although their function is not known. It is possible that high frequency whistles of killer whales are used in a similar way during socializing but further work will be necessary to understand what their function may be.

Fig. 1. Example spectrograms of extracted fundamental frequency contours of high frequency whistles from Iceland and Norway. Note the high similarity between both contours despite being recorded in two separate locations.
The whistles of captive bottlenose dolphins (*Tursiops truncatus*) during a 24 hour cycle: A comparison between two aquaria

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Acoustic behavior analyses have been extensively studied on marine mammals during day time. However, analyses during 24 h cycles are remarkably scarce for marine mammals. This study is the first known one to report and describe the whistles of captive bottlenose dolphins (*Tursiops truncatus*) at night. Whistles are frequency modulated sounds almost omnidirectional, with duration between 0.1 and 3.6 s and a fundamental frequency between 1 and 35 kHz (Bazúa Durán 2010). It appears that whistles are only used in communication between individuals, to maintain contact within individuals of a herd, and to coordinate herd movements (Janik & Slater 1998).

In this study we analyzed the whistles recorded during a 24 h cycle at a sampling rate of 88 or 96 kHz with 16 bits in format files .wav in the presence of four bottlenose dolphins in two aquaria in Mexico City, two at Six Flags and two at Atlantis. Dolphins from Atlantis were young and from the Gulf of Mexico, while those of Six Flags were adults from the Pacific Ocean. Whistles were analyzed to measure whistle occurrence and to categorize them in whistle types using an automated categorization method (Deecke & Janik 2006). Comparisons during day and night (day was from 6:30 to 20:30, night was from 20:30 to 6:30), and between the two aquaria were made.

For the 24 h cycle we recorded 277 whistle s in Six Flags, and 447 whistle s in Atlantis. Whistling in Six Flags occurred only during day time (Fig. 1A), continuously from 08:38 to 11:20 at 1.7 whistles/min, with a 24 h whistling rate of 0.2±1.1 whistles/min, a day time rate of 0.3±1.4 whistles/min, and 18.7 h of continuous silence (the silent period constituted 94.6% of the 24 h). Whistling in Atlantis occurred during both day and night (Fig. 1B), having a 24 h whistling rate of 0.3±1.5 whistles/min, a day time rate of 0.4±1.6 whistles/min, a night time rate of 0.2±1.2 whistles/min, and a continuous silent period of 9.3 h (the silent period constituted 92.3% of the 24 h). Of the whistles emitted in Atlantis during the day, three whistling bouts were noticed at 6.0 whistles/min for 53.9%, at 0.6 whistles/min for 14.3%, and at 2.1 whistles/min for 31.8% of the day time whistles. At night, 84.6% of the night time whistles were recorded between 01:51 and 02:05 at 5.1 whistles/min. Overall, whistling has higher in Atlantis than in Six Flags (Mann-Whitney U-Test: 24 h Z-stat adjusted=5.50, P<0.001; day time Z-stat adjusted=-1.23, P=0.22; night time Z adjusted-stat=-4.39, P<0.001). In Atlantis, both dolphins were active during both day and night, swimming and interacting with other dolphins (the two activities during which whistling is high, López Rivas 2010), while in Six Flags both dolphins were only active during day time (when dolphins were resting they did not whistle; López Rivas 2010). Therefore, whistling for the captive dolphins at both aquaria seems to be related to dolphin activity and to age (when dolphins were younger they whistled more).

In Six Flags the whistle repertoire consisted of 38 whistle types, representing 0.137 of the whistles recorded during 24 h (or during day time). In Atlantis the whistle repertoire consisted of 50 whistle types, representing 0.112 of the whistles recorded during 24 h (27 types corresponded only to day time, 0.166 of the whistles recorded, 36.5% of Atlantis whistles; 5 types only to night time, 0.122 of the whistles recorded, 9.2% of Atlantis whistles; 18 types to both day and night time, 0.074 of the whistles recorded, 54.3% of Atlantis whistles). Therefore, the whistle repertoire for 24 h in Atlantis was larger than in Six

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Flags and whistle types were used more often in Atlantis (Fig. 2). In Six Flags the four whistle types mostly used (61.6% of the whistles) were of less variability than the four mostly used in Atlantis (26.6% of the whistles) (Fig. 2), suggesting that adult bottlenose dolphins have a smaller repertoire of less variable whistles. Our results also suggest that the activities Atlantis dolphins engaged in may be similar during both day and night (whistle types are related to dolphin activity, López Rivas 2010).

This study showed that some dolphins whistle at night, but others do not, and when whistling at night dolphins are probably performing similar activities than during day time.

Fig. 1. Whistle occurrence during 24 h. A. Two bottlenose dolphins at aquarium Six Flags and B. Two bottlenose dolphins at aquarium Atlantis. The gray region indicates the night time period.

Fig. 2. Use of whistle types during 24 h. A. Two bottlenose dolphins at aquarium Six Flags and B. Two bottlenose dolphins at aquarium Atlantis.

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References
Stereotyped calls in long-finned pilot whales (*Globicephala melas*)

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Surprisingly little is known about the vocal repertoire of either short-finned (*Globicephala macrorhynchus*) or long-finned (*Globicephala melas*) pilot whales. In 1969, in the earliest published study of short-finned pilot whale calls, Caldwell and Caldwell reported that a captive whale produced a stereotyped call that was made up of two components, a tonal whistle and a pulsed lower frequency component. We now recognize that this signal structure is similar to the low and high frequency components reported for killer whales. Following the Caldwells’ work, two studies focused on tonal “whistle” sounds of long-finned pilot whales, but grouped these sounds into seven broad categories, without showing structural details of the calls. Here we categorized calls produced by two simultaneously tagged long-finned pilot whales in the western Mediterranean (Alboran Sea) based on their structural details, and found that they produce highly stereotyped, complex calls consisting of pulsed, tonal, and non-linear components (see abstract by Wu-Jung Lee et al.).

Whales were tagged with digital acoustic and movement logging DTAGs. We focused on high signal to noise calls greater than 0.5 sec in duration, thus not including short pulsed sounds such as rasps (see abstract by Frants Jensen et al.). Calls were categorized visually, by viewing spectrograms. In an approximately 278 min tag record, 306 calls were recorded; of these, 141 were attributed to the tagged whale and 165 to other whales, with the majority of the latter being attributed to a second, simultaneously tagged whale. Call attributions were made by comparing amplitudes of calls on the two tags. Of the 306 calls, 76% (232) were categorized as the same call type, called type “A”. Within type A, however, there were three different variants: the predominant call type, which accounted for 78% of the calls, the “pulse only” variant, which accounted for 13%, and the “multi-loop” variant, which accounted for 9%. One tagged whale produced all three of these variants, and the other produced only two. These stereotyped calls were highly likely to overlap and to occur in sequences, with 88% occurring within 10 sec of another type A call, and 71% occurring within 5 sec of another (see Figure 1).

The two tagged whales were very closely associated; in 81% of scored surface intervals they were nearest neighbors, and in 71% of scored surface intervals they were less than 3 body lengths apart. They also showed high synchrony in both shallow and deep dives (see Jensen et al. abstract). The two simultaneously tagged whales dove together for six of the seven deep foraging dives in the tag record. In only one of these dives did one whale undertake a deep foraging dive while the other stayed near or at the surface. During this separation, 58 (25%) of the 232 type A calls were recorded. All occurred during the
174 sec ascent phase of the dive, with the ascending whale producing 41 calls (at a rate of 14 calls per minute). All but two of the remaining calls were produced by the ascending whale’s “partner” near the surface. Calls produced during the separation were of very high amplitude; calls were audible at the surface even when produced at almost 400m depth.

These high call rates when the whales were separated suggest that stereotyped calls are used to maintain group cohesion, an idea that is further supported by the fact that no type A calls were recorded when the two whales were observed together at the surface. However, many of these calls were produced when the whales were only separated by small (<5m) vertical distances, indicating that they are likely to play other roles in mediating pilot whale social interactions as well.

Fig. 1. Spectrogram of a sequence of type A calls, produced by several different whales.
Responses to Chorus Noise and their Functional Significance in the Gray Treefrog, *Hyla versicolor*

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Male anurans often vocalize in choruses replete with background noise produced by the calls of conspecific males advertising to attract a mate. At breeding sites of the gray treefrog, *Hyla versicolor*, noise levels commonly range between 70 – 80 dB SPL (RMS), although they may be higher very close to groups of callers. Previous studies have demonstrated that males increase the number of pulses within calls and simultaneously lower call rate when acoustically stimulated by the calls of other individuals. In laboratory-based phonotaxis tests, females have showed a robust discrimination in favor of longer relative to shorter calls presented at identical call rates, although this preference can be reduced or absent under some experimental conditions, especially when call rates are lowered to stabilize pulse effort (call pulse number x call rate). In this study, we tested the hypothesis that adjustments males make in call duration render their calls less easily masked in noise and in this way facilitate communication under the less than ideal acoustic conditions of the chorus environment. We also tested whether the dynamic shifts in male calling behavior required changes in background calling, per se, or could be elicited through changes in the level of filtered background noise of appropriate spectrum.

