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Massachusetts Institute of Technology
Woods Hole Oceanographic Institution

Joint Program in Oceanography/ Applied Ocean Science and Engineering

DOCTORAL DISSERTATION

Relating Behavioral Context to Acoustic Parameters of Bottlenose Dolphin (*Tursiops truncatus*) Vocalizations

by

Rebecca Elizabeth Thomas

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RELATING BEHAVIORAL CONTEXT TO ACOUSTIC PARAMETERS OF BOTTLENOSE DOLPHIN (*TURSIOPS TRUNCATUS*) VOCALIZATIONS

By

Rebecca Elizabeth Thomas
B. S. Duke University, 1995

Submitted in partial fulfillment of the requirements for the degree of

Doctor of Philosophy

at the

MASSACHUSETTS INSTITUTE OF TECHNOLOGY

and the

WOODS HOLE OCEANOGRAPHIC INSTITUTION

August 2001

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Relating Behavioral Context to Acoustic Parameters of Bottlenose Dolphin (*Tursiops truncatus*) Vocalizations

by
Rebecca Elizabeth Thomas

Submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy at the Massachusetts Institute of Technology and the Woods Hole Oceanographic Institution

Abstract

This thesis presents methods to analyze the function of vocalizations of the bottlenose dolphin, *Tursiops truncatus*. The thesis uses the social interaction as the basic unit of analysis, and maintains a deliberate focus on quantitative and replicable analyses throughout.

A method for determining identity of the vocalizing animal in a lagoon was developed. This method combined passive acoustic localization with video sampling to determine which animal vocalized. It fills an urgent need for unbiased identification of vocalizations of undisturbed dolphins where details of social interactions can be followed without affecting the behavior of the subjects. This method was implemented in a captive lagoon with 6 dolphins: two adult females, their two male calves, and a juvenile male and a juvenile female.

This thesis also reviews the current state of analysis of the bottlenose dolphin acoustic repertoire, highlighting the need for a detailed, quantitative, and consistent study of the entire vocal repertoire. It does not attempt to do a comprehensive repertoire study, but uses several new quantitative methods to parameterize vocalizations and relate these to behavior from dolphins. Vocalizations within the lagoon tended to occur around the time of onset of behaviors produced by the focal dolphin. A comparison of vocalizations during affiliative and agonistic interactions revealed that the association of group vocalizations with the behavior of a focal animal was related to agonistic but not affiliative interactions.

Using the localization/video method, vocalizations in a time window around submissive behaviors were localized and classified as having come from either dolphins engaged in the interaction or dolphins not engaged in the interaction. Vocalizations were emitted by interactants more often than expected, and by non-interactants less often than expected. Use of different vocalization types was found to vary depending on the context of the agonistic interaction. In addition, the sequence of vocalizations with respect to behaviors within the interaction mattered, with more vocalizations occurring after than before submissive behaviors. These results demonstrated that group-based analyses of vocalizations are insufficient and one must use techniques designed to focus on the level of the interaction in order to study communication and social behavior in dolphins.

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There are an incredible number of people who deserve my gratitude for helping me develop and live through this thesis. I am sure that I cannot fit them all in here, but I will try.

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Table of Contents

List of Figures

List of Figures

List of Tables

Chapter 1: Introduction

1.1 Introduction:

Hinde (1976) proposed a conceptual framework for the study of the dynamics of social structure that involved three levels: interactions, relationships, and "surface structure." The most basic element of social structure in this framework was the interaction. The interaction is described by what the individuals are doing together ("content") as well as by how they do it ("quality"). Examples of "content" would be talking or hugging for humans, and whistling or gentle rubbing for dolphins. The notion of "quality" addresses the nature of the behavior being performed, e.g. talking loudly for humans, or gentle touching for dolphins. Interactions involve at least two individuals, and at least one social behavior. Identifying which interactant produced which behavior further assists in the understanding of the interaction.

Relationships are made up of a succession of interactions between two individuals. Describing a relationship not only involves describing the interactions involved, but also specifying their absolute and relative frequencies as well as the timing and sequence of the interactions with respect to each other. In Hinde's framework, the term "relationship" can refer to specific modes of interactions between specific individuals, or to generic patterns of behavior between individuals, such as the mother-calf relationship. The "surface structure," or social structure, of a group is described by the content, quality and patterning of the relationships within it. Like relationships, the surface structure also contains a time dimension.

Hinde's framework has been adapted for use in the study of cetacean social behavior by Whitehead *et al.* (2000). As noted by Whitehead *et al.* (2000), the basic building block of the interaction can be difficult to observe and measure in cetaceans. Identifying and following individuals of many cetacean species, not to mention measuring specific aspects of their interactions, may be hampered by a variety of problems, including speed of movement of the animals, murky water, and difficulty in identifying or following individuals in real time. Detailed observations of interactions have been possible in captivity (Samuels and Spradlin 1995, Samuels and Gifford 1997), and under some conditions, such as those with dolphins in Shark Bay, Australia (e.g. Mann 2000). However, for those difficult to study species, many cetacean researchers assume the "gambit of the group" for studying social organization (Whitehead *et al.* 2000). This assumes that when animals are clustered, they are interacting. This assumption may be reasonable under some circumstances. For example, Whitehead and Dufault (1999) suggest that this may be reasonable if most interactions take place within groups, where different groups are separated by more than the maximal range of communication. As acoustic signals can travel several kilometers, this separation of groups may be difficult for observers to ascertain.

The challenges of obtaining and interpreting a visual record of behavior are amplified when one attempts to integrate the acoustic component of social interaction, a dimension that is very important to these animals (Tyack 1997). Even under captive conditions or exceptional conditions in the wild, it is difficult to follow the acoustic components of a social interaction at the same time as the visible components of the same interaction. The number of studies of cetaceans that have simultaneously followed the acoustic and visual display aspects of interactions is very limited. Many cetacean researchers have also followed the "gambit of the group" strategy when studying acoustic behavior (Overstrom 1983 , Weilgart and Whitehead 1990 , Jacobs *et al.* 1993). Because sound typically travels much further than light underwater, an acoustic "group" of marine mammals may be much larger than what is perceived by a human watching from a boat.

Due to difficulties in determining which animal is vocalizing in acoustic recordings from a group, researchers often assume that when vocalizations are clustered in time, the vocalizations are part of the same social interaction. Researchers may also assume that vocalizations from a group are acoustic components of concurrent interactions being recorded by visual observers. These may or may not be reasonable assumptions depending on the circumstances. If all vocalizations are of the same type, all animals are exhibiting the same behavior, and vocalizations recorded come from the group under observation, then these assumptions may be valid. However, seldom can one count on all of these conditions being met. In addition, there are specific problems with the second item, determining the behavior of a group of animals. As pointed out by Mann (1999), there are inherent biases when an observer attempts to continuously follow and record all behaviors from all animals in a group. It may be possible to accurately record group activity for a small group if all animals are cohesively grouped and engaged in the same activity and activities are grossly defined. However, it may be difficult to determine if some animals within the group are engaged in a different activity. For example, some behaviors may be much more obvious to observers than other behaviors, resulting in biased sampling as well as vocalizations being incorrectly associated with behavioral interactions. The reverse can also occur, with behavioral interactions being incorrectly associated with obvious or loud vocalizations.

By correctly linking vocalizations with associated behavioral interactions, it can be determined how the acoustic repertoire is associated with social organization. This can occur on many levels, from visual displays being associated with concurrent vocalizations of various call types within an interaction, to relationships being associated with functional categories of vocalizations, to how elements in the acoustic repertoire are used by animals occupying different levels in the social structure. An adaptation of Hinde's 1976 framework to illustrate this concept is shown in Fig. 1.1.

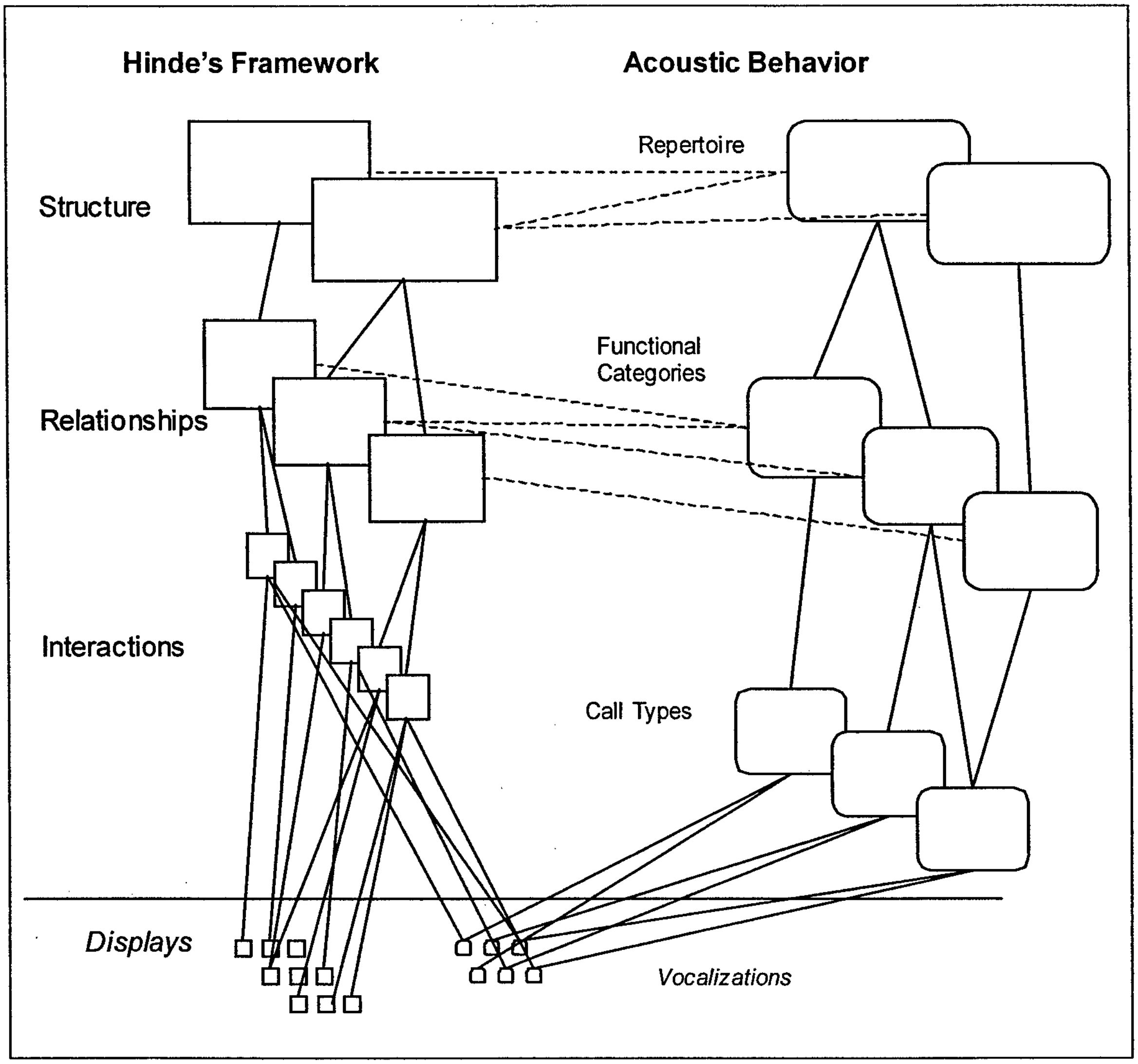

Figure 1.1 Adaptation of Hinde 1976's framework for studying social structure including acoustic relationships as well as the role of displays and vocalizations in interactions

1.2 Thesis structure:

One of the technical difficulties involved in associating vocalizations with their use in an interaction is the problem of determining the identity of the vocalizing animal, at least to the extent of determining whether or not the vocalizer was associated with the interaction. In Chapter 2, a solution to this problem is described and demonstrated for bottlenose dolphins, *Tursiops truncatus*, in a captive environment. A combined system combining acoustic localization and overhead video was used to determine which animal was vocalizing by overlaying the location from which the sound was emitted to the concurrent video image. Using this technique, the identity of the vocalizing animal can be determined, or if the animals are too close together, as may occur during an interaction, one can determine whether the vocalization came from one of the interactants. This system can be even more powerful when combined with concurrent behavioral sampling to associate specific vocalizations with specific behavioral interactions.

One difficulty with using the localization/video technique with the framework in Fig. 1.1 is that the bottlenose dolphin acoustic repertoire is currently not well defined. Even though the vocal repertoire of the bottlenose dolphin is better studied than that of any other cetacean species, few quantitative repertoire studies have been performed to date. Historically the acoustic repertoire has been loosely classified into three categories: echolocation clicks, burst-pulsed calls, and whistles. Unfortunately, these categories are not entirely distinct, having been defined by a combination of structural and functional analyses. For example, echolocation clicks were named for their function in echolocation, whereas burst-pulsed calls have been usually described as serving a function in social communication. These two categories have historically been separated by supposed function, but have similar acoustic structures, which has caused much confusion. Repertoire analysis of the bottlenose dolphin has also been confused by analyses that were performed piece-meal or were inconsistent from one researcher to the next. Analyses have tended to be focused on a narrow setting and one behavioral context. It is important that repertoire analyses be done on a more general contextual scale. The primary goal of Chapter 3 is to develop a consistent and replicable method for linking acoustic characteristics of bottlenose dolphin vocalizations to their social context. The effect of using the acoustic "gambit of the group" is also discussed in Chapter 3.

Having identified potentially interesting links between vocalizations and behavior types using the method described in Chapter 3, I refine the analysis in Chapter 4 by linking sound types to their use in interactions involving a specific type of behavior, the submissive behavior. Aspects of Hinde's notion of "quality," or how the vocalizations are used in the interaction, are addressed. This includes which vocalization types are used by the participants in the interaction, as well as the timing of vocalizations with respect to submissive behaviors. The use of whistles in relation to submissive behaviors by different age/sex classes is also explored.

In Chapter 5, the concluding chapter, results from Chapters 2 - 4 are summarized, conclusions are drawn from overall results of the thesis, and contributions of this thesis to the field of marine mammalogy are listed. Avenues for future research are also discussed.

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Chapter 2: Linking Dolphin Vocalizations to Movements and Behavior Using a Passive Acoustic Array and Video Recordings

2.1 Introduction:

Studies of animal communication and social behavior ideally use methods in which signals and actions can be associated with individuals. Only under these conditions can one study social interactions involving signal and response. However, studies of marine mammal communication have been hampered by the difficulty of identifying which animal produces each sound. Marine mammals generally do not open their mouths when they vocalize underwater, nor do they regularly release bubbles in association with vocalizations. In addition, humans cannot normally use their auditory capabilities to localize underwater sounds directly. However, these practical difficulties have not deterred interest in studying marine mammal vocalizations. Acoustic communication is especially important for whales and dolphins, because they are often out of sight of each other, but can remain in acoustic contact at long ranges.

Several solutions have been proposed to solving the problem of determining the identity of the vocalizing animal when studying cetacean communication. One of the earliest approaches involved isolating an animal (Lilly and Miller 1961, Caldwell and Caldwell 1965) to ensure that recorded vocalizations were emitted by that individual. While this technique was useful, the animals were not in a normal social situation and could not interact directly with other animals. These conditions of involuntary isolation may also be stressful for the subjects. In addition, vocalizations have also been studied during spontaneous (i.e. animal-mediated) separations, reducing the bias present in studies on forcibly isolated animals. For example, Janik and Slater (1998) used amplitude comparisons to determine which animal produced each sound during spontaneous separations of animals into separate pools. They found that each dolphin produced signature whistles during spontaneous separations from the group, but that signature whistles were seldom produced among animals when they were all swimming in the same pool. However, their success with this technique depended upon conditions that are not widely encountered.

Another solution to the problem of determining identity of the vocalizing animal involves attaching a tag to the animal. Various attachments have been suggested e.g. (Evans and Sutherland 1963) and actually used on dolphins e.g. (Tyack 1991, Tyack and Recchia 1991, Nowacek *et al.* 1998). These methods either require that the animal be trained to wear the tag, or involve involuntary attachment of the tag to the animal. The mere act of wearing a tag, whether or not this involves training, may cause changes in the animal's behavior and those animals that interact with it.

Identifying the vocalizing animal by bubblestream emissions during vocalizations is another method that has also been used by several researchers (Dahlheim and Awbrey 1982, McCowan 1995, McCowan and Reiss 1995, Herzing 1996). Drawbacks to this method include the fact that bubblestream emissions only occur during a small percentage of vocalizations, bubblestreams themselves may function as a behavioral display, and vocalizations produced with bubblestreams may not be a random subsample of all the vocalizations (Fripp 1999).

Linear arrays for sound beamforming to determine the direction to a sound source and dispersed arrays for localization of sounds are solutions that are becoming more practical with recent increases in computing power and reduction in the cost of components. Beamforming using towed linear arrays is often suitable for field work at sea to study free-ranging animals, because the array can be easily towed while maintaining fixed distances between hydrophones. When the length of the array is small relative to the distance to the sound source, the bearing to the source can be obtained. This bearing indicates angle relative to the line of the array, so the locus of possible locations is a cone. With careful positioning of the array relative to the animals, focal follows of acoustic behavior of individual animals can be performed (Miller and Tyack 1998). Miller and Tyack (1998) followed wild killer whales while beamforming their vocalizations using a small towed array.

Watkins and Schevill (1974) used a drifting 3-dimensional array to determine x-y positions of finback whales, right whales, and white-beaked dolphins. Although the technique used passive acoustic localization, this method required the use of intermittent pings to determine hydrophone locations. The calibration pings had the effect of temporarily halting sperm whale sound production (Watkins and Schevill 1975). Instead of a drifting array, Clark *et al.* (1986) used a fixed array to study bowhead whales during the whales' spring migration off Pt. Barrow, Alaska. Placing the hydrophones at fixed locations under the ice eliminated the need for intermittent pings. Spiesberger and Fristrup (1990) developed a method combining passive localization of vocalizing animals with acoustic tomography, a technique which allowed for localization of vocalizing animals in addition to construction of maps of sound speed and wind (or current) fields. However, their technique has yet to be implemented in its entirety for studies of cetacean communication. Freitag and Tyack (1993) demonstrated the feasibility of acoustic localization of bottlenose dolphin vocalizations in a captive environment. Although they were able to localize vocalizations, their study demonstrated that reverberation presents a problem for localization in captive environments. Janik (2000) demonstrated the feasibility of a two-dimensional acoustic localization system for determining positions of vocalizing wild bottlenose dolphins passing through a channel. Reverberation did not appear to be a significant problem in this study, most likely due to the fact that the fixed array was located in a large channel rather than in a more confined space. Brensing *et al.* (2001) designed a system of two pairs of closely spaced hydrophones to localize dolphins within a pool, although the resolution of their system is unclear. Few, if any, studies have been able to link locations of specific sounds to a detailed record of behavior.

Video recording systems can be used to supplement observations, provide an archival record of behavior, or serve as the sole source of observational data. The technique presented here projects acoustic localization results onto a video recording of dolphin locations and behavior. The identity of the calling animal can be determined, and the behavioral context of the call can be revisited.

2.2 Methods:

2.2.1 Study site:

This research was performed at Dolphin Quest Bermuda's interim facility at the Maritime Museum in the Naval Dockyards on Ireland Island, Bermuda, in the fall of 1999. At that time, the dolphins' social group was composed of two mother-calf pairs, a juvenile male, and a juvenile female, for a total of 6 animals. The lagoon facility measured roughly 30 meters by 45 m and was roughly 3-5 m deep, depending on the tide. The sides of the lagoon were composed of irregular limestone bricks, covered with algae and other organisms. The ramparts of the Naval Dockyards directly abutted the lagoon on one side. The hydrophones were placed around three sides of the lagoon, and the video camera was placed on the ramparts overlooking the lagoon, approximately 9 m high (Fig. 2.1). A separate hydrophone was connected to the video camera and was not used in acoustic localization. The lagoon was connected to the ocean via a short channel with a gate on the lagoon side, allowing the water level in the lagoon to change with the local tides.

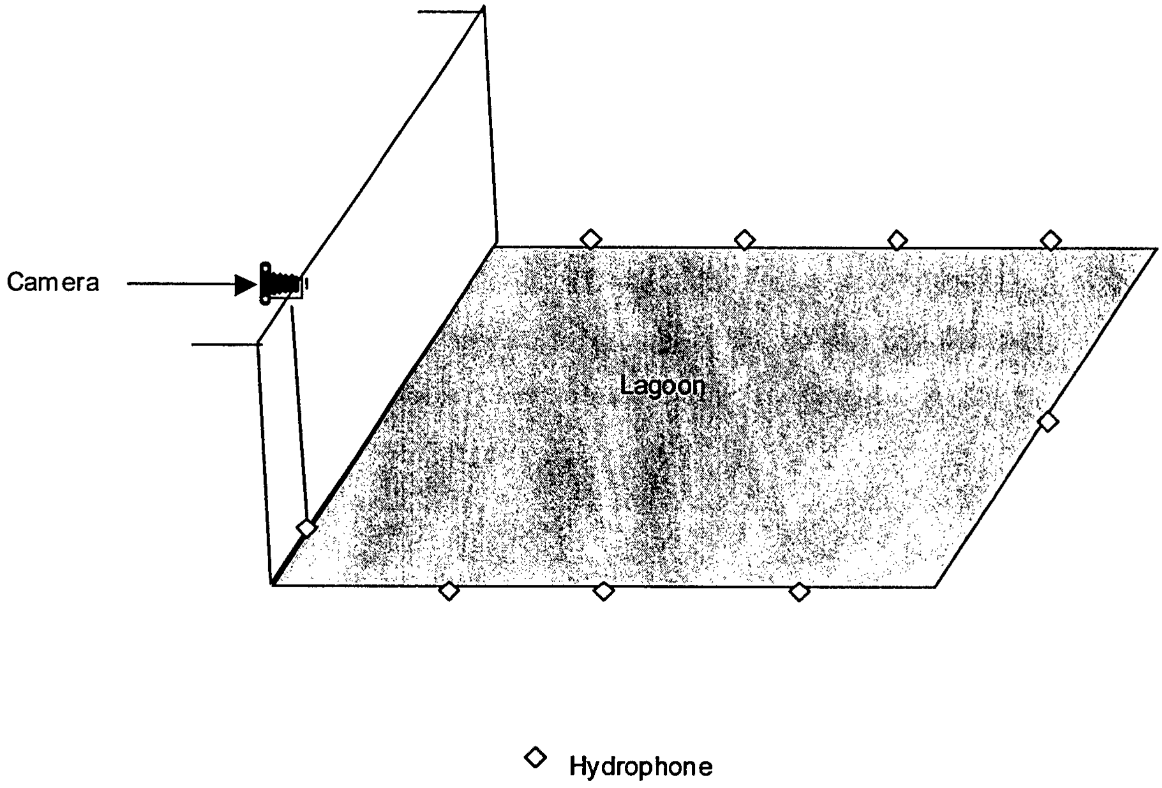

Figure 2. 1 Schematic of the lagoon with hydrophone and camera placements.

The speed of sound in water is affected by temperature, salinity, and depth (Urick 1983). Temperature has a much larger effect on the speed of sound in water than salinity and depth. The change of speed of sound per unit change of temperature, salinity, and depth is + 2.7 m/s per °C, + 1.2 m/s per ppt, and + 1.6×10^{-2} m/s per m, respectively ((Urick 1983), converted into metric units). It should be noted that while the ocean varies in temperature over several tens of degrees, it only varies in salinity over a few parts per thousand. The water temperature was recorded each day of observation from a mercury thermometer. Because salinity and depth have less significant effects than temperature, salinity was assumed to be fixed at 36.6 ppt, and the depth of the animal in the shallow lagoon was assumed to be constant at 0 m. The change in sound speed that occurs over the depth of the lagoon (0-5 m) is only 0.08 m/s, so this choice of depth is insignificant compared to temperature. The speed of sound, *c*, was calculated as following (Urick 1983):

$$c = 1492.9 + 3(T-10) - 6\times10^{-3}(T-10)^2 - 4\times10^{-2}(T-18)^2 + 1.2(S-35) - \\ 10^{-2}(T-18)(S-35) + D/61$$

where T is temperature in degrees Celsius, S is salinity in parts per thousand, and D is depth in meters.

2.2.2 Acoustic localization:

Eight hydrophones (High Tech Inc. HTI-94-SSQ) for acoustic localization were placed at measured locations around three of the four sides of the lagoon. The fourth side of the lagoon directly abutted the ramparts of the Dockyard fort, with no convenient spot to anchor a hydrophone. An eight-channel TASCAM DA-88 multitrack digital recorder was used for recording the signals from the hydrophones. The TASCAM DA-88 has a flat frequency response (± 0.5 dB) from 20 Hz to 20 kHz.

Signal selection process:

The tapes were digitized to computer using the "Translator Plus" digital audio format converter from Spectral with Studio Tracks XP Software on a computer running Microsoft Windows. A suite of Matlab (MathWorks 1984-1999) programs was used for performing the various aspects of signal selection. A flowchart of signal selection is shown in Fig. 2.2. An energy detector running on the computer detected, extracted, and saved sounds above a preset energy threshold (modified from Fripp *et al.* (1997)). Due to variability in wind and water conditions, the energy threshold had to be set by the operator before detection for each recording session. A level of three standard deviations above an average noise energy was used for the threshold. The detected cuts were parameterized by ACOUSTAT (Fristrup and Watkins 1992). A linear classifier was used to automatically select a subset of cuts based upon their ACOUSTAT parameters (see Appendix for classifier details). Note that this involves linear processing of a data set that largely consists of non-linear parameters. This selection of signals was needed because the energy detector triggered on snapping shrimp clicks as well as dolphin vocalizations. As the received levels of whistles often appeared to be lower than that of echolocation clicks, a separate detector for whistles was specifically designed to detect whistles based upon their narrow bandwidth (using higher order zero crossings, (Kedem 1994)). For both detectors, the goal was not to be able to detect every single event, but to be able to easily gather a suitably sized sample of vocalizations. In other terms, this system tolerated missing some signals of interest in order to exclude most of the acoustic clutter in the environment.

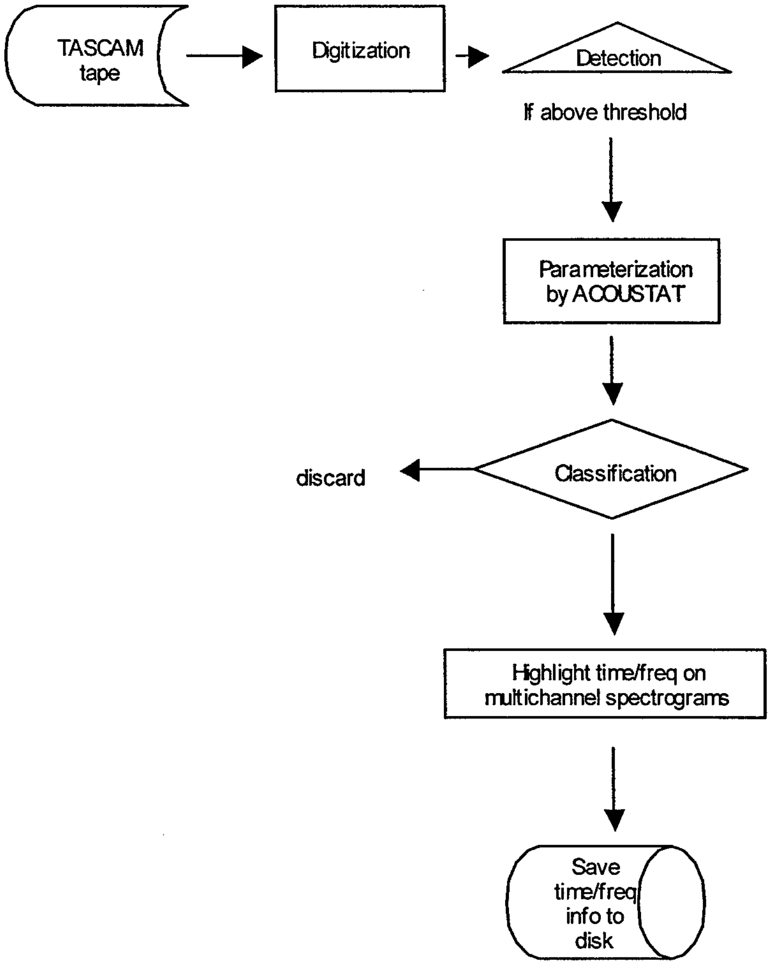

Figure 2. 2 Flowchart of signal selection process

The operator viewed 8-channel spectrograms of the cuts obtained from the detection step. The operator would discard any cut if it contained only noise or if it was a dolphin vocalization excessively contaminated by transient signals (e.g. snapping shrimp clicks). Otherwise, the operator would highlight the vocalizations in time and frequency. These time and frequency parameters were saved for the localization step.

Localization algorithm:

Summary of algorithm: The algorithm used cross-correlation functions to determine the point in space that corresponded to maximal beamformed signal energy (Fristrup and Dunsmore *in prep*). Time delays, τ_{ij}, were calculated for each candidate location and hydrophone pair, (*i,j*). The time delays were calculated using geometry and the speed of sound. These τ_{ij} were then used to extract the value of the cross-correlation function at this time delay τ_{ij}. The sum of the correlation values at the calculated τ_{ij} for all pairs of hydrophones was used to measure the summed squared value of the beamformed signal for the assumed position. A stochastic search algorithm (Vose 1999) was used to identify the location where the summed squared beamformed energy attained the global maximum. A minor variant of this procedure was used for the results reported here. The correlation values were cubed before they were summed which had the effect of emphasizing the larger correlation values and reducing the impact of the smaller values. A flowchart of this procedure is provided in Fig. 2.3. Note that this approach finds locations corresponding to large average values for the cross-correlation functions, in contrast to alternative schemes in which the time delays associated with the peaks of each cross-correlation function are taken and a least-squares fit is performed to obtain a location estimate from these time delays (Spiesberger and Fristrup 1990). A description of the algorithm as used for this study is provided below; details are provided in Fristrup and Dunsmore *in prep*.

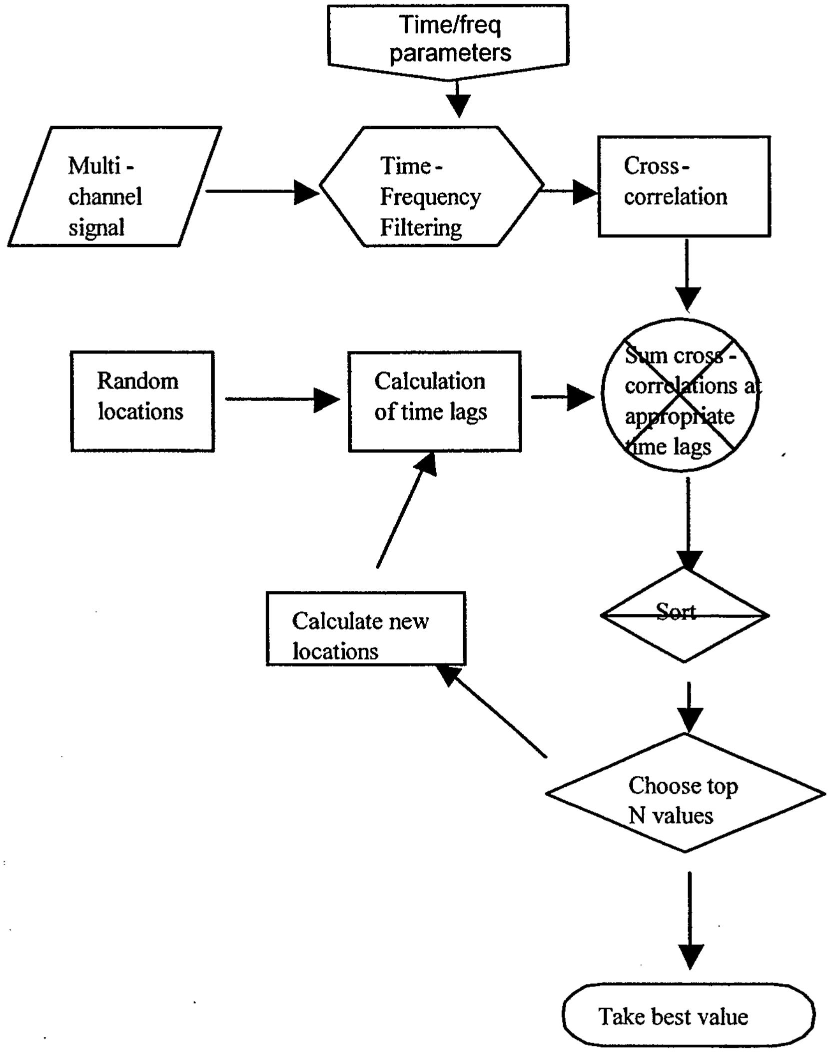

Figure 2. 3 Flowchart of localization algorithm

Details of algorithm: For the results reported in this paper, after signal selection the sounds were filtered and cross-correlations from all channel pairs were calculated. A stochastic search algorithm was used to find the point in space that corresponded to the highest values in all the cross correlation functions. An initial set of randomly chosen potential source locations was generated. For each estimate *k* of potential source location, the distances to all of the hydrophones were calculated. These distances were used to predict the relative arrival times at the microphones, and hence the expected time delays for each pair of hydrophones. These time delays were used to extract the appropriate value from the cross correlation functions for each pair of microphones. These cross-correlation values were transformed by cubing them, and then were summed. Figure 2.4 shows an example of this process. As shown, the time it would take for a sound to travel from the random location to each hydrophone *i* is calculated to yield a set t_i. The differences in travel times between each hydrophone pair *i* and *j*, $\tau_{ij} = t_i - t_j$, are calculated. For each pair of hydrophones *i* and *j*, the value of the cross-correlation function R_{ij}, at the time delay τ_{ij}, is extracted to obtain $R_{ij}(\tau_{ij})$. The $R_{ij}(\tau_{ij})$ over all sets of hydrophone pairs *ij* are transformed and summed to yield S_k, where $S_k = \sum_{ij} \left(R_{ij}(\tau_{ij})\right)^3$. For this study, the transform used was x^3, which biased the search to give greater weight to correlations with large values. The transform that is used can vary depending on the user's preference. The summed values S_k for each location *k* were compared, and the largest N values were chosen. Thus if the location chosen were near the actual origin of the sound, the summed transformed values would all add up to a large number. These largest N values served as parents using a genetic algorithm (Vose 1999) for choosing the next sets of locations in the lagoon. This algorithm was then iterated a predetermined number of times, and the position corresponding to the largest S_k was used as the final localization position. The S_k term for the chosen location was also saved with each localization, as it quantified the quality of the localization.