In the experiment with males, we found that subjects altered the number of pulses in their calls while adjusting call rate in a fashion similar to that reported during broadcasts of calls. In phonotaxis tests with females using unmodulated background noise, noise amplitude-modulated like that of a natural chorus, and calls (10, 20, 30, or 40 pulses long) presented at either unequal or equal pulse efforts, we failed to find significant differences in noise levels at call detection thresholds with increases in call duration. However, calls were more easily detected (i.e. noise levels at detection thresholds were higher) when the noise background was modulated as compared to the unmodulated condition. Our results and those of an earlier study by our laboratory indicate that changes made by males of *H. versicolor* to the components of calling effort in response to changes in calling and background noise within choruses likely do not function to ameliorate the problems of signal detection or degradation due to interference. Accordingly, a small advantage accruing to males due to an inherent, albeit context-dependent, female preference for long calls (even at low call rates) may account for the dynamic calling behavior of male gray treefrogs.
Fig. 1. Noise levels at detection thresholds for female gray treefrogs presented with calls of 10 – 40 pulses (65 dB SPL RMS) under four different conditions (calls types presented at equal calling effort or unequal calling effort and with background noise unmodulated or modulated).
Harmonic misalignment in echoes causes image defocusing and masking release from clutter interference in the FM bat, *Eptesicus fuscus*

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Big big brown bats (*Eptesicus fuscus*) emit multiple-harmonic FM biosonar sounds with multiple-harmonics (*e.g.*, FM1, FM2) for orientation. When they fly in cluttered surroundings, echoes from off to the sides cause “blind spots” (clutter interference) that obscure perception of an open path forward. Nevertheless, big brown bats can fly and orient effectively in densely-cluttered surroundings, including in laboratory flight tests with arrays of obstacles having varying densities and spatial extents. Due to broadcast beaming and atmospheric absorption, echoes from off-axis or far-away clutter always are lowpass-filtered compared to flat-spectrum echoes from objects immediately to the front. The key to understanding how bats resist clutter interference is the relation between echo amplitude changes related to lowpass filtering and corresponding changes in the timing (latency) of neural responses evoked by lowpass echoes. For flat-spectrum echoes, delay acuity in “ordinary” two-choice discrimination tests normally is about 50 µs. When harmonics are misaligned (FM2 delayed by 3 µs or more re FM1), the bat’s delay acuity degrades sharply to 800 µs (Fig. 1, black diamonds). This effect amounts to a blurring or defocusing of the bat’s delay images for echoes with misaligned harmonics compared to the focused images for echoes with aligned harmonics. FM1 and FM2 always arrive at the same acoustic delay because air is a nondispersive medium over distances up to 10 m. However, neural coding of for lowpass echoes, such as from clutter, causes neural responses evoked by FM1 and FM2 to become misaligned in time by amplitude-latency trading (-16 µs/DB). Consequently, spikes evoked by FM2 always lag spikes evoked by FM2, in effect shifting FM2 to a later time within the bat’s auditory system. This internal auditory misalignment of harmonics defocuses the bat’s echo-delay images in the same fashion as acoustic misalignment. Experiments on masking-release reveal that, although defocusing makes the bat’s delay acuity much worse, it also suppresses clutter-induced blind spots that mask the presence or absence of flat-spectrum echoes from the critical region immediately in front of the bat. Both normal delay acuity and clutter masking are restored when neural responses to FM1 and FM2 are electronically realigned by adjusting FM2 earlier to offset amplitude-latency shifts. Bats use the harmonic structure of their sonar beam to delineate a frontal region for flat-spectrum, focused delay acuity surrounded by a region of defocused images and suppressed clutter interference from lowpass echoes. [Research supported by ONR and NSF grants, a Brown Univ. Dissertation Fellowship, and a JSPS fellowship]
Fig. 1. Performance in echo delay discrimination experiments for (1) deliberately misaligned harmonics (black diamonds) that cause degraded delay acuity (defocusing of delay image), (2) clutter-like lowpass-filtered echoes that misalign harmonics by amplitude-latency trading (white circles) combined with deliberate compensation of latency trading by shifting FM2 earlier than FM1, and (3) performance curve shifted to right by amount of amplitude-latency trading (gray circles) to demonstrate reciprocal relation between masking and defocusing.
Fish Sounds in the Southern California Bight

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Passive acoustic studies have been conducted in the Southern California Bight (SCB) for over 60 years, but most of the effort has been focused on marine mammal sound production. More than 100 families of fishes are known to produce sounds, as well, but their sound repertoires are better described for the species found in the Atlantic than in the Pacific Ocean. Fish produce sounds for a variety of reasons including mate attraction, agnostic interactions, and feeding. Their sounds mostly consist of low frequency pulses of variable duration, number, and repetition rate.

Two types of passive acoustic recorders have been deployed throughout the SCB since 2005: High-frequency Acoustic Recordings Packages (HARPs) and AURALs. The AURALs were deployed at 14 locations over a short term (1-40 days) in 2007 and HARPs were deployed repeatedly at two locations over a longer term (2-4 months) between 2008 and 2010. Both types of instruments were deployed between Santa Rosa Island and San Diego on shallow waters reefs (<300 m), where fish encounters are most likely. Automatic detection and manual scanning methods were used to identify fish sounds in these data. The automatic detection method used was spectrogram correlation; it was applied to sounds with long (> 1s) durations. Before manually scanning data, long-term spectral averages were first calculated from the data to allow quick access to sounds of interest. Presence of shorter pulsed sounds was then examined visually. Frequency and temporal characteristics of calls were measured and averages were calculated. Call rates were calculated based on the total number of sounds detected per hour of recording effort and daily and seasonal patterns in those rates were investigated.

Fish sounds produced in Southern California Bight were generally low frequency (<500 Hz), relatively low intensity, and consisted of repetitive pulses (Figure 1). A number of these sounds were produced by rockfishes, the most vocal of which appears to be bocaccio (*Sebastes paucispinis*). The spatial and temporal pattern of recorded fish sounds varied across the SCB and some sounds exhibited strong diel patterns. The daily pattern of sound production by bocaccio, with peaks in calling after sunset and before sunrise, has not changed for more than four decades.

Seasonal and diel patterns of sound production offer insights to the function the sound plays in the life of the fish. However, more directed studies are needed on the behavioral context of sound production in many species of fish found offshore of southern California. Such behavioral information would also facilitate the use of passive acoustic monitoring for long-term studies of fish population dynamics. Finally, these long-term recordings could provide information on the large-scale changes in the ecosystem through comparisons in the soundscape of a reef over time.
Fig. 1. Spectrograms of common fish sounds recorded in the Southern California Bight including sounds from bocaccio (*Sebastes paucispinus*) (upper left) and two unknown, but likely fish, sources. Lighter gray denotes stronger intensity sound.
In search of the neural template for birdsong in a bat brain?

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Singing is rare among mammals, having been reported for only a few primates, cetaceans and bats. The Mexican free-tailed bat (Tadarida brasiliensis) sings an elaborate, flexible, hierarchically-organized polysyllabic courtship song that bears striking resemblance to the songs of oscine songbirds. The neural network that underlies birdsong production is well characterized, but homologous circuits have yet to be identified in any mammal. A central question is where in the bat brain the neural template exists for coordinating the syllable sequences that comprise bat songs. In the songbird brain a region known as the Higher Vocal Center (HVC) contains the template for producing syllables, phrases and songs, and although HVC is often compared to the dorsolateral prefrontal cortex in humans, it has no clearly analogous structure in mammals. Since bats sing songs, do bats have a brain area that is functionally equivalent to the avian HVC?

Few details are known about the neural networks controlling complex vocalizations in mammals. At the highest level of the mammalian vocal motor pathway is the anterior cingulate motor cortex (ACg), from which both communication and echolocation calls can be evoked by microstimulation. We examined whether pharmacological excitation of ACg could reveal a mechanism for vocal complexity by testing whether syllable timing, temporal patterning or sequence production depended upon anatomical location of the injection, the type of drug injected, or drug dosage. We used stereotaxically-positioned glass micropipettes in restrained animals to first identify the best location for evoking vocalizations, and secondarily we used chronically-implanted injection cannulae in unrestrained (tethered) bats to test the effects of drug and dosage on the types and patterns of vocalizations generated. Post-injection vocalizations were recorded for two hours and compared to control saline injections, and any additional non-vocal locomotor side-effects were also characterized.