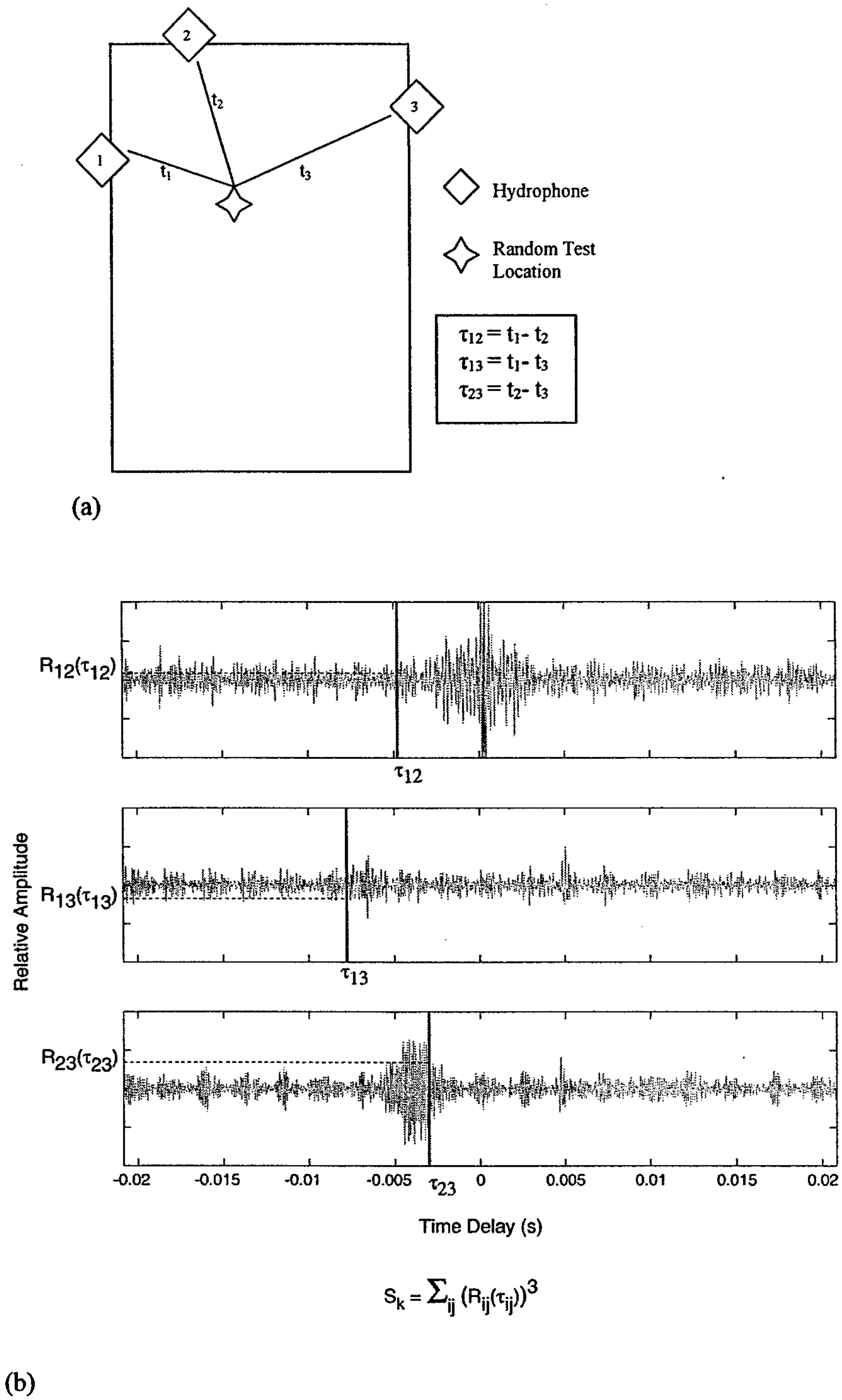

Figure 2. 4 Example of using time delays from a random location to estimate value in the cross-correlation.

(a) The time delays from a test location to the hydrophones are calculated. For simplicity, only three of the eight hydrophones actually used are shown here. (b). The cross correlation values corresponding to these time delays are transformed and then summed. It should be noted that the time delays are a function of a random variable, namely the location of the random test location, and are not directly measured from the cross-correlation function.

Calibration of acoustic localization system - Locations of hydrophones:

At the time of initial placement, the inter-hydrophone distances were measured using a tape measure to obtain approximate hydrophone positions. To obtain more precise locations, a calibration signal set was played at each hydrophone (ostensibly yielding a time delay of 0 for that hydrophone). The calibration signal consisted of a set of 5 barker codes (Peterson and Weldon 1972) (11 point) and a set of 4 upsweeps (4-7 kHz). Spectrograms of the signals and their autocorrelations are shown in Fig. 2.5. The Barker code is a series of 1's and –1's that has good autocorrelation properties with a high main lobe and low sidelobes. The 11 point Barker codes each lasted about 0.1 s, and the upsweeps each lasted about 1 s. Received calibration signals at each hydrophone were selected using an energy detector in a manner similar to that described in the signal selection process. These signals were then saved as multichannel sound cuts along with the time of detection. Localization was performed on each sound cut to obtain a series of estimates of hydrophone locations. The time delays that were used for calculation of these estimates were also saved. Outlier localizations were removed, yielding a set of localizations and corresponding sets of time delays for each of the 8 hydrophones. The time delays were converted into distances using the speed of sound, yielding 8 sets of inter-hydrophone distances. These sets were condensed into the matrix $\mathbf{D}_{\mathbf{exp}}$. The matrix $\mathbf{D}_{\mathbf{exp}}$ is the 8 x 8 matrix of inter-hydrophone distances. To determine the best-fit x-y positions that would yield these distances, a multidimensional unconstrained nonlinear minimization (Nelder-Mead, (Press et al. 1999)) was performed in Matlab. This type of minimization requires no assumptions about the function to be minimized. The function to be minimized was $\left\|\mathbf{D}_{\mathbf{pos}} - \mathbf{D}_{\mathbf{exp}}\right\|$, minimizing over $\mathbf{D}_{\mathbf{pos}}$. $\mathbf{D}_{\mathbf{pos}}$ is the set of inter-position distances between a set of 8 x-y positions. The $\mathbf{D}_{\mathbf{pos}}$ which minimizes $\left\|\mathbf{D}_{\mathbf{pos}} - \mathbf{D}_{\mathbf{exp}}\right\|$ should be the distances between the correct hydrophone positions. In the minimization, $\mathbf{D}_{\mathbf{pos}}$ was initialized as the set of distances between the tape-measured hydrophone positions. For reference in the real world, one hydrophone was arbitrarily set to (0,0), and the x-coordinate of an adjacent hydrophone set to 0. The rest of the hydrophone coordinates were calculated from these two hydrophone locations and the best-fit $\mathbf{D}_{pos}$ resulting from the minimization.

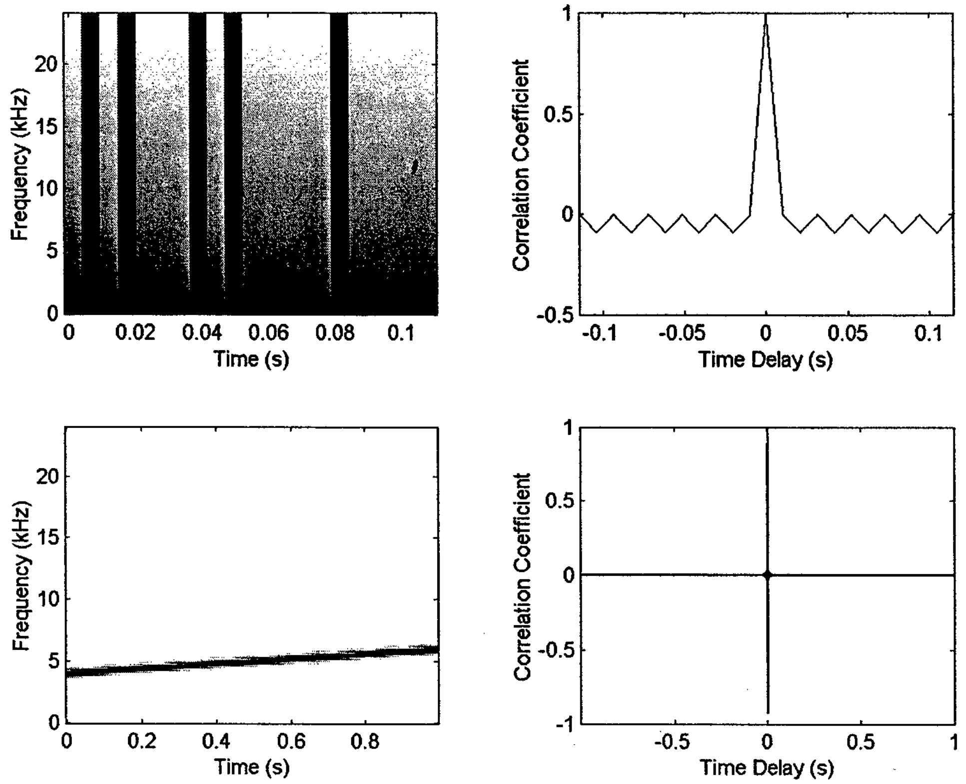

Figure 2. 5 Calibration signals

(a) Spectrogram and cross-correlation function of the 11 point barker code signal used as part of the calibration set. (b) Spectrogram and cross-correlation function of the upsweep signal used as part of the calibration set.

Calibration of acoustic localization system - Accuracy and precision:

Transects were performed along a dock that separated the lagoon into two parts as well as along a side wall of the lagoon (See Fig. 2.6 in results). A sound source was played at set locations along three transect lines, transect 1, transect 2, and transect 3. The lines were measured using a tape measure. The same calibration signal as used for calibrating the hydrophone locations was played at each location. The timing of each cut in the acoustic record was matched to the timing of source signal playback. Thus each sound cut could be linked to the location where it was played. The algorithm kept localizations above a threshold of $S_k = 5$. This heuristic threshold was implemented to remove outliers caused by poor localization quality. The mean and standard deviation of the locations (obtained from the localization algorithm) at each position along the transect line were calculated. The error was calculated as the distance from the mean localized position to the actual position (calculated using tape measured lines). The standard deviation was calculated as the standard deviation of localization results for that source position. The error can be thought of as accuracy of localization, and two standard deviations as precision.

2.2.3 Video System:

The video camera was placed at a height of approximately 9 m on the side of the lagoon abutting the ramparts. The camera was placed in approximately the same position each day. A wide angle lens (KVC-05 0.5 x) and polarizing filter were attached to the 3 ccd digital video camcorder (SONY TRV-900) used for recording video. At the beginning of each recording session, the timestamps on the video and audio recorders were synchronized to a digital chronometer. Video recordings were later imported into a PC computer using a DVRaptor card and Adobe Premiere software.

There were two steps involved in calibrating the camera image. The first was the intrinsic calibration, in which the internal geometric and optical workings of the camera were calibrated. As long as the focal length was kept constant, intrinsic parameters would not vary when different images were recorded. The second step in calibrating the camera image was the extrinsic calibration. In this calibration, parameters such as distance to objects in the world frame coordinate system, rotation, etc. were calibrated. Since the same configuration of lenses and filters, and no zoom, was used every day, the intrinsic calibration only needed to be performed once. The camera was installed each morning and then not moved for the day, so the extrinsic calibration needed to be performed once for each day of observation. A camera calibration toolbox for Matlab obtained from Cal-Tech (Bouguet 2000) was used for both the intrinsic and extrinsic calibrations. The calibration toolbox was designed based upon several sources (Heikkila and Silvén 1997, Sturm and Maybank 1999, Zhang 1999). The projection feature of the calibration toolbox transformed the real world coordinates of localizations into video space.

Intrinsic calibration:

The camera calibration toolbox included a checkerboard that was attached to stiff matting board. The checkerboard was videotaped from a variety of angles and distances. Twenty images representing a diversity of video angles and distances were used for the intrinsic calibration. The toolbox, with some initial user input, automatically finds the corners of the checkerboard boxes and performs the intrinsic calibration. Parameters from this calibration were saved in a file for later use.

Extrinsic calibration:

After solving for the intrinsic parameters, the extrinsic parameters were calculated by relating known points in the world coordinate system with their pixel analogs in the video image. Video frame pixel coordinates were obtained by plotting the image in Matlab and using the mouse to click on locations in the image. We chose 5 easily recognizable locations to be used for daily calibration. The daily calibration yielded the extrinsic calibration parameters for that day.

One way of measuring the error of the video sampling system is in terms of the projection error, which is the difference between the actual position and the projected position. Using a tape measure we determined the world coordinates at 100 set locations along transect lines (videotaped on 11/1/99). The real world positions of these transect coordinates were termed $\mathbf{X}_{ti}$ (in meters). These positions were projected (from the extrinsic parameters calculated from the five specified points) into video frame coordinates. We called these projected coordinates $\mathbf{x}_{ti}$ (in pixels).

From the video image we determined the pixel location of the transect coordinates by plotting the image in Matlab and using the mouse to click on each transect location in the video frame. We termed these video frame coordinates $\mathbf{x}_{mi}$. We backprojected $\mathbf{x}_{mi}$ to real world coordinates, $\mathbf{X}_{mi}$ (in meters) for comparison with $\mathbf{X}_{ti}$. The projection error in terms of real world coordinates was calculated as $\mathbf{E}_i = \mathbf{X}_{ti} - \mathbf{X}_{mi}$. The error in terms of pixels is $\mathbf{e}_i = \mathbf{x}_{ti} - \mathbf{x}_{mi}$. The error in terms of both coordinate types is presented in the results section.

2.2.4 Method for fusion of acoustic localization and video sampling:

The localizations were projected onto the water's surface, taking into account daily tidal fluctuations. The tidal height was assumed not to change significantly over the two hour observation period. The projected positions were plotted in Matlab against a blue background and exported as numbered picture files. These files were then imported into Adobe Premiere as an animated video clip. The video sequence from the same time sequence as the localizations was also imported. The two video sequences were overlayed by setting the blue background in the animated localization clip to transparent. This resulted in the localized positions appearing as rings on the video clip (See Fig. 2.13 in results).

A set of source playbacks on a transect line (transect 1 in Fig. 2.6) across the lagoon was videotaped to compare positions obtained from both acoustic localization and video imaging. Pixel positions of the acoustic source were recorded directly from the video images by clicking the mouse on the position of the source where the cable exited the water. The difference in localized position and video frame position was calculated for each playback location.

Dolphin localization: A set of 222 vocalizations from dolphins swimming freely in the lagoon was localized. Of the subset of these vocalizations that could be localized to a dolphin or a group of dolphins, ten vocalizations of each of three call types were randomly chosen. The three call types were echolocation clicks, burst pulsed calls, and whistles. For each vocalization, the error was calculated as the distance between the localized position and the nearest dolphin. When possible, the blowhole was used as the reference point for the dolphin. If more than one dolphin was in the immediate area, the error was calculated as the distance between the localized position and the mean position of the two nearest dolphins. Instances when more than two dolphins were in the immediate area were not used.

2.3 Results:

This section presents the results of a combined acoustic localization and video imaging system. The results are broken down into three categories: acoustic localization results, video imaging results, and combined acoustic localization and video imaging results. The results of the combined system are broken down into two categories: results from the artificial sound source, and results from dolphins.

2.3.1 Error of acoustic localization system:

The error and standard deviation of the acoustic localization system were determined by comparing known source playback locations along the transect lines to the corresponding positions calculated from acoustic localization. The histograms of error and standard deviation are shown in Fig. 2.7.

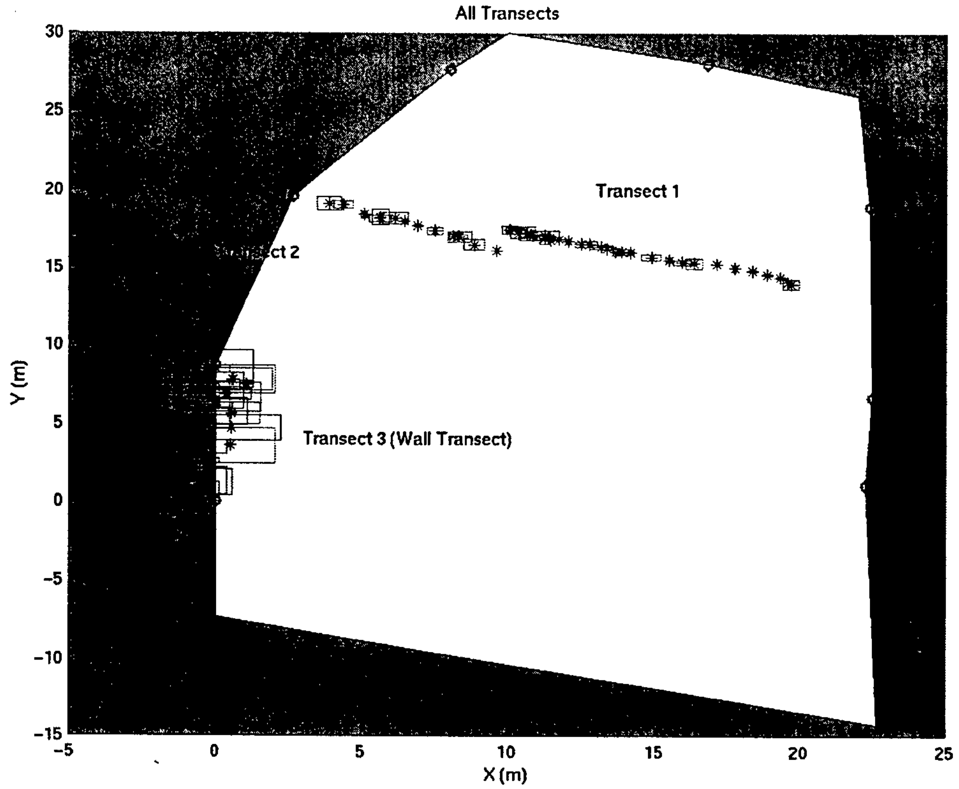

Figure 2. 6 Locations of hydrophones and transects lines in the lagoon

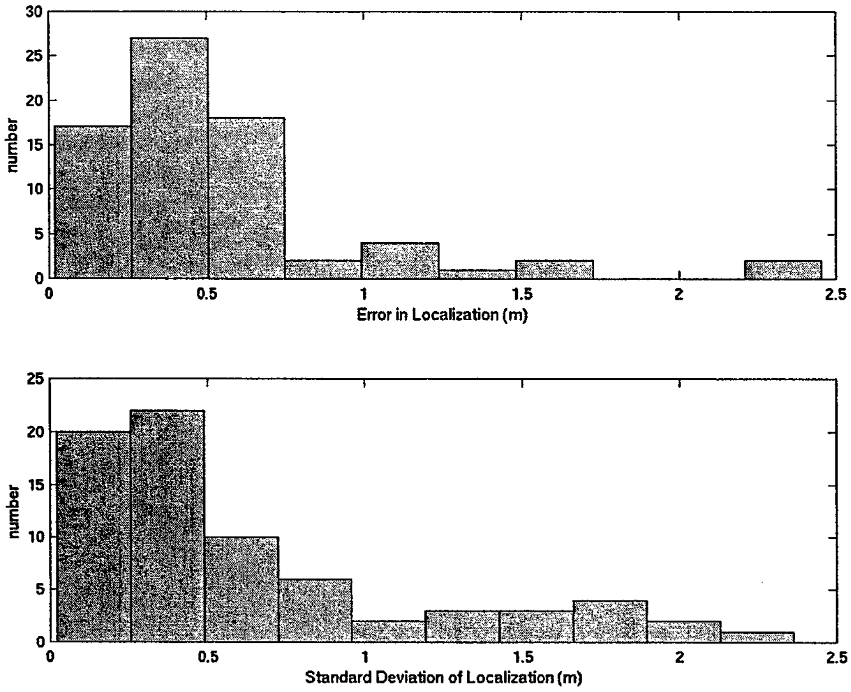

Figure 2. 7 Histograms of error and standard deviation of the acoustic localization system.

The localization error in terms of distance was less than 1.5 meters for 95% of the measurements (mean error = 0.54 meters). Thus the accuracy of the localization system can be thought of as being <1.5 m. The mean standard deviation was 0.64 m. Thus the precision of localization can be thought of as being two standard deviations, or 1.28 m.

The error (Fig. 2.8) and standard deviation (Fig. 2.9) were plotted vs. distance from the centroid of the array as well as vs. distance from the nearest wall. The error and standard deviation appeared to increase both with increasing distance from the centroid of the array as well as with decreasing distance to the nearest wall.

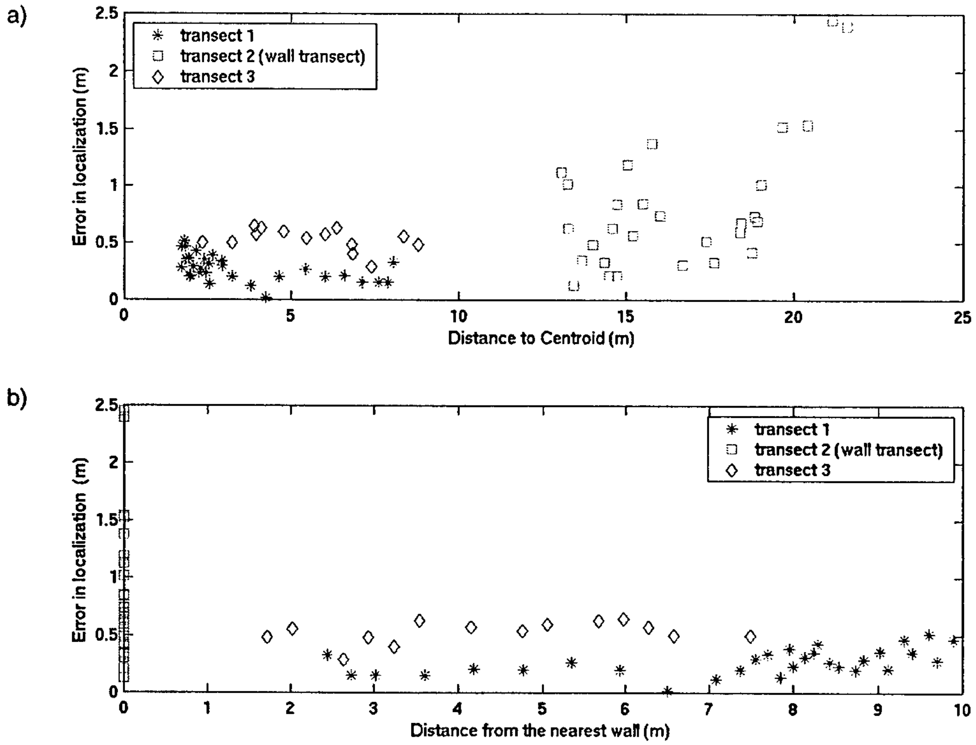

Figure 2. 8 Localization error

a) Error in localization plotted vs. distance from source position to centroid of array. (b) Error in localization plotted vs. distance from the nearest wall.

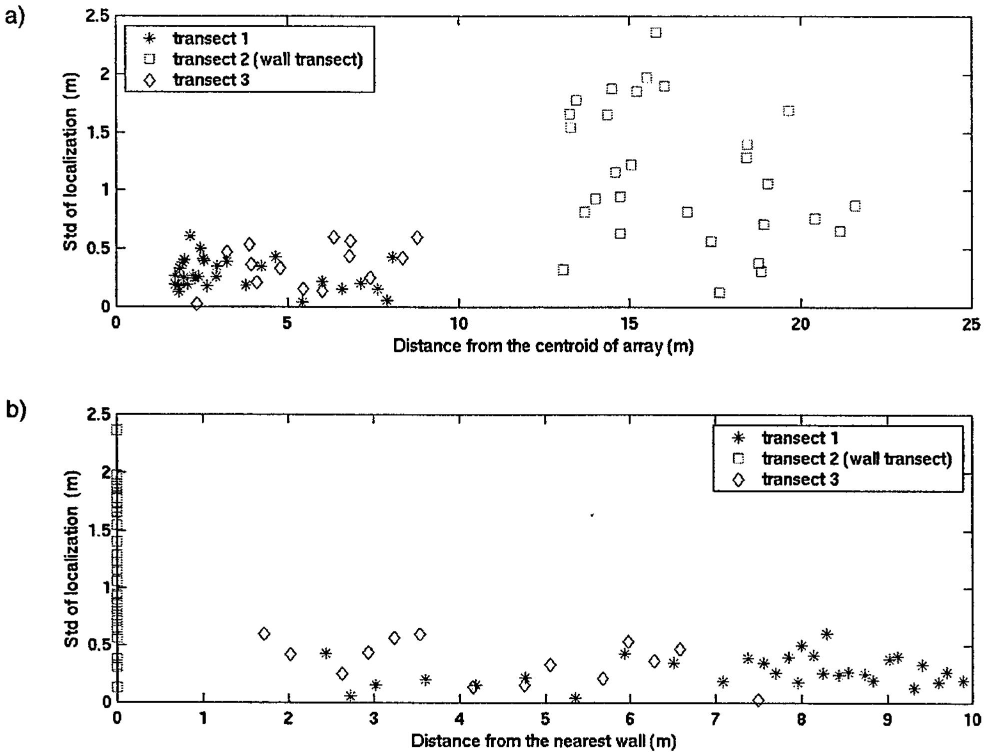

Figure 2. 9 Standard deviation of localized positions

(a) Standard deviation of positions plotted as a function of distance from the centroid of the array. (b) Standard deviation of positions plotted as a function of distance from the nearest wall.

2.3.2 Error of video imaging system:

The histogram of the video projection error in terms of pixels is shown in Fig. 2.10. The size of each video image in pixels was 480 x 720. Of the absolute error in the x dimension, 95 % was less than 11.6 pixels. This was less than 1.6 % percent of the image size in the x dimension. Of the absolute error in the y dimension, 95 % was less than 6.4 pixels, which is less than 1.3 % of the image size in the y dimension. The mean absolute error is 6.0 pixels in the x dimension and 2.4 pixels in the y dimension.

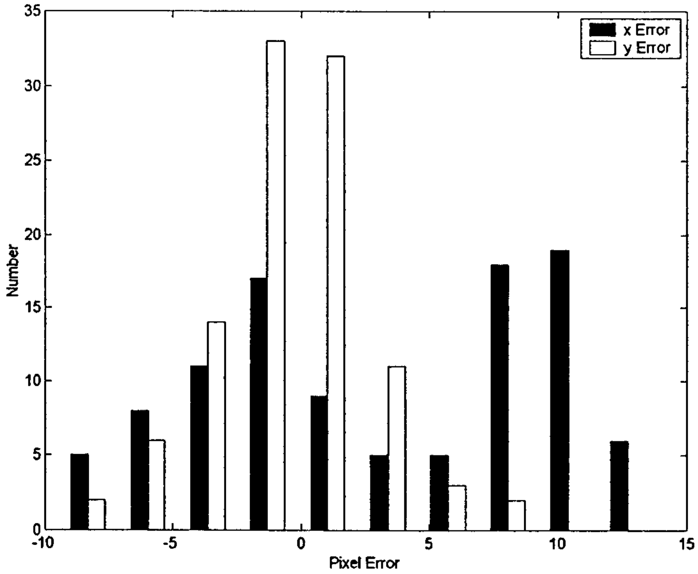

Figure 2. 10 Histogram of projection error of the video system in terms of pixels. The video frame is 480 x 720 pixels.

The projection error was calculated in terms of real world coordinates. The histogram of this error is shown in Fig. 2.11. Of the projection error, 95 % was less than 0.9 m in the x axis, and 2.0 m in the y axis. The mean absolute error was 0.5 meters in the x axis and 0.7 m in the y axis. The overall 2-D projection error was less than 2.1 meters for 95 % of the measurements. The mean 2-D projection error was 0.9 meters.

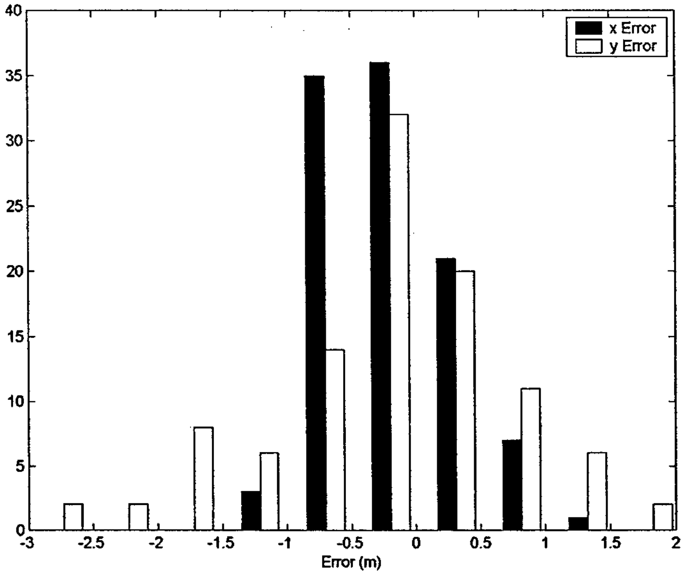

Figure 2. 11 Histogram of the projection error in terms of real world coordinates (m)

2.3.3 Synthesis of acoustic localization and video:

Artificial sound source

Video recordings were performed during acoustic calibration transect 1 across the center of the lagoon. This allowed direct comparison of the positions projected from the acoustic localizations to positions obtained directly from video images. Histograms of the differences in these two sets of positions for both pixel and real world coordinates are shown in Fig. 2.12. The error between the localized position and the video frame position was calculated in terms of both pixel and real world coordinates. Of the error measurements in the x and y axes, 95 % were less than 10.0 and 9.8 pixels respectively. In real world coordinates this corresponds to errors less than 0.9 m and 2.0 m respectively. The mean errors in the x and y axes were 4.7 and 7.5 pixels respectively. In real world coordinates this corresponds to mean errors of 0.4 m and 1.7 m in the x and y axes respectively. The 2-D error between the localized and video frame positions was less than 2.1 m for 95 % of the measurements. The mean 2-D error was 1.8 m.

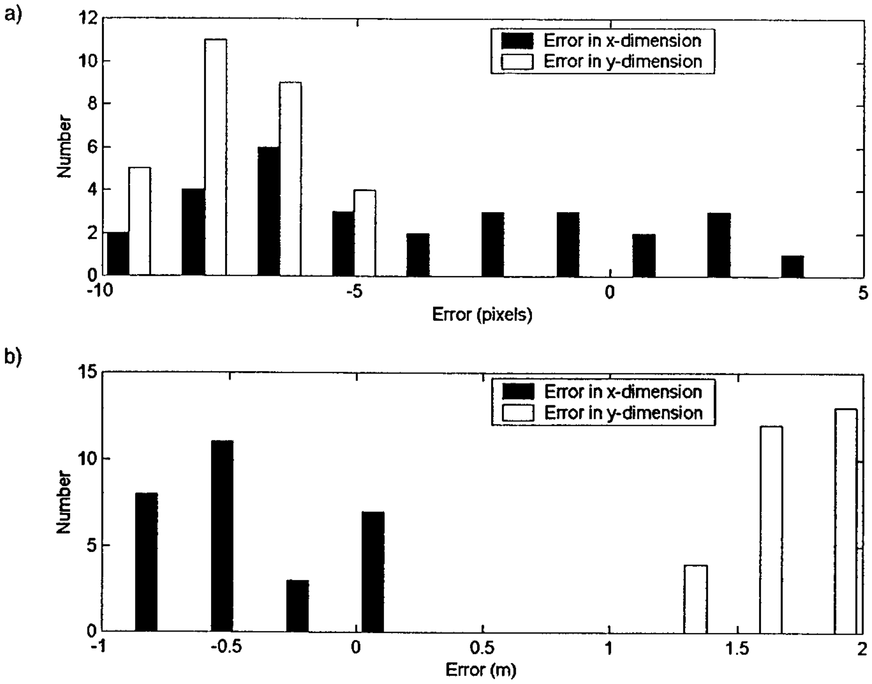

Figure 2. 12 Histograms of error in terms of pixels

(a) Difference in calculated pixel position of the acoustic source using acoustic localization and video imaging. (b) Difference in meters of calculated position of the acoustic source using acoustic localization and video imaging.