Injections of the glutamate agonists kainic acid (KA) and DL-homocysteic acid (DLH) and the GABA antagonist bicuculline (BIC) each evoked calling when injected into a focal region of the ACg, and the type, number and pattern of vocalizations was found to vary with drug, dose and time after injection. When injected into the ACg just above the genu of the corpus callosum, low doses (≤1 mM) of each drug evoked rapid trains of echolocation pulses. Injections of KA at doses greater than 1 mM always produced super-stereotyped polysyllabic vocal sequences closely resembling the free-tailed bat’s courtship song. Using a range of BIC concentrations we were able to extract a broad repertoire of the bats natural vocal patterns. Intermediate concentrations (1-5 mM) evoked steady streams of doublets, multiplets and trills. 5-10 mM BIC initially evoked trills and buzzes but these were subsequently replaced by vocal sequences closely resembling natural foraging sequences, including the repetition of a progressive emission of search, approach, and buzz phase echolocation pulses. Surprisingly however, foraging sequences were not the highest level of output of the system. Injections of 10 mM BIC rapidly induced trills, buzzes and foraging sequences, but these were soon replaced by the repetitive production of courtship songs. As the drug effects waned this pattern of increasing vocal complexity reversed, going from song back to buzzes and trills, pairs of communication calls, then to multiplets, doublets, and finally returning to individual echolocation pulses. Similar patterns were evoked from either side of the brain, and we were also able to evoke courtship songs from two females. The results indicate that vocal
complexity is tightly coupled to level of excitation in the vocal control center of the ACg. It also indicates that both courtship songs and foraging sequences uttered by adult bats reflects activation of hard-wired motor templates that can be executed outside of a natural context. It is hypothesized that different levels of vocal complexity reflect different activation states of a distributed cortical network controlling the bat vocal motor pathways, and that this network appears to be centered in the ACg. In this sense then, the bat ACg is functionally equivalent to the songbird HVC.

![Fig. 1. Spectrogram of the repetitive singing behavior evoked by chemical microstimulation of the free-tailed bat cingulate cortex.](image)

However, these results only illustrate that the network can be activated through the ACg and does not demonstrate that the neural template for song is actually housed in the ACg. Using c-fos immunohistochemistry we asked what other brain areas were activated as a result of microstimulation of the ACg. In addition to all the previously reported components of the mammalian vocal motor pathway, we found high levels of immediate early gene expression in the contralateral caudate nucleus, globus pallidus, mediodorsal thalamus, and contralateral ACg. These results are consistent with a hypothesis that similar to songbirds, bat song production may require activation of a forebrain straitothalamic feedback loop that might participate in the determination of syllable selection, timing, and sequencing. Ongoing research is testing this hypothesis.
The acoustic ecology of the California mantis shrimp (*Hemisquilla californiensis*)

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Acoustic communication plays a major role in the behavioral ecology of various marine organisms, yet little attention has been given to acoustic communication in marine crustaceans. Furthermore, the interplay between anthropogenic noise and the acoustic ecology of crustaceans remains virtually unexplored. In this study we investigated the acoustic environment of a benthic stomatopod crustacean, the California mantis shrimp (*Hemisquilla californiensis*, Crustacea, Stomatopoda).

The first documentation of the “rumbles” produced by *H. californiensis* was a laboratory-based study in 2006 (Patek and Caldwell 2006). Rumbles lasted less than 2 seconds and the mean dominant frequency was $45 \pm 10$ s. d. Hz ($n = 53$ rumbles). The general function of this sound and whether or not females are capable of generating it remains unknown, as females did not produce rumbles in the study. While the laboratory-based recordings provide a starting point for characterizing this sound, field recordings are essential for interpreting the rumble’s function and role in the ecology of mantis shrimp.

The three primary goals of this study were to: 1) describe the sounds of *H. californiensis* in its natural habitat; 2) explore diel patterns of behavior and sound production; 3) examine the presence of anthropogenic noise in the acoustic habitat of the California mantis shrimp. We employed several tools and techniques to accomplish these goals, including a coupled audio-video system and an autonomous recording unit.

Recordings were obtained in the naturally occurring communities of *H. californiensis* off the coast of Santa Catalina Island, CA, USA, in March of 2009. A coupled audio-video system was placed in front of several animal burrows by a SCUBA diver, and the resulting footage was later imported into digital audio files for analysis. These recordings (48 kHz, 16-bit sampling rate) were used to describe general characteristics of the rumbles. The average rumble had a dominant frequency of $167 \pm 0.66$ s. e. Hz, and lasted $0.2 \pm 0.0013$ s. e. sec ($n = 3858$ rumbles from an undetermined number of individuals). We found that the rumbles were typically produced in groups of twos, threes, and fours, which we will now refer to as “rumble groups” (Figure 1). The leading rumble of each group was louder by an average of $5 \pm 0.7$ dB and longer in duration by an average of $0.093 \pm 0.05$ seconds than the second rumble in the group ($n = 304$ rumbles from approximately 17 individuals).

Despite these general similarities, recordings from various individual burrows yielded rumbles that differed in dominant frequency, number of rumbles per group, and temporal patterning. We also recorded co-occurring and overlapping rumble bouts (Figure 2), suggesting that multiple individuals within the vicinity of the hydrophone were rumbling at the same time. Our recordings took place during the early part of the mating season, when males are highly competitive for burrow space and actively attempt to recruit females into their burrows to mate (J. Engle, pers. comm., Basch and Engle 1993). Therefore, it is possible that individuals use rumbles to establish territories and/or attract potential mates.

In the second step of this investigation, an autonomous recording unit (Clark and Clapham 2004) was deployed and run continuously (32 kHz, 16-bit sampling rate) for an 8-day period. We scanned this recording’s spectrogram both visually and aurally and found distinct trends across the 8 days. During crepuscular periods, loud, rhythmic rumbles were audible. At this time of day, *H. californiensis* is typically found guarding its burrow entrance (Basch and Engle 1993). At night, the mantis shrimp were acoustically active, but their rumbles were lower in both frequency and received level than during the day. Because the burrow is typically closed at night for protection from predators (Basch and Engle 1993),
these recordings of quieter rumbles suggest that sound production may continue even while the burrow is closed.

![Figure 1](image1.png)

Figure 1. Typical *Hemisquilla californiensis* rumble group, consisting of three rumbles (labeled 1, 2, and 3). Spectrogram parameters: Hann window, 256 samples; 3 dB filter bandwidth, 11.2 Hz; DFT, 8192 samples; 50 - 500 Hz bandpass filter.

![Figure 2](image2.png)

Figure 2. Spectrogram of coincident rumble groups of *Hemisquilla californiensis*, labeled a or b. Boxes surround rumble groups, not single rumbles. Spectrogram parameters: Hann window, 256 samples; 3 dB filter bandwidth, 5.62 Hz; DFT, 1024 samples; 50 – 500 Hz bandpass filter.

The waters near Santa Catalina Island are frequented by small boats and large shipping vessels, which collectively produce a tremendous amount of acoustic energy in the communication band of *H. californiensis* (i.e. 100-500 Hz). During periods of intense vessel noise, we could not determine whether mantis shrimp ceased rumbling or whether we were simply unable to detect them. However, given the fact that vessel noise was detectable during a large portion of the day, we suspect that acoustic masking is a frequent phenomenon in this habitat. Given the potential deleterious effects of acoustic masking in other taxa, this omnipresent and acoustically overlapping vessel noise may substantially impact the acoustic ecology of the California mantis shrimp. Marine invertebrates should be included when considering the effects of anthropogenic noise on aquatic animals.

**References**


Passive acoustic tracking of singing humpback whales (*Megaptera novaeangliae*) on a North Atlantic feeding ground

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Humpback whale song occurs extensively on higher-latitude feeding grounds outside of the winter breeding season or migration routes. The impetus for singing behavior on the feeding grounds is unclear and may be linked to low-cost opportunistic male advertising, intra-sexual display and/or hormone levels. To date there have been very few observations of singer behavior outside of the breeding grounds. This study utilizes passive acoustic tracking methods to investigate the movement patterns and swimming speeds of humpback whale singers on a North Atlantic feeding ground.

Continuous recordings were obtained from an array of 10 autonomous marine acoustic recording units deployed in Stellwagen Bank National Marine Sanctuary throughout 2009. During periods of peak song occurrence in April-May and October-November, individual singing whales were localized and tracked throughout the array. A spectrogram correlation sum estimation method (Cortopassi & Fristrup, unpublished) was used to compute locations from song across multiple recording units. A new location was computed every 1-2 minutes for the duration of a song session, which was defined as a continuous period of song from a particular singer without a pause of more than 5 minutes. Tracks were constructed for 36 distinct song sessions. Song sessions were selected from different days spanning month-long periods in both spring and fall, to increase the probability of including multiple individuals in the analysis. Each track was analyzed to determine the distance traveled, swimming speed, directionality, and space use of the singer. Additional singers apart from the one tracked were often present during tracked song sessions, but were usually outside the array and therefore too far away to be tracked. On 4 occasions when two singers were within the array they were tracked simultaneously to examine singer interactions. A high level of variation in singer movement patterns was found; ranging from slow, apparently directionless meandering to faster, highly directional movement. Tracked song sessions were 30 minutes to several hours in duration, and singers traveled distances ranging from 0.9 km to 20.1 km. Mean swimming speed was 2.1 ± 0.98 km/hr, and is comparable to values reported by previous studies conducted on breeding grounds and migration routes. Patterns and rates of movement indicated that most singers were actively swimming, rather than remaining stationary or passively drifting. There were no clear differences in singer behavior between the April-May period when males had recently arrived on the feeding grounds and the October-November period when they were preparing to depart for the breeding grounds.
The changing acoustic environment in the ocean and its relation to baleen whales is a current topic of interest that is being studied using a variety of methods. Non-invasive acoustic tags allow recordings to be made directly at the focal animal’s location, and these recordings can then be compared with the animal’s behavior. To this point, research on the humpback whale breeding ground, which is an important and potentially sensitive habitat, has only focused on adult whales. Limited acoustic recordings from calf groups have been made by snorkelers (Pack et al. 2005; Zoidis et al. 2009), but there has been no directed, close range recording project focusing on calf acoustic behavior, and associated calf underwater behavior is completely unknown. We attempted to fill this knowledge gap by deploying acoustic tags on humpback whale calves on a breeding ground.

Non-invasive, suction cup acoustic tags (DTAGs; Johnson and Tyack 2003) were attached to three humpback whale calves on the Hawaiian breeding grounds in February and March of 2011. Calves were less than six months old, but care was taken to avoid approaching very young calves that indicated any signs, physical or behavioral, of birth within one month or who showed a particularly close pair bond with the mother. All three calves were with their mothers and were part of social groups containing between zero and three male escort whales. Tag attachment durations ranged from 3 to 4.5 hours.

Analysis of a subset of the data (one tag of three) showed a moderate rate of sound production: lower than that of adult whales on the feeding grounds but much higher than that of adult whales on the breeding grounds (Stimpert 2010). During periods of rest or stationary behavior, the sound production rate was approximately 12 sounds/hour, whereas during more active periods when other male adults were present (a more competitive environment), the sound production rate was approximately 28 sounds/hour. These sounds cannot be definitively attributed to the calf because of the close proximity of other whales in the group, but further analysis of sound levels and type will elucidate this.

In addition to standard sounds recorded, an acoustic signature believed to be physical contact, or gentle rubbing, between the mother and calf was also heard. This “rub” sound was more common during periods of rest or stationary behavior (17 rubs/hour) than during periods of competition with more than one adult whale present (10 rubs/hour).

Lastly, some previously undocumented sounds were recorded at the time that another male escort joined the group. This was coincident with surface activity from the primary escort, and a sudden increase in swim speed by the calf. The sounds were high intensity, high frequency, and “alarm-like”, and may have been a signal from one of the adults or a reaction to the social interaction.

These preliminary analyses suggest that acoustic communication is relatively common in mother/calf groups, and we speculate that the increase is due to elevated sound exchange between the mother/calf pair, especially during periods of active behavior change, such as when multiple male escorts join or leave the group. The ability to identify instances of physical contact between mother and calf via the acoustic record is also encouraging, and the decrease of this type of behavior during active periods of the group indicates that physical contact may be impeded by the presence of other adults.
References


Some reflections on chorusing

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Chorusing is most commonly associated with concurrent vocalizations of conspecifics within an identified proximity of mutual influence. The artifacts are identifiable group pattern behavior. In this presentation chorusing is examined from an acoustical response perspective rather than a vocalization behavior. In this context chorusing occurs not only in arthropods, anurans, sciaenids, humans, and some mysticetes, but also in the flight synchronization of birds and shoaling of fishes.

Sound and song production in many animals is sexually dimorphic inasmuch as the males of most species either exclusively produce sounds, or produce the more complex sounds of the species. As a consequence chorusing is commonly framed under the competitive rubric of advertizing breeding fitness. But chorusing also allows an individual singer to conceal their presence to predators within the sound field of the chorusing group, pointing to a cooperative aspect of chorusing.

Vocal chorusing can be either synchronous (common in many stridulating insects) or asynchronous (common in anurans and fish). Synchronous chorusing is facilitated by neural blanking in the individual, synchronized with their sound, thus the animal does not hear their sound or the sounds of synchronized conspecifics, but does hear sounds outside of their blanking interval and thus out of sync – providing them with a “negative target” with which to sync. As bio-oscillators tend toward synchronization the mechanism that drives asynchronous chorusing to not synchronize has yet to be determined.

The cooperative aspect of chorusing suggests that other strategies may also be present, including collective annunciation of the group fitness, physical extents, and identification of external threats to the chorusing “acoustic community.”

Signal attributes such as phase complex, spatially ambiguous signals, or “triggering sequences” can give cues to the group purposes of chorusing. Auditory systems such as lateral lines of fishes or large cranial fenestra in birds also suggest the input systems of acoustical stimulus that facilitate spatial chorusing. Acoustical interruptions to chorusing cues such as impulse noise or broad-band masking may have un-accounted biological costs to chorusing animals.
Gain control of Emitted Intensity in Echolocating Bats.

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Echolocating bats adjust their sonar calls to the constraints of habitat, prey and capture behavior. A large number of studies on many bat species have demonstrated how spectral and temporal parameters are constantly adjusted to adapt the biosonar to the context. In general the calls are shorter, more broad banded and repeated at a higher rate, the closer the bats fly to background or prey.

The directionality of bat echolocation calls defines the width of bats’ sonar “view,” while call intensity directly influences detection range since adequate sound energy must impinge upon objects to return audible echoes. Both directionality and intensity are thus crucial parameters for understanding biosonar signal design. Recent results have shown that bats actively control also these acoustic features of their sonar calls. They adjust the emitted intensity and directionality to the habitat, such that bats hunting for prey out in open space emit an intense narrow sonar beam for long range sonar, while bats hunting closer to background in more confined space emit less intense and less directional calls (Fig.1).

![Fig. 1. Echolocation calls of Daubenton’s bat (*Myotis daubentonii*) are louder and more directional in the open compared to the cluttered space of the lab. The curves on the right show sonar beam directionality in the field (inner narrow beam, grey/red) and in the lab (outer broader beam, black) at 55 kHz (Surlykke et al. 2009).](image)

Bats do not only adjust the emitted intensity to habitat, but also dynamically from call to call in response to sensory feed back as they approach objects. A decrease in output intensity with decreasing distance has been verified in all bat species studied so far. The results have suggested a logarithmic relationship between distance and emitted intensity, with a slope of the decrease close to -6dB / halving of distance, which would keep intensity impinging on the object approximately constant (Fig.2). However, the logarithmic model implies a source level, which is ever increasing with distance, which is physically and biologically impossible.

Here we present new data to show, that the slope is much steeper, i.e. that in most situations bats reduce their output level by much more than -6dB per halving of distance, often by more than -20dB per...
halving of distance, when approaching objects, in particular if the start compensation close to the object. We fitted our model to data from individual flight. Previously, models have been fitted to pooled data, which may produce incorrectly shallow slopes. Thus, the results presented here strongly emphasize the importance of analyzing single events.

Fig. 2. When bats approach objects and background, they reduce their emitted intensity, the source level (SL); the shorter the distance to the object the lower the SL. Pooled data, left, are for Noctilio leporinus from Panamá (Surlykke & Kalko, 2008). The data are fitted to a logarithmic relationship between distance and emitted intensity, with a slope of the decrease close to -6dB / halving of distance. On the right is an individual flight of Phyllostomus hastatus showing much steeper slope and better fit, R²=0.9 (Nørum, Brinkløv, Surlykke in prep)

It is a biological reality that no bat can increase its source level ad infinity. Thus, we developed a new model for source level distance compensation, which includes the concept of a maximum source level. The model offers a method for estimating the maximum output and also for estimating the bat’s detection distance, which is assumed to be the distance, where source level compensation starts.

Bats flying close to background or in cluttered space can improve the echo-to-clutter ratio for the echo-object at which they point their sonar beam, both by adjusting emitted intensity and directionality. Decreased output intensity will reduce echoes from objects at longer range. Increased directionality will reduce echoes from off-axis objects (Brinkløv et al. 2011). Thus, bats have a high degree of dynamic control of the echo-scene they perceive. The results are discussed in light of habitat constraints and interaction between bats and their eared prey.