Dolphin vocalizations

The final set of results pertains to matching localized vocalizations with the identities of the vocalizing dolphins. An example of matching a localized vocalization to a dolphin is shown in Fig. 2.13. The results from the comparisons of localized positions to video frame positions are shown for each of the three call types in Table 2.1. The results were analyzed in terms of the errors in the x and y dimensions as well as the 2-D error. The mean errors were calculated for each call type as well as over all three call types. 95 % of the errors were less than 0.8 m in the x-dimension, 2.5 m in the y-dimension, and 2.9 m in the combined dimensions (2-D). The mean error of echolocation clicks appears to be lower than that of the other two call types, although the difference in error between the call types is not statistically significant (ANOVA, $p = 0.068$, shown in Fig. 2.14).

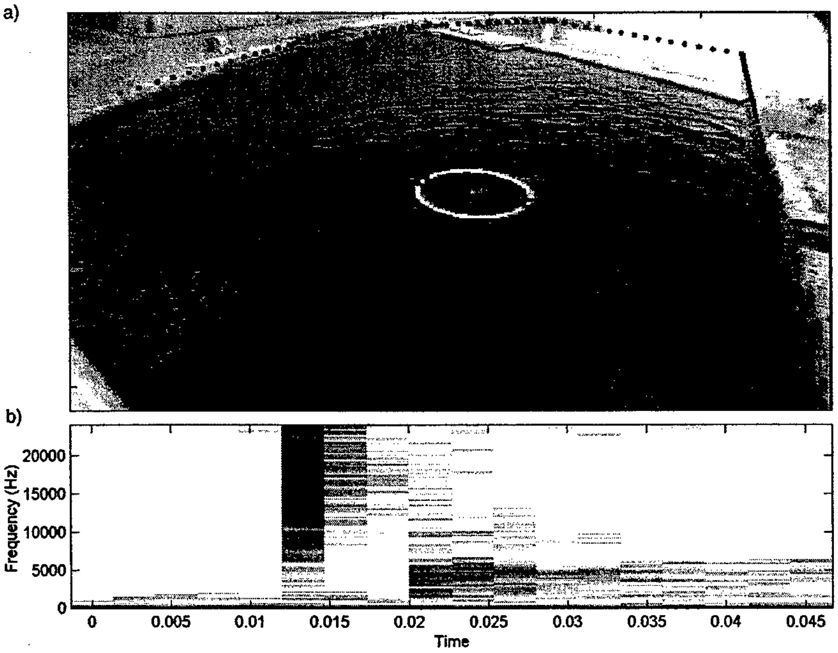

Figure 2. 13 Example localization of a dolphin vocalization

(a) The dot with a ring around it overlaid onto the video image shows the localized position of the vocalizing dolphin. (b) Spectrogram of the vocalization (echolocation click) that was used for the localization. Only frequencies above 10,000 Hz were used for this particular localization.

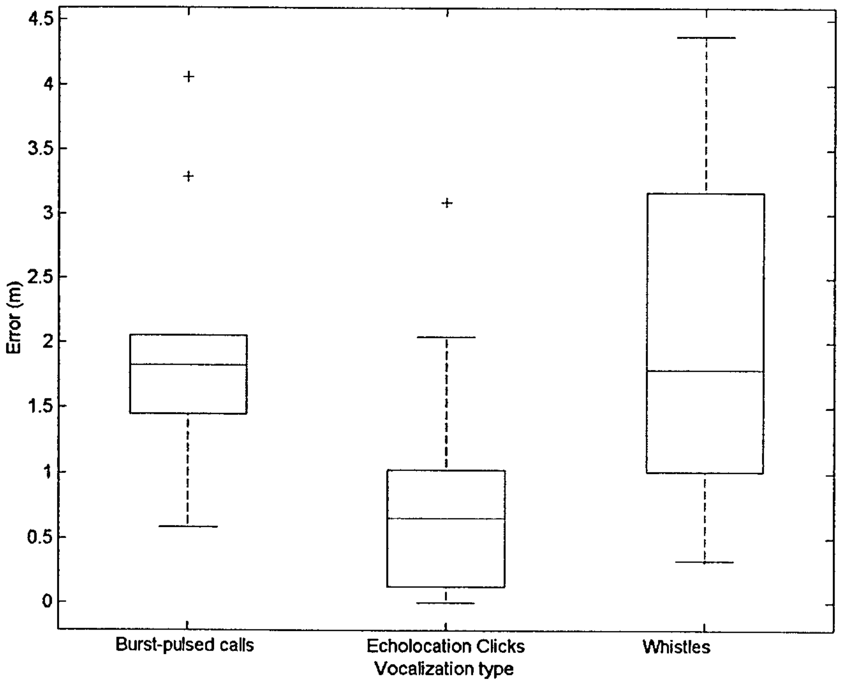

Figure 2. 14 Error (in terms of distance) between localized and video frame positions for each of three vocalization types.

Note: Outliers are represented by + symbols. The whiskers represent 1.5 multiplied by the interquartile range, which is a robust estimator of the spread of the data.

Table 2. 1 Mean error between localized and video frame positions for each of three vocalization types, the mean error over all three vocalization types, and the 95% error limit over all three vocalization types.

	X Dimension (m)	*Y Dimension (m)*	*2-D (m)*
Burst pulsed calls	0.33	1.29	1.34
Echolocation clicks	0.52	0.65	0.83
Whistles	0.34	1.24	1.28
Overall mean	0.40	1.06	1.13
95% error limit	0.75	2.52	2.91

In addition to determining the errors between localized positions and video frame positions of vocalizing dolphins, the percent of localized vocalizations that could be attributed to a dolphin or a group of dolphins was also calculated (Table 2.2). Since in some areas the video image did not extend to the bottom of the lagoon, there were occasions when a dolphin was believed to be in the area, but the presence of the dolphin could not be confirmed. A dolphin might be believed to be in the area if the path between the dolphin's previous and following surfacings crossed the area around the localized position. At other times, more than one dolphin could be seen within 1.5 m of the localized position. In these instances the vocalization could only be identified as coming from that group of dolphins. When only one dolphin was in the immediate vicinity of the localization (no other dolphins were within 1.5 m) the vocalization was determined to be from that individual.

Table 2. 2 Number and percentage of localized vocalizations that could be attributed to a dolphin or group of dolphins.

	Number (Total = 222)	*Percentage*
Can not determine if dolphin in area:		
No reason to believe there is a dolphin:	8	3.6 %
Reason to believe there is a dolphin:	27	12.2 %
Can identify to group of dolphins:	101	45.5%
Can identify to individual dolphin:	86	38.7%

2.4 Discussion:

The localization error of 95 % of the measurements from source playback transects was less than 1.5 m. This is less than the average length of an adult bottlenose dolphin (1.9-3.9 m (Read et al. 1993, Cawardine 1995)). The error is not constant at all points within the array, but increases towards the wall of the lagoon. This trend was observed primarily in transect 2. Transects 1 and 3 showed no discernible trend of increase or decrease in error with decreasing distance from the wall or with increasing distance from the centroid (Fig. 2.8). Transect 2, which was along the wall, was also the transect furthest from the centroid. Thus it is not strictly possible to separate the effects of decreasing distance from the wall and increasing distance from the centroid. However, the tight linkage between error greater than about 0.75 meters and proximity to the wall suggests that the wall may have been the main factor. Reflections of sound off the wall can confuse the localization algorithm. This problem with reverberation was also seen in Freitag and Tyack (1993), albeit with a different localization algorithm. Confusion is likely to be greatest when the sound originates near the wall and the reflected sound cannot be isolated from the direct path. There are several ways to reduce this problem. Localized positions from reflected sounds will appear to come from outside the lagoon, which we know is not possible. Another solution would be to keep the dolphins away from the walls, which in this setting was not practical.

The standard deviation of the transects (Fig. 2.9) followed the same trend as the error, with increasing standard deviation towards the wall and away from the centroid of the array. The precision of the source playback transects is 1.28 m. In this sense, we should be able to distinguish sound sources that are greater than 1.28 m apart.

The error of the video system was measured in terms of pixels (Fig. 2.10) and then projected into meters (Fig. 2.11). The absolute pixel error appeared to be the greatest in the x axis. However, the errors in terms of percentage of image size were similar for both the x and y axes. When the error of the video system was projected into real world coordinates, the error was greater in the y dimension (Fig. 2.11). Error in the y dimension appeared to increase with increasing y position (which was also increasing distance from the camera). The transects were performed around the perimeter of lagoon, which was longer in the y dimension than in the x dimension. The necessity of fitting more of the y-axis into the image resulted in less resolution and greater error at the limits. This skewed distribution of error could be improved by placing the video camera higher and at less of an angle to the lagoon (e.g. suspend the camera from an overhead blimp Nowacek (1999). An interesting feature of Fig. 2.10 is the bimodality of the x error. Due to practical considerations of the lagoon, the x axis was sampled more heavily at the extremes than at the middle. If one side were better calibrated at the expense of the other side, it would result in the observed bimodality of the x-error.

The error of the overall system must take into account the errors of both the acoustic localization and video projection components. The 95 % error bound calculated from the combined acoustic localization and video transect is 2.1 m. Comparison of this error bound to the 2.1 m error bound for the video transect and the 1.5 m error bound from the acoustic transects suggests that the video component of the system is the dominating source of error.

Although the transects using calibration sounds from a mechanical source demonstrate that the system ostensibly had an error less than 2.1 m, the true test of the system is with vocalizations from the dolphins. The 95 % error bound for the dolphin vocalizations is 2.9 m, roughly the length of an adult dolphin's body. The errors in video position and localized position of dolphin vocalizations are worse than those from calibration sounds from a mechanical source. This is probably due to a combination of several factors. The first factor has to do with the signal itself. The barker codes and frequency upsweeps used for calibration sounds are specifically designed to be easily locatable, while dolphin sounds may or may not be. In addition, many of the dolphin vocalizations may have lower signal to noise ratios than the calibration sounds, making localizations more susceptible to contamination from ambient noise, such as snapping shrimp clicks. Another factor is the movement of the dolphins themselves. This may result in smearing of the localization due to the dolphin's movement while vocalizing. Also, if the synchronization between the acoustic localization and the video imaging is not perfect, rapid movements of the dolphin will result in increased error in matching the localization position to the video image. The third factor concerns the limited visibility of the water column. For the dolphin vocalizations, most of the matches between the localizations and the dolphin image on the video were to whatever portion of the dolphin's anatomy was visible. Since dolphins can be up 4 m long, this could cause significant error. In addition, although the operator attempted to keep track of all the dolphins in the pool, it is possible that limited visibility may have resulted in incorrect or missed identification.

This system of acoustic localization using a fixed array combined with elevated video imaging has several benefits. The elevated video enables increased visibility into the water column, along with possibilities for more detailed behavior analyses. The localization component enables matching of the vocalization to concurrent behavior. Another advantage of this system is that it is not necessary for human observers be near the animals under observation. This may be important as the animals were fed by human trainers, and the presence of any humans may interrupt the dolphins' normal social routine. In practice, it may be difficult to obtain identification of individual dolphins without human observers or without marking the dolphins. The primary disadvantage of this system is that fixed arrays and elevated video cameras can be difficult to implement in ocean situations with free-ranging dolphins.

There are several avenues for improvement of the system. Increased resolution would enable determination of the vocalizing dolphin when dolphins are closer together. The video projection error appears to be the dominating source of error. However, since the video calibration error can be over ten pixels, the solution is probably not to increase image resolution. In one sense, this level of video error is not inherent to the system, and the results could probably be easily improved by superior camera placement and improved camera calibration. Placing the camera directly overhead the lagoon (e.g. suspended from a blimp (Nowacek 1999)) would reduce the error in at least one dimension. Using more than 5 points to perform daily calibrations, as well as using points spaced more evenly in the image, would probably increase accuracy of the calibration as well. Reducing this video error would be a relatively easy way to increase resolution of the entire system.

Increasing resolution of the acoustic localization system would also be helpful. Use of even slightly incorrect hydrophone positions can cause significant errors in localization. Thus, any method of improving calibration of hydrophone positions would likely decrease localization error. Placing the source a known distance from each hydrophone instead of directly adjacent to each hydrophone might avoid possible hydrophone overloading, near-field effects, as well as strong reverberation effects from the wall next to each hydrophone. The localization algorithm could be improved, to reduce its sensitivity to reverberation. The algorithm that was used in this study could only localize when one source was active at a time. Dolphins often vocalize simultaneously, so an algorithm capable of localizing simultaneous sources would also be useful.

2.5 Concluding remarks:

The combination of acoustic localization and video sampling techniques allows us to link a specific dolphin vocalization with the identity of the vocalizer. If the behavior of the vocalizing animal is known, either from the video record or from more detailed behavioral sampling, vocalizations can be linked to the contexts under which they were made. This is very important if we desire to ascertain the functions of vocalizations. Possible uses of this system include studying numerous aspects of the social contexts and behavioral function of vocal behavior as well as purely acoustic aspects of vocalizations (e.g. directionality) under normal social conditions. There are several avenues for improvement of the system. However, many new and interesting questions about marine mammal behavior can be answered with the current resolution.

2.6 Contributions:

Specific contributions of this chapter are:

I. Capability for localization of vocalizations of captive dolphins to vocalizing dolphin, or group of possible vocalizing dolphins

II. Capability for studying vocalizations from an individual (or a group of closely spaced dolphins) in an unbiased social setting (in captivity).

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Appendix 2.1: Classifier

Snapping shrimp clicks are short in duration and are relatively broad-band in frequency. In these features they resemble dolphin echolocation clicks. For the training set we chose a section of recording that was high in both numbers of snapping shrimp clicks and echolocation clicks. The operator first went through the cuts from the training set and classified the cuts as "desirable signal" or "noise" based upon snapping shrimp click content and signal-to-noise ratio. Next, ACOUSTAT parameters were calculated for all of the cuts. The data were normalized, and a principal components analysis transform was performed on the data. The 11 components that in total accounted for 95 % of the variance were kept. Linear discriminant analysis to distinguish desirable signals was performed on the components. The factors from the discriminant analysis were used to determine whether to keep or discard all subsequent cuts.

Chapter 3: Functional Acoustic Repertoire of the Bottlenose dolphin, *Tursiops truncatus*

3.1 Introduction:

One of the first steps in studying acoustic communication of a species is to determine its acoustic repertoire in order to provide a foundation for further studies. Even though the vocal repertoire of the bottlenose dolphin is better studied than that of any other cetacean species, no quantitative studies of the complete repertoire have been performed. The repertoire of the bottlenose dolphin has traditionally been broken down into three main categories: whistles, echolocation clicks, and burst-pulsed sounds. These categories are not entirely distinct, which is not surprising since the repertoire has been categorized by a confusing combination of structural and functional analyses. Whistles have a tonal structure, usually with harmonics. Echolocation clicks are pulsed calls that have been designated as such because of their assumed function in echolocation, while burst-pulsed calls are usually described as serving a communicative function. Burst-pulsed calls, which are a series of clicks like echolocation clicks, are termed as such because of their acoustic structure: bursts of pulses. These latter two categories have historically been separated by supposed function, but have similar acoustic structures. This has caused much confusion. For instance, Wood (1953) put into the burst-pulsed category a "rusty-hinge" sound that is now thought to be echolocation.

3.1.1 Literature review of the bottlenose dolphin acoustic repertoire

Table 3.1 provides a review of the literature describing various elements of the bottlenose dolphin acoustic repertoire. The purpose of this review is not to make sense of the current repertoire system, but rather to demonstrate that a coherent and replicable system is not in place. For example, various terms may have been used for the same vocalization, some terms may have been used for a number of different vocalizations, and other terms are just not clear. I will not attempt to relate the vocalization types to each other as I do not have access to the original data. I have expanded to include two more categories, "single impulse signals" and "compound signals." These categories were added since a number of the vocalization types did not fit in with the standard whistle/echolocation/burst-pulsed call categorization scheme.

One of the earliest descriptions of bottlenose dolphin acoustic behavior came from McBride and Hebb (1948). They described three types of sounds made by dolphins: "a snapping noise made with the jaw" (jaw clap), whistles, and "barking" (now thought to be a combination of the categories of burst-pulsed sounds and echolocation). These three categories were expanded upon by Wood (1953), such that "barking" was subdivided into four categories, "rasping and grating" sounds, "mewing and rasping" sounds, "barking" sounds, and "yelping" sounds. The first two categories were probably echolocation click trains. "Rasping and grating" sounds included the "rusty hinge" sound used by dolphins when examining objects. The "mewing and rasping" sounds, also click trains which were described as sounding similar to the "rasping and grating" sounds above, were specifically associated with feeding (Wood 1953). The other two categories appeared to be communicative. "Barking" has been reported to be associated with play, feeding, sexual activity (Wood 1953), and agonism (Herzing 1996). "Yelping" may also have been associated with sexual activity (Caldwell and Caldwell 1967). These latter two categories were probably what we would now call "burst-pulsed sounds" since they appeared to primarily be communicative signals but also had a pulsed acoustical structure.

Dolphin sonar (echolocation) was first published as a possibility in 1952 (Kellogg and Kohler 1952), although it had been postulated as early as 1947 by McBride (1956). Several early investigations were published in the 1950's (Schevill and Lawrence 1956, Kellogg 1958), but the study leading to its experimental confirmation was not published until 1961 (Norris *et al.* 1961). The classification of the bottlenose dolphin acoustic repertoire into the broad groups of whistles, echolocation clicks, and burst-pulsed sounds coalesced gradually, and by 1980 was the dominant paradigm (Popper 1980).

From Table 3.1, it is obvious that the descriptors of various elements of the acoustic repertoire are not standardized. There are many different types of measurements in both the time and frequency domains, with researchers probably selecting those they thought were most pertinent to the specific vocalization or context. Frequency range (minimum to maximum frequency) was often used as a frequency descriptor, although the frequency of peak energy, mean frequency, and textual descriptors were also used. It should be kept in mind that the maximum frequency measurements in many of the referenced studies were probably limited by the equipment used. For instance, the upper frequency limit of the system used in the Caldwell and Caldwell (1967) study on pulsed sounds was 6 kHz, while the equipment used in the Au *et al.* (1974) study extended to over 200 kHz.

Duration was often used as a time descriptor, although other time descriptors were used, including number of pulses/clicks per second (for pulsed sounds), interclick interval, repetition rate, time interval between vocalizations, and textual descriptors. The lack of standardization of descriptors makes comparison across categories very difficult. In addition, the various names for elements of the repertoire are not standardized, and researchers may not be using these names in the same way.

The confusion in the repertoire analysis of the bottlenose dolphin is partially due to inconsistency and piece-meal analysis. Analyses have also tended to focus on a limited physical setting and one behavioral context. It is important that repertoire analyses be done on a more general contextual scale. For instance, "pops" have been recorded during a study of sexual consortships in Shark Bay, Western Australia (Connor and Smolker 1996), "thunks" have been heard during studies of mother/infant interactions in captivity (McCowan and Reiss 1995), "low creaks" have been recorded in the Sado Estuary, Portugal (dos Santos *et al.* 1990), and "bangs" have been recorded in several different locations (Marten *et al.* 1988). These vocalizations were all reported as low-frequency impulses. They may or may not be basically the same vocalization produced during different contexts, but it is difficult to know unless the same groups of animals are studied under a variety of contexts, and the vocalizations compared.

Our understanding of the entire bottlenose dolphin repertoire would greatly improve if an appropriate structural-acoustic categorization scheme were consistently and quantitatively applied. The accessibility of rapid computerized techniques has now made it much more feasible to characterize acoustic signals objectively and consistently (Fristrup and Watkins 1992, Thomas and Tyack 1998). In previous repertoire analyses, classification by acoustic form as well as by guesses as to function of vocalizations have often been applied at the same time, muddying the analysis. This is true even at the broad category level. *Whistles* are named for their tonal structure and *echolocation clicks* are named for their function. The category of *burst-pulsed* sounds is an amalgam of all the calls that are not tonal and do not appear to serve an echolocation function. This term probably comes from Lilly's description (Lilly and Miller 1961) of three categories of dolphin sounds: whistles, slow trains of clicks, and a class of complex sounds "emitted in bursts." Lilly's original class of sounds "emitted in bursts" probably included some echolocation signals as well, but by 1980 (Popper 1980) the term burst-pulsed sound was appropriated to include only social pulsed signals, which is how it is currently used.

The cut-off between the three groups is not distinct. A dolphin may produce clicks concurrently with a whistle. Some burst-pulsed sounds appear to have tonal components, possibly resulting in confusion with whistles. Both burst-pulsed calls and echolocation signals are generally made up of click trains. The distinction between burst-pulsed sounds and echolocation is based upon interclick interval (or pulse repetition rate) and intensity (Au 2000). Since intensity is difficult to measure when the location of the animal is not known, most researchers use interclick interval or pulse repetition rate to distinguish the two call types. Despite this, the cut-off in interclick interval or pulse-repetition rate that is appropriate for distinguishing echolocation click trains from burst-pulsed click trains is not clear.

The lack of clear acoustic distinction between echolocation signals and burst-pulsed calls is a weak point of the current repertoire system. As mentioned above, one of the primary differences between what is currently considered a burst-pulsed sound and what is considered an echolocation signal is that of function (whether or not it serves an echolocative function). Click trains that are associated with foraging and feeding are generally assumed to be echolocation. However, other non-click train vocalizations may be associated with feeding as well. For instance, loud bangs have also been hypothesized to be associated with feeding as described by the acoustic stunning hypothesis (Norris and Mohl 1983). Brays, a combination of tonal sounds and grunts (classified as a burst-pulsed sound (Janik 2000)), are communicative calls that are also associated with feeding (Janik 2000).

It is often not possible to know the behavioral context of the vocalization, and thus researchers often cannot classify the vocalization by its function. Therefore researchers have also endeavored to use acoustic descriptors to classify vocalizations. A descriptor that appears to have been commonly used to distinguish between burst-pulsed sounds and echolocation signals is the interclick interval (Overstrom 1983, Murray *et al.* 1998, Au 2000). Traditionally, attempts to distinguish between echolocation clicks and burst-pulsed calls have been made aurally by humans, probably based on the interclick intervals. If the click rate is low enough that the human listener can distinguish individual clicks, then the series is often classed as echolocation clicks. If on the other hand the click rate is so high that the human hears a buzzing burst of pulses, the series may be classed as a burst-pulsed sound. Since the critical interclick interval beyond which humans and dolphins are unable to distinguish paired clicks differs, humans and dolphins will necessarily hear a range of these sounds in different ways. The critical interclick interval for dolphins has been shown to be in the range of 0.25 - 0.3 ms (3333 –

4000 clicks/sec) (Zanin and Zaslavskii 1977, Dubrovskiy 1990). By contrast, the critical interclick interval for humans appears to be about 6 ms, reviewed in Ralston and Herman 1989), about 20 times longer than that for dolphins. Interclick intervals in bottlenose dolphin echolocation clicks have been reported to be anywhere in the range of 2.5 ms to 50 ms (20 – 400 clicks/sec), with most measurements in the range of 15-22 ms (45 – 67 clicks/sec). From Table 3.1 we see that when the click rate of burst-pulsed calls was noted, it was in the range of 50-2000 clicks/sec, with an average range of 86 to 1333 clicks/sec. This translates to an average interclick interval range of 11.6 to 0.75 ms. Humans may be able to distinguish individual clicks at the low end of this click rate range, but definitely will not be able to isolate clicks aurally as the click rate increases. Thus at some click rates the burst-pulsed calls will sound pulsed to humans, whereas at faster rates they will not. On the other hand, dolphins should be able to distinguish the individual clicks over most of this range. Even at the fastest click rate listed (2000 clicks/sec, corresponding to an interclick interval of .5 ms), dolphins should theoretically be able to distinguish individual clicks. Over the entire range of interclick intervals of burst-pulsed sounds, dolphins should still be able to hear them as a train of individual clicks. Thus some of the confusion in the functional repertoire resulting from humans attempting to aurally (rather than functionally) distinguish between echolocation clicks and burst-pulsed sounds may result from the dichotomy between how we perceive the signals and how the dolphins perceive them.

Dolphins may emit functionally similar signals with differing acoustic structures, depending on the individual animal as well as on very specific circumstances. As mentioned above, the interclick interval for echolocation clicks can vary widely. The details depend on the phase of the echolocation activity (search, targeting, etc.) as well as on the distance between the dolphin and the target (Au 1993). Signal details may vary widely depending on individual experience for social signals as well. For instance, signature whistles are thought to be learned and individually distinctive (Caldwell *et al.* 1990, Sayigh *et al.* 1995). If dolphins retain the ability to learn new signals throughout their life, and if they can imitate arbitrary sounds in their environment (Richards *et al.* 1984), then the bottlenose dolphin acoustic repertoire may be open-ended and not finite, like some avian acoustic repertoires (Kroodsma 1979). The large amount of individual variation in addition to the lack of a coherent general acoustic repertoire prompts a focus on analyzing more general acoustic categories that will be applied to this chapter.

The lack of distinction between the structural and functional analyses of the bottlenose dolphin repertoire at a more detailed level is apparent in Tables 3.1 and 3.2. Table 3.2 shows the elements of the repertoire that have been given a functional description, with the proposed functions arranged by general sound type (tonal signals, burst-pulsed signals, clicks/echolocation signals, single impulse signals, and compound signals). Many of the structural elements of the repertoire are named according to, or connote possible function, such as the "fight squawk," the "whimper," and the "sex yelp." Including postulated functional categories in the repertoire classification before the supposed function is confirmed can be dangerous and misleading (Martin and Bateson 1993), as illustrated by the problems discussed so far concerning the bottlenose dolphin repertoire

Table 3. 1 A summary of the literature description of the elements of the acoustic vocalization repertoire of *Tursiops truncatus*.

Vocalization	Description in Frequency	Description in Time	Proposed Function	Context/ Comments	Reference
***1*: Whistles and Tonal signals**					
1.A Whistle	4-6 kHz^t	< .2 s^t			(Jacobs *et al.* 1993)
				separated into contour types	(Dreher 1966)
	4-18 kHz, usually 9-12 kHz^t	.1s - .4s (mode = .25s)^t		sine-wave type	(Lilly and Miller 1961)
	Mostly > 1.5 kHz, mean variation in freq. = 7.76 kHz^t	Mean duration = .40 s^t			(Schultz *et al.* 1995)
	Min: 3 kHz, Max: >16 kHz^t (over all 17 contour types). Included initial and final freq. for each contour type	Duration range: 225-2400 ms^t		Continuous, tonal sounds	(dos Santos *et al.* 1990)
1.A1 Signature whistle	Mode Frequency sweep: 7 kHz^t Min Freq: 1 - 9 kHz (mode = 5 kHz)^t Max Freq: 8 - >24 kHz (mode 13-15kHz)^t	Ave. Duration: .96 s^t	Broadcast identity of whistler		(Caldwell *et al.* 1990)
1.B Scream	Freq. Range = 5.8 - 9.4 kHz, Overlapping FM whistles^t	Duration = 2.5 - 4.0 s^t	Agonistic and aggressive		(Herzing 1996)
1.C LFN: Low-frequency, narrow- band	Fund. Freq. Range: 260 Hz – 1280 Hz, mean variation in frequency = 41 Hz^t	Duration = .01 -.41 s, mean =.05 s^t			(Schultz *et al.* 1995)
1.D Chirp	pure tone, often with upward FM^t	Brief^t		didn't classify it as a whistle	(Caldwell and Caldwell 1967)

***2:* Burst-pulsed signals**					
2.A Quack type sounds (class iii)		50 -800 clicks/sec, .1 -3 s, Emitted in bursts ^{t}			(Lilly and Miller 1961)
	Freq. Range: 2-9 kHz ^{t}	.05 s ^{t}	Social?	Correlated with social behavior	(Jacobs *et al.* 1993)
2.B Yelp	high-pitched ^{t}		Sexual/ Aggressive	Loud. Related to sexual behavior, dominance?	(Wood 1953)
2.B1 "sex yelp"	~ DC to 5 kHz ^{s}	.2 -.4 s ^{s}	Sexual	From male making advances to female	(Caldwell and Caldwell 1967)
2.B2 Creak	most energy < 2.5 kHz ^{t}	Pulse rate > 40 pulses /sec ^{t}		labeled as continuum: click trains->creaks -> moans.	(dos Santos *et al.* 1990)
2.B3 Squawk		Emitted in bursts, click rates up to 800 /sec ^{t}			Lilly and Miller 1961
	.2 - 12 kHz "broad-band" Main energy 1.1 – 2.4 kHz ^{t}	.2 - 1.0 s 200-1200 clicks/s ^{t}	Agonistic and aggressive, Sexual play		(Herzing 1996)
2.C1 "chase squawk"	Freq. Range: 0 - 2 kHz ^{s}	Duration: .4 s ^{s}	Aggression, play	During a chase	(Caldwell and Caldwell 1967)
2.C2 "fight squawk"	Freq. Range: 0 –2.5 kHz ^{s}	Duration: .4 -.5 s ^{s}	Aggression	During a fight. Sounds shows only minor difference from chase squawk	(Caldwell and Caldwell 1967)
2.C3 "low-frequency squawk"	Freq. Range: 0 - 6 kHz ^{s} (cut off at 6 kHz)	Duration: .6 -.8 s ^{s}	Agitation /disturbance	From adult female carrying still-born calf.	(Caldwell and Caldwell 1967)
2.C4 "synchronized squawk"	Freq. Range: .1 - 15 kHz Main energy .1 - 2.2 kHz ^{s}	Duration: .9 - 1.0 s ^{s}	Agonistic and aggressive		(Herzing 1996)

2.D Bark				Quite loud	(McBride and Hebb 1948)
	slightly falling inflection ^{t}			2-12 repeated rapidly	(Wood 1953)
		Prolonged click train^t			(Lilly 1962)
	Freq. Range: .2 - 2.0 kHz ^{t}	Duration: .5 - 1.0 s ^{t}	Agonistic and aggressive		(Herzing 1996)
2.E Soft Bark	main energy <2 kHz (6 kHz cutoff) ^{s}	<.1 s ^{s}		similar to squeak, but softer	(Caldwell and Caldwell 1967)
2.F Squeak, or high-pitched bark	main energy <3 kHz (6 kHz cutoff) ^{s}	<.1 s ^{s}		Dumbbell was suspended over pool	(Caldwell and Caldwell 1967)
2.G Whimper	.5 - 3 kHz, ^{s}	.3 s ^{s}	Appeasement	when new animal introduced to tank.	(Caldwell and Caldwell 1967)
2.H Short Bursts		Duration: < 1 s ^{t}	Aggression		(Overstrom 1983)
2.I Long Bursts		Duration: >1 s ^{t}	Aggression		(Overstrom 1983)
2.J Buzz effect		No click structure found using analysis at 3.8 cm/s ^{t}		modification of other sounds, making them noisy, with the appearance of a buzzing wasp.	(dos Santos *et al.* 1990)
2.K Jaw clap sound			Threat		(McBride and Hebb 1948)
2.L Blasts	noisy	3 bursts, each last ~150 ms, for ~700ms total ^{t}			(dos Santos *et al.* 1990)
2.M Buzz	Freq. Range: 2-7 kHz ^{t}	Duration: 0.5 s ^{s}	Travel?	associated with travel	(Jacobs *et al.* 1993)
2.N Genital Buzz	Freq. Range: 1.2 - 2.5 kHz ^{t}	Duration: 6-20 s 8-2000 clicks/s ^{t}	Discipline		(Herzing 1996)

***3:* Clicks and echolocation signals**					
3.A Rusty-hinge		Duration: Generally 1-3 s ^{t}	Novelty	when new object introduced	(Wood 1953)
3.B Raspings and Gratings	toneless and grating to high-pitched, musical meandering ^{t}	Duration: brief to 2-3 s ^{t}		(related to rusty-hinge). Apparently intergrade to a considerable extent	(Wood 1953)
3.C Mewing				during provisioning of fish	(Wood 1953)
	up to at least 6 kHz ^{t}	.7 s ^{t}	Fine-discrimination echolocation	associated with echolocation - doing difficult tasks	(Caldwell and Caldwell 1967)
		click train prolonged over seconds ^{t}		also termed "wailings"	(Lilly 1962)
3.D Click		> .001 s ^{t}	Echolocation	Used for sonar	(Kellogg 1961)
	Peak frequency: 110-130 kHz ^{t} 3 dB bandwidth: 30 – 40 kHz ^{t} (dolphin/location dependent)	Duration: 40 – 70 µs ^{t}	Echolocation	Also directional, average directivity index of 24.8 dB ^{t}	(Au *et al.* 1974, Au *et al.* 1978, Au 1980, Au 1993)
			Foraging		(Nowacek, 1999)
3.E Click Trains		1-800 clicks/sec ^{t}		slow, buzzings	(Lilly and Miller 1961)
		.5 -1 s (for train) ^{t}			(Lilly and Miller 1961)
3.F Click-creakings			Echolocation	find food, navigate	(Lilly and Miller 1961)
3.G Razor Buzz	Freq. Range: 2.0 – 6.0 kHz ^{t}	200 click/s sustained for minutes ^{t}	Echolocation, Foraging		(Herzing 1996)

***4:* Single Impulse**					
4.A Jaw-clap			Threat	Visual and acoustic component	(McBride and Hebb 1948),
			Threat	May be associated with a very short sharp series of loud clicks	(Lilly 1962)
4.A1 jaw-clap (Hawaii-NOSC)	range .5 - 3.7 kHz ^{t} mean 1.8 kHz ^{t} SD = .6 kHz ^{t}	mean = 9 ms ^{t} SD = 8 ms ^{t}	Social	"social impulse sound"	(Marten *et al.* 1988)
4.A2 jaw-clap (Florida-Marineland)	range 0 - 2.5 kHz ^{t} mean = 530 Hz ^{t} SD = 444 Hz ^{t}	mean = 44 ms ^{t} SD = 21 ms ^{t}	Social	"social impulse sound"	(Marten *et al.* 1988)
4.B Thunk	Peak: 273-350 Hz ^{t} Range: 129-5556 Hz ^{t}	Range: 21-171 ms ^{t}	Maternal aggressive contact vocalization		(McCowan and Reiss 1995)
4.C Crack	more energy in low freq band (.1 -8 kHz) than ech. click		Fear		(Caldwell *et al.* 1962)
4.D Pop		<.1 s (on sg)		same as crack, but lower intensity	(Caldwell and Caldwell 1967)
	max power at mean=1166 Hz (range 320-2160 Hz) ^{t}	4-11 ms (main part), mean interval between pops =118ms (range 68-285 ms) Rep. rate 6-12 /sec ^{t}	Sexual/threat	Hypothesized to function as threat vocalization - induces fem. remain by male during courtship	(Connor and Smolker 1996)
	Concentrated at 2 kHz, some sound near 6 kHz ^{t}	0.005 s^t	Feeding, socialization?	Associated with feeding	(Jacobs *et al.* 1993)
			Foraging		(Nowacek 1999)

4.E1 Bang	broadband (freq. response up to 20 kHz)	about 20 ms		authors think resembles Caldwells' "cracks and "pops"	(dos Santos *et al.* 1990)
4.E2 Bang ("predatory")	broadband; range 50 Hz - 1.0 kHz mean = 580 Hz, SD = 132 Hz ^{t}	mean = 46 ms SD = 24 ms ^{t}	Feeding	predatory	(Marten *et al.* 1988)
4.F Loud clicks			Aggression	described as "loud clicks", look like a crack, described as having a threat function	(Lilly 1962)
5: Combined Vocalizations					
5.A Whistle-squawk	whistle: about 5 kHz (cut-off), upsweep ^{t} squawk: 0 - 4-5 kHz ^{s} freq. range	whistle: short, up to about .2 s ^{s} squawk: .1 -.5 s ^{s}		First whistle, then squawk. Both components "individually-characteristic"	(Caldwell and Caldwell 1967)
5.B Bray		Mean time interval between squeak and grunt: 390 ms ^{t}		squeak-like sounds followed by grunts. Sometimes preceded by creak or noisy sound	(dos Santos *et al.* 1990)
			Feeding	Describes as burst-pulsed sound	(Janik 2000)

^{t} = from description in text
^{s} = approximated from spectrogram

Others:
chirps, grunts, squeals, snorts, clucking noises, noises like a bulb horn, sounds like voice (Wood 1953)

Table 3. 2 A summary of the literature description of the functions associated with general vocalization types

Acoustic Structure

Function

	Whistles/Tonal Signals	***Burst-pulsed Signals***	***Clicks and Echolocation Signals***	***Single Impulse Signals***	***Compound Signals***
Aggression	screams (Herzing 1996)	squawks (Caldwell and Caldwell 1967, Herzing 1996), barks (Herzing 1996), genital buzz (discipline) (Herzing 1996), jaw-clap (McBride and Hebb 1948, Lilly 1962)		Thunk (McCowan and Reiss 1995), pop (Connor and Smolker 1996)	
Sexual		sex yelp (Caldwell and Caldwell 1967), squawk (Herzing 1996)		Pop (Connor and Smolker 1996)	
Submission		whimper (Caldwell and Caldwell 1967), crack (fear) (Caldwell and Caldwell 1962)			
Unspecified Social	signature whistles (Caldwell *et al.* 1990)	quack (Jacobs *et al.* 1993)		Bang "social" (Marten *et al.* 1988)	
Contact	signature whistles (Caldwell *et al.* 1990)				
Echolocation			echolocation (Kellogg 1961)		
Foraging			Clicks (Nowacek, 1999)	Bang "predatory" (Marten *et al.* 1988), pop (Nowacek 1999)	Bray (Janik 2000)
Other		buzz (Jacobs *et al.* 1993), disturbance, low-frequency squawk (Caldwell and Caldwell 1967)			

There is no one-to-one mapping from acoustic to functional categories in Table 3.2. Table 3.2 also glaringly points out the difficulties involved in classifying some sound types by their function and others by their acoustic structure. A large number of the vocalization elements that were named and placed in the burst-pulsed category appear to be the result of a single study in which a certain type of pulsed train vocalization was observed to occur during a specific social context (yelp, sex yelp, chase squawk, fight squawk, low-frequency squawk, synchronized squawk, bark, and whimper). This study did not systematically test the association of each sound across all functional contexts. It is quite possible that the same vocalization type could occur in other contexts and therefore be given a different label (e.g. Caldwell and Caldwell (1967) could not distinguish acoustically between a fight squawk and a chase squawk).

The literature review summarized in Tables 3.1 and 3.2 clearly demonstrates the need for a consistent and replicable classification of the acoustic repertoire. This does not necessarily preclude situations in which human observers may be used to classify sounds (e.g. Sayigh *et al.* 1995, Janik 1999). However, the objectivity introduced by using an automated computer system would aid in consistency of classification across researchers. Such a classification scheme would also be easily replicable. Thus, the primary goals of this chapter are to describe a consistent and replicable method for linking acoustic characteristics of bottlenose dolphin vocalizations to their context and to describe results from the method. This new method can be used to explore in more detail the distinction between burst pulsed calls and echolocation signals as well as between pulsed calls and whistles.

3.1.2 Parameterization

Behaviorists tend to classify behavior into discrete and exclusive categories for ease of later analysis. For instance, Martin and Bateson (1993), in their well-known introductory guide to measuring behavior, suggest that behavioral categories should generally be independent of one another. Categories are necessary abstractions for pooling data for analysis (Fentress 1973). In addition, the formation of categories may be a trait common to all organisms (Marler 1982, Harnad 1987). A discrete categorization makes sense when the animals themselves perceive the categories as discrete. As stated by Fentress, "categories *must be formed*, but the investigator *must not believe them*" (Fentress 1973). Every discrete category of biological signals still contains variation (Marler 1976). If signals appear (to humans) to be graded rather than discrete, the problem may be even more difficult. Animals may or may not classify what we perceive as graded signals into discrete categories, but without studies on categorical perception of the species, it may be difficult to determine the appropriate cut-offs, if any.

An alternative to the formation of discrete categories is parameterization. The parameters themselves can later be used to form categories if desired. Possible advantages of parameterization include automated analyses, an explicit focus on certain signal characteristics, and the ability to retain the graded characteristics of signals for further analyses. An example of use of parameters in studying acoustic behavior comes from Todt (1988). Todt calculated various acoustic parameters of the crying process of a Barbary macaque infant, and investigated how these parameters changed with time and external behavioral events. He determined that the temporal dynamics found in the analyzed processes did not correlate with contextual variables, and interpreted the results as being a reflection of the signaler's internal state. Extending this research to humans, Todt found that there were responses of human judges to parameters of cries of human infants. For instance, headturn responses of the judges positively correlated to occurrence of noisy cries.

The parameters used will usually depend on the signal in question. While Morton's motivational-structural rules (Morton 1977) are a topic of debate, his rules suggest clearly that pitch and bandwidth may be important components of acoustic signals. Signals have been theorized to have certain design features dependent on their function (Bradbury and Vehrencamp 1998). For instance, acoustic threat signals may be low frequency, while acoustic courtship and alarm signals may be composed of higher frequencies. Any investigation of signals which are proposed to serve certain functions would be well advised to include parameters relevant to the appropriate theorized design features.

In this thesis chapter I investigated the acoustic repertoire of the bottlenose dolphin. Bottlenose dolphins are thought to have two separate sound-producing mechanisms producing whistles and pulsed sounds (Dormer 1976, Cranford *et al.* 1997). Therefore it makes sense to use two separate parameters, one for tonal and one for pulsed sounds, to investigate functional usage of the repertoire. Using time series for the behavior and acoustic data explicitly keeps the time dependent nature of each data set as well as the synchronicity between the two data types. This will allow for later analysis of timing of behaviors with respect to vocalizations.

This computerized system for classifying dolphin sounds gets around the issue of the lack of repertoire classification by first allowing a very general description of sounds that can then be linked to behavioral context. The parameterization step calculates acoustic parameters of interest without limiting the analysis to one specific vocalization type. This is of special use in a situation such as the bottlenose dolphin repertoire where specific vocalization types are not well defined or in situations when different vocalizations may be combined.

The method offers an overall picture of what types of vocalizations (in a very general sense) are being used in the lagoon at the time of certain behaviors. This then allows us to flag interesting correlations for further study. The temporal associations between behaviors and vocalizations have not been well studied. Correlating the behavior and parameter time series allows determination of whether behaviors and parameterized vocalizations are associated in time as well as what time scales are appropriate for analyses. This method also allows determination of offsets between the time series (i.e.

anticipation or delay). The method can also be used to look at associations in time between different vocalization parameter types.

Another major goal of this chapter is to determine whether vocalization patterns of all animals within the group correlate well with activities measured from one dolphin randomly selected within the group, or whether it is important to focus on associating specific vocalizations with specific individuals that are engaged in specific interactions. The data acquired in this thesis consisted of several components, including focal follows of behavior from one randomly-selected dolphin at a time and multichannel acoustic recordings from the entire lagoon. Although we follow the behavior of one dolphin at a time, vocalizations in this chapter could have come from any of the dolphins in the lagoon, and not necessarily from that one dolphin. If the behavioral context of one dolphin is sufficient to determine the bulk of the vocalization types, then the repertoire can probably be analyzed on the group level, and individual identification is not important. If the behavioral context of the dolphin is not sufficient to discriminate among the vocalization types, then further splitting of the vocalization types or analysis on the level of the individual is required for repertoire analysis. This issue of analysis on the level of the group vs. individual will be further discussed in Chapter 4.

3.1.3 Overview of methods:

A brief overview of the methods to be used in this chapter is given here, and summarized in Fig. 3.1.

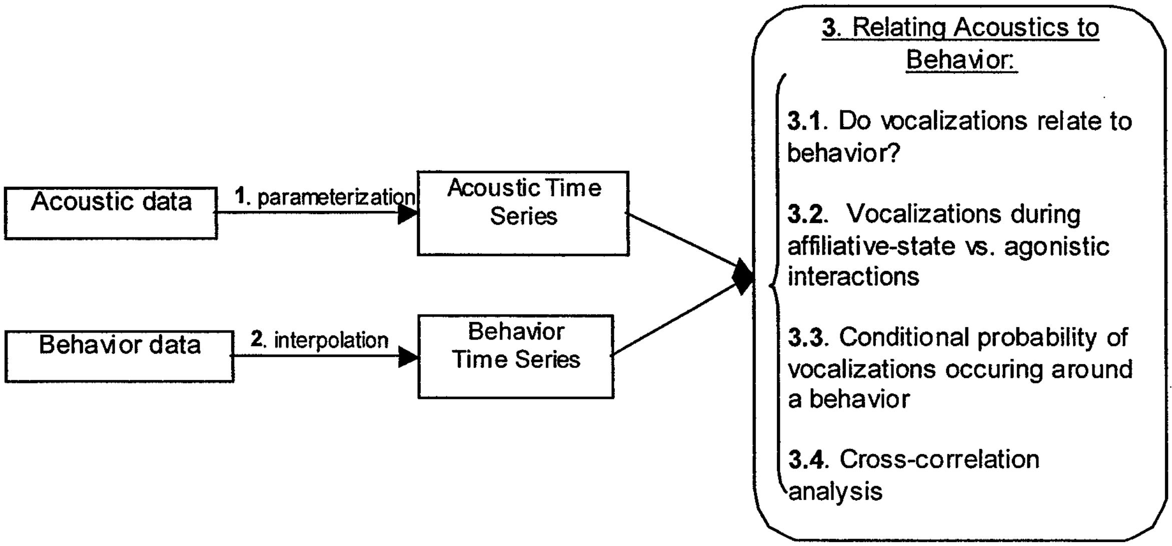


Figure 3. 1 Overview of methods

1. Parameterization: The acoustic data were first parameterized. The parameters that were used for this method were the tonality and broadband nature of the acoustic record. The time resolution of the parameterization was 0.1 s. The tonality parameter was chosen because it already appears to be useful candidate for classification of the bottlenose dolphin repertoire. There appears to be general agreement across researchers that whistles are a reasonably distinct group. The broadband parameter will allow exploration of the pulsed sounds and how they are used in various behavior contexts. Amplitude might also be an interesting parameter, but was not used in this study. Amplitude measures would have to account for transmission loss, a significant practical obstacle.

The acoustic recordings from each day of observation were parameterized and then concatenated into one time series for each of the two parameters. The parameters measured the extent of the tonal and broadband energy. A quantization step was performed for each parameter time series. Values above a certain threshold were given a value of 1, and values below the threshold were given a value of 0. For example, for the tonal parameter there should be values of 1 in that time series for the times when a whistle occurred. This simple quantization step was performed for two reasons. Since in this chapter I analyzed only timing of vocalizations, parameter intensity data were not needed. Also, parameter intensity will vary independently of the source level of the sound based upon the location of the vocalizing animal. If the location of the animal were known, the intensity at the source could be calculated and used to correct the parameter values.

The parameterization method is objective and can be performed entirely by the computer, but at certain stages human intervention was required. The extremely loud source level of snapping shrimp (recorded in Hawaii as loud as 189 dB re:1 μPa @ 1 m (Au *et al.* 1998)) caused problems with the parameterization step. For the whistle parameter, an observer double-checked each sound cut to be sure the parameterization was picking up tonality of a sound, not merely the energy from a very loud snapping shrimp. Despite the removal of most of the broadband energy, due to the loud source level snapping shrimp click energy sometimes could not be completely removed with the filter used. Although snapping shrimp were also a problem in calculation of the broadband parameter, an additional filter retained only broadband sounds which were longer in duration, eliminating the need for double-checking against the presence of snapping shrimp clicks. A special case study was made of a call type that was frequently identified by both the tonal and broadband parameters. This call type was identified manually, by techniques similar to those used in standard studies of animal behavior.

2. Interpolation: The behavioral records from the focal follows for each day of observation were concatenated to form a time series in a similar manner to the parameterizations of the acoustic recordings. The time resolution of the behavioral time

series was 1 s, while the time resolution of the acoustic time series was 0.1 s, so interpolation of the behavior data to the 0.1 s resolution was performed.

3) Relating behavior to acoustics: Tests for associations between the two acoustic parameter time series (representing times of tonal and broadband vocalizations) and the behavioral time series can be performed in a variety of ways. The analysis was rooted in the number of vocalizations around a behavior, rather than vice versa. This choice was made based on the fact that roughly 30 % of the time the focal animal was out of sight. Whenever we have behavior data, we always have acoustic data. However, the reverse is not true. When the focal animal was out of sight, we have acoustic but not behavior data. Therefore analysis was rooted in the number of vocalizations around a behavior.

(3.1) First it was tested whether times of vocalizations of all types were associated with times of behaviors of all types.

(3.2) Next it was tested whether vocalizations were associated with two major types of interactions, affiliative interactions and agonistic interactions. Next a couple of exploratory techniques were used.

(3.3) Conditional probabilities of occurrences (within a certain time window) of tonal and broadband vocalizations given the occurrence of each type of behavior were calculated and tested for significance.

(3.4) Cross-correlations of the parameter time series and the behavior time series over both short and long scales can be performed.

For this thesis, only cross-correlations over short time scales, seconds and minutes, were performed. However, this method allows analysis over long time scales as well. Cross-correlation over short time scales allows analysis of the linkage between vocalization and behavioral context on a second by second basis. If vocalizations are acoustic components of a behavioral interaction, we might expect a fairly tight linkage (on the order of seconds) between vocalizations and behavioral displays. For instance, jaw-clap sounds are usually associated with a jaw-clap display. For this association, we might expect a sharp peak around a time lag of zero. However, we expect that the logging of behaviors by observers will lag behind the occurrences of the behaviors, so we might expect a sharp peak with sounds "anticipating" the visual logs. Thus we might expect the cross correlation to exhibit a peak at a slight lag from zero. Expectations and interpretations of correlation results will be discussed in more detail in the methods section.

In general, if vocalizations are closely associated with specific behavioral displays we will expect the cross correlation over short time scales to exhibit a peak at a slight lag from zero. Over scales of longer time lags we might expect to see additional associations. For instance, if an animal is sexually receptive, we might expect to see a general increase in vocalizations associated with sexual behavior due to endogenous changes in motivational state. It might be useful to study this kind of correlation on a seasonal basis over periods as long as a year or more. In general for cross-correlations over minute to diurnal time scales, we might expect to see more gradual trends due to underlying motivational factors.

Case Study:

A special case study was made of a common call type that was identified by both the tonal and broadband parameters. Although the call type is broadband, due to the relationship between the high repetition rate of the pulses in the call and the spectrogram windowing, the call type was often selected by the tonal parameterization/quantization step as well. This call type was selected for special analysis and for this thesis has been called burst-pulsed call Type I (BP Type I). All of the cuts identified by the broadband parameter were reviewed to select those that contained BP Type I calls. This step to identify this call type is similar to standard techniques used in studies of animal behavior, while the parameterization method is a relatively novel technique. Using the same conditional probability and correlation analyses on both sets of data should illuminate the strengths and weaknesses of the parameterization method as compared to the more traditional classification method.

3.2 Methods:

3.2.1 Data collection:

Study site:

These data were collected at DolphinQuest Bermuda's facility at the Naval dockyards in Bermuda. For details of the study site, see Chapter 2. There were 8 dolphins in the original group (Table 3.3) at DolphinQuest Bermuda. Due to Hurricane Gert, which hit Bermuda Sep. 22, 1999, 4 animals escaped the lagoon; Cirrus and Nimbus were recovered, but Dolber and Gibbs were not. Thus the group of dolphins after September 22 no longer contained an adult male or an adult female without a calf. Four of the six remaining dolphins were members of a mother-calf pair, which may skew the results. The animals were in process of adapting to new social conditions and the results presented in this thesis should not be regarded as being representative of captive dolphin social groups in general. All of the behavior and acoustic data were collected after Sep. 22, 1999, so the dolphins present during the data collection are highlighted in bold in Table 3.3.

Table 3. 3 Dolphins at DolphinQuest Bermuda pre-September 22, 1999

Dolphin	*Code*	*Date of Birth*	*Sex*
Nimbus	**C**	**1999**	**Male**
Bailey	**B**	**1989**	**Female**
Somers	**S**	**May 22, 1998**	**Male**
Caliban	**L**	**March 17, 1993**	**Female**
Cirrus	**R**	**~1974**	**Female**
Dolber	D	~1965	Female
Gibbs	G	~1976	Male
Khyber	**K**	**1992**	**Male**

Note: Dolber and Gibbs were no longer a part of the group after Sep. 22, 1999.

Behavior Data:

In focal animal sampling, the observer focuses on one individual at a time for a specified period, recording behavior about that individual (Altmann 1974). The focal animal sampling sessions used in this thesis lasted 10 minutes. The 10 minute session length was chosen to allow at least 1, and possibly 2, focal sessions on each animal each day of observation. The order of observation of the animals varied from day to day based on a pre-determined randomized schedule. This randomization reduced bias which would result from the selection of the focal animal based upon its behavior, as well as bias based upon time of day, although all sessions were performed during the morning hours. The data were gathered after sunrise and before trainers arrived for the morning feeding (generally between 6 AM and 9:30 AM). A total of 142 focal sessions were performed, although only 135 of these were used; the first three were not used as there were no acoustic recordings, and others were not used due to observer mistakes. A few sessions ran over 10 minutes, and a few were stopped early for external reasons. This yielded approximately 1350 minutes (22.5 hours) of simultaneous focal behavior and acoustic array recordings. Appendix 3.1 shows the time and dates of behavioral follows, the clarity of the lagoon on a scale of 1 to 10, the pools the focal animal had access to, the social group that the focal animal could interact with, the identity of the focal animal, and any pertinent comments for that focal follow.

In each focal sampling session, two types of behavioral sampling were performed simultaneously. The first was point sampling (Altmann 1974). Point samples were taken at one minute intervals. The following information was recorded: location of focal, nearest neighbor identity, nearest neighbor distance, and activity state. Continuous behavioral sampling was also performed (Altmann 1974), in which all occurrences of specified behaviors by the focal were recorded. Specified solitary behaviors were recorded as well. See Appendix 3.1 for details of the behavioral sampling protocol and definitions of the behaviors. Not all behaviors listed in the protocol were observed at DolphinQuest Bermuda.

As in Samuels and Gifford (1997), for the purposes of the focal follow a social interaction was defined as when two animals were within 1 m of each other and a dolphin directed one or more of the specified behaviors towards another. Samuels and Gifford chose this 1 m criterion based upon preferential association patterns being discernible in a captive group at 1, but not 2 meters. Acoustic (and some behavioral) interactions may occur over longer distances, but would be difficult to define. Table 3.4 lists the behaviors that were used in the ethogram and their categorization by behavior type for purposes of comparison with vocalization types. These behaviors and categories are taken from ethograms designed by Amy Samuels and Cindy Flaherty for use at the Brookfield Zoo facility.

Behavioral observers often make an artificial distinction between behavioral "states", which last long enough for the observers to note the onset and termination of the behavior, and behavioral "events", which have durations so short that the observers just note a time of occurrence for the whole behavior. In this thesis I primarily recorded behaviors as events with zero duration, although a few behaviors were coded as states with an associated duration. The distinction between events and states is not absolute, since no behavior takes zero amount of time to perform. However, when the behavior had a duration of roughly a second or less, it was recorded as an event. Some behaviors lasted longer than 1 second. Whenever possible these longer behaviors were recorded as state behaviors, with associated onset and offset times. Recording of behavioral events as well as states was desired to allow for fine time scale association between vocalizations and behaviors. Most of the behaviors listed were pre-defined to be event behaviors, some were pre-defined as state behaviors, and a few behaviors could be recorded either as events or states. For example, some affiliative behaviors were states: swim together, rest together, and contact swim. These three behaviors were the only behaviors in the ethogram that were necessarily state behaviors, and were by definition only recorded when they lasted longer than 10 s. The 10 s rule was used so that the observer could be positive that the dolphins were actually engaged in that behavior (e.g. swimming together instead of swimming by). The rub is an example of an affiliative behavior that could be used as an event, although rubs could last for several seconds and thus could also be recorded as state behaviors. Other behaviors, including object manipulate, white water, and root, could be recorded both as events and as states. The average length of each behavior, shown in Table 3.4, was calculated assuming a duration of 0 for events, and used the average difference between onset and offset times for behaviors that were (at least occasionally) recorded as state behaviors. Any behavior which has an average length of behavior greater than 0 in Table 3.4 was sometimes recorded as a state behavior. During times when the animal could not be seen, it was labeled as "out of sight." Animals were out of sight 30% of the time on average. For purposes of comparing behaviors across individuals, the sample size of each behavior is given in Table 3.2.2 in Appendix. 3.2

Table 3. 4 Summary of recorded behaviors

Code	**Behavior**	**Behavior Type**	**Average Length of Behavior (s)**	**Sample Size**
QA	**Quick Approach**	**Abrupt-Social**	**0.0**	**2**
SH	Spy Hop	Abrupt-Solitary	0.0	147
TA	Tail slap (solitary)	Abrupt-Solitary	0.0	16
LT	Look Tourist	Abrupt-Solitary	3.2	44
CF	Chuff	Abrupt-Unknown	0.0	16
QS	**Quick Swim**	**Abrupt-Unknown**	**0.0**	**24**
PS	**Flipper Slap**	**Abrupt-Unknown**	**0.0**	**10**
BR	**Breach**	**Abrupt-Unknown**	**0.0**	**3**
PO	**Porpoise**	**Abrupt-Unknown**	**0.0**	**31**
ST	**Swim Together**	**Affiliative**	**75.8**	**564**
CS/ST	**Contact swim**	**Affiliative**	**50.7**	**39**

RT	**Rest Together**	**Affiliative**	**28.4**	**37**
RB	**Rub**	**Affiliative -Event**	**1.9**	**158**
MH	**Mouth Threat**	**Agonistic-Aggressive**	**0.0**	**1**
CH	**Chase**	**Agonistic-Aggressive**	**5.8**	**13**
HI	**Hit**	**Agonistic-Aggressive**	**0.0**	**52**
BI	**Bite**	**Agonistic-Aggressive**	**0.0**	**3**
HT	**Head Threat**	**Agonistic-Aggressive**	**0.0**	**10**
TS	**Tail slap**	**Agonistic-Aggressive**	**0.0**	**91**
TH	**Threat**	**Agonistic-Aggressive**	**0.0**	**32**
BS	**Body Slam**	**Agonistic-Aggressive**	**0.0**	**8**
MO	**Mouth Open**	**Agonistic-Aggressive**	**0.0**	**59**
FL	**Flinch**	**Agonistic-Submissive**	**0.0**	**57**
FE	**Flee**	**Agonistic-Submissive**	**6.0**	**13**
WW	**White Water**	**Agonistic-Unknown**	**5.2**	**81**
DW	**Deep Water**	**Agonistic-Unknown**	**4.9**	**67**
CT	**Casual Touch**	**Brief Touch**	**0.0**	**107**
SB	**Snout to Body**	**Brief Touch**	**0.0**	**180**
BU	Bubble	Bubble	0.0	7
CI	**Circling**	**Calf**	**17.0**	**1**
NU	**Nurse**	**Calf**	**3.6**	**6**
JW	Jawing	Foraging	0.0	26
FC	Fish Chase	Foraging	0.0	10
RO	Root	Foraging	2.9	9
SC	Scan	Foraging	0.3	56
SG	**Snout-to-Genital**	**Genital Interest**	**0.0**	**54**
VA	**Ventrum Away**	**Genital Interest**	**0.0**	**15**
VP	**Ventrum Present**	**Genital Interest**	**0.0**	**3**
OM	Object Manipulate	Object	57.6	34
ER	**Erection**	**Sexual**	**0.0**	**1**
IM	**Intromission**	**Sexual**	**0.0**	**1**
MT	**Dorsal Mount**	**Sexual**	**0.0**	**7**
TR	**Thrust**	**Sexual**	**0.0**	**14**

VM	**Ventral Mount**	**Sexual**	**0.0**	**6**

Note: Behaviors in bold could be used as social behaviors.

Details of the acoustic array system are given in Chapter 2. The sampling rate of the recordings was 48,000 Hz. An eight-channel TASCAM DA-88 multitrack digital recorder was used for recording the signals from the hydrophones. The TASCAM DA-88 has a flat frequency response (± 0.5 dB) from 20 Hz to 20 kHz. Parameterization calculations were all carried out on the recordings from channel 2. This channel was chosen because its associated hydrophone was located approximately in the center of one of the sides of the lagoon, and was also not near a potential source of noise, such as a dock or a gate.

3.2.2 Parameterization of vocalizations:

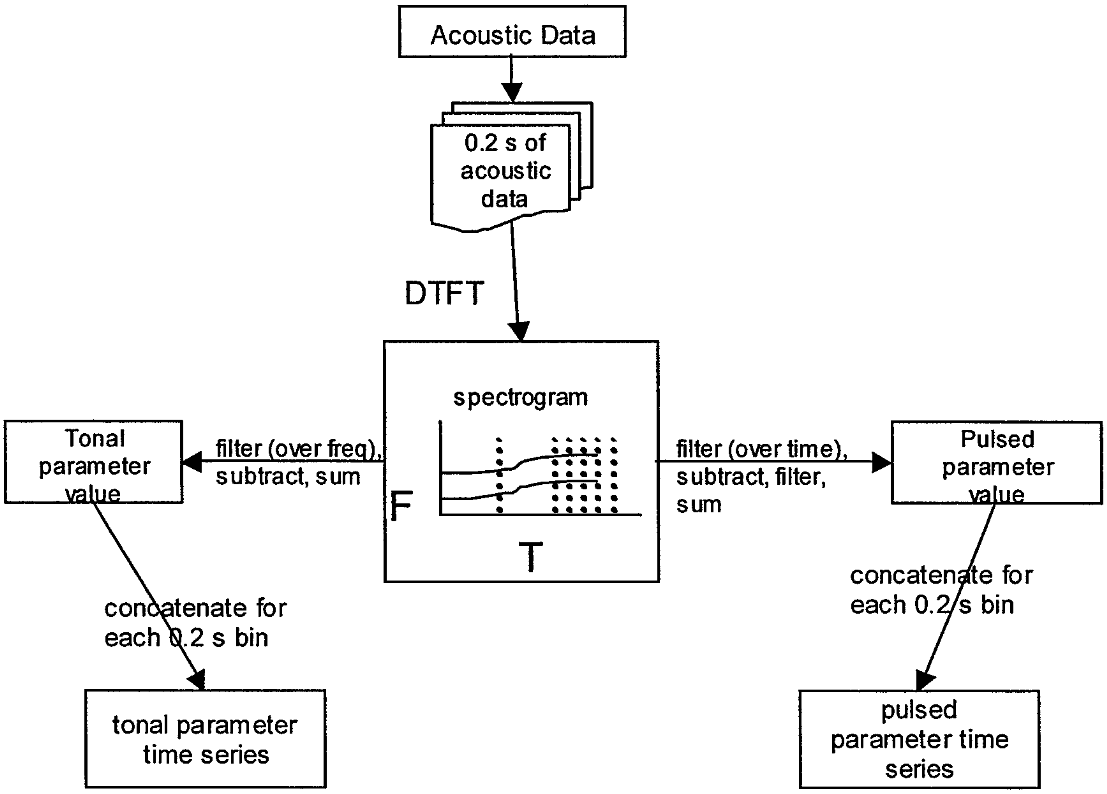


Figure 3. 2 Overview of parameterization

An overview of the parameterization technique is shown in Fig. 3.2. Two sets of parameters were calculated. The first quantified the tonality, or narrow-band nature, of the sound. The second quantified the broad-band nature of the sound. Before any parameterization, the sound was chunked into 0.2 s chunks. The choice of chunk size was not critical, but a chunk size of less than or equal to 1 s was desired, as the behavior sampling resolution was 1 s. A choice of chunk size less than 0.1 s proved intractable because of memory limitations of the computer used for analysis, since as the chunk size becomes smaller, the parameter vector becomes longer. These 0.2 s chunks were overlapped by 0.1 s, half of the chunk size. Thus the time resolution, or sampling rate, of the parameter time series was 0.1 s. The spectrogram was calculated for each 0.2 s chunk, using an FFT size of 256 points, a Hanning window, and no overlap. (The FFT stands for the Fast Fourier Transform, a quick algorithm for calculating the Fourier transform (Oppenheim and Schafer 1989).) The spectrogram is the Time-dependent Fourier transform (Oppenheim and Schafer 1989). (Technically speaking, it is the display of the of the Time-dependent Fourier transform of a signal, but for this paper we will use the term spectrogram to mean the Time-dependent Fourier Transform of the signal). The spectrogram has a time resolution of about 5.5 ms. The FFT bins are spaced about 188 (48000/256) Hz apart, but as the data were processed with a Hanning window, the frequency resolution based upon the window mainlobe width (Chap. 11, Oppenheim and Schafer 1989) is 764 Hz. The parameterization step was performed on the spectrogram calculated from each 0.2 s chunk. Any sound lasting longer than 5.5 ms would necessarily span more than one FFT time bin in the spectrogram. In addition, any sound with an inter-pulse interval less than 5.5 ms (more than 188 pulses per second) would make the sound appear to have a tonal component (Watkins 1967), which might lead to parameterization of the sound as a tonal signal as well as a pulsed signal. Watkins (1967) showed that signals with a repetition rate of pulses faster than time resolution of the spectrogram would appear to have a harmonic at the pulse repetition rate. This frequently occurs with burst-pulsed calls, and should be kept in mind on the section of parameterization of pulsed calls.

Tonality parameter:

This parameterization step quantified the narrowband nature of the sound chunk. Specifically, the goal was to select sounds that in previous studies had been classified as whistles in addition to other tonal sounds. Due to an abundance of low-frequency noise, the DC and 15 lowest frequency bins were discarded (equivalent to implementing a high-pass filter), leaving bins $k = 16$ to 128, corresponding to frequencies of 3,000 Hz to 24,000 Hz (Nyquist frequency). One study calculated that the mode for the lowest frequency component of whistles is 5 kHz, and the mode for the highest frequency component of whistles is 13-15 kHz (Caldwell *et al.* 1990). This discarding of the lowest frequency bins should not adversely affect the results.

Calculation of parameter for each time block: The general idea for calculation of the tonality parameter was to determine all the non-tonal energy of the sound and subtract this non-tonal energy from the total sound energy, leaving only the tonal energy. A cartoon of this is shown in Fig. 3.3.