References:


Mating decisions have substantial fitness consequences for sexual organisms. However, organisms experience potentially-conflicting pressures during the process of mate choice. Males within a species generally vary in ways that are important to females but the aspects of the male phenotype that females can assess to discriminate among males are often similar in multiple co-occurring species. Females responding to the most attractive signals run the risk of incompatible heterospecific matings if co-occurring species have more extreme values of attractive traits. Choosing a high quality conspecific can be beneficial to females, but responding to a heterospecific male represents an even bigger fitness cost. Consequently, females may be faced with trade-offs between identifying optimal conspecifics and discriminating against similar heterospecifics.

This potential conflict can be resolved in several ways. First, in the presence of heterospecifics, females may evolve to use one set of traits to discriminate conspecifics from heterospecifics and rely on a different set of traits to differentiate among conspecifics. In this scenario, females are predicted to show closed preferences where the female preference optima match the male trait mean for traits involved in discriminating conspecifics from heterospecifics. Female preferences will be open-ended for traits used to differentiate among conspecifics. A second possible outcome of trait overlap among species is that female mating preferences are constrained by the presence of heterospecifics, resulting in decreased capacity for females to differentiate among conspecifics. Finally, discrimination and choice rules may also depend on how many species occur in a community, since this will influence how crowded the signaling space is, and how much overlap there is between the signals of different species.

I am using tree crickets in the genus *Oecanthus* to investigate how mate choice is shaped by co-occurring species. There are approximately 20 species of *Oecanthus* in North America and up to seven congeners can be heard in one place at one time. Males in this genus use relatively simple stereotyped calls to attract females (Figure 1) and females respond phonotactically by walking toward preferred males. Males produce sound by rubbing their two front wings. One wing has a scleratized region with many small teeth (the file). When this portion is drawn across a hardened region of the other wing (the scraper), the impact induces resonance in the wings. The two predominant call characteristics are the pulse rate and dominant frequency (perceived as pitch) and both are highly repeatable across time. Pulse rate corresponds to the number of wing closures per second while dominant frequency is related to wing size.
Fig. 1. Many tree cricket species have similar call structure. Each panel contains an oscillogram (upper trace) and a spectrogram (lower trace) created from 0.5 second of calling. Oscillograms show the amplitude of the signal and spectrograms show the amount of energy present at a given frequency (pitch) at a given time. Calls are consistent over much longer periods of time. In these species, there is no higher temporal structure to the calls and the amplitude and dominant frequency are relatively consistent within calls. Numeric frequency values in each panel represent the dominant frequency. Higher frequency bands are harmonics (integer multiples of the dominant frequency).

To determine whether female preferences for male calls are open ended (females prefer the most extreme value available) or closed (females look for an exact value of the male trait), I am measuring female responses to synthesized calls with varied combinations of male call characteristics. By comparing preferences of the same focal species when found with different background species, I am investigating which, if any, preference components change in response to the species composition. I am also assessing whether regional variation observed in male traits is reflective of variation in female preferences for these traits.

To determine whether the species composition affects the variance of signals, I am comparing the variability of male signals in populations with few and many species. Assessing the variance in the male signal, the morphology underlying the male signal, aspects of morphology not related to calling, and female morphology, will allow me to parse whether the level of male variability is consistent with acoustic niche partitioning in some or all call characteristics.
‘Syntactic’ Rule Learning in Zebra Finches?

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A key requirement for language learning is the ability to detect structure and the rules underlying structure when exposed to a stream of speech sounds. Major advances in understanding this ability originate from experiments using Artificial Language Learning (ALL), in which subjects are exposed to artificially constructed strings of speech sounds (e.g. syllables) devoid of any meaning, but structured according to a particular algorithm. While animals don’t apply rules of any great complexity in producing vocalizations, it is unclear how far their abilities reach when it comes to detect the presence of underlying rules in perceiving structured acoustic stimuli.

A specific example concerns rule learning of the form XYX, where the first element is identical to the last one in the sequence and differentiating it from XXY and XYY. Marcus et al (1999) showed that seven month old infants can distinguish XYX from XYY speech stimuli. Regarding the abilities of non-human animals to detect such structure, the results are ambiguous. Also, the emphasis in experiments on rule learning was on showing that the animals could transfer from a training set of specific Xs and Ys to a novel set, rather than exploring the exact rule used by the animals to distinguish these patterns. The XYX vs XXY task can be resolved in various ways, e.g. by responding to presence or absence of a repeated element, by noticing that first and last element of the sequences are either the same or different, etc..

Arguably the best, but surprisingly hardly used model species for ALL research are songbirds. In contrast to most mammal species, songbirds have complex, learned vocalizations, and birdsong researchers have discovered remarkable cognitive, neural and genetic parallels between the processes involved in the production, perception and development of language and birdsong. Against this background, we examine whether, and if so how, a songbird, the zebra finch, is able to discriminate three-element sequences ABA and BAB (A and B being particular elements) from AAB, ABB, BAA and BBA sequences.

We show that zebra finches can learn this discrimination. Next we examine two questions: (1) what is the ‘rule’ used by zebra finches to distinguish the stimuli, and (2) can they transfer the acquired distinction to novel types of elements? To this end we tested the birds with deviant probe sequences, novel element types and also presented them with subsequent training and testing on more complex and longer sequences. We discuss our findings in relation to those obtained by studies of similar rule learning in other species.
Cetacean Communication

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The ocean provides a different sensory environment than we are used to on land. Chemical signals disperse more slowly in water than in air, vision underwater is limited to ranges of tens of m, but underwater sound can travel for hundreds of km. Cetaceans are large and mobile, with many species routinely swimming >100 km each day. They have evolved modes of acoustic communication that can mediate interactions over relevant separation distances from hundreds of m to hundreds of km. Baleen whales such as blue and fin whales disperse during their breeding season into temperate and tropical oceans. These whales, which can be widely separated, produce low frequency songs that can be heard hundreds of km away. Other species such as humpback whales, which congregate on higher-density breeding grounds, produce more complex songs with higher frequency components that are audible over tens of km. These reproductive advertisement displays mediate male-male competitive interactions and interactions between males and females. While full-bandwidth songs of humpbacks only carry tens of km, the acoustic structure of song forms a vocal tradition that can carry thousands of km over years.

Most cetaceans regularly swim out of visual range from partners (e.g. mother and dependent young, strongly bonded individuals, members of stable groups). They use contact calls to maintain cohesion when out of sight and to reunite after separation. The acoustic structure of these calls depends upon the range over which they must function, upon the ambient acoustic environment, and upon the social structure typical of the species. Right whales produce a frequency-modulated upsweep to maintain contact. This call uses a frequency range that overlaps with low frequency shipping noise. When shipping noise increases, the whales call more loudly, and as shipping noise has increased over the past 50 years, right whales have elevated the frequency of these calls out of the dominant noise band. These mechanisms to compensate for noise are an underappreciated selection pressure for vocal production learning, in which animals can learn to modify their vocal output based upon auditory input.

Sperm whales use rhythmic series of modified echolocation clicks, called codas, for their communicative calls. Sperm whales grow up in matrilineal family units, but most groups sighted at sea are composed of more than one of these family units. When one unit joins another unit, they select a unit that shares their coda repertoire. All of the units that share the same coda repertoire are called a vocal clan. Vocal clans may extend over thousands of km, but several different clans may be sympatric. These results suggest that sperm whale units use codas as they decide which other units to join.

Delphinid cetaceans produce stereotyped calls used to maintain individual-specific social relationships and group cohesion. I will describe an example where pilot whales separate when they make deep foraging dives together. They use bursts of echolocation clicks, called rasps, to come together at the start of their ascent to the surface. When one pilot whale dives alone, it produces a stereotyped call as it ascends. Members of its group at the surface respond, with call exchanges as they reunite. Killer whales have complex group-distinctive repertoires of stereotyped calls, with independent high- and low-frequency components. The high-frequency components are more directional than the low. By comparing the amount of energy in the high and low frequencies, any whale that knows the usual proportions can tell whether the caller is moving towards or away, which may make it easier for animals to alter their
movement patterns to stay together. While each killer whale has its own group-distinctive repertoire of these complex calls, the calls may be made up of a few dozen subunits. There is some evidence that these subunits may be shared among different killer whale populations. The subunit view suggests that killer whales construct complex calls by combining unique sequences of subunits.

Bottlenose dolphins produce frequency modulated tonal whistles. When a dolphin is separated from its group, it will tend to produce a stereotyped whistle, called a signature whistle, which is individually distinctive. Bottlenose dolphins have a fission-fusion society in which relationships between specific individuals such as a mother-calf pair, or pairs or trios of adult males in an alliance, can be very stable. As males form an alliance, their whistles become more similar. This pattern of convergence of calls as animals form a group has been observed in a relatively broad array of birds and mammals. In addition, dolphins with strong social bonds sometimes imitate the signature whistle of their partner. These whistle copies have the overall contour of the other animal’s signature whistle, but also have features that identify them as copies, so they are not thought to be used for deception. Song matching can be used for agonistic interactions between songbirds, but signature whistles are imitated in more affiliative contexts. Dolphins can use imitations of arbitrary synthetic signals to label manmade objects; it has been hypothesized that they may copy signature whistles to label other individuals.

Many cross-taxon comparative reviews of vocal learning and communication emphasize birds and terrestrial mammals. This is surprising, as the abilities of marine mammals to learn to produce novel sounds are much better developed than those of non-human terrestrial mammals. Marine mammals use vocal learning to compensate for noise, in the development of sexually selected songs, and to develop individual- or group-distinctive calls. The songs of whales involve complex sequences of signals with a hierarchical structure every element of which changes over time. The subunit view of killer whale calls suggests that these calls may also be formed by learning many different sequences of shared subunits. Opportunities to compare the sequencing of song units and call subunits with syntactic properties of communication signals in humans and other animals is underexploited. The convergence of contact calls as animals form a group has parallels with birds and terrestrial mammals, but there is less evidence for mimicry of individually distinctive calls. While there are strong indications that dolphins may use imitations of signature whistles to label other individuals, an important unanswered question involves whether dolphins make referential use of imitated signatures.
A Robust Technique for Detection, Classification, and Localization of Marine Mammals

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Automatic detection, classification, and localization (DCL) techniques play an important role in passive acoustic monitoring of marine mammals. The basic problem associated with automatic DCL techniques design is the lack of a priori information about the signals and the presence of noise transients overlapping with signals in time and frequency domains. Another problem is locating a single or multiple acoustic sources producing similar signals closely spaced in time domain, see Fig. 1. Finding time difference of arrival (TDOA) estimates for similar closely-spaced signals over different channels may be a difficult task. The traditional approach to this problem is based on computing the peaks of pair-wise cross-correlations of waveforms or spectrograms. The presence of similar closely-spaced signals may result in outliers in TDOA estimates which, in turn, produce outliers in the position estimates. As a result, in a multi-signal situation the probability of outliers produced by traditional TDOA-based location techniques can be unacceptably high.

In this presentation, the problem of automatic detection, classification, and localization of marine mammals using large arrays of hydrophones is considered. The goal of this work is to design a robust DCL technique reducing the outlier rate. The proposed solution is based on a multistage hypothesis-testing technique using a spectrogram-based detector, a feature-vector testing algorithm, and a TDOA-based locator.

In the initial stage, the spectrogram-based detector is applied to each channel. In the second stage, a feature vector is extracted and tested for classification of signals of interest. The TDOA-based localization of signal sources is implemented in the final stage. The main contribution of this work is a robust algorithm for computing TDOA estimates. To reduce the rate of outliers, a weight function for each cross-correlation peak is computed. The weight function is based on using such non-energetic signal parameters as signal duration, peak frequency, etc. Using weight processing can reduce the peak levels produced by different signals. As a result, the outlier rate of position estimates can also be decreased.

To test the proposed technique, the problem of DCL of North Atlantic right whales, *Eubalaena glacialis*, is considered. The technique was applied to the data set collected from February 18 to May 16, 2009, in Cape Cod Bay, MA. As an example, the spectrograms of the sensor outputs containing multiple closely-spaced signals from the same North Atlantic right whale are shown in Fig. 1 (left). The location estimates obtained by the traditional and the proposed location algorithms are shown in Fig. 1 (right).

Test results show that the proposed DCL technique makes it possible to detect 70% – 90% of signals and to locate 95% – 99% of sources closely spaced to the array. It provides a 2 – 3 times lower outlier rate as compared to the conventional location algorithm. The technique can also be adjusted to detect and localize fin whales, humpback whales, bowhead whales and other marine mammals producing low-frequency calls.
Fig. 1. Spectrogram of detected North Atlantic right whale (*Eubalaena glacialis*) vocalizations (left) and corresponding location estimates (right) obtained by the proposed technique. Outliers provided by the conventional algorithm are shown by red squares.
The relative role of noise and hybridization in shaping the advertisement call of the poison frogs Oophaga histrionica and Oophaga lehmanni

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Factors promoting geographic variation in communication signals can promote phenotypic divergence between populations and eventually reproductive isolation. Among vertebrates, poison frogs (Dendrobatidae) represent good models to study the evolutionary biology of multicomponent signals and its implications in speciation for two reasons. First, they use multicomponent signals to communicate with conspecifics and heterospecifics. Second, multicomponent signals used by poison frogs commonly exhibit intraspecific geographic variation. Among the mechanisms supposedly promoting geographic variation in multicomponent signals of poison frogs are divergent female choice preferences, adaptation to local predators, mimetic processes, and genetic drift. However, noise on streams and hybridization has not been proposed yet as a selective factor shaping and promoting intraespecific variation in a multicomponent signal such as the advertisement call.

To test potential causes promoting the variation in multicomponent signals in poison frogs, we characterized the geographic variation in the temporal and the spectral features of the advertisement call of three populations of Oophaga histrionica (Naranjo, Delfina, Danubio) and two populations of Oophaga lehmanni (Red and Yellow morph) (see Figure 1). These poison frogs live in tropical wet forest where males usually establish territories, call and mate in places away from streams. However, two populations live in riparian forest (Naranjo, Red lehmanni), places in which the acoustic environment is influenced by noise produced from large streams. Moreover, previous cross-breeding experiments and molecular evidence have shown that at least one population (Danubio) resulted from hybridization between populations of O. histrionica (Delfina) and O. lehmanni (Yellow).

We conducted fieldtrips of 3-8 days each, from April 2009 to January 2010 to four study areas in the western Andes of the department of Valle del Cauca, Colombia. In each study area we located calling males, and recorded their advertisement calls under natural conditions except for individuals of Yellow lehmanni that were recorded in laboratory. Body size, temperature, and ambient noise level in calling places under natural conditions were registered for each male recorded. We obtained nine call records for Naranjo, eight for Delfina, nine for Danubio, ten for Red lehmanni and seven for Yellow lehmanni.

Multivariate analysis showed that advertisement calls of populations differed in spectral and temporal features. On one hand, the two populations (Naranjo and Red lehmanni) living in noisy habitats close to streams and rivers exhibited higher peak frequency, than populations living away from those water bodies. These results support a previously unconsidered role of noise on streams as a selective force promoting an increase in call frequency in poison frogs, although pleiotropic effects and other selective factors acting in body size cannot be discarded. On the other hand, variation of temporal call features was according to expected by the phylogenetic relationship among populations. This means, temporal call features were more similar between most related populations (Naranjo and Delfina, Yellow and Red lehmanni) than between less related populations. Contrary to our expectation, spectral and temporal call features of the hybrid population (Danubio) were not distinctive, but were very similar to respective call traits of Yellow lehmanni, one of the parental populations.

Overall, our results suggest that advertisement call on the studied populations is a multicomponent signal shaped by extrinsic and intrinsic factors acting simultaneously and semi independently. This
means, spectral components are shaped by environmental cues (i.e. noise on streams), while temporal components tend to reflect the relationship among populations (i.e. hybrids, hybrid parental populations, no parental populations). Whether this geographic variation in advertisement call, in conjunction with the high variation in coloration exhibited by these populations, is promoting reproductive isolation deserves more study.

Fig. 1. Habitat preference (riparian habitats and forest away from streams), and phylogenetic relationships among the three populations of *Oophaga histrionica* (Naranjo, Delfina, Danubio) and the two populations of *O. lehmanni* (Yellow and Red morph) included in this study. The topology is based on mitochondrial markers COI and 16S using Bayesian and maximum likelihood methods (Medina 2008). Molecular analyses based on microsatellites indicate that Danubio is a hybrid population produced by crossbreeding between Delfina and Yellow *lehmanni* (Medina 2010).
Talkative males are more attractive: relation between vocal behaviour and mating success in the Lusitanian toadfish

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Many studies on communication systems have centered on the relationship between signals and reproductive success. Determining the characteristics of signals that lead to enhanced mating success may help understanding how a communication system may have evolved and how sexual selection may have shaped signaling (Andersson 1994). Although the relation between acoustic signaling and reproductive success has been considerably explored in several taxa, it has been scarcely studied in fish, despite the behavioral evidences that point to female preferences for specific acoustic features (eg. Myrberg et al. 1986).

In the Lusitanian toadfish (Halobatrachus didactylus), nesting males depend on acoustic signals (boatwhistle) to attract females for mating and advertise their quality (condition) primarily with boatwhistle calling rate and calling effort (Amorim et al. 2010). In this study we relate the vocal behaviour with the reproductive success in the Lusitanian toadfish.