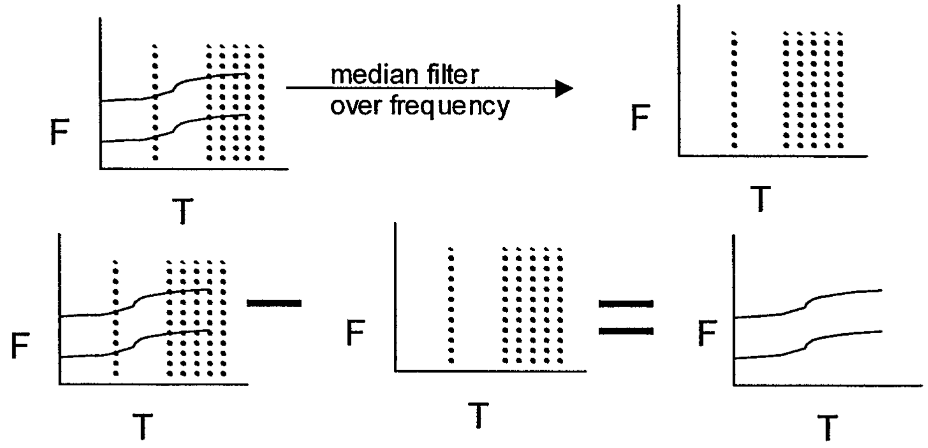


Figure 3. 3 Cartoon of the process of removing non-tonal energy from the total sound energy

For each time chunk *t*, X is the spectrogram with X_{ik} being the squared value in the *k* th FFT bin and *i* th time bin. *A* median filter operation (Gallagher *et al.* 1981) and a subtraction were performed on X. These operations were performed to exclude short-term (in time) energy while simultaneously selecting for narrowband (in frequency) energy. The filter size was 2n+1 bins, where n = 3, or 1313 Hz. (The bandwidth of a whistle band very roughly covers 3 bins. This is equivalent to 563 Hz, although due to windowing effects, the actual bandwidth of a whistle is probably less than this). For each *i,k*, Y_{ik} was calculated as $Y_{ik} = \text{Median}(X_{i,k-n}, \ldots, X_{i,k+n})$ over *k*. Values of 0 were assumed for the edge points ($X_{i,k-n}$ and $X_{i,k+n}$ when k-n<1 and k+n > 128).

$A_{ik} = X_{ik} - dY_{ik}$ where d was a constant multiple. The exact value of d was not critical; what was important was that the constant be large enough to remove all the noise that was associated with Y. Since Y is calculated from median values, not all of the noise is captured in Y. For this study, a multiple of $d = 40$ was used. For each time chunk *k*, we calculated $r_t = \sum_{ik} A_{ik}$ to yield a time series $\mathbf{r}$.

Broad-band parameter:

This parameterization step is similar to the one above, with the difference being that it quantifies the broad-band nature of the sound block. For this, the median filter is taken over time instead of frequency. The filtering over time instead of frequency (and ensuing subtraction) selects for energy that is dispersed in frequency rather than in time. In addition, since higher repetition rate broad-band sounds were of primary interest, another median filter operation over time was performed before final energy calculation. A cartoon of this is shown in Fig. 3.4. Due to low-frequency noise, the DC and 8 lowest frequency bins were discarded, leaving bins k = 9 to 128. The remaining frequencies range from 1,688 Hz to 24,000 Hz (Nyquist). Burst-pulsed calls and echolocation clicks, which were the general sound type we were trying to detect here, appear to have more frequency components in the 1688 – 3000 Hz range than whistles, so fewer bins were discarded.

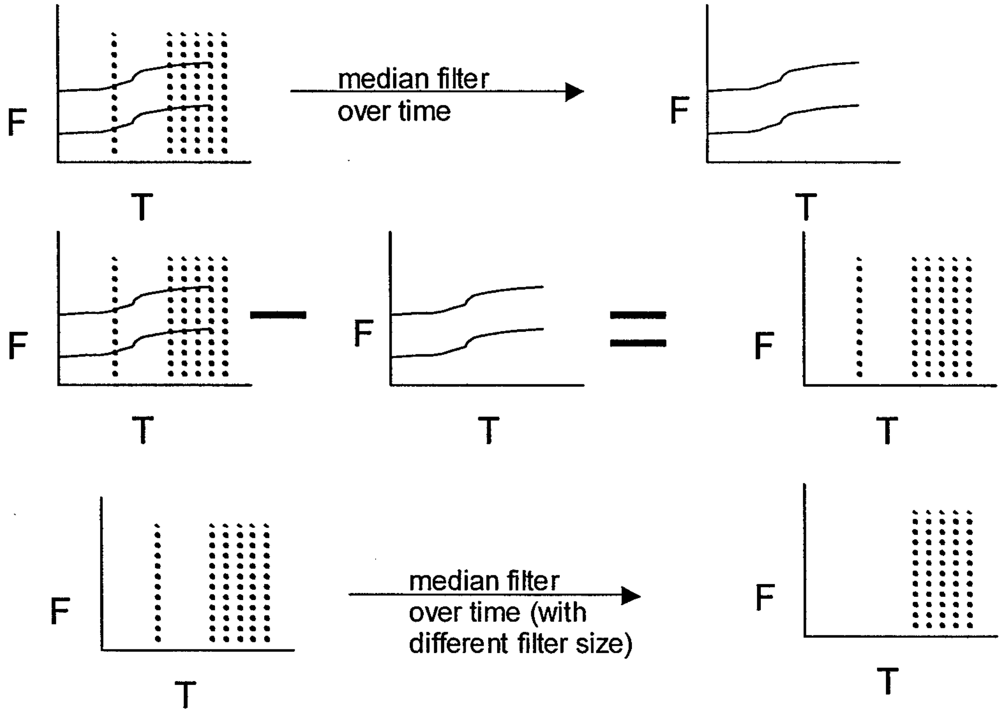


Figure 3. 4 Cartoon of the process of removing tonal energy from the total sound energy, leaving broadband energy.

Calculation of parameter for each time block: As with the tonality parameter, for each time block *t*, X is the spectrogram, with X_{ik} being the squared value in the *k* th FFT bin and *i* th time bin. A median filter operation and a subtraction were performed on X. The filtering over time instead of frequency (and ensuing subtraction) selects for energy that is dispersed in frequency rather than in time. The filter size is 2n+1 bins, where n = 8 (17 bins), which corresponds to a filter size of about 91 ms. Even with windowing effects and some reverberation, the apparent duration of echolocation clicks is generally less than 8 time bins (about 43 ms). The filter was chosen to err on the large side to account for windowing and reverberation effects. For each i, k, Y_{ik} was calculated as

Y_{ik} = Median($X_{i-n,k}$, …, $X_{i+n,k}$) over i. Values of 0 are assumed for the edge points ($X_{i-n,k}$ and $X_{i+n,k}$ when i-n<1 and i+n > number of time bins in the chunk). We then subtract a weighted version of Y from X to get $B_{ik} = X_{ik} - dY_{ik}$ where d is a constant multiple. The exact constant used is somewhat arbitrary. For this study, a multiple of $d = 1$ was used. After this, a median frequency filter operation across time was performed, with no ensuing subtraction. This operation used a larger filter size, which removed short clicks that were not shortly followed by other clicks.

This filter operation had two effects. The first effect, and primary purpose of the filter, was to remove the effects of snapping shrimp. Snapping shrimp tend to make one loud solitary snap. Although there were many snapping shrimp in the lagoon, they snapped randomly, and did not have a constant inter-snap interval. The snaps therefore tended to occur as solitary snaps. The second effect was to exclude slower click trains: those that would have been classified structurally by humans by their interclick intervals as single pops or slow echolocation, and not as burst-pulsed calls. This may slightly bias the sample set by removing slow trains of clicks, but was necessary to reduce the effects of snapping shrimp. The filter size is 2n+1 bins, where n = 5 (11 bins, or about 59 ms).

We would like to be able to calculate the interclick interval at which this filter will start to retain clicks as belonging to a pulsed call instead of throwing them out as solitary clicks. If the clicks occupy more than half of the total filter window (occupy >n+1 bins), then the clicks will be retained by the filter. Therefore, if the click width is greater than n+1 bins (e.g. Fig. 3.5(a)), the click will automatically be retained, regardless of the interclick interval. Assuming that most clicks are not this long (would require the clicks to be longer than 6 bins = 31.8 ms), we can calculate the maximum interclick interval possible for the clicks to still be retained. For the purposes of calculating maximum interclick interval, we assume that twice the click width will be greater than n+1 bins, that is 2 Cw > n+1 (Fig. 3.5(b)). It is possible that it would take 3 or more clicks to satisfy the requirement that the total click energy occupy more than n+1 bins, but to fit into the filter window, this interclick interval would be smaller than the interclick interval between two clicks. Since we are concerned with the maximum interclick interval, we will calculate the maximum interclick interval based on the assumption that two clicks are enough to satisfy the requirement that the total click energy occupy more than n+1 bins (2 Cw > n+1). If n+1 bins must be occupied by clicks, that leaves 2n+1 – (n+1) = n bins for the interclick interval. For this filter, this would be n=5. With an FFT size of 256 points, and no overlap, we get the equivalent of 187 points per second. 187 points/5 would give a maximum click rate of 37.4 points per second. 1/(37.4 per second) gives a maximum interclick interval of 26.9 ms. Therefore most of the echolocation click trains should be included, excepting the very slowest, and all of what has traditionally been classified as burst pulsed calls, according to their interclick intervals, should be included. For each time block *t*, we calculate $s_t = \sum_{ik} A_{ik}$ to yield a time series $\mathbf{s}$.

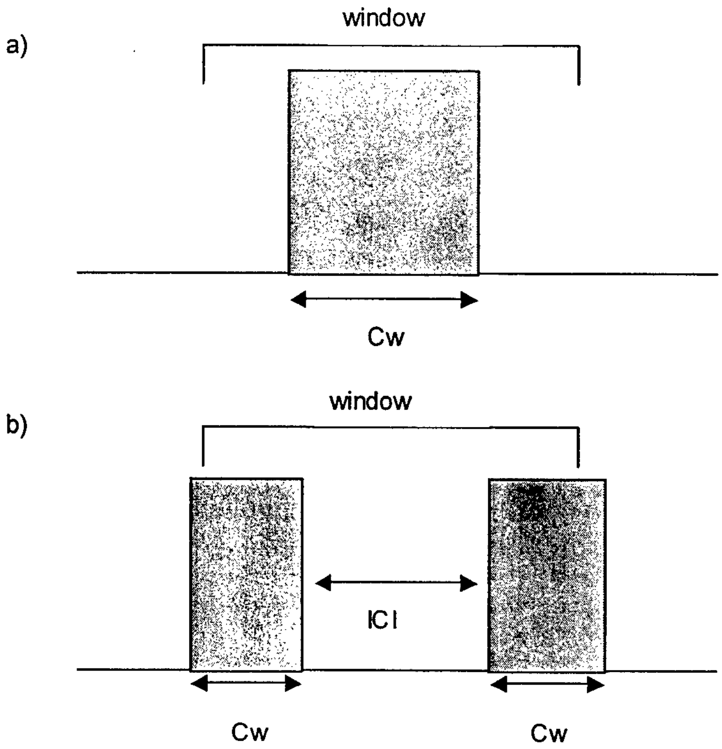


Figure 3. 5 Determination of click width and interclick interval to identify clicks with a median filter

An example of the spectrograms before and after the filter and subtraction steps for the tonal and pulsed parameterization algorithms is shown in Fig. 3.6. This spectrogram shows a sound cut in which pulsed calls overlapped with whistles. The bottom two plots show how the tonal parameterization emphasizes tonal features while the pulse parameterization emphasizes broadband features. Even though the tonal spectrogram appears to fragment each whistle, the energy is summed over 0.2 s intervals. This example used a 1 s chunk instead of the 0.2 s chunk to illustrate details of variation of these features. Energy would be summed over a 0.2 s chunk for use in the quantization step.

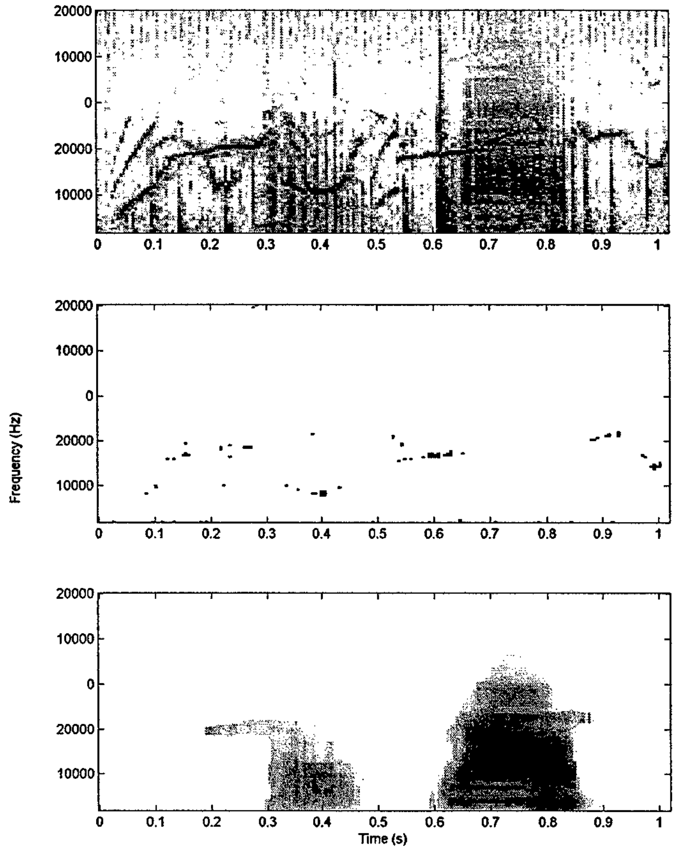


Figure 3. 6 Example of the effects of the filter sequences on a sound cut containing both tonal and pulsed sounds as well as snapping shrimp clicks.

Note: The top plot contains the spectrogram of the sound cut. The second plot contains the spectrogram of the sound cut after the filtering used for calculating the tonal parameter. The third plot contains the spectrogram of the sound cut after the filtering used for calculating the broadband parameter.

Quantization:

After parameterization of each tape in the acoustic record to obtain the parameter time series $\mathbf{r}$ and $\mathbf{s}$, the time series from each tape of recordings were concatenated. Direct concatenation of unrelated acoustic time series may have a spurious effect on correlations of the parameter series to behavior series, for instance, if acoustic events at the beginning or end of a tape correlated with behavioral events occurring at the beginning of the next tape or the end of the previous tape. However, the behavior series always had at least a few minutes of time without recorded behaviors between concatenated time series, so this effect should only be seen with longer term correlations between the behavior and acoustic parameter time series and any correlations between acoustic parameter series. Since each tape of recordings should theoretically be statistically independent, this concatenation may have the effect of causing a bit of noise in the correlation data, but should not unduly affect the results. After concatenation a detection step was performed. Times with parameter values that exceeded set thresholds were given values of 1. All others were given values of 0. This resulted in a total of 19204 detections from $\mathbf{r}$. However, snapping shrimp and burst-pulsed calls (such as BP Type I) formed some of these detections, so these detections were double-checked by eye. 13889 out of 19204 cuts (72.3%) were kept. Due to the extra median filter in the broadband filter, $\mathbf{s}$ was not double-checked by hand. There were a total of 19603 detections in $\mathbf{s}$ over the entire acoustic record. The binary-valued time series were denoted as $\dot{\mathbf{r}}$ and $\dot{\mathbf{s}}$. This step yielded an average of 10.0 detections/minute in $\dot{\mathbf{r}}$ and 7.1 detections/minute in $\dot{\mathbf{s}}$. These time series $\dot{\mathbf{r}}$ and $\dot{\mathbf{s}}$ were used for comparison with the behavior time series.

BP Type I:

A special case study was made of a common call type that was identified by both the tonal and broadband parameters. The call type is broadband, but with a sufficiently high repetition rate to cause triggering (due to windowing and reverberation effects) by the tonal parameterization (Fig. 3.7). I noticed this sound type commonly triggering the tonal parameter during double-checking of the sound cuts. 226 of 2747 (8.2 %) of 0.1 s chunks that were identified as having both tonal and broadband energy were of this call type. It appeared to be a distinct call type, and for this thesis has been called burst-pulsed call Type I (BP Type I). This situation of an observer noticing what appears to be a distinct call type and pulling it out for further analysis is common among marine mammal and animal behavior studies. However, as evidenced by Table 3.2, it is important to systematically relate the call type to the rest of the repertoire.

The sound cuts detected by the broadband parameter were inspected by the observer to determine which were BP Type I calls. In the case study of this call type, I investigated the extent of usefulness of relating a specific call type to behavior of an individual when the identity of the vocalizer is not known. This also allowed comparison to the dominant method in this chapter of relating general vocalization types recorded from all animals in the lagoon to behavior of an individual (when the identity of the vocalizer is not known). 2671 of 19603 (13.6%) pulsed calls were of this call type. The set of BP Type I calls were pulled from the set of pulsed calls, and therefore all BP Type I calls were pulsed calls. A spectrogram of a typical BP Type I call is shown in Figure 3.7. The times of occurrences of BP Type I calls were used to form a time series $\dot{\mathbf{r}}$, which is also binary (1's and 0's) and on the same time scale as the time series $\dot{\mathbf{p}}$ and $\dot{\mathbf{q}}$.

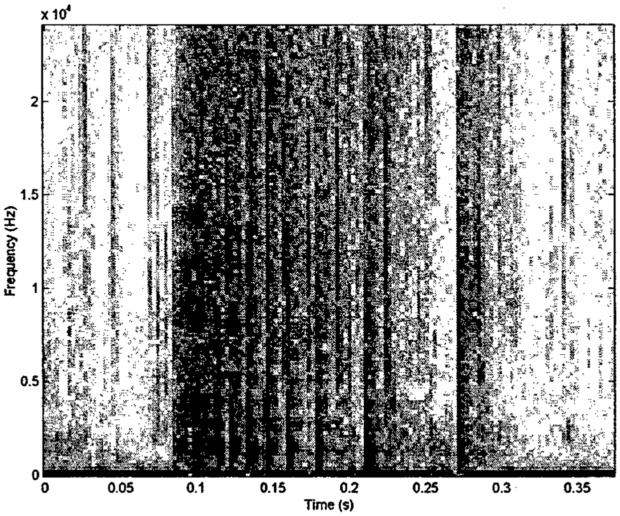


Figure 3. 7 Spectrogram of a BP Type I call.

A few acoustic characteristics of the BP Type I call are shown in Table 3.3. The median frequency and envelope duration were calculated by Acoustat (Fristrup and Watkins

1994). The median duration and peak frequency were measured by the observer using Matlab.

Table 3. 5 Acoustic Characteristics of BP Type I calls

Parameter	**Value**
Peak frequency (median value)	3375 Hz
Median Frequency	11484 Hz
Median duration	.051 s
Envelope duration (using median 75%)	.078 s

3.2.3 Behavior time series:

To facilitate analysis, the behaviors that were recorded in the focal animal sampling were categorized into 15 categories. The groupings of behaviors are shown in Table 3.4. A time series was synthesized for each behavioral type from the data. The behavioral data were sampled at no more finely than one second intervals. Points in time during which a behavior was occurring were given a value of 1. Points in time during which no behavior was occurring were given a value of 0. As most of the behaviors were events, the time of the event was given a value of 1. This yields an implicit duration of behavioral events as 1 s. For behavior states, values of 1 were given for the entire time that the animal was in that state. We will term these time series $\mathbf{H}_k$, with k =1 to 15 for each of the 15 behavior types in Table 3.4.

3.2.4 Relating behavior events to sound detections:

As mentioned in the introduction and shown in Tables 3.1 and 3.2, it might be expected that certain types of behaviors would appear be associated with certain types of vocalizations. However, due to difficulties in identifying the vocalizer, as detailed in

Chapters 1 and 2, bottlenose dolphin vocalizations have only been very generally linked to function. Whistles are thought to be associated with social interactions, although the function of other tonal signals is unclear. Signature whistles are hypothesized to serve a contact function (Janik and Slater 1998), for instance, by broadcasting individual identity and location (Caldwell *et al.* 1990), or functioning in mother/calf reunions (Smolker *et al.* 1993). From these reports it is not clear with which class of behavior (agonistic, affiliative, etc.) we would expect whistles to be associated. Burst-pulsed calls have been reported to be associated with agonism (Caldwell and Caldwell 1967, Overstrom 1983), sexual behavior (Caldwell and Caldwell 1967), disturbance (Caldwell and Caldwell 1967), and travel (Jacobs *et al.* 1993). Therefore we might expect that BP Type I calls would serve a social function, although it would be difficult to predict which type. Pulsed signals, which would likely include both echolocation signals and burst-pulsed signals, might be expected to be associated with both foraging and social interactions. Therefore, from available reports we have only very limited predictions of associations of classes of behaviors with vocalization types.

Vocalizations during Affiliative states:

The first analysis was performed for the behaviors that were always state behaviors: swim together, contact swim, and rest together. These behaviors were grouped into the "affiliative state" category (in contrast to the affiliative-event category). The number of vocalizations (defined by a break of ≥ 0.1 s) of each call type that occurred during affiliative states was determined. Vocalizations usually last longer than 0.1 s. The occurrence of each vocalization type (including all types pooled into one category) was tallied for the affiliative state and for all other times (including times when the focal was out of sight) and the counts tested by Chi-squared analysis (Table 3.6) for deviation from expected based upon the amount of time actually spent in each category.

Table 3. 6 Chi-squared analysis table for analysis of vocalizations during and not during affiliative states

	Affiliative State	**Not in Affiliative State**
Observed	Number of vocalizations in *affiliative state*	Number of vocalizations *not in affiliative state*
Expected	Number of vocalizations *expected* based upon percent time in *affiliative state*	Number of vocalizations *expected* based upon percent time *not in affiliative state*

Vocalizations during Agonistic interactions:

A similar analysis as above was performed for agonistic interactions. Since agonistic behaviors were not coded as states, a 10 s chain rule was used to define an agonistic interaction. That is, if longer than 10 s occurred between behaviors, the subsequent sequence of behaviors was defined as a new interaction. This is the same criterion that was used by Samuels and Gifford's (1997) study of agonistic interactions for assessment of dominance relations. The number of vocalizations (defined by a break of ≥ 0.1 s) of each call type that occurred during agonistic interactions was determined. The amount of time that different vocalization types occurred during agonistic interactions was calculated and tested for deviation from expected based upon the same kind of analysis as just described for affiliative interactions.

The previous methods described were used in confirmatory analyses to obtain statistical inference. In this chapter, the following methods are used as exploratory methods for analyzing data, and they should be regarded as exploratory data analyses in the sense of Tukey (1977). They are not confirmatory statistical analyses, and therefore should not be regarded as methods for obtaining statistical inference. Exploratory methods can be very useful in determining overall trends and understanding general patterns in the data. The first methods we used (conditional probabilities) resembled more traditional behavior analyses, and the last method (cross-correlations) was less conventional. In the following analyses, 95 % indicator lines are used to give an idea of which results might be important. As these are exploratory analyses, these 95 % indicator lines should not be confused with testing for statistical significance.

Conditional probabilities:

Analyzing conditional probabilities of vocalizations occurring during behavioral states is a common technique, especially in the cetacean literature where a group rather than an individual is often the subject of observation. As mentioned in Chapter 1, although this method is commonly used, it does have drawbacks and is subject to bias. When observing a group, its behavior is often recorded as being in one of several general activity states, such as resting, feeding, traveling, etc, although not every single member of the group may be engaged in this activity. Vocalizations from the group can be related to these states by comparing the number of vocalizations emitted during each state, thereby possibly inferring vocalization function. As most of the behaviors in this study were coded as events rather than states, we adapted the standard technique described above to this study by using a time window of ± 10 s around the behavior. The numbers of vocalizations in each window were counted and compared.

The use of conditional probabilities for this method was slightly different than traditional behavior analyses, as a time window around each behavior event was used. This contrasts with analyses that calculate conditional probabilities of occurrences of vocalizations when the animal is in a behavior state. Since this was a primarily event-based study, and the behavior sampling likely had some variance in the time of calling of behaviors, a time window around behavior events was used instead of just the time of the event. A ± 3 s window has been used by other researchers to analyze dependencies of vocalizations (Janik 2000). However, this thesis involves associating visual observations of behaviors with acoustic records, which is more problematic than just comparing the timing of vocalizations within the same acoustic record. Since it often takes the observer a few seconds to identify and record the behaviors under observation, a longer window was needed. Selection of a longer window also allows detection of more loosely coupled associations of sound and behavior.

Conditional probabilities were used to determine the probability of a certain call type occurring within a certain time period of a given behavior type. To rephrase that mathematically, $P(V_i \mid B_k)$ is the conditional probability that vocalization type V_i will occur given that behavior type B_k has occurred. For our purposes, we would like to determine the conditional probability that vocalization type V_i will occur within ± 10 s of behavior type B_k. In other words, given that a certain type of behavioral event (or onset of a state) has occurred, what is the probability that a certain vocalization type will occur within ± 10 s of the behavior? It is easier to ascertain whether this might differ from expected using frequencies rather than probabilities. The number of times that each of the vocalization types occurred within 10 s of each of the 15 behavioral types was tallied. In order to determine whether each of these was different from expected, we determined what the expected value was of a vocalization type occurring near a behavior for each behavioral type. Since vocalizations often occurred in bouts, it was not valid to use the mean frequency of occurrence of the vocalization type in conjunction with a time window to calculate the expected frequency. Rather, it was more appropriate to take the time structure into account. This was done by looking at random times in the data and determining the mean frequency of occurrence of the vocalization type within the ± 10 s window of those random times. I took a random number (N=10000) of points and for each of these calculated the frequency of occurrence that each of the vocalization types occurred within ± 10 s of that point. That is, to put it mathematically, for each random time t, I calculated:

$$\mathbf{F}_i(t) = \begin{cases} 0 \text{ if there is no vocalization (of type } i) \pm 10 \text{ s of t} \\ 1 \text{ if there is a vocalization (of type } i) \pm 10 \text{ s of t} \end{cases}$$

for each behavior type B_k. So for each behavior type, $\mathbf{F}_i(t)$ is a time series of 1's and 0's, where a 1 indicates that there is a vocalization of type *i* within 10 s of t, and a 0 indicates that there is no vocalization of type *i* within 10 s of t. So the expected probability of a vocalization of type *i* occurring within ± 10 s of a random time t is $E_i = \sum \mathbf{F}_i(t) / N$. Thus the product of E and N is the expected frequency of occurrence of vocalization within ± 10 s of a behavior for each behavioral type B_k. This expected frequency was calculated for each behavior type, and a Chi-squared analysis was performed for whistles, burst pulsed calls, and BP type I calls. However, since the Chi-squared analysis was performed repeatedly, results must be considered to be exploratory, and the 95 % level used is an indicator rather than a significance level.

Cross-correlations:

The second technique more explicitly preserves the timing in the behavior and vocalization time series. Cross-correlation of behavior time series is an underused method in animal behavior. Heiligenberg (1973) successfully used this method in the early 1970's to analyze sequential behavior of a cichlid fish. This method has the advantage of easily displaying the relation in timing within a large data set of events. However, the results can sometimes be difficult to interpret. The technique is somewhat similar to lag sequential analysis, although the computation is different. Lag sequential analysis shows the conditional probability of one event happening at progressively longer time lags from another. Cross-correlation shows the multiplication of two time series over a range of lagged values. The value used is not important, but both in Heiligenberg (1973) and in this thesis, 1's were used to denote times of the behavior event. The shape of peaks in the cross-correlation can be important, both in terms of the robustness of the peaks, as well as in the interpretation of the underlying mechanism leading to the peaks. For instance, in the top plot of figure 3.8 below, generated from synthetic data, the peak at 1 s is rather narrow and tight, indicating a tight correlation in time between two time series. In this case, one event almost always occurred about one second after the other. In the lower plot, the peak at 5 s is broader, indicating that the correlation in time between two time series is not tight. While one event may have tended to occur 5 s after the other, time lags of 0 to 10 s were not uncommon.

For some associations of vocalizations with behavior, we might expect a tight time correlation of vocalization and behavior. For methodological reasons, we might expect a tight time correlation of a vocalization with a bite, flinch, or rub, which are event behaviors, and might not expect a tight time correlation with a swim together, which is a state behavior. For behaviors and vocalizations with a tight cause and effect scenario, we would expect a tight correlation. For instance, since a jaw clap display usually has an acoustic component, we would expect a sharp peak for the correlation between the visual display and vocalization. Other vocalizations and behaviors might have a looser time correlation. Take, for instance, signature whistles associated with mother/calf reunions (possibly evidenced by the start of a swim together). The correlation of signature whistles and reunions might show a broader peak than the visual and acoustic components of jaw claps, as the calf may vary in the amount of time that it takes to reunite with the mother and start a swim together. For some behaviors, we might expect a trough or no peak in the correlation function. For instance, if echolocation is only used for foraging or navigation, there would be no reason to expect gentle rubbing and echolocation to be related, resulting in a trough or no peak in the cross-correlation function.

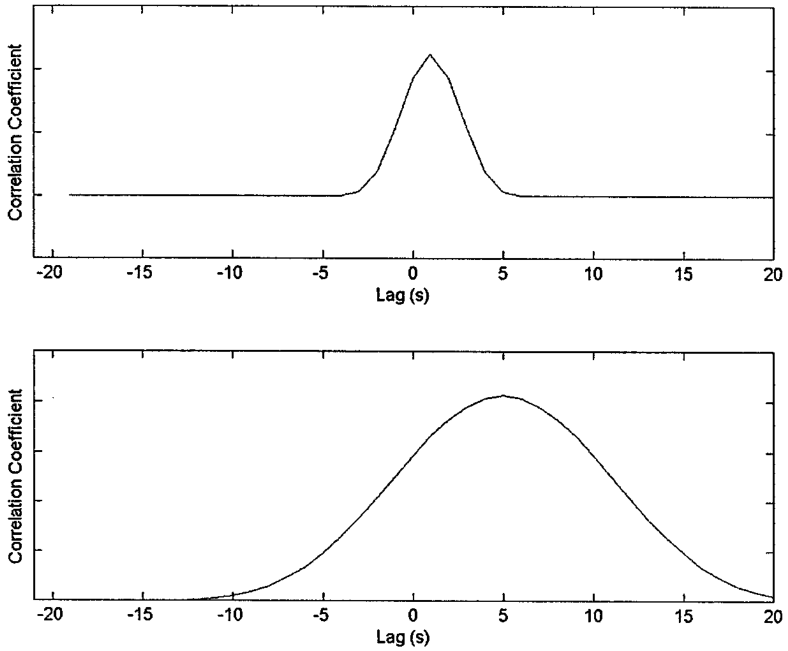


Figure 3. 8 Depiction of tight and loose correlations.

Note: The top plot depicts a possible tight correlation. The bottom plot depicts a looser correlation.

In order to associate behaviors with vocalizations over a finer time scale than the conditional probability analyses, the time series of the behavioral record $\mathbf{H}_k$ for all *k* was interpolated and then correlated with $\dot{\mathbf{r}}$ and $\dot{\mathbf{s}}$. This type of analysis may allow, for instance, discrimination between echolocation and social signals, based upon which types of signals occur with solitary foraging behaviors, and which occur only with social behaviors. In order to perform the correlations, the behavioral record $\mathbf{H}_k$ (which had a resolution of 1 s compared to the 0.1 s resolution of the parameter time series) was first interpolated to yield $\mathbf{h}_k$. This was performed by taking each time point and sub-sampling at 0.1 s, using the value of the original time point for each 0.1 s subsample. To look at the immediate association of behaviors and vocalizations, the cross-correlations between $\dot{\mathbf{r}}$ and $\dot{\mathbf{s}}$ and the interpolated behavioral records $\mathbf{h}_k$ were calculated for lags of ± 30 s. The unbiased cross-correlation was calculated by

$${}_{p}X_{k}(t)=\frac{1}{T-|(j-t)|}\sum_{j}\mathbf{h}_{\mathrm{k}}(j)\dot{\mathbf{r}}(j-t)$$ over all $j = t$ -30 to t +30, and

$${}_{q}X_{k}(t)=\frac{1}{T-|(j-t)|}\sum_{j}\mathbf{h}_{\mathrm{k}}(j)\dot{\mathbf{s}}(j-t)$$, over all $j = t$ -30 to t +30, where T is the length of $\mathbf{h}_{\mathrm{k}}$ (also the lengths of $\dot{\mathbf{r}}$ and $\dot{\mathbf{s}}$)

Indicator Levels Using Stochastic Resampling: In order to determine levels beyond which correlation peaks or troughs could be interpreted as being meaningful, two stochastic resampling techniques were used. The first randomized behavior types, but used the same start times of behaviors. The second used the same behavior types, but randomized the start times of the behaviors. Both techniques should give a similar significance level unless there were peculiarities in timing, either from the bout structure or resulting from artifacts of the concatenation of parameter time series, we might see different results.

For this first technique, the time of start of each behavior was held constant, but the complete set of behaviors, and their associated durations were randomly permuted (keeping the duration associated with the behavior) and placed at the same behavior start times. Put another way, the start times in the behavioral record were held constant, but another behavior (retaining its duration) was placed at that start time. This retains the bout structure observed, but randomizes behavior type. The behavior type was chosen randomly, but without replacement. This randomized behavior series was then correlated with the parameter set calculated from the real data for ± 30 s lags from time 0. This correlation was saved. This randomization and subsequent correlation calculation was performed 100 times, with the correlation being saved each time. The upper and lower 2.5 percentiles for each time lag were calculated (to yield overall 95 % indicator levels) for comparison with the data cross-correlations.

For the second technique, the start time was randomized within each behavior type, with each behavior retaining its duration as with the previous technique. That is, the set of behaviors, and their associated durations, were placed at random behavior times. By randomizing timing, this second method eliminates any bout structure present in the observed data. Once again, each randomized behavior series was correlated with the parameter set calculated from the real data for ± 30 s lags from time 0. The randomization and subsequent correlation calculation was performed 100 times, with the correlation being saved each time. The upper and lower 2.5 percentiles for each time lag were calculated (to yield overall 95 % indicator levels) for comparison with the data cross-correlations.

Indicator levels using Kolmogorov-Smirnov analyses: The Kolmogorov-Smirnov two-sample test is a non-parametric technique for looking at differences in two distributions. This technique determines whether the two distributions arise from the same underlying distribution. The distributions to be compared were the data cross-correlations (of the behavior and vocalization time series) and the cross-correlations generated from the stochastic resampling simulations. The distributions were first sorted, then cumulatively summed to form cumulative frequency distributions. The differences between the distributions at each point in the distribution were calculated. The value at the point of largest difference was compared to a 95 % indicator level, to evaluate whether the distributions might be considered to be different (Sokal and Rohlf 1981).

Correlations (over > 30 s time scale):

Correlations over longer time scales were also investigated. A time lag of ± 5 minutes was used to determine longer-term associations between behavior types and vocalizations. It should be possible to look at longer time scales, although the 10 minute length of the focal follow would limit its application in the data set collected for this thesis. If some motivational factors act on a short-term basis, and others on a long-term basis, then the changing of focal animals as per the protocol might confuse the analysis.

95 % indicator levels were calculated using stochastic resampling techniques similar to those used for the correlations on a short time scale.

3.3 Results:

3.3.1 General association of vocalizations with behaviors

The first analysis was to determine whether vocalizations (of all types) were associated in time with behaviors (of all types). The conditional probability of any vocalization (of any type) occurring ± 10 s of the onset of any behavior (of any type) is 0.44. This is higher than the overall probability, indicating that vocalizations tended to occur within this window more often than expected by chance. This corresponds to frequencies of occurrence significantly different from expected (chi-squared test, $p << .01$).

This analysis determined that vocalizations were associated with behaviors on a general level, but we would like to look more deeply at the factors involved. On this general level, it might be expected that tonal signals would be associated with some behaviors, and broadband signals with others. For instance, as some types of whistles are believed to serve a contact function, it might be expected that tonal signals would be associated with affiliative interactions, such as the onset of a swim together. As pulsed signals will likely be composed of both echolocation and burst-pulsed signals, it might be expected that pulsed signals would be associated with foraging and social behaviors, including agonism. We therefore also looked at the association of vocalizations with two major types of interactions, affiliative-state and agonistic interactions.

3.3.2 Vocalizations during Affiliative states:

For the affiliative state behaviors, the number of vocalizations (defined by a break ≥ 0.1 s) of each call type that occurred during affiliative states was determined (Table 3.7). Tonal signals, pulsed calls, and lumped vocalizations of all types occurred significantly less often than expected during affiliative states ($p < .017$, based upon Bonferroni correction (p must be < .05/3)). Note that this is *during* behavioral states, not within a ± 10 s window of the onset of a behavior. BP Type I calls also occurred less often than expected, but this result was not significant.

Table 3. 7 Number of vocalizations (defined by a break ≥ 0.1 s) of each call type occurring during affiliative state interactions.

	Tonal Signals	Pulsed Calls	BP Type I	All Vocalizations
Observed	863	1008	322	2193
Expected	998	1388	343	2730

Note: Shaded columns indicate results that are statistically ($p<.017$ – Bonferroni adjustment) different than expected.

3.3.3 Vocalizations during Agonistic interactions:

A similar analysis as above was performed for agonistic behaviors. Since agonistic behaviors were not coded as states, the 10 s chain rule was used to define an interaction. That is, if longer than 10 s occurred between behaviors, the new sequence of behaviors was defined as a new interaction. For the agonistic behaviors, the number of vocalizations (defined by a break ≥ 0.1 s) of each call type that occurred during agonistic interactions was determined. All types of vocalizations occurred significantly more often than expected during agonistic interactions ($p < .017$).

Table 3. 8 The number of vocalizations (defined by a break ≥ 0.1 s) of each call type occurring during agonistic interactions.

	Tonal Signals	Pulsed Calls	BP Type I	All Vocalizations
Observed	180	250	77	507
Expected	65	90	22	177

Note: Shaded columns indicate results that are statistically ($p<.017$ – Bonferroni adjustment) different than expected.

3.3.4 Conditional probability results:

The results of the conditional probability analyses are shown in Figs. 3.9 – 3.12.

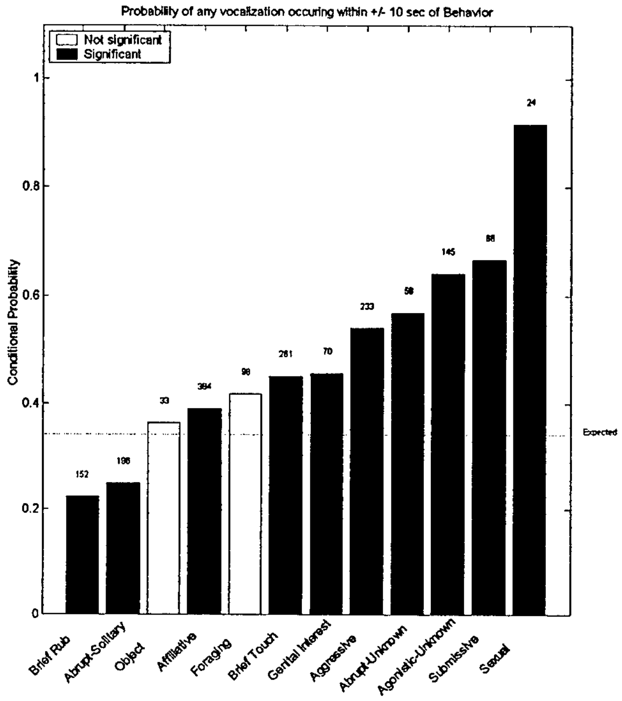


Figure 3. 9 The probability of any vocalization occurring within ± 10 s of the start of the behavior type.

Note: Bars in black represent results that were different from expected based upon 95 % indicator thresholds (note that this is not statistical inference). The numbers above the bars are the sample sizes for that behavior type.

The conditional probabilities of any vocalization occurring within ± 10 s of the start of a behavior for each behavioral type are shown in Fig. 3.9. Vocalizations were more likely to occur within ± 10 s of all of the agonistic behaviors (aggressive, submissive, and unknown), affiliative behaviors, sexual behaviors, genital interest behaviors, brief touches, and abrupt-unknown behaviors. Vocalizations were less likely to occur within ± 10 s of brief rub or abrupt-solitary behaviors. Vocalization rates did not differ from expected within ± 10 s of foraging behaviors and object-oriented behaviors.

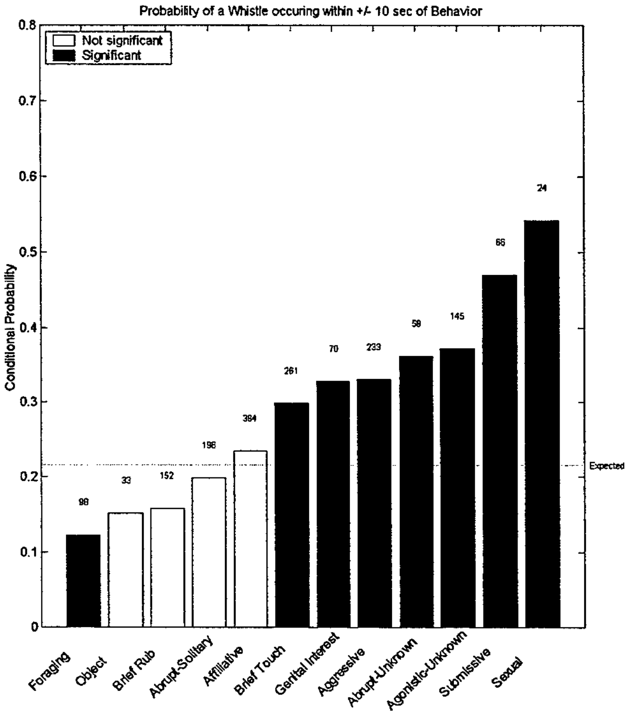


Figure 3. 10 The probability of a whistle occurring within ± 10 s of the start of the behavior type.

Note: Bars in black represent results that were different from expected based upon 95 % indicator thresholds (note that this is not statistical inference). The numbers above the bars are the sample sizes for that behavior type.

The conditional probabilities of a whistle vocalization occurring within ± 10 s of the start of a behavior for each behavioral type are shown in Fig. 3.10. A whistle was more likely to occur within ± 10 s of all of the agonistic behaviors (aggressive, submissive, and unknown), sexual behaviors, genital interest behaviors, brief touches, and abrupt-unknown behaviors. A whistle was less likely to occur within ± 10 s of a foraging behavior. Whistles were not likely to occur differently from expected within ± 10 s of affiliative behaviors (affiliative state and brief rub), abrupt-solitary behaviors, and object-oriented behaviors.

The conditional probabilities of a pulsed vocalization occurring within ± 10 s of the start of a behavior for each behavioral type are shown in Fig. 3.11.

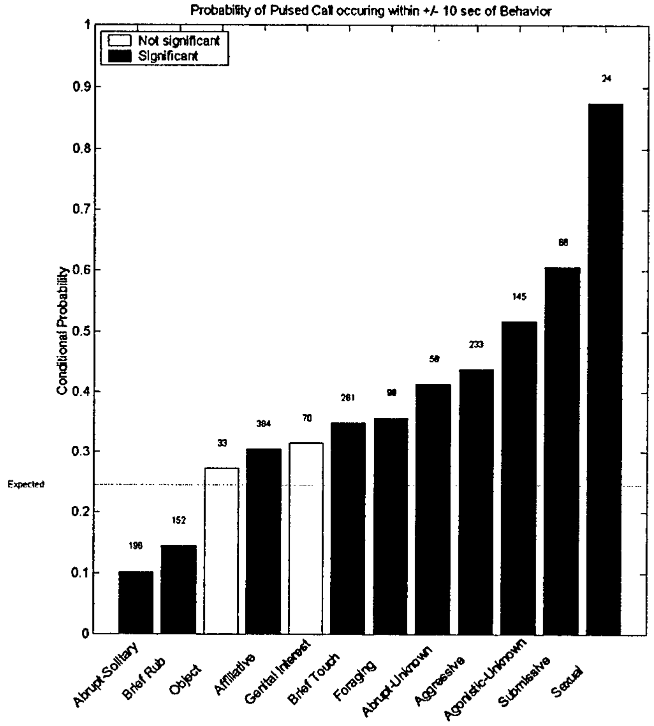


Figure 3. 11 The probability of a pulsed vocalization occurring within ± 10 s of the start of the behavior type.

Note: Bars in black represent results that were different from expected based upon 95 % indicator thresholds (note that this is not statistical inference). The numbers above the bars are the sample sizes for that behavior type.

A pulsed call was more likely to occur within ± 10 s of all of the agonistic behaviors (aggressive, submissive, and unknown), sexual behaviors, foraging, brief touches, and abrupt-unknown behaviors. A pulsed call was less likely to occur within ± 10 s of a brief rub or an abrupt-solitary behavior. Pulsed vocalizations were not likely to occur differently from expected within ± 10 s of object-oriented behaviors and genital interest behaviors.

The conditional probabilities of a BP type I vocalization occurring within ± 10 s of the start of a behavior for each behavioral type are shown in Fig. 3.12.

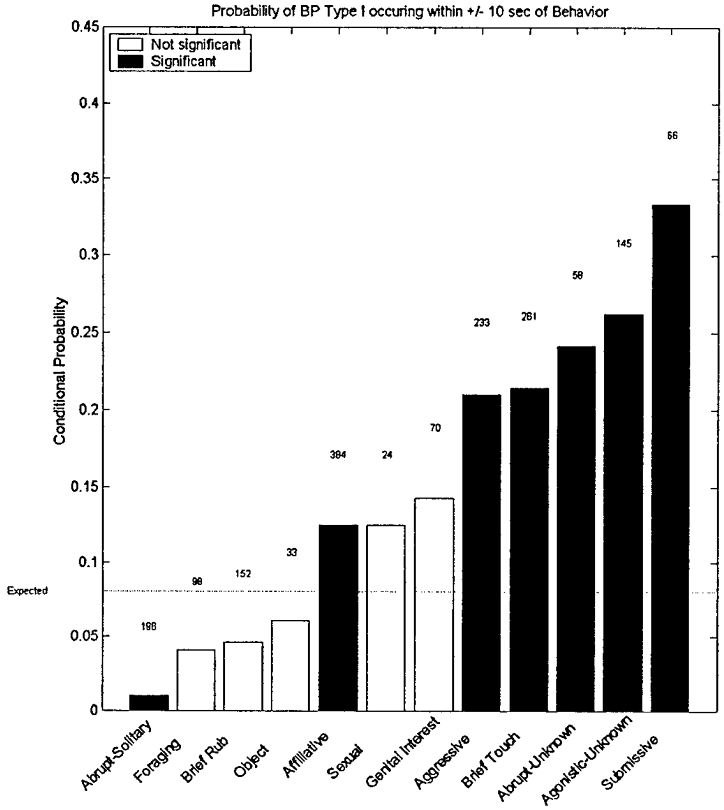


Figure 3. 12 The probability of BP type I vocalizations occurring within ± 10 s of the start of the behavior type.

Note: Bars in black represent results that were different from expected based upon 95 % indicator thresholds (note that this is not statistical inference). The numbers above the bars are the sample sizes for that behavior type.

A BP Type I vocalization was more likely to occur within ± 10 s of all of the agonistic behaviors (aggressive, submissive, and unknown), affiliative (state), brief touches, and abrupt-unknown behaviors. A BP Type I vocalization was less likely to occur within ± 10 s of an abrupt-solitary behavior. BP Type I vocalizations were not likely to occur differently from expected within ± 10 s of foraging, sexual behaviors, brief rubs, object-oriented behaviors and genital interest behaviors.

Summary: Whistles and BP type I vocalizations were not strongly associated with foraging, while pulsed calls were. Whistles and pulsed vocalizations were strongly associated with sexual behaviors, while BP type I vocalizations were not. All vocalization types were strongly associated with agonistic, brief touch, and abrupt unknown behaviors. A summary of the associations is given in Table 3.9.

Table 3. 9 Summary of Conditional Probability Results

	All Vocalizations	**Tonal Signals**	**Pulsed Signals**	**BP Signals**
Agonistic-Aggressive	+	+	+	+
Agonistic-Submissive	+	+	+	+
Agonistic-Unknown	+	+	+	+
Sexual	+	+	+	+
Genital Interest	+	+	**o**	**o**
Brief Touch	+	+	+	+
Brief Rub	-	**o**	-	**o**
Affiliative	+	**o**	+	+
Abrupt-Unknown	+	+	+	+
Abrupt-Solitary	-	**o**	-	-
Foraging	**o**	-	+	**o**
Object	**o**	**o**	**o**	**o**

Note: The symbols indicate the sign of association between vocalizations and behavioral types. + indicates an increase in vocalizations in the time window around the behavioral type, - indicates a decrease, and **o** indicates no trend.

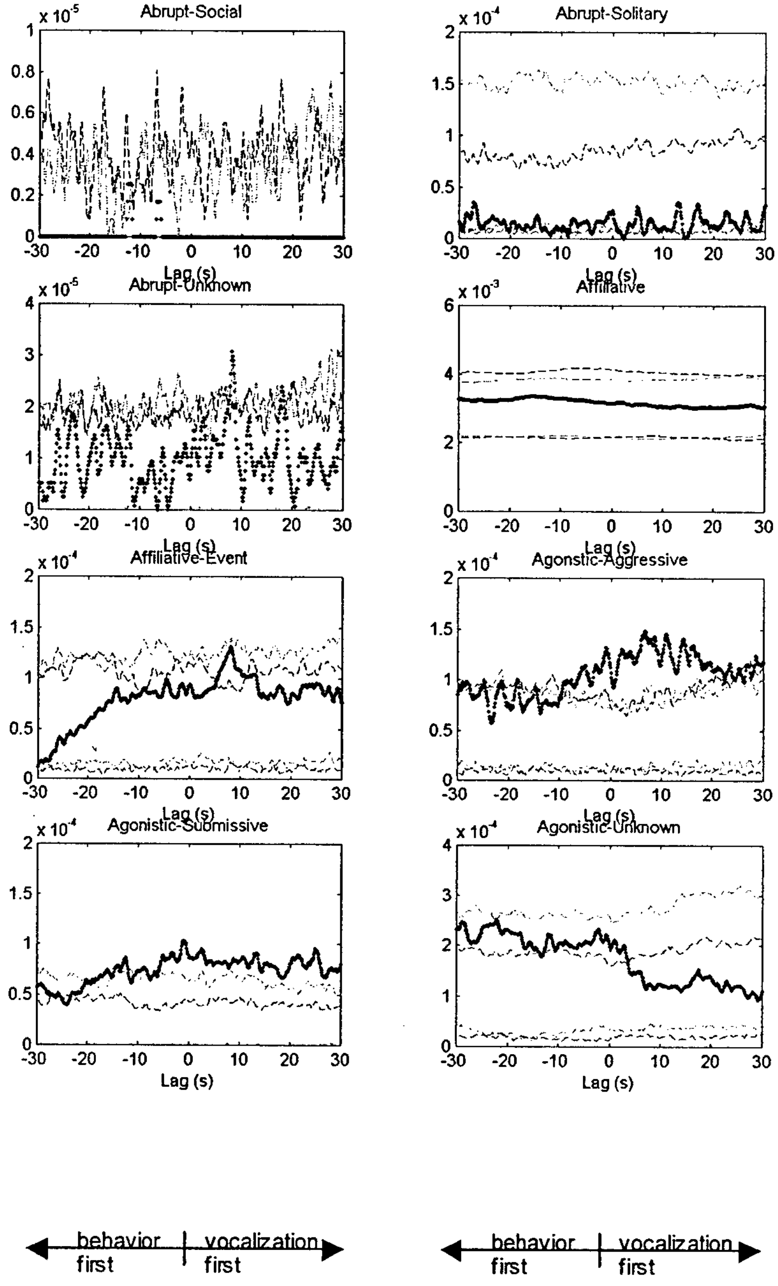
3.3.5 Cross-correlation results:

Stochastic resampling:

The cross-correlation results for the parameter time series with the behavior time series are shown in Fig. 3.13 – 3.15. The 95 % indicator lines generated from the stochastic resampling are also plotted on Figs. 3.13 – 3.15. As the results from the two types of stochastic simulations were similar, they are both plotted as dashed lines in Figs. 3.13 – 3.15.

Tonal signals:

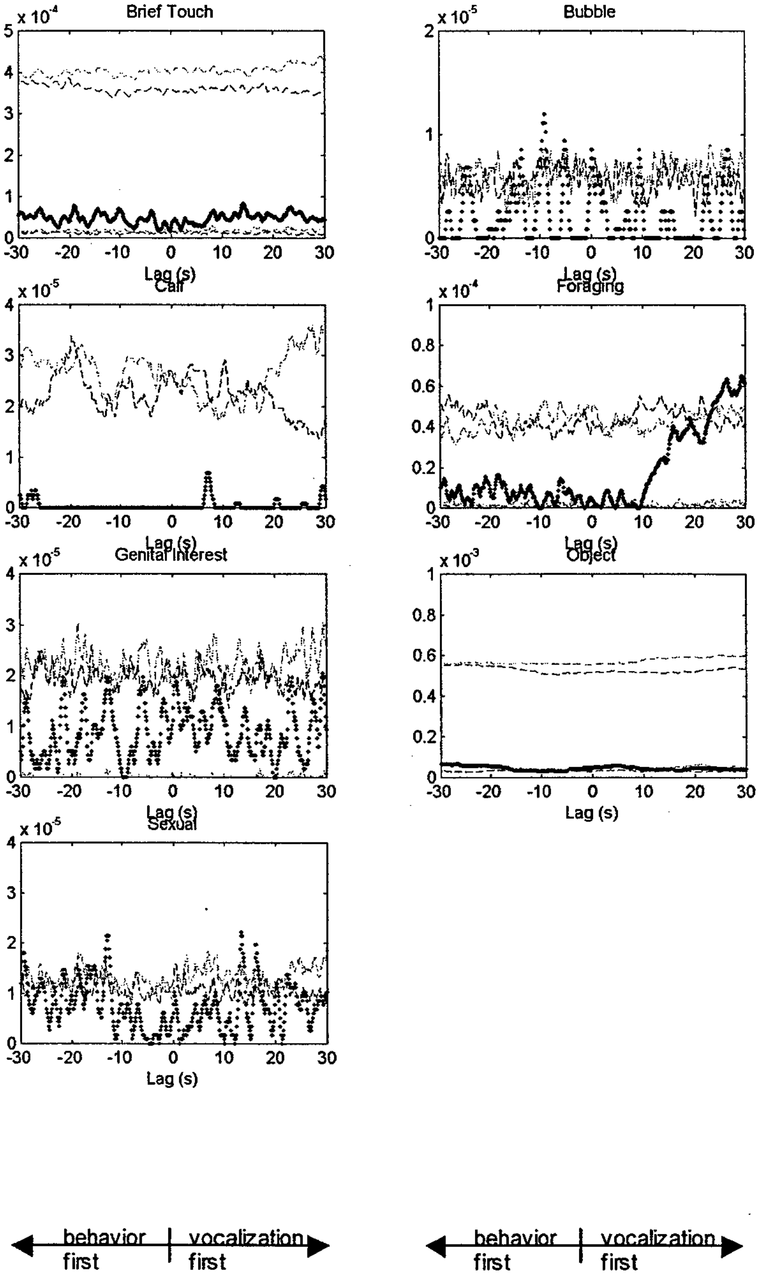
The behavior types that show strong correlations are affiliative events, all of the agonistic behaviors, and foraging behaviors (Fig. 3.13 (a) and (b)). The cross-correlation for the affiliative events has a peak around 8 s, indicating a possible tendency for a whistle to occur, then a rub involving the focal animal to occur 8 s later. The cross-correlation for the agonistic-aggressive behaviors is right-skewed. This means that there may be a tendency for whistles to happen mainly before the aggressive behavior. The correlation for the agonistic-submissive behavior is generally elevated for the entire 60 s window, with the exception of the -20 to -30 s time lags. The cross-correlation for the agonistic-unknown behaviors is left-skewed. This means that there may be a tendency for first the behavior to occur, then the whistle. The cross-correlation for the foraging behavior is generally low for most time lags, then is elevated for time lags from + 20 to + 30 s. This indicates a possible trend in foraging events happening 20 to 30 s after a whistle. Upon closer examination of the affiliative event and foraging behavior cross-correlation data, it appeared that the aforementioned peaks in the correlations may have resulted almost entirely from the events of one day. This does not necessarily mean that these results were spurious, but that the association was very strong one day, and not others, and may not be generalizable. Further investigation into the more specific context of isolated results like these may yield interesting results. Brief touch and object-oriented behaviors showed sustained low correlation levels, indicating that these behaviors may only rarely occur in association with whistles.



(a)

Figure 3. 13 Cross-correlations for lags of ± 30 s of the tonal parameter time series with the behavior time series for each behavior type.

Note: The dark dotted line is the cross-correlation of the observed data. The lighter dashed lines are the 95% indicator levels from the stochastic resampling. Correlations below the lower pairs of lines are in the bottom 2.5 % of the data from stochastic resampling. Correlations above the higher pairs of lines are in the bottom 2.5 % of the data.



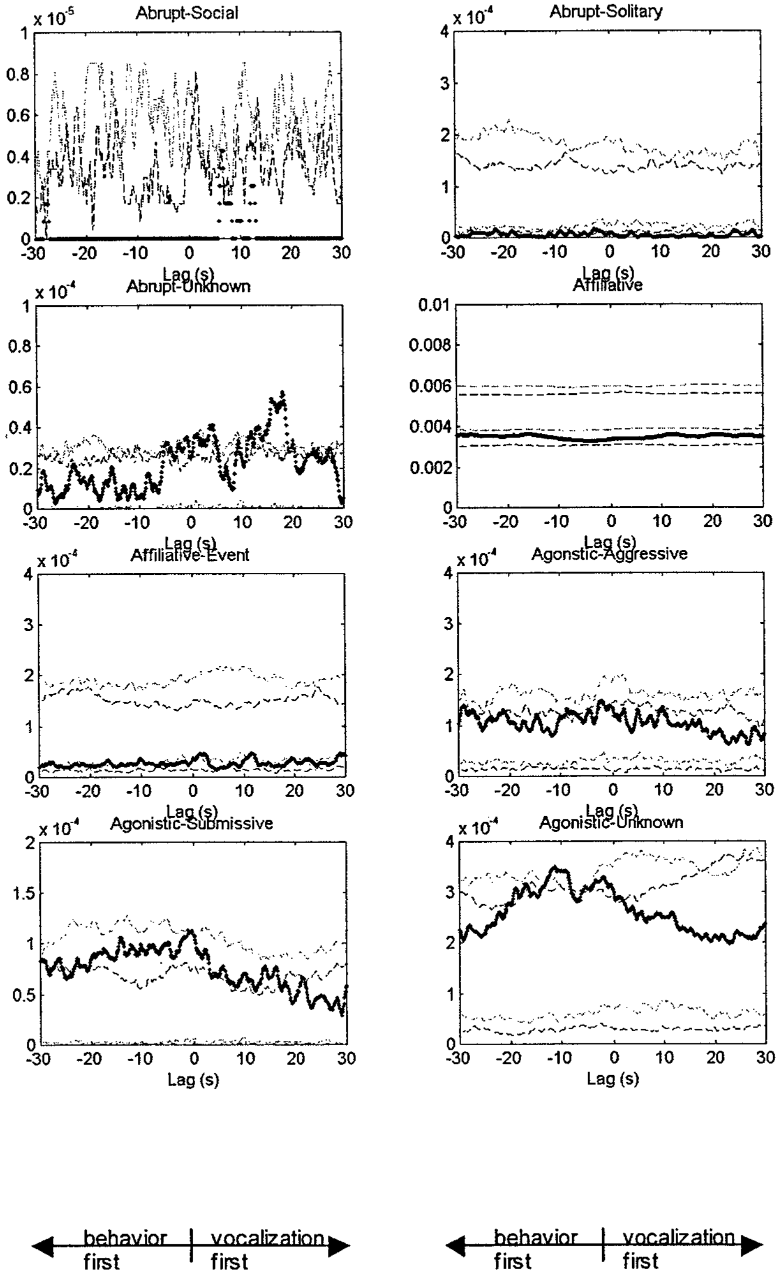
(b)

Figure 3. 13 Cross-correlations for lags of ± 30 s of the tonal parameter time series with the behavior time series for each behavior type.

Note: The dark dotted line is the cross-correlation of the observed data. The lighter dashed lines are the 95% indicator levels from the stochastic resampling. Correlations below the lower pairs of lines are in the bottom 2.5 % of the data from stochastic resampling. Correlations above the higher pairs of lines are in the bottom 2.5 % of the data.

Pulsed signals:

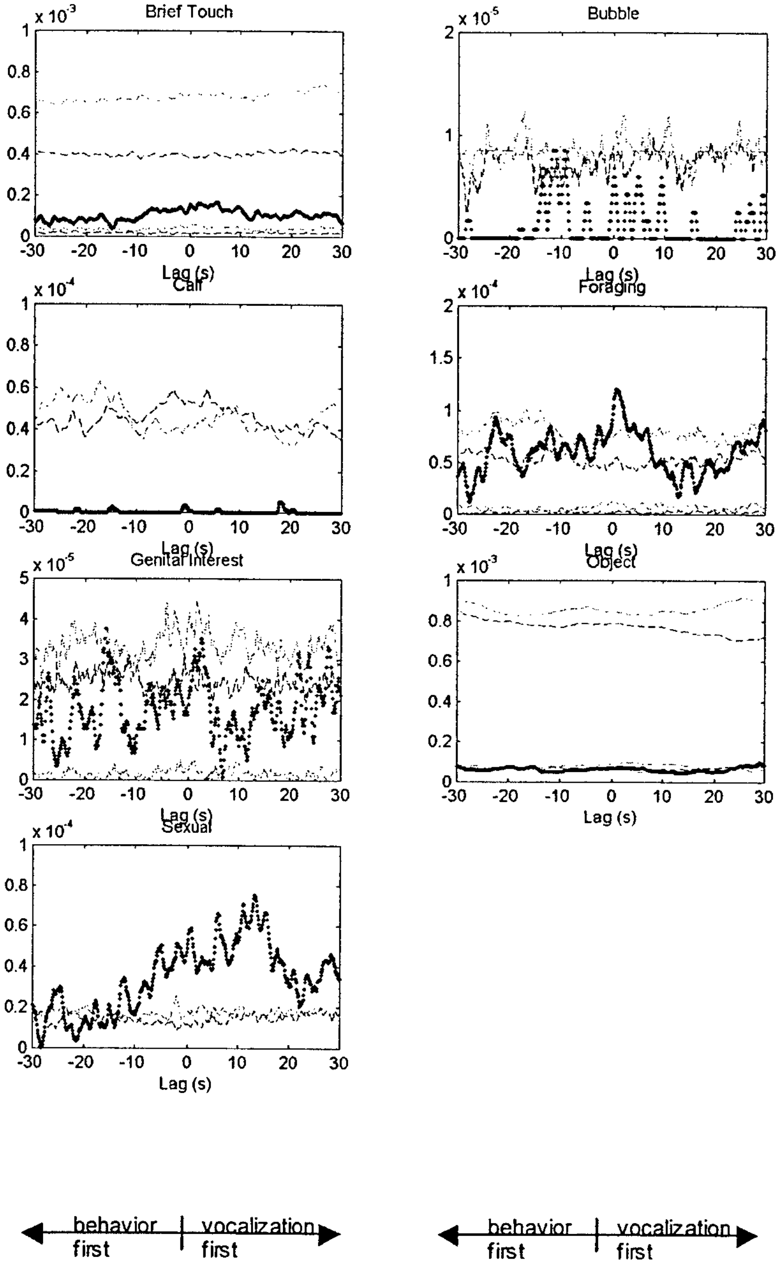
While there may have been associations of pulsed sounds with abrupt-unknown behaviors and agonistic behaviors (Fig. 3.14 (a)), the most striking results came from the foraging and sexual behavior cross-correlations (Fig. 3.14(b)). The cross-correlation for the abrupt-unknown behaviors with pulsed signals shows two separate peaks, one around zero, and one at a little under 20 s. All of the agonistic behaviors show peaks above the 95 % indicators, with the event behaviors (aggressive and submissive) possibly showing peaks around zero. The cross-correlation for the foraging behaviors shows a definitive peak around zero. This suggests a close link in time between pulsed signals and foraging behaviors. The cross-correlation for sexual behaviors appears to increase before zero, and peak around 15 s. This peak at 15 s suggests the occurrence of the pulsed vocalizations first, with sexual behaviors occurring within 15 s afterwards. Affiliative events, affiliative states, abrupt-solitary, and object-oriented behaviors show sustained low correlation levels, indicating that these behaviors may only rarely occur in association with pulsed calls.



(a)

Figure 3. 14 Cross-correlations for lags of ± 30 s of the pulsed parameter time series with the behavior time series for each behavior type.

Note: The dark dotted line is the cross-correlation of the observed data. The lighter dashed lines are the 95% indicator levels from the stochastic resampling. Correlations below the lower pairs of lines are in the bottom 2.5 % of the data from stochastic resampling. Correlations above the higher pairs of lines are in the bottom 2.5 % of the data.