We confined 56 type I (parental) toadfish males in artificial nests over circa two weeks during the peak of the breeding season and recorded their vocal behaviour. Nests were wrapped with a plastic net to prevent males from escaping and to ensure individual identity throughout the recordings (Fig. 1a). A small opening (10 cm x 5 cm) was created at the nest’s entrance to allow the access of females, sneakers or smaller type II males and prey items. The number of mate advertising calls (boatwhistles) emitted throughout the recording period and the number of eggs in the nest was quantified for each male. Calling rate (number of boatwhistles min⁻¹) and calling effort (percentage of time spent calling) were determined.

From the total of 56 toadfish males confined in the artificial nests, 51 toadfish (91.1%) showed vocal activity and 16 specimens (28.6%) presented clutches in their nest indicating successful attraction of gravid females. Nesting males also attracted other conspecific males, which were in a position typically occupied by sneakers (type II males) - see Fig. 1a. These males, however, were mostly type I males (n=10, 91%), but with significantly lower TL (Mann-Whitney U test: U = 89, n<sub>nesting fish</sub> = 11, n<sub>nest parasite fish</sub> = 7, p = 0.008) and body condition (Mann-Whitney U-test: U = 2, n<sub>nesting fish</sub> = 11, n<sub>nest parasite fish</sub> = 7, p < 0.001, Fig. 2a) relative to the vocalizing nesting type I males.

The mean and maximum calling rates were significantly higher in nesting toadfish males with eggs than in males without any clutches (Mann-Whitney U test: U = 66.5-70, n<sub>eggs</sub> = 14, n<sub>noeggs</sub> = 40, p < 0.001). The calling effort also differed significantly between these two fish groups (t-test: t=-3, n<sub>eggs</sub> = 14, n<sub>noeggs</sub> = 40, p ≤ 0.001). In a multiple linear regression model (stepwise procedure), calling rate and calling effort were the best predictors of the number of eggs in a nest, and morphometric features such as total length, relative gonad mass, relative sonic muscle mass and male condition did not enter the final model (linear regression, R²=0.581, F<sub>1,53</sub>= 35.32, p < 0.001).
Fig. 1. (a) Experimental setup showing a parental toadfish male confined inside the artificial nest. A hydrophone (H) was placed 10 cm from the nest in order to record male’s vocal activity. Note the female inside the nest laying eggs and a satellite male that was often found outside the nest close to the entrance. Illustration by Marta Bolgan. (b) Relation between the maximum calling rate and the number of eggs. The number of eggs are square-root-transformed and the maximum calling rate are log-transformed.

We provide first evidence that the vocal behaviour strongly determines reproductive success in a teleost fish and suggest that acoustic signaling at higher rates and in a regular fashion may operate as indicator of elevated motivation/readiness for reproduction in Batrachoididae.

References
Dusky dolphin vocalizations: A comparison between populations in New Zealand and Argentina

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Categorization of a species’ vocalizations is a key first step to understanding proximate functions of vocalizations. Here, we quantitatively categorize and describe dusky dolphin (*Lagenorhynchus obscurus*) vocalizations off New Zealand and Argentina. We also compare broadband vocalizations (0-200 kHz) to their down-sampled narrowband counterparts (0-16 kHz), to quantify bias in the narrowband dataset. We found that only 26% of broadband vocalizations were present in down-sampled narrowband recordings. However, there were distinct quantitative differences between these low versus high frequency vocalizations. Low frequency vocalizations had shorter durations, more clicks per vocalization, shorter inter-click intervals, larger duty cycles, lower center frequencies, and more narrow 3-dB bandwidths than did high frequency vocalizations. These parameter differences suggest differences in functions, and lower frequency vocalizations may be more often used for communication while higher frequency vocalizations may be more often used for echolocation. Inter-click intervals were the most robust parameter between broadband and down-sampled narrowband vocalizations; we thus used this parameter to categorize New Zealand and Argentina narrowband vocalizations. In New Zealand, distribution of inter-click intervals was bimodal around burst pulses (< 9.25 ms) and click trains (≥ 9.25 ms). In Argentina, distribution of inter-click intervals was uni-modal around burst pulses. In both locations, a similar percentage of vocalizations were burst pulses and click trains, and a smaller percentage was click train-burst pulse combination vocalizations. Burst pulses were more likely than the other vocalization types to have a constant inter-click interval, and their durations were shorter than click trains and click train-burst pulses. Sequences of burst pulses also occurred, which contained 2-14 burst pulses that were highly similar aurally and visually. The short durations of burst pulses combined with the wide diversity of burst pulses and sequences suggest that these vocalizations were used for communication. Dusky dolphins may use burst pulses for many communication roles for which other species commonly use whistles, since we did not observe whistles in this study.
Humans and nonhuman animals often communicate in social aggregations that include several signalers and receivers, such as cocktail parties, bird dawn choruses, and frog breeding choruses (Schwartz & Freeberg 2008). For species that communicate acoustically, the mixture of signals from unattended signalers is a potent source of auditory masking and leads to errors in communication (Brumm & Slabbekoorn 2005). Because these social aggregations often form in the context of reproduction, the ability to recognize and discriminate among individual signals has important fitness consequences. Hence, natural selection should favor signaling behaviors and perceptual mechanisms that diminish the effects of auditory masking (Brumm & Slabbekoorn 2005; Bee & Micheyl 2008).

Among the potential mechanisms by which receivers may separate signals from background noise include an ability to exploit features of the signal and the noise. For instance, human listeners experience higher levels of speech intelligibility when the amplitude of the background noise fluctuates in time (Gustafsson & Arlinger 1994; Bacon et al. 1998). The release from masking obtained in amplitude-modulated noise is attributed to the ability of listeners’ to extract short but meaningful acoustic “glimpses” of the target signal at moments when the background noise momentarily dips to low levels. This phenomenon, known as “dip-listening,” is one key mechanism that allows humans to solve the “cocktail-party problem” of understanding speech in multi-talker social environments. The extent to which similar mechanisms operate in the acoustic communication systems of non-human animals has received little attention. In this study of Cope’s gray treefrogs (Hyla chrysoscelis), we asked whether mechanisms akin to dip-listening allow females to solve their own “cocktail-party-like” problem.

Cope’s gray treefrog males aggregate around ponds and form dense choruses where they produce loud advertisement calls to attract females. The calls produced by males of this species are comprised of series of pulses (32 on average) delivered at a rate of ~45 Hz. In a first experiment, we estimated the minimum effective call duration for call recognition. In the absence of background noise, we presented females with series of synthetic mating calls that had, on average, 2.25, 4.5, 9, 18 or 36 pulses (Figure 1). Our results suggest that glimpses of more than five consecutive pulses are necessary for eliciting positive phonotaxis by female frogs. In a second phonotaxis experiment, we tested the hypothesis that amplitude fluctuations in the background noise influence thresholds for recognizing male mating signals. We estimated signal recognition thresholds in the presence of “chorus-shaped noises” (i.e. noises with the long-term frequency spectrum of Cope’s gray treefrog choruses) that were either unmodulated or sinusoidally amplitude modulated (SAM) at rates of 0.625 Hz, 1.25 Hz, 2.5 Hz, 5 Hz, 10 Hz, 20 Hz, 40 Hz, or 80 Hz (Figure 1). Consistent with the dip-listening hypothesis and the results from the first experiment, signal recognition thresholds in SAM noises were ~4dB lower than in the unmodulated control when amplitude dips were long enough to include “glimpses” of nine or more consecutive pulses. We did not find evidence for dip-listening when the dips in SAM noises included five or less consecutive pulses. Because the sounds of frog choruses fluctuate in amplitude (Vélez & Bee 2010), female frogs might benefit from dips in the background noise to recognize signals in natural social environments.
Fig. 1. (Left) Waveforms of synthetic mating calls comprising 36, 18, 9, 4 or 5, and 2 or 3 pulses (top to bottom, respectively), used in experiment 1. (Right) Waveforms of a 32-pulse advertisement call (black) in the presence of chorus-shaped noises (gray) that were either unmodulated (top) or sinusoidally amplitude modulated (SAM) at rates of 0.625 Hz (middle) or 5 Hz (bottom). The solid gray line depicts the sine wave used to modulate the noises, and the dashed black line illustrates the values at which the amplitude modulated maskers reach 50% of the maximum amplitude; these values were used to measure the numbers of pulses falling within dips of fluctuating maskers.

References
Rules for taking calling turns in a gregarious songbird: A study of communal vocalizations in the zebra finch (Taeniopygia guttata)

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Colonies or communities of animals such as fishes, frogs, seabirds, or marine mammals can be noisy. Indeed, the simultaneous vocal activity of several individuals results in apparently uncoordinated communal vocal production. Although vocal communication between clearly identified sender(s) and receiver(s) has been well studied, little is known about the information potentially conveyed by such a background sound resulting from a network of vocalizing animals (i.e., multiple senders and receivers).

In the present study, we first tried to relate some acoustic properties of the noisy sound that results from the acoustic network of a group of animals to the social relationships between individuals and/or the group composition. Using custom-written software for automatic detection of vocalizations occurring over many hours of recordings, we report acoustic features of communal vocal activities in a gregarious species, the zebra finch (Taeniopygia guttata).