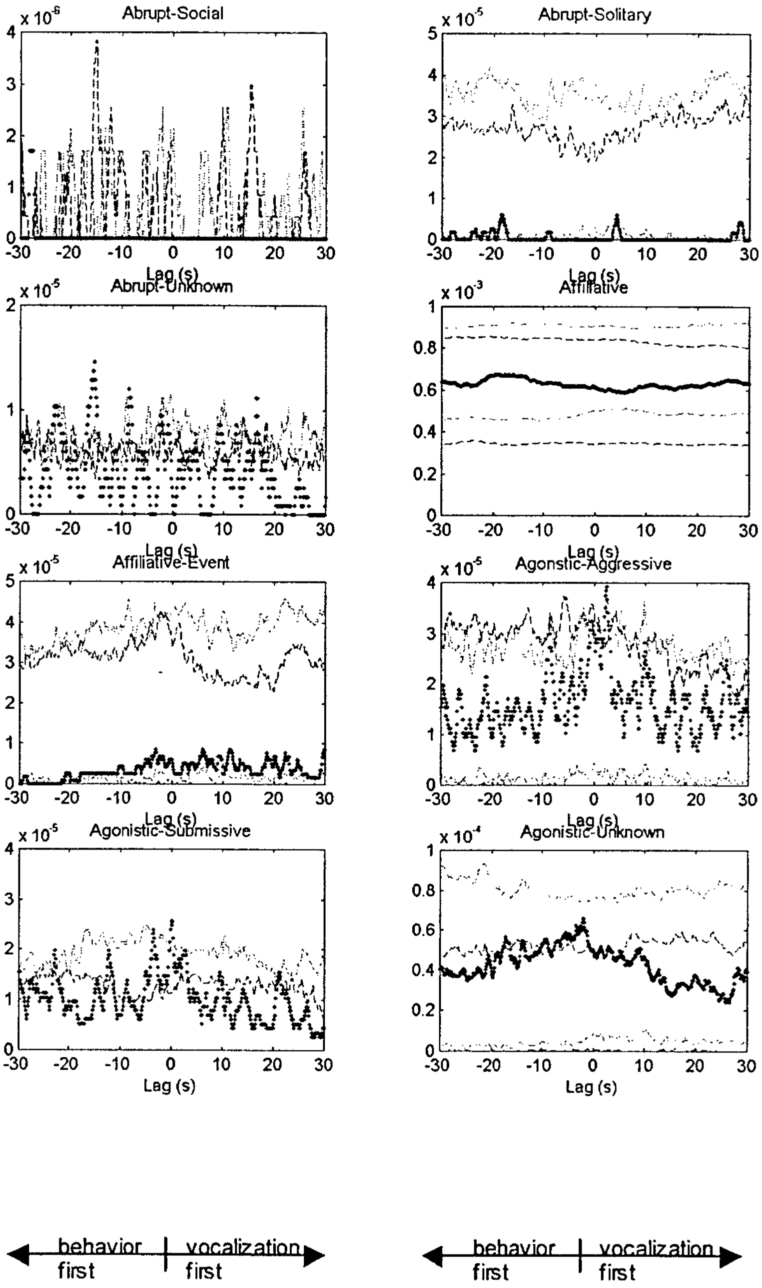
(b)

Figure 3. 14 Cross-correlations for lags of ± 30 s of the pulsed parameter time series with the behavior time series for each behavior type.

Note: The dark dotted line is the cross-correlation of the observed data. The lighter dashed lines are the 95% indicator levels from the stochastic resampling. Correlations below the lower pairs of lines are in the bottom 2.5 % of the data from stochastic resampling. Correlations above the higher pairs of lines are in the bottom 2.5 % of the data.

BP Type I signals:

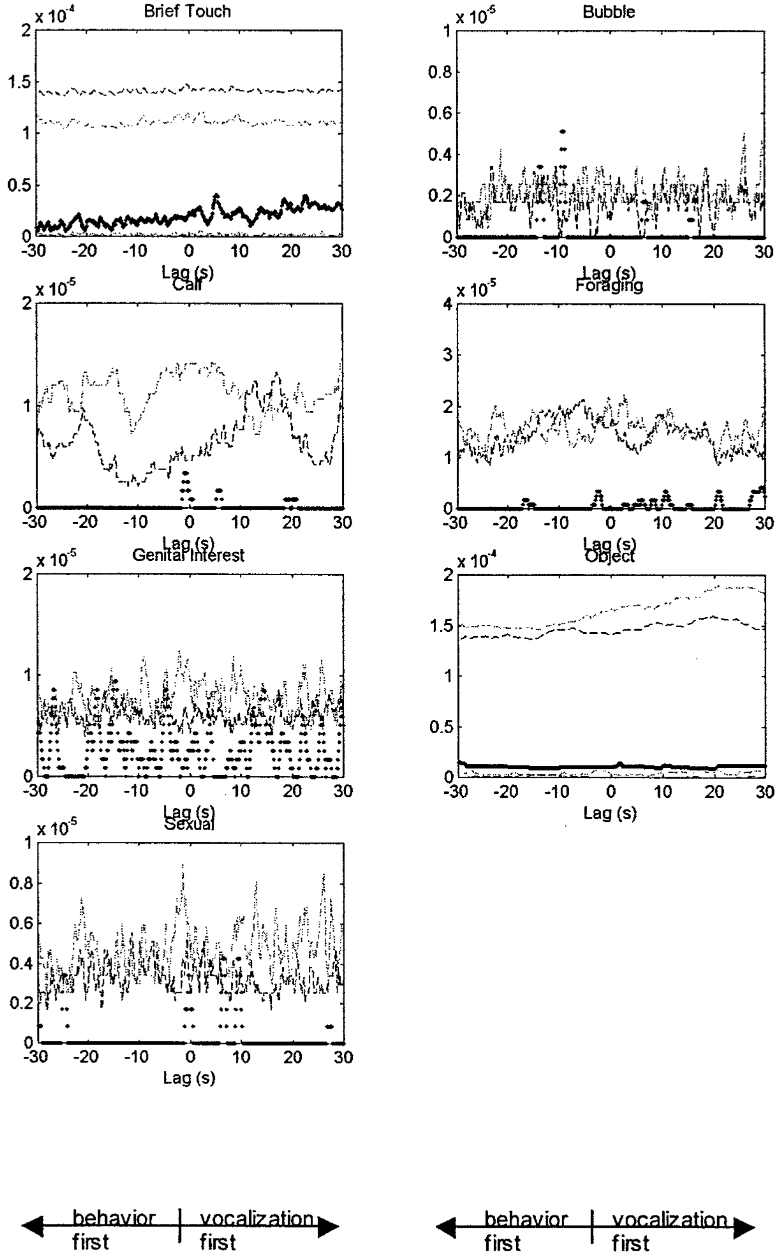
The cross-correlation for the abrupt-unknown behaviors with the BP type I time series is very peaky (Fig. 3.15(a)). There appears to be some underlying oscillation, although it is difficult to tell whether this reflects genuine trends in the underlying data (perhaps caused by regular repetition of one or the other of these behaviors in bouts) or a spurious result. The cross correlations for the agonistic behaviors all have peaks in the region of 0 lag. This suggests a close linkage in time of BP type I vocalizations to agonistic behaviors. Affiliative events and object-oriented behaviors show sustained low correlation levels, indicating that these behaviors may only rarely occur in association with BP I calls.



(a)

Figure 3. 15 Cross-correlations for lags of ± 30 s of the BP Type I time series with the behavior time series for each behavior type.

Note: The dark dotted line is the cross-correlation of the observed data. The lighter dashed lines are the 95% indicator levels from the stochastic resampling. Correlations below the lower pairs of lines are in the bottom 2.5 % of the data from stochastic resampling. Correlations above the higher pairs of lines are in the bottom 2.5 % of the data.



(b)

Figure 3. 15 Cross-correlations for lags of ± 30 s of the BP Type I time series with the behavior time series for each behavior type.

Note: The dark dotted line is the cross-correlation of the observed data. The lighter dashed lines are the 95% indicator levels from the stochastic resampling. Correlations below the lower pairs of lines are in the bottom 2.5 % of the data from stochastic resampling. Correlations above the higher pairs of lines are in the bottom 2.5 % of the data.

Summary:

The results of the cross-correlations are summarized in Table 3.10. Summarizing the large amount of data from the cross-correlations is difficult, so only very broad generalizations were made. Each result from the cross-correlations was described by one of the following: vocalizations tended to occur before behaviors, behaviors tended to occur before vocalizations, behaviors and vocalizations tended to occur at the same time, the correlation was in general high, the correlation was in general low, the data were unclear, or the data did not appear to be different than expected.

Table 3. 10 Summary of cross-correlation results

	Tonal Signals	Pulsed Signals	BP Signals
Agonistic-Aggressive	**V →B**	+	**V=B**
Agonistic-Submissive	+	**B →V**	**V=B**
Agonistic-Unknown	**B →V**	**B →V**	+
Sexual		**V →B**	
Genital Interest			
Brief Touch	-		
Brief Rub (Affiliative-event)	**V →B**	-	-
Affiliative		-	
Abrupt-Unknown		**V →B**	
Abrupt-Solitary	-	-	-
Foraging	**V →B***	**V=B**	
Object	-	-	

Note: The correlation results have been very generally summed in the above table. **V →B** indicates that the vocalization tended to occur before the behavior, **B →V** indicates that the behavior tended to occur before the vocalization, **V=B** indicates that the behavior and vocalization occurred about the same time, **+** indicates that the correlation was in general elevated, with no clear trend of vocalization or behavior occurring first, **-** indicates that the correlation in general was low with no clear trend of vocalization or behavior occurring first. Blank squares indicate that either the results were unclear or the correlations did not appear to differ from expected.
*= this result may not be generalizable

Kolmogorov-Smirnov:

The results from the Kolmogorov-Smirnov analysis for difference in distributions is shown in Table 3.11. Results which exceeded 95 % indicator levels (.8860) are denoted by cells with thick borders. As this is an exploratory analysis, these results cannot be considered to be statistically significant, although they are likely to be of interest. Results which exceeded 80 % indicator levels (0.7360) are denoted by cells with intermediate borders. Although these were also not considered to be significant, they may indicate areas for further research. For cells with values above 80 % indicator levels, shading and hatching indicate how the distribution differed from expected. Shaded cells indicate that the two distributions differed with the data distribution exceeding the expected distribution over portions of the distribution range. Hatched cells indicate that the two distributions differed from the data distribution by the data distribution being lower than the expected distribution over the entire distribution range.

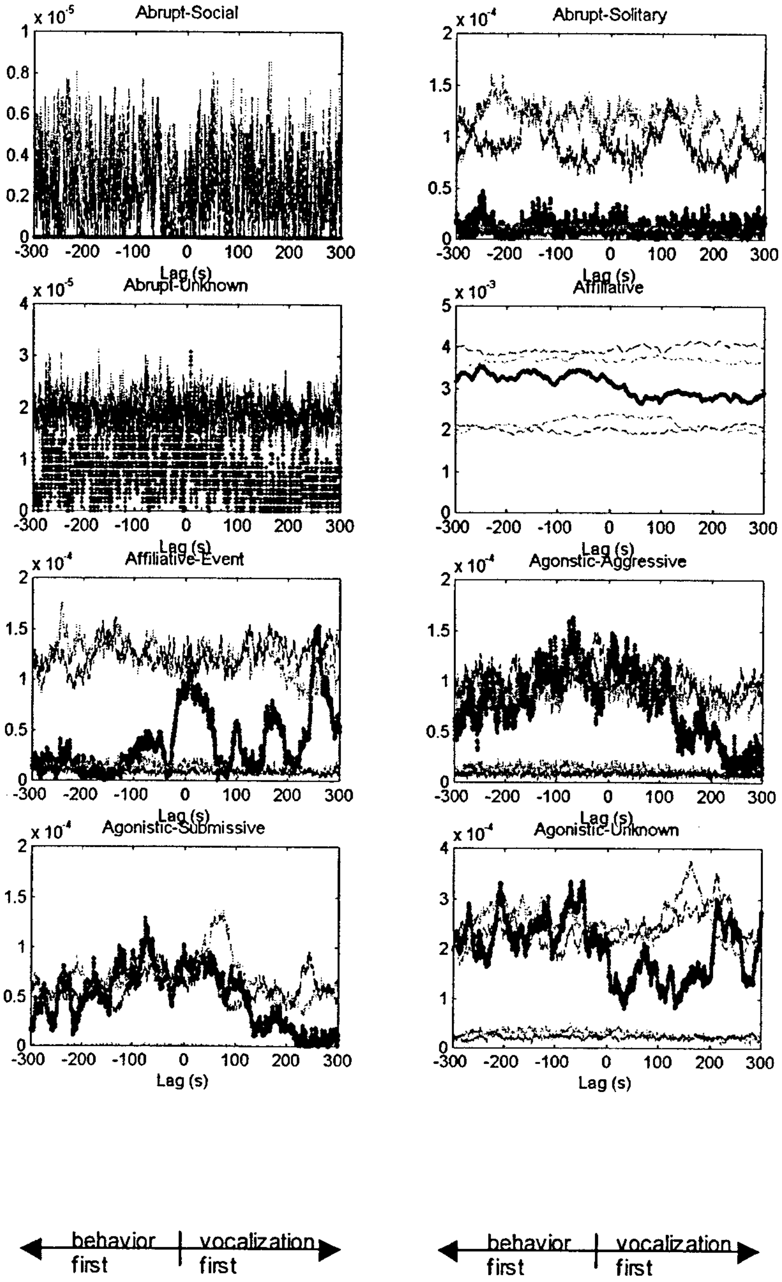
Table 3. 11 Results of the Kolmogorov-Smirnov Test for Difference in Distributions

Behavior Type	Whistle	Pulsed Signal	BP Type I
Abrupt-Social	0.0491	0.0216	0.0098
Abrupt-Solitary	0.5207	0.9208	0.6898
Abrupt-Unknown	0.3233	0.4482	0.4658
Affiliative	0.5441	0.8078	0.5598
Affiliative-Event	0.6473	0.6278	0.4479
Agonistic-Aggressive	0.9015	0.7905	0.6724
Agonistic-Submissive	0.9643	0.8486	0.8101
Agonistic-Unknown	0.7309	0.8541	0.7602
Brief Touch	0.3498	0.4062	0.3663
Bubble	0.4009	0.1585	0.0216
Calf	0.2943	0.3949	0.0899
Foraging	0.2271	0.7743	0.4278
Genital Interest	0.1881	0.4885	0.2418
Object	0.8613	0.8954	0.6653
Sexual	0.4966	0.8293	0.0819

Note: Cells with bold borders indicate results which exceeded 95 % indicator levels (.8860). Results which were above 80% indicator levels (0.7360) are denoted by cells with intermediate borders. Shaded cells indicate that the two distributions differed with the data distribution exceeding the expected distribution over portions of the distribution range. Hatched cells indicate that the two distributions differed from the data distribution by the data distribution being lower than the expected distribution over the entire distribution range.

3.3.6 Cross-correlations (± 5 min):

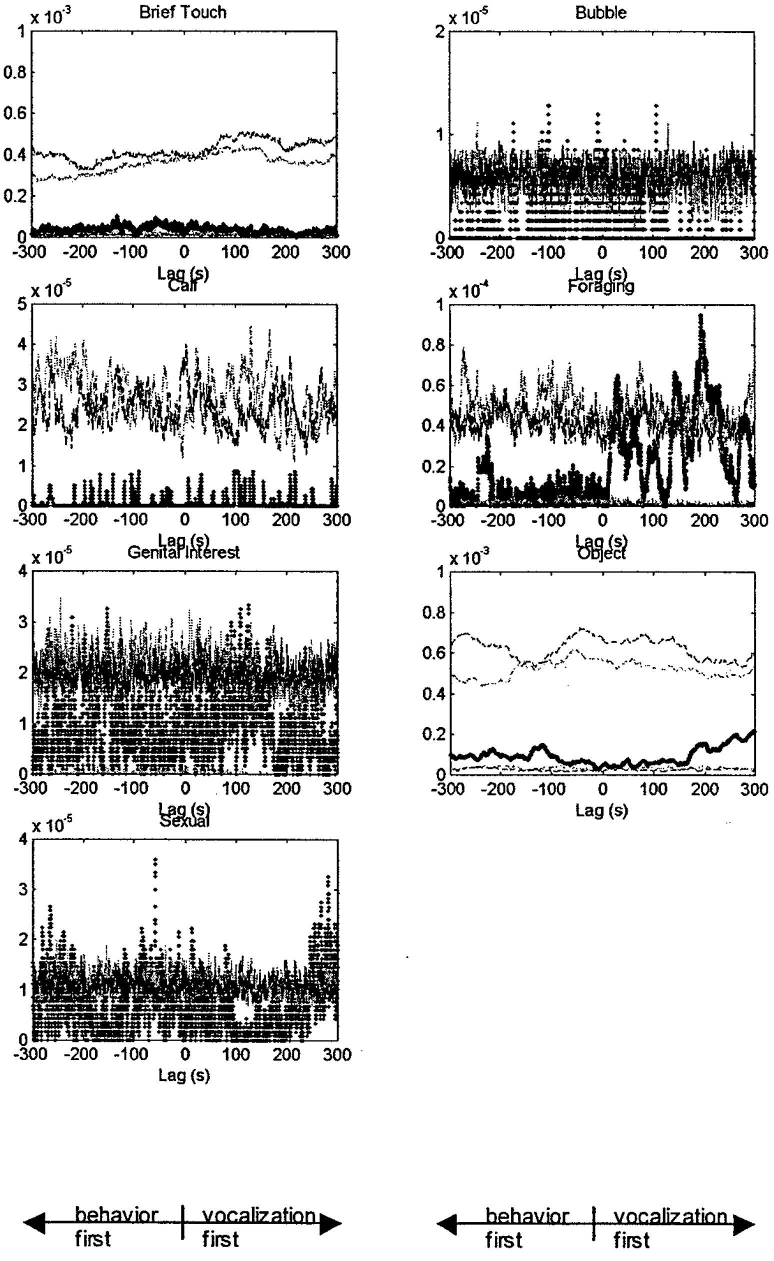
The cross-correlations for lags of ± 5 min (± 300 s) of the parameter time series with the behavior time series for each behavior type are shown in Figures 3.16 – 3.18. These results are somewhat difficult to interpret, so I will focus on peaks in the affiliative, agonistic, and sexual behaviors.



(a)

Figure 3. 16 Cross-correlations for lags of ± 5 min (± 300 s) of the tonal parameter time series with the behavior time series for each behavior type.

Note: The dark dotted line is the cross-correlation of the observed data. The lighter dashed lines are the 95% indicator levels from the stochastic resampling. Correlations below the lower pairs of lines are in the bottom 2.5 % of the data from stochastic resampling. Correlations above the higher pairs of lines are in the bottom 2.5 % of the data.

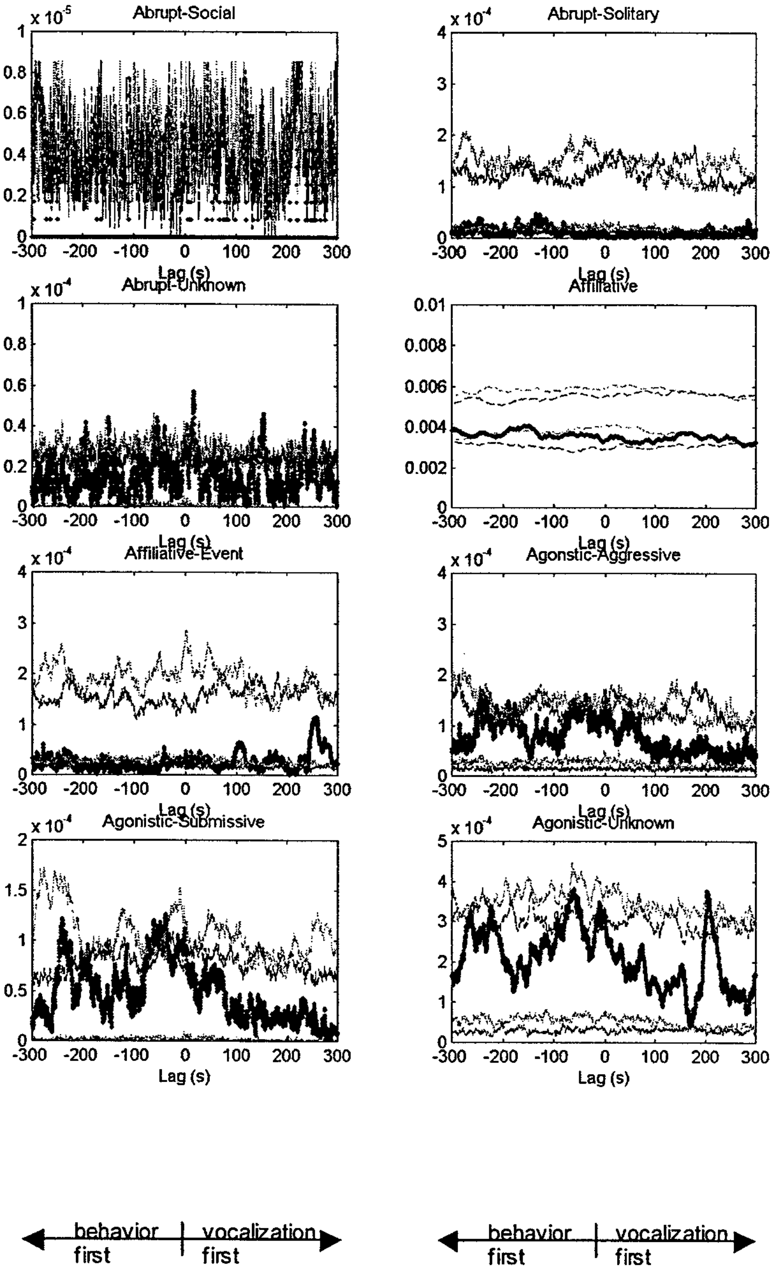


(b)

Figure 3. 16 Cross-correlations for lags of ± 5 min (± 300 s) of the tonal parameter time series with the behavior time series for each behavior type.

Note: The dark dotted line is the cross-correlation of the observed data. The lighter dashed lines are the 95% indicator levels from the stochastic resampling. Correlations below the lower pairs of lines are in the bottom 2.5 % of the data from stochastic resampling. Correlations above the higher pairs of lines are in the bottom 2.5 % of the data.

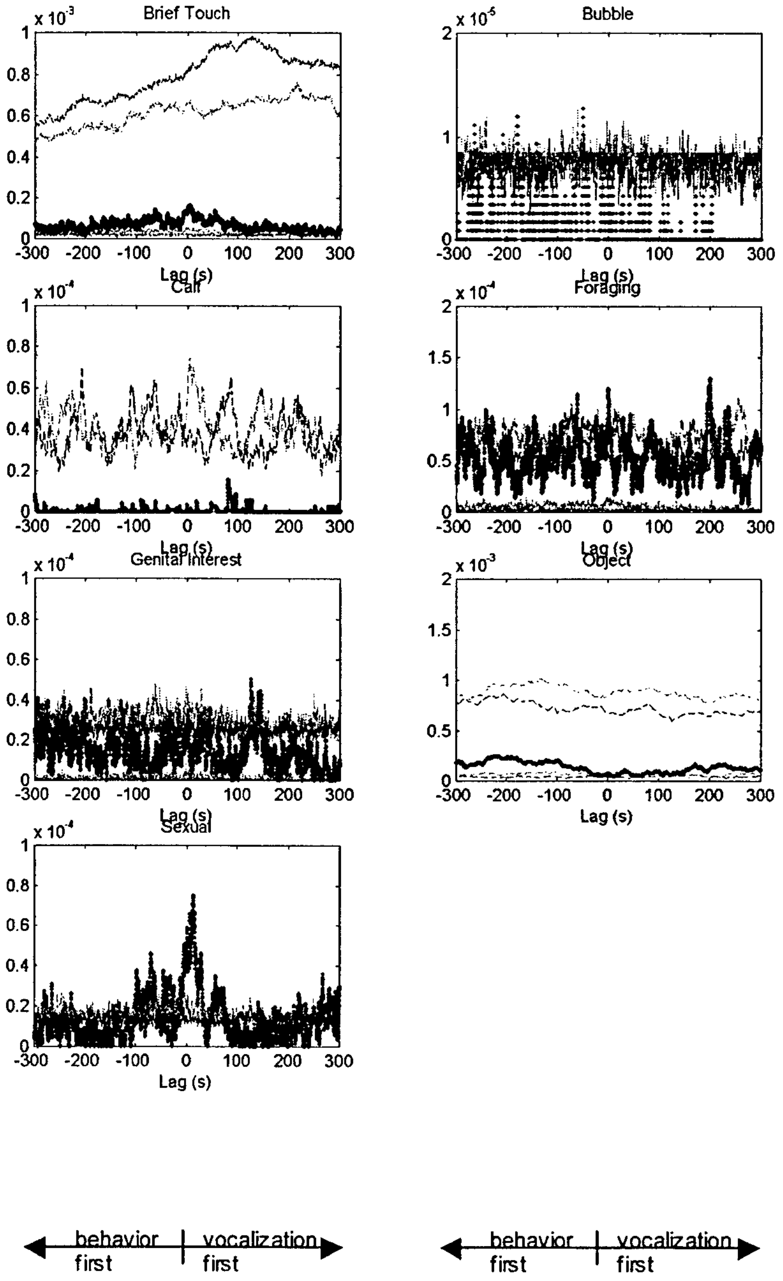
The cross-correlation of affiliative-event behaviors with the time series of tonal vocalizations gives a peak about 50 s wide around the time lag of zero (Fig. 3.16 (a)). The peak is slightly offset in the positive direction, indicating that the tonal vocalization was more likely to occur before the behavior started. However, it should be noted that this peak is an increase from low numbers, and only near 0 does the peak cross the 95 % indicator line from stochastic resampling. The peaks are fairly broad around the aggressive and submissive behaviors, indicating at least a minute-scale association of tonal vocalizations and behaviors.



(a)

Figure 3. 17 Cross-correlations for lags of ± 5 min (± 300 s) of the pulsed parameter time series with the behavior time series for each behavior type.

Note: The dark dotted line is the cross-correlation of the observed data. The lighter dashed lines are the 95% indicator levels from the stochastic resampling. Correlations below the lower pairs of lines are in the bottom 2.5 % of the data from stochastic resampling. Correlations above the higher pairs of lines are in the bottom 2.5 % of the data.

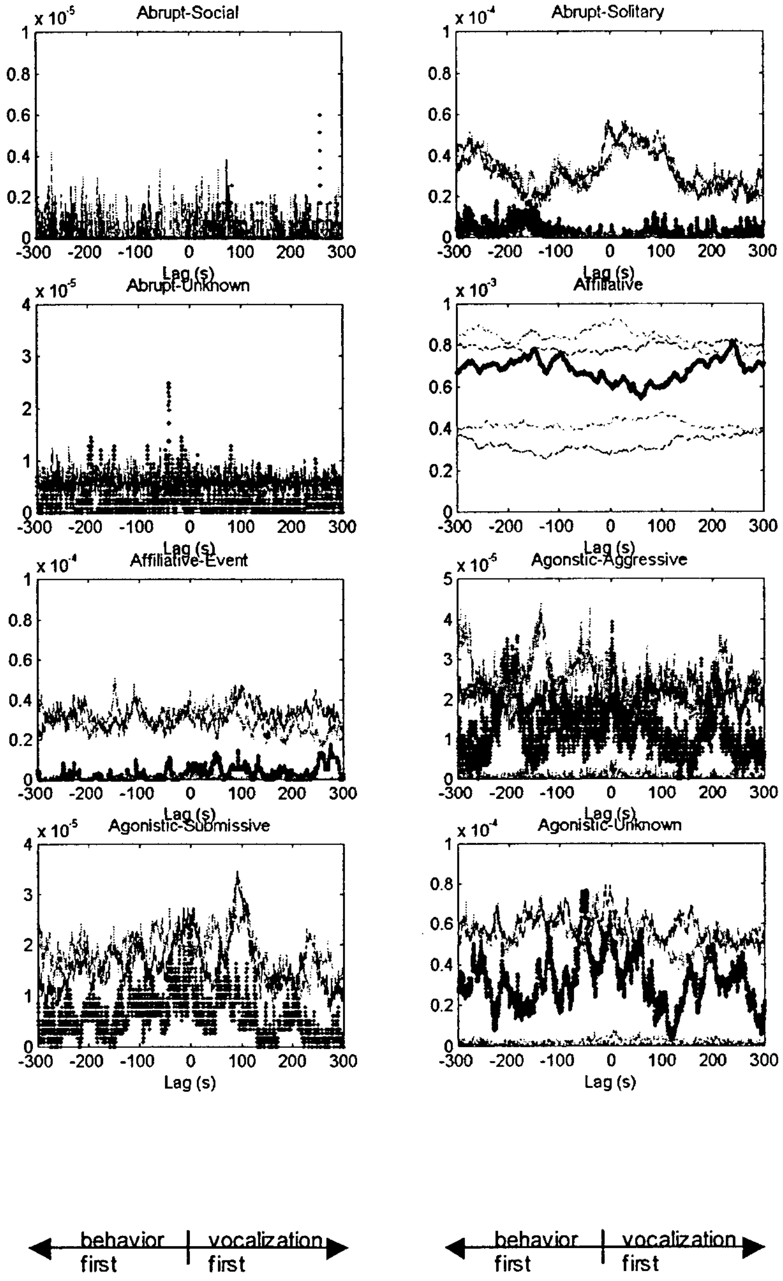


(b)

Figure 3. 17 Cross-correlations for lags of ± 5 min (± 300 s) of the pulsed parameter time series with the behavior time series for each behavior type.

Note: The dark dotted line is the cross-correlation of the observed data. The lighter dashed lines are the 95% indicator levels from the stochastic resampling. Correlations below the lower pairs of lines are in the bottom 2.5 % of the data from stochastic resampling. Correlations above the higher pairs of lines are in the bottom 2.5 % of the data.

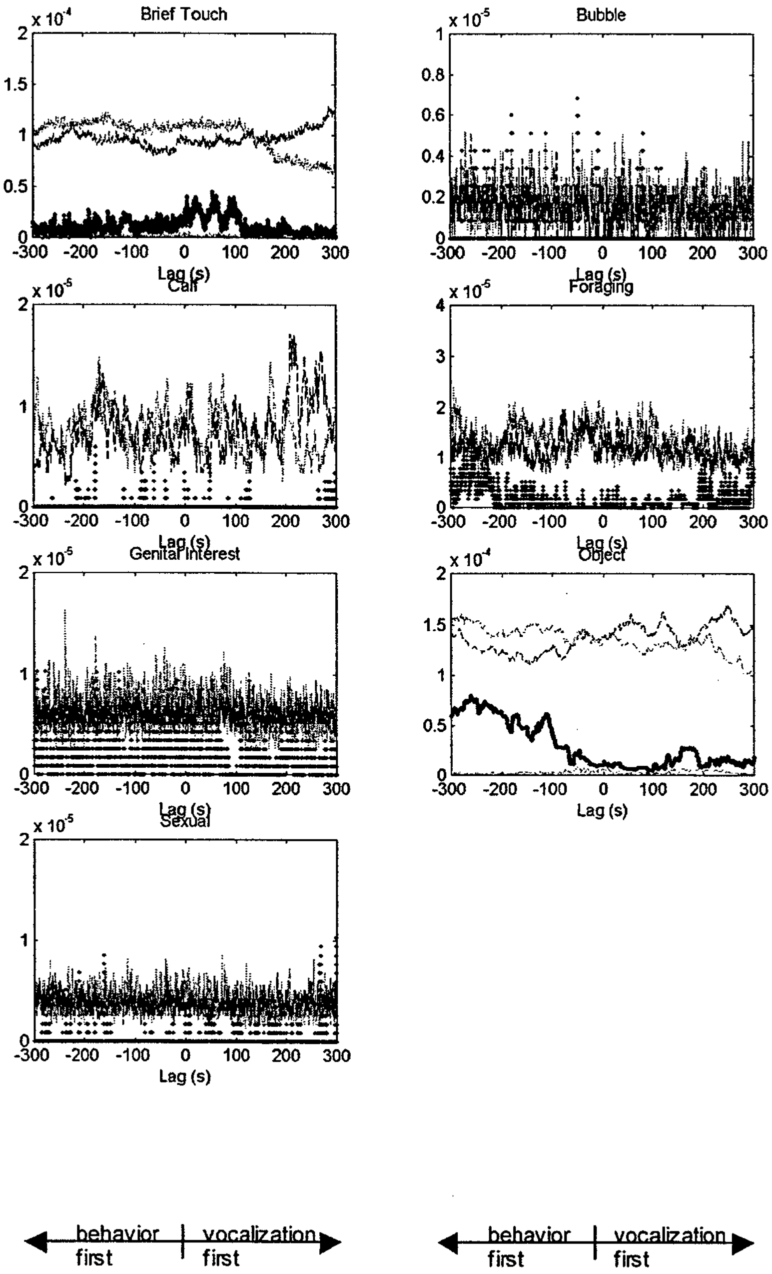
In Fig. 3.17 (a), the wider peaks around 0 for the agonistic-aggressive and agonistic-submissive behaviors may indicate a longer-term association of pulsed vocalizations and behavior, whereas the narrower peak (Fig. 3.17 (b)) around 0 for the sexual behavior may indicate a shorter term association.



(a)

Figure 3. 18 Cross-correlations for lags of ± 5 min (± 300 s) of the BP Type I time series with the behavior time series for each behavior type.

Note: The dark dotted line is the cross-correlation of the observed data. The lighter dashed lines are the 95% indicator levels from the stochastic resampling. Correlations below the lower pairs of lines are in the bottom 2.5 % of the data from stochastic resampling. Correlations above the higher pairs of lines are in the bottom 2.5 % of the data.



(b)

Figure 3. 18 Cross-correlations for lags of ± 5 min (± 300 s) of the BP Type I time series with the behavior time series for each behavior type.

Note: The dark dotted line is the cross-correlation of the observed data. The lighter dashed lines are the 95% indicator levels from the stochastic resampling. Correlations below the lower pairs of lines are in the bottom 2.5 % of the data from stochastic resampling. Correlations above the higher pairs of lines are in the bottom 2.5 % of the data.