Six groups of zebra finches with varied social structures were set up. Five of them had various sex ratios and sizes, and were housed in communal cages allowing social relationships. A control group was made of males housed in individual cages, allowing visual and acoustic contact but no physical interaction, thus preventing socialization within this group.

The results showed that the rate of emission and the acoustic dynamic (i.e., patterning of vocalizations over time) both depended on the social structure. In particular, the vocal activity of a group of zebra finches depended mainly on the number of unpaired birds, i.e., individuals not part of a stably bonded pair. The percentage of unpaired birds in social groups was positively correlated with the vocalization rate (Fig. 1.). Thus, the unpaired birds drive the communal acoustic activity in a group of zebra finches and acoustic parameters linked to the rhythm of emission of vocalizations represented good probes of the pairing status of birds within groups. In addition, these acoustic features well distinguished the most extreme perturbation of social links (physical isolation) from other social conditions. Compared to males housed in the same cage, the acoustic environment of the individually housed males was noisier (higher vocalization rate), extremely correlated, and burst-like (Fig. 2.).

As a second step in the study of communal vocalizations in zebra finches, we tried to relate the calling order between individuals to their social relationships. We placed birds with previously known relationships in adjacent individual cages, each equipped with a microphone. The resulting microphone array allowed to identify calling individuals on hours of recording. We will discuss how calling slots relate to birds social bonds.
Fig. 1. Vocalization rate (number of vocalizations per min) versus percentage of unpaired individuals. The black line is the linear regression which yields an R²=0.84. 6M6F, 8M4F, 11M1F, 9F and 9M are five social groups of varied sex-ratio and number of birds (xM and yF being the number of males and females, respectively).

Fig. 2. Instantaneous rate of vocalization of the two all-male groups 9M (social group of 9 males, black curve) and 10IM (group of 10 isolated males in adjacent cages, grey dashed curve). For each group, the average rate was substracted from the instantaneous rate to allow comparisons.
Acoustic Duetting in insects with special emphasis on *Scudderia pistillata*, a counting katydid

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Members of the insect order Orthoptera (grasshoppers, crickets, and katydids) are best known for their acoustic courtship behavior, typically with males sending their songs through the air to receiving females who then respond by phonotaxis to approach the signaling male. Duets in which both the male and female signal during courtship is relatively rare for acoustically communicating organisms using an airborne signal. More commonly acoustic duets are produced by organisms signaling through a dense substrate, such as vegetation and water. Acoustic duets, however, are quite common within the katydid subfamily Phaneropterinae and also in the ephippigerines. The male signal typically precedes the female’s response which is often just a brief, simple sound. The timing between the signal emission and receiver response is often important in species identification and the latency from the end of his signal until the beginning of hers often depends upon the length of his signal.

An exemplar acoustic duetter is the Broad Winged Bush Katydid, *Scudderia pistillata*. Male *S. pistillata* produce sounds in the form of a pulse, one strike of a file on his left forewing against a plectrum on his right forewing. These pulses are arranged in a phrase. Between phrases are periods of silence on the order of a few seconds with sequential phrases organized into a bout. The timing between phrases is fairly consistent, with much longer and more varied periods of silence between bouts. The female produces a tick via a separate sound producing apparatus consisting of a few disorganized teeth on the caudal vein of her right forewing. Her response always follows the male’s phrase and she typically responds to every phrase in a bout.

An elaboration towards complexity in acoustic duetting is quite common in many groups. With each subsequent phrase in a bout, male *S. pistillata* adds one to two pulses, with the first phrase consisting of 3 pulses and then sequentially added pulses until 7-10 pulses are produced in a single phrase. Thus the males count up during a bout. Analysis of over 500 recorded male bouts shows individual males are stereotypic in the pulse sequence they produce, and that there is variability between bouts of individual males that are associated with their overall size.

Compared to most duetting katydids, female *S. pistillata*’s acoustic response is highly affected by the male’s call. Typically, duetting females produce one to three acoustic ticks in response to the male’s call with a consistent latency between the end of his call and the beginning of her response. Female *S. pistillata* in response to each phrase produce multiple ticks in reply. The number of ticks a female produces, as well as the timing of her response is dependent on the number of pulses the male produced, with longer phrases receiving a shorter latency. In playback studies, females were found to be unaffected by the sequence in which the pulses arrive. They showed no preference in terms of number of ticks produced to male calls with n+1 pulses added to each phrase compared to inconsistent counters. They also do not show a change in acoustic preference to a bout with a typical counting sequence of 3 to 8 pulses versus a bout consisting solely of 8 pulse phrases. The adaptive significance of the counting sequence is of great interest and is currently being studied. Further analysis of both female acoustic and phonotaxic response to manipulated male bouts is currently underway to determine what effect adding pulses to each phrase has on female mating decisions.
Fig. 1. Waveform (above) and spectrogram (below) of a courtship duet between a male and female Broad winged bush katydid (*Scudderia pistillata*) recorded in Ithaca, New York. The first sound is a male 9 pulse phrase presented in playback and is followed by the recorded response of a live female.
Invited Speaker

Tiger Bioacoustics: An Overview of Vocalization Acoustics and Hearing in *Panthera tigris*

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Unlike its smaller relatives, the tiger is known as a roaring cat, a distinguishing vocal attribute shared only with other species belonging to the genus *Panthera*. Roaring, however, is but one of numerous calls in the tiger’s vocal repertoire. Hissing, grunting, growling, snarling, gasping, chuffing and long distance advertisement calls (also referred to as moaning or intense mews) are also prominent utterances that are used to express attitudes and intentions in a variety of social settings (2-4). Some calls, like the full-throated roar, are impressively loud, while others, like chuffing, are barely audible within a few feet of the source. This wide dynamic range is largely a manifestation of the tiger’s larynx; the flat and broad medial surface of its massive vocal folds (1,5,8) enables the big cat to produce surprisingly low phonation thresholds and extraordinary output (5).

The tiger is also the largest of the big cats. The body mass of an adult, male Amur tiger can exceed 300 kg. Its height at the shoulder can be as large as one meter and its snout-to-tail-tip length has been measured at 13 meters. The dimensions of the vocal tract and the larynx in particular, are equally impressive, as is the diameter of the trachea. It is not particularly surprising, therefore, that the bulk of acoustic power radiated in voiced calls is frequently carried by a relatively narrow low-frequency band of energy. This is illustrated spectrographically in the case of a long distance advertisement call in figure 1. While the call contains elements of nonlinearity as part of its acoustic structure, it is largely tonal in character, expressing robust harmonic and sub-harmonic structure. The average fundamental frequency of the long distance call is approximately 158 Hz, while the peak frequency is slightly higher averaging approximately 284 Hz (7), acoustic features that support its propagation over large distances. Although the low frequency character of tiger calls can be thought of as a general acoustic feature, some calls, like prusten and roaring, contain acoustic energy over a very wide frequency band.

The low-frequency nature of utterances like the long distance advertisement call suits the solitary lifestyle of free-ranging tigers inhabiting large territories well and appears to be a function of the body size of the animal, not a vocal tract adaptation. However, the observation that many calls in the tiger’s vocal repertoire are dominated by intense bands of low-frequency acoustic energy does raise an interesting evolutionary question related to hearing: Is the tiger an auditory generalist taking advantage of its overall soundscape, or is the big cat an auditory specialist paying particular attention to and taking advantage of a specific feature, or features, of its sound environment. The shape of the tiger’s threshold-frequency curve suggests that it is a generalist; there is no evidence suggesting that sensitivity to a particular frequency band is notably exaggerated. However, an interesting and unexpected physiological finding associated with response latency may suggest that the specialist question should be reconsidered in the case of the tiger. Specifically, the well recognized and generally accepted inverse relationship
between neural response latency and stimulus frequency may not hold in the case of the tiger. Auditory brainstem response findings suggest that response latencies to lower frequency stimulation are as short as response latencies to higher-frequency stimulation. The outcome of findings from a neural masking study suggests that the cochlear base makes a substantial contribution to responses to low-frequency stimuli in the tiger (6). The biological implication of this observation is that the inner ear of the tiger may have undergone adaptation in the course of its evolution leading to faster response times for lower frequency acoustic signals. The ethological significance of this finding is unknown, but possibilities, including the possibility that the adaptation confers a hunting advantage, will be considered.

![Figure 1](image)

**FIGURE 1.** A: An example of the temporal waveform (upper panel) and spectral characteristics (lower panel) of three consecutive long distance advertisement calls produced by an adult male Amur tiger. B: Distributions of average fundamental frequency (upper panel) and average peak frequency (lower panel) for long distance advertisement calls. Means and standard deviations are indicated in each panel.

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