The peaks around 0 for the agonistic behaviors are fairly narrow (Fig. 3.18(a)) for the cross-correlation of the BP I time series. This probably indicates a tighter correlation in time between BP type I parameter vocalizations and agonistic behaviors than between the other vocalization types and agonistic behaviors.

3.3.7 Caveat on exploratory analysis:

Results from analyses in this chapter which repeatedly use the same statistical test or 95% threshold on a different subset of data should be regarded as exploratory, not confirmatory analyses. Tukey in his book on exploratory data analysis (Tukey 1977) emphasizes the importance of exploratory analysis and its use for extracting new insights that can then be confirmed. Most of the analyses in this chapter are exploratory. Foremost are the conditional analyses of association of vocalizations with different behavior types, and the cross-correlation analyses of the acoustic parameter time series with the behavior time series. The chi-squared test associated with the conditional probability analyses was repeated for each behavior type. The thresholds from stochastic resampling are 95% thresholds that are used for comparison against each time lag in the cross-correlation. The Kolmogorov-Smirnov analysis associated with the cross-correlation analyses was repeated for each behavior type. Use of repeated testing does not invalidate the analyses, but the results should not be regarded as final confirmation. Specific analyses in this chapter which are confirmatory and not exploratory, are the analysis of association of vocalizations with any behavior type (first conditional probability analysis), and analyses of vocalization types during affiliative-state and agonistic interactions.

3.4 Discussion:

3.4.1 General association of vocalizations with behaviors

In general, the frequency of occurrence of all vocalizations in the lagoon is greater than expected in the 10 s time window around the onset of behaviors by the focal dolphin. It is not clear whether these vocalizations are from all the dolphins in the lagoon or primarily from the focal (or dolphins interacting with the focal). The question of whether these vocalizations were emitted by the focal dolphin or a dolphin interacting with the focal will be addressed in Chapter 4. Does this pattern of occurrence of vocalizations in the 10 s time window around the onset of behaviors by the focal dolphin hold for all types of behavior? To address this question, we first look at vocalization usage during two major types of interactions, affiliative states and agonistic interactions.

3.4.2 Vocalizations during Affiliative states vs. Agonistic interactions:

The number of vocalizations of all types is significantly greater than expected during agonistic interactions, but significantly less than expected during affiliative states (Tables 3.7 and 3.8). Agonistic interactions tend to be composed of high-energy behaviors, while affiliative states usually consist of two or more dolphins swimming calmly around the pool. If vocalization rate in the lagoon is related to the energy level in the interaction, or to the arousal level of the interactants, this would yield the obtained result of more vocalizations during agonistic interactions and fewer during affiliative states.

3.4.3 Conditional probability analyses:

The conditional probability of all vocalization types occurring within 10 s of any behavior was greater than normal. This means that in general vocalizations tended to occur within 10 s of when the focal animal produces a behavior that observers could see. When this is narrowed down by behavior type, we see that most behavior types tended to be associated with an increase in vocalizations (Fig. 3.9). The exceptions were brief rub and abrupt-solitary behaviors, which were actually associated with fewer vocalizations. Foraging and object behaviors were not associated with either an increase or decrease in vocalizations. For the affiliative state it should be kept in mind that the slight, though significant, increase in conditional probability of occurrence of vocalizations is in relation to the 20 s window around the start of the behavior, not to the entire duration of the affiliative state. This slight increase in conditional probability of occurrence of vocalizations in relation to the onset of the affiliative state should therefore be considered to be related to the start of swim-togethers or rest-togethers, or to reunions.

The conditional probabilities of a tonal vocalization occurring within ± 10 s of the start of the behavior were greater than expected for agonistic behaviors, sexual behaviors, genital interest behaviors, the brief touches, and abrupt-unknown behaviors (Fig. 3.10). Although it might have been expected that tonal vocalizations would occur more often within ± 10 s of the onset of affiliative behaviors, this was not the case. It is possible that vocalizations in general are more strongly associated with intense behaviors and interactions. This would lead to all vocalization types being strongly associated with agonistic behaviors and other intense behaviors. From Figures 3.10 to 3.12, this appears to be the case. Tonal vocalizations occurred less often within ± 10 s of the onset of foraging behaviors. This might be expected as tonal vocalizations are not thought to be heavily involved with foraging, in contrast to echolocation signals.

The conditional probabilities of pulsed vocalizations occurring within ± 10 s of the behavior were different than expected for all of the behavior types with the exception of object-oriented behaviors and genital interest behaviors (Fig. 3.11). As we expect that pulsed calls will include a variety of social signals as well as echolocation signals, this is not too surprising. Echolocation may be associated with social behaviors if the dolphin is using sonar to locate another dolphin. Pulsed calls were not associated with abrupt-solitary and brief rub behaviors. As abrupt-solitary behaviors would not be expected to involve echolocation or social signals, and the dolphin may often have its head out of the water, this lack of association might be expected. The result that pulsed calls occur more often within ± 10 s of the onset of an affiliative state, but not of brief rub behaviors (often event behaviors) is interesting. It is possible that if a dolphin wishes to enter an affiliative state with another dolphin, it may use echolocation to target or detect the other dolphin. In the case of a swim together, the two dolphins might be separated across the lagoon. By contrast, rubs generally occur during a swim together, when both dolphins are probably aware of the location of the other, and thus there would be no need for echolocation to locate each other.

Object-oriented behaviors often involved a hula hoop on some portion of the dolphin's anatomy. This is an activity that would likely not require echolocation or social interaction. However, the lack of echolocation or socially related vocalizations in association with genital interest behaviors suggests that the genital interest behaviors are associated with visual rather than acoustic inspection. Future research focusing on the relation of pulsed vocalizations to snout-to-genital behaviors might address this question.

BP type I vocalizations had an increased probability of occurring within ± 10 s of the agonistic behaviors and affiliative-state (but not brief rub) behaviors (Fig. 3.12). Thus it appears that BP type I vocalizations tended to be associated with agonistic behaviors. The conditional probability of BP type I vocalizations was highest for agonistic-submissive behaviors. It is possible that this could be due to BP type I sounds being used as submissive signals in the deciding or de-escalation phases of agonistic interactions. To answer this question, we would need to know the identity of the vocalizing dolphin and whether it was the focal dolphin, as well as the dolphin's role (if any) in the interaction. It is likely that many agonistic interactions will include both aggressive and submissive behaviors, and quite possibly agonistic-unknown behaviors as well, as shown in Table 3.4.1 (Appendix 3.4).

BP Type I calls also had an increased probability of occurring within ± 10 s of brief touch and abrupt-unknown behaviors (Fig. 3.12). The abrupt-unknown behaviors included breach, chuff, porpoise, flipper slap, and quick swim. The brief touch behaviors included casual touch and snout-to-body behaviors.

The conditional probability of BP type I vocalizations was also higher than expected for within 10 s of the onset of an affiliative state (Fig. 3.12). This contrasts with the result from Table 3.7 showing that the number of BP type I calls was less than expected during the entire affiliative state. However this result was not above the 95 % indicator threshold. The difference likely stems from the fact that one analysis counted vocalizations within a ±10 s window around the start of the affiliative state, and the other analysis counted vocalizations during the entire affiliative state. The result that the number of BP type I vocalizations was greater than expected in a ±10 s window around the start of the affiliative state, and less than expected during the entire affiliative state suggests that BP type I vocalizations may be occurring right before, but not during the affiliate state.

It is possible that BP type I vocalizations associated with agonistic interactions being performed by animals might cause other animals (such as a mother-calf pair) to join a swim together. In order to test this hypothesis, identity of the vocalizer would need to be known.

From these conditional probability figures (Figs 3.9 – 3.12), it appears difficult to discriminate agonistic, and abrupt-unknown behaviors by the parameter types; they appear to be associated with all of the parameter types. It is also possible that the (± 10 s) time window, parameter quantization step, or other factor may have contributed to the above difficulty. The affiliative and sexual behaviors are also not well delineated by parameter type. As mentioned above, this might be due to increased vocalizing within the entire group during the occurrence of intense behaviors. By contrast, foraging behaviors appear to segregate well by parameter type. Tonal vocalizations have a less than expected probability of occurring within ± 10 s of foraging behaviors. By contrast, pulsed calls have a greater than expected probability of occurring within ± 10 s of foraging behaviors. It is evident that there is not enough detail in these data to segregate social behaviors by parameter type. This is to be expected if one cannot determine that the signal came from the focal animal. To discriminate in more detail the relationship between behavior types and vocalizations types, it is necessary to identify the vocalizer. Then specific vocalizations can be linked to their specific behavior contexts to develop functional categories of vocalizations.

3.4.4 Cross-correlation analyses:

The correlation results for ± 30 s lags are shown in Figs. 3.13 to 3.15. While the 95 % indicator lines are plotted on these figures, it is important to consider the shape of the cross-correlation as well. Peaks in very peaky cross-correlations are more likely to be flukes than more smooth peaks. Smoother peaks probably reflect a higher underlying sample size leading to that peak. In addition, as mentioned earlier, it should be remembered that the narrower the peak, the tighter the correlation is in time, the broader the peak, the less consistent the correlation is in time.

The sample sizes for bubble, calf, and abrupt-social behaviors were very small, and the correlation plots are included only for completeness. No conclusions should be drawn from these three plot sets. The 95 % thresholds from the two stochastic resampling variations do not appear to vary greatly, so the discussion of the two sets of results will be combined.

Tonal parameter:

The cross-correlation of the tonal parameter with the abrupt-unknown behaviors is very peaky and should be interpreted with care (Fig. 3.13 (a)). The cross-correlation for the affiliative events (brief rubs) shows a possibly significant peak at around eight seconds. This means that the tonal vocalization occurred first, then the affiliative event. In this case, it is possible that a whistle may solicit a rubbing behavior. If identity of the vocalizer were known, it might prove fruitful to look at which animal whistles, and which animal gives the rub. Peaks in the cross correlations for the agonistic-aggressive and agonistic-submissive plots are of longer duration, and may reflect an overall association of tonal vocalizations with the entire agonistic interaction rather than with specific behaviors. The cross-correlation for the foraging behaviors shows a peak near 30 s. Upon further exploration of the data, this peak appears to arise from one prolonged foraging event on one day, and appeared not to occur during other periods of foraging.

Pulsed signals:

The cross-correlation for the abrupt-unknown behaviors with pulsed signals shows two separate peaks, one around zero, and one at a little under 20 s (Fig. 3.14 (a)). The abrupt-unknown behaviors include quick swims, breaches, and porpoises, all of which may be associated with agonism. All of the agonistic behavior correlations s show peaks above the upper 95 % indicator levels, with the aggressive and submissive behavior correlations possibly showing peaks around zero. The peaks in the agonistic behavior cross-correlation plots might suggest a close link between these agonistic event behaviors and pulsed vocalizations. The cross-correlation for the foraging behaviors shows a definitive peak around zero. This suggests that pulsed vocalizations often occur at the same time as foraging behaviors. As the pulsed signals include echolocation signals, this is consistent with the use of echolocation for foraging. The cross-correlation for sexual behaviors appears to increase before zero, and peak around 15 s. This peak at 15 s suggests the occurrence of the pulsed vocalizations first, with sexual behaviors occurring within 15 s afterwards. The role of pulsed signals in sexual behavior is not well known, although Caldwell *et al.* (Caldwell and Caldwell 1967) did suggest that several types of burst-pulsed signals might play a role in sexual behavior.

BP Type I signals:

The cross correlations for the agonistic behaviors all have peaks in the region of 0 lag (Fig. 15 (a)). This suggests a close linkage in time of BP type I vocalizations to agonistic behaviors. This may indicate that BP type I vocalizations and agonism tend to occur the same time.

In general for the cross-correlation results for < 30 s, we observe the same trend as for the conditional probability results, with agonistic behaviors being associated with all of the vocalization types, but foraging only being associated with pulsed calls. Pulsed calls comprise echolocation clicks as well as social signals. This method cannot delineate between the two; the question remains of how this would be done. As the interclick interval between echolocation clicks has been demonstrated to vary with the distance between the dolphin and the target (Au 2000), one would need to know details about the location of the dolphin and the spatial relationship between the dolphin and objects and other animals in its environment. A high-resolution acoustic localization and video system would provide these details. In addition, the interclick interval would need to be explored more explicitly as a vocalization parameter (Amundin 1991).

An important question to consider is why the results from the conditional probability analyses and the cross-correlation analyses differ in some respects. First, they are performed over different sets of time lags. The conditional probability analysis takes into account the entire ± 10 s time window, while the cross-correlation considers more precise timing over a ± 30 s time window. The conditional probability analysis will blur the ± 10 s time window into one result which may be easy to interpret, but which may obscure more precise timing. The cross-correlation yields a time lag-dependent set of results, which can be very powerful in linking precise timing of vocalizations to behaviors, but can also be more difficult to interpret.

The Kolmogorov-Smirnov analysis yielded only a few results which exceeded 95 %

indicator levels (Table 3.11). The distributions of the cross-correlations of the time series of tonal parameters with the time series of agonistic aggressive behaviors and agonistic-submissive behaviors were different from predicted. In addition, the distributions of the cross-correlations of the time series of pulsed parameters with the time series of object-oriented behaviors and abrupt-solitary behaviors were different from predicted. However, as can be seen from the cross-correlation plots, the whistle results showed a positive association with agonistic-aggressive and agonistic-submissive behaviors, while the pulsed call results showed a negative association with object-oriented behaviors and abrupt-solitary behaviors.

Inspecting the results that did not exceed 95 % indicator levels, but which did exceed 80 % levels may help in illuminating interesting avenues for future research. The cross-correlation for object-oriented behaviors with whistles was different from expected. From the cross-correlation plots, we see that whistles appear to have a negative association with object-oriented behaviors. The same negative association holds true for the relationship between pulsed signals and affiliative behaviors. However, pulsed calls and agonism, foraging, and sexual behaviors appeared to be positively related. In addition the BP Type I calls appeared to be positively related to both the agonistic-submissive and agonistic-submissive behaviors.

In many respects, the Kolmogorov-Smirnov analyses merely confirm the general results from the other analyses. Agonistic behaviors appeared to be associated with all call types. Other types of behaviors associated with intense interactions also appeared to associated across call types. Pulsed calls appeared to be associated with foraging while none of the others were. Object-oriented behaviors did not appear to be associated with any of the call types.

3.4.5 Correlation results (± 5 min lag):

The cross-correlation results over the longer lags are shown in Figs. 3.16 to 3.18. In this section I will not repeat what has been discussed previously about cross-correlations on time lags less than 30 s but focus on the time period between 30 s and 5 min.

Tonal vocalizations:

There is a peak about 50 s wide around the time lag of 0 in the cross-correlation of affiliative-event behaviors with the time series of tonal vocalizations (Fig. 3.16). The peak is slightly offset towards a positive time lag indicating that the tonal vocalization was more likely to occur before the behavior. Once again, a more in-depth investigation of the relationship of whistles and rubs might prove fruitful.

BP Type I vocalizations:

The cross-correlation of affiliative state behaviors and the BP type I vocalization time series yields a minimum at a time lag of 60 s (Fig. 3.18). This minimum at a positive time lag means that if the BP type I vocalization occurs, the affiliative state is less likely to happen over the next minute. There also appears to be some underlying periodicity in the cross-correlation of the agonistic-unknown behaviors. This could be due to sampling biases of the observer, or could be due to underlying processes in the agonistic interaction.

Pulsed vocalizations:

The cross-correlations of the pulsed call time series with the agonistic-aggressive and agonistic-submissive behaviors demonstrate a prolonged peak with a width on the order of 200 s roughly centered on the time lag of 0 (Fig. 3.17). This might indicate a general level of arousal for agonistic behaviors on the order of 200 s.

3.4.6 Behavioral categories:

As a final topic of discussion, we should consider the fact that the behavioral categories were chosen subjectively. If they were chosen differently, the analyses in this chapter might lead to different results, both in terms of the conditional probability analyses and the correlation analyses. For instance, if associations of vocalizations exist with some behaviors in a behavioral category, and not from others in the same category, this could obscure the association results which would be clearly seen if the category were properly split. Behaviors could be placed in different categories, or categories could be split or combined. For instance, the brief touch behaviors could be included in the abrupt-social category, or the abrupt-solitary, abrupt-social, and abrupt-unknown categories could be combined into one larger category. Behaviors could also be broken down into contact vs. close proximity behaviors. One way to rearrange the categories would be to determine which behaviors tend to occur close in time to other behaviors, and place these behaviors in the same category. Timing of behaviors in these new categories could then be compared to timing of vocalization types. In addition, if the sample size of some behaviors is sufficiently large, timing of each such behavior could be compared to timing of vocalizations.

In addition, some behavior types might take longer to be noticed and recorded by the observer. For instance, a tail slap is very obvious, and would probably be noticed and recorded immediately, whereas a rub might take a bit longer (on the order of 1 to a few seconds) to be noticed and recorded. This differential recording of behaviors would result in the blurring (widening) of correlation peaks of timing of behaviors and vocalizations.

3.5 Conclusion:

The main result from this chapter is that the probability of vocalizations in the lagoon increased in a ±10 s time window around the onset of behaviors performed by the focal dolphin. The rest of the chapter was devoted to exploring why this occurred. The number of vocalizations was greater than expected during agonistic interactions, and less than expected during affiliative states. Therefore, this increase in vocalization probability may be more specifically associated with agonistic rather than affiliative interactions. The two results just mentioned are the results of confirmatory statistical analyses, and can be regarded as final. The following results should be regarded as exploratory, not confirmatory. From the conditional probability analyses, we see that vocalizations of all types appeared to be associated with agonistic behaviors, but pulsed sounds were primarily associated with foraging behaviors. Pulsed and BP I calls, but not whistles, were weakly associated with affiliative behaviors. From the cross-correlation analyses, we also see most of the trends described above, but with a greater detail of timing. Whistles and pulsed calls appear to be associated with agonistic behaviors over broader time lags, while BP I calls appear to be more tightly linked with agonistic behaviors around a time lag of 0. BP I calls may therefore be directly associated with the specific agonistic behavior, while whistles and pulsed calls may play a more general role within the agonistic interaction.

In conclusion, the methods presented in this chapter yielded useful results for narrowing down interesting questions and potentially fruitful areas of further study. The results were obtained using replicable and almost entirely quantitative methods. However, the methods were not extremely useful for delineating social behaviors by specific parameter types, although this may partially result from analyzing vocalizations from a group with respect to focal behaviors from an individual. The method did demonstrate that foraging was only primarily associated with pulsed calls. Some gradations in differential use of parameter types by social behavior were also suggested, but this was not clearly shown. It was also demonstrated that many more questions could be answered if the identity of the vocalizer were known. Determining the relationship between tonal vocalizations and rubbing, differentiating between burst-pulsed calls and echolocation clicks, and achieving more detail on the relationship between agonism and BP type I calls would all likely be possible if the identity of the vocalizers were known. Examples of how this might be done will be shown in the following chapter.

3.6 Contributions:

Contributions of this chapter to the field include:

I. Quantitative Methods: Used quantitative and replicable methods for parameterizing vocalizations and relating them to observed behavior.
    a. Developed methods for relating vocalization parameters to focal behavior:
        i. Parameterization of vocalizations into tonal and pulsed parameters
        ii. Relating time series of vocalization parameters to time series of behavior
            1. Conditional probability analyses with time window
            2. Cross-correlation analyses
    b. Focus on *quantitative* and *objective* techniques

II. Group vocalization usage during affiliative states and agonistic interactions:
    a. *Fewer* vocalizations of all types (produced by the group in general) occurred during affiliative states (involving the focal) and *more* occurred during agonistic interactions (involving the focal).

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Appendix 3.1 Behavioral Protocol

FUNCTIONALITY OF THE ACOUSTIC REPERTOIRE OF THE BOTTLENOSE DOLPHIN: PROTOCOL FOR BEHAVIORAL OBSERVATIONS AT DOLPHINQUEST BERMUDA

September 1999

Purpose: The behavior and vocalizations of the dolphins will be recorded simultaneously to determine the behavioral correlates of vocalizations in the dolphins' repertoire. This protocol is concerned with the recording of visual behavior.

Focal Animal Sampling: Focal animal sampling techniques will be used to record the dolphins' behavior. All dolphins will be sampled, with each dolphin being sampled twice daily if possible. Focal sessions will be 10 minutes per animal, for a total of 20 minutes per animal per observation day.

Subjects:

Dolphin	*Code*	*Date of Birth*	*Sex*
Calf (Nimbus)	C	1999	Male
Bailey	B	1989	Female
Somers	S	May 22, 1998	Male
Caliban	L	March 17, 1993	Female
Cirrus	R	~1974	Female
Dolber	D	~1965	Female
Gibbs	G	~1976	Male
Khyber	K	1992	Male

Observation Order:

The order of observation of the dolphins will be pre-determined and randomized within the morning and afternoon sessions. Each dolphin will be observed once in the morning and once in the afternoon. This randomization will prevent observer bias and bias based upon time of day as well as assuring equal coverage of all the dolphins.

NOTE: Although the protocol currently stipulates morning and afternoon observations, it may be that only one of these is possible due to scheduling at DQ.

Observation Site: The dolphins will be observed from the cliff above the lagoon.

Data Recorded in Each Focal-animal Sample:

Information for each sample:

1. Date and time of observation
2. Focal dolphin
3. Social grouping - dolphins with access to the same pools as the focal
4. Pools available to focal dolphin (codes MN (Main), FH (Far holding), NH (Near holding), MD (Med pool)
5. Observer
6. Visibility (water)- scale of 1 to 10
7. Weather

Amount of Sun	Amount of Rain
Sunny	
Partially cloudy	Rain
Mostly cloudy	No Rain
Cloudy	

8. Nearest Low and High Tide
9. Comments about any special circumstances

Data Recorded About the Focal Animal:

1. **Point Sampling:** Record information at one minute intervals
    a) Location of focal (NS, FS, NM, FM, NW, FW) (see map)
    b) Nearest neighbor identity
    c) Nearest neighbor distance
    d) Social Activity
2. **Continuous Sampling:** Record all specified actions/interactions of the focal dolphin

Information Recorded for Each Point Sample:

Social activities:

Details of interactions that occur on-the-interval are annotated in the descriptions of interactions by placing a "*" in the [#] column.

ST **Swim Together**: coordinated swimming of one or more dolphins, usually within 1 m (although may temporarily separate to >1 m) for ≥10 s.

RT **Rest Together:** two or more dolphins stationary (floating, hovering, or lying on pool bottom) within 1 m of each other for ≥ 10 s.

BP **Baby Position:** swimming pattern of mom-calf pair in which the calf is below the mother with its head positioned near the mammary area, must last at least 10 seconds and may include constant or intermittent contact.

FO **Foraging:** any of the behaviors listed under foraging behaviors.

OM **Object Manipulate:** manipulation of objects (not including dolphins) using any part of the anatomy.

SO **Social:** all affiliative, aggressive, sexual, and other behaviors not included in ST, RT, or BP, usually within 1 m. Specify behaviors and participants on-the-interval in the [With] and [Behavior] columns (see behaviors defined on the following pages)

- On-the-interval social interactions may include components that are occurring without break immediately before or after the interval: record all behaviors in sequence including the behavior(s) occurring on-the-interval. E. g. recorded interaction is "B/W >W CH>EE" even though only "W/N EE" occurred on-the-interval.

Swim Patterns with Calf

BP **Baby Position**: calf swims below mom with head positioned near mammary area.

AH **Calf-at-head**: calf swims next to or slightly ahead of mom's head; sometimes with /SW

CI **Circling**: calf swims alone in circles

SL **Slipstreaming**: **ST** but calf rides in mom's pressure wave, little or no fluking by calf except at surfacings (to catch up).

ST **Swim Together**: calf and mom swimming side-by-side, both fluking

SW **Switching**: calf switches back and forth more than 2 times from one side of mom to the other; may be associated with nursing or may be done around her head and dorsal fin.

ZG **Zigzagging**: calf swims alone in zigzags, seemingly without much directional control.

Non-social activities:

These are activities that are not coordinated with anyone else. These activities are typically solitary, but on-the-interval another animal may be within 1 m of the focal.

SS	**Solitary Swim:** movement is not coordinated with swimming pattern of another, although other individual may be nearby.
RE	**Solitary Rest:** float, hover, or rest on bottom with no effort exerted to move forward; no individuals resting within 1m although others may be nearby.
UU	**Unknown:** unknown activity, usually because focal is out of sight.

Social Interactions Recorded Continuously

(1) Affiliative Behaviors:

CR **Contact Rest**: two or more dolphins resting in contact, or intermittent contact, usually with the flipper of one animal touching the side, dorsal fin, or peduncle of the other, usually for ≥ 10 seconds.

CSST **Contact –Swim Position**: swimming side-by-side in contact, or intermittent contact, usually with the pec of one animal touching the side, dorsal fin, or peduncle of another (may or may not have contact).

RB **Gentle Rub:** gentle movement against the body of another, usually body against other's flipper; may be brief or prolonged, alternation or one-way, and may include genital area.

SB Snout-to-Body: gentle touching (or near-touching) or rostrum to other's body, not including genital or face, may be brief of prolonged.

RT Rest Together: two or more dolphins stationary (floating, hovering, or lying on pool bottom) within 1 m of each other for ≥ 10 s.

ST Swim Together: coordinated swimming of 2 or more dolphins, usually within 1 m, (although may temporarily separate to > 1 m) for ≥10 seconds.

CT Casual Touch: brief gentle touching (or near-touching) or brushing against another. Rubs are not included in this.

(2) Aggressive/Submissive Behaviors:

BS Body Slam: abrupt and potentially injurious contact (or near-contact) of side of body or dorsal fin to another.

CH Chase: rapid pursuit of another for ≥ 10 seconds, usually unidirectional and within 1-2 m; may include rapid approach or charge posture.

DW Deep Water: agonistic interaction including circling and/or flailing bodies or tails; use to indicate that some or all interactions are occurring at depth and are not clearly visible.

EE Flee: immediate departure of one dolphin in response to presence of behavior of another; other dolphin must be within 1 m, departure must occur immediately following other's action, and departure distance must be ≥ 1 body-length

FL **Flinch**: abrupt jerking of head or whole body away from another, as immediate response to actions of another.

HI **Hit**: abrupt and potentially injurious contact (or near-contact) of tail to another.

HT **Head Threat**: Threat using the head, with mouth closed; abrupt head-jerk display with closed mouth or body-lunge display at another within 1 m.

MH **Mouth Threat**: Threat using the mouth: a mouth-open, bite, or jaw-clap display at another within 1 m

RA **Ram**: abrupt and potentially injurious contact (or near-contact) or head or rostrum to another.

TS **Tail Slap**: slap water surface with tail once or repeatedly in response to actions of another.

WW **White Water**: agonistic interaction including lots of splashing, circling, and/or flailing bodies or tails; use to indicate that some or all interactions are obscured by churning water.

(2b) Aggressive Behaviors Toward Calf:

FP **Flip or Toss**: abrupt, seemingly dangerous flipping of calf into the air with rostrum.

PI **Pin**: hold calf to bottom.

(3) Explicit Sexual Behaviors:

ER **Erection**: penile erection

IN **Intromission**: insertion of erect penis into genital slit.

MT **Dorsal Mount**: ventral-to-dorsal contact (or near-contact) usually with one animal draped over another.

TR **Thrust**: abrupt and sometimes repeated genital contact (or near-contact) of one animal to another with genital-to-genital contact or orientation.

VM **Ventral Mount**: ventrum-to-ventrum contact (or near-contact) often associated with the thrusting.

(4) Other Sexual Behavior:

BC **Beach**: haul body out of water on to dock or beach in response to another's actions.

BH **Butt Heads**: two animals move rapidly towards each other and ram their heads together.

LP **Lie Passive**: hang limp in water column or on pool bottom in response to behavior of another within 1 m; often animal lies passively on side.

VA **Ventrum Away**: turn ventrum away from another.

VP **Ventrum Present**: present ventrum towards another.

(5) Behaviors associated with nursing:

AT **Attempt to Nurse**: usually takes the form of one or repeated gentle nudges to mom's side, ventrum, or mammary/genital area.

MN **Mammary Nudge**: mom bumps calf with her mammary region.

NU **Actual Nursing**: when calf is 'locked on' to the mammary slit and presumably getting milk; usually indicated by a change in the calf's posture and fluking pattern; use ?NU when you think the calf might be nursing but you are not sure it's on-the-mammary slit.

VA **Ventrum Away**: mom tilts ventrum and mammary region away from the calf's head, not cooperating with calf's attempt to nurse.

VP **Ventrum Present**: mom tilts her ventrum and mammary region towards the calf's head, cooperating with the calf's attempt to nurse.

Other:

BR **Breach**: Animal jumps out of the water to land on its side, usually from a relatively stationary position, often away from another animal. If away from another animal, indicate so. E. g. S/K BR : Somers breaches away from Khyber

BU **Bubble**: Animal releases bubbles from blowhole while blowhole is underwater.

CA **Carry**: mom swims upside-down at the surface, carrying the calf on her ventrum; mom's pecs are held up (to hold calf?), calf flukes rapidly in and out of water.

CF **Chuff**: Rapid and forceful exhalation of air from the blowhole.

PO **Porpoise**: Energetic leap or bow while swimming. Re-entry to water is normally head-first.

PS **Pec Slap**: animal slaps pectoral fin on the water, usually making a loud sound that can be heard in air.

PU **Push:** rostrum or head is used to gently propel or prod another.

SG **Snout-to-Genital**: gentle touching (or near-touching) of rostrum to genital area of another, may be brief of prolonged.

SH **Spy Hop:** head (including eyes) is vertically out of water, with none or little else of the body above the water.

TA **Tail slap (solitary):** Like TS (tail slap) but not directed towards or in response to another animal.

/AB **Abrupt Behavior**: use this code to modify **any** behavior code when a normally-gentle behavior is done abruptly or roughly, e.g. CT/AB, RB/AB.

Non-Social Interactions Recorded Continuously:

Sightability:

IS **In Sight**: Focal animal that was previously out of sight is now in sight (and include behavioral state).

OS **Out of Sight**: 10 s has elapsed since focal animal was last seen.

Foraging Behaviors:

FC **Fish Chase:** dolphin is chasing after a fish

FM **Fish in Mouth:** fish visible in the mouth

JW **Jawing**: little mouth open and close movements not directed at another animal

PW **Pin Wheel**: rapid change of direction not directed at another animal; usually turns greater than 270 degrees while side-swimming.

RO **Root**: tail up, nose down vertical body position, whole body in the water.

SC **Scan:** lateral, back and forth head movement

(9) Behavior with Objects:

GC ***Genital Carry***: dolphin moves objects through water by pushing genitals against object or hooking object onto genitals.

GR ***Genital Rub on Object***: rocking, rubbing and/or thrusting genitals on objects, floor, grates, etc.

OR **Object Rub**: rubbing body on objects, floor, or grates. When predominantly genital areas, use “GR”, genital rub on object.

OP **Object Push**: push object with rostrum or other (non-genital) part of body.

Appendix 3.2

Table 3.2. 1 Summary of Focal Follows

Date	Clarity	Pool	Social	Focal	Comments
10/12/99 12:12:21	6		BKLS	K	
10/12/99 1:36:51 PM	6		BKLS	S	
10/12/99 1:48:53 PM	7		BKLS	B	
10/23/99 2:14:11 PM	3	NH/FH	BCKLRS	B	
10/23/99 2:25:26 PM	5	NH/FH	BKLS	K	
10/23/99 2:36:09 PM	5	NH/FH	BKLS	R	
10/23/99 2:47:28 PM	5	NH/FH	BKLS	L	
10/29/99 8:00:49 AM	6	NH/FH	BCKLRS	L	
10/29/99 8:13:47 AM	6	NH/FH	BCKLRS	R	
10/29/99 8:38:06 AM	6	NH/FH	BCKLRS	S	
10/29/99 8:49:11 AM	6	NH/FH	BCKLRS	K	
10/30/99 8:11:51 AM	7	NH/FH	BCKLRS	K	
10/30/99 8:23:38 AM	7	NH/FH	BCKLRS	B	
10/30/99 8:35:49 AM	7	NH/FH	BCKLRS	L	
10/30/99 8:48:09 AM	5	NH/FH	BCKLRS	R	Animal orienting to people by side of pool
10/30/99 8:59:40 AM	5	NH/FH	BCKLRS	C	Session ended early due to rain
10/30/99 9:17:42 AM	4	NH/FH	BCKLRS	S	People still around
10/31/99 6:55:40 AM	7	NH/FH	BCKLRS	S	
10/31/99 7:06:32 AM	7	NH/FH	BCKLRS	L	Stopped early due to trainers on dock
11/2/99 7:36:10 AM	4	FH	BS	B	BS in FH, CKLR in NH
11/2/99 7:48:50 AM	4	NH	CKLR	C	BS in FH, CKLR in NH
11/2/99 7:59:25 AM	5	NH	CKLR	R	BS in FH, CKLR in NH
11/2/99 8:18:45 AM	6	FH	BS	S	BS in FH, CKLR in NH
11/2/99 8:29:51 AM	6	NH	CKLR	L	BS in FH, CKLR in NH
11/2/99 8:40:43 AM	6	FH	BS	B	BS in FH, CKLR in NH
11/2/99 8:53:29 AM	7	NH	CKLR	R	BS in FH, CKLR in NH
11/2/99 9:04:34 AM	7	FH	BS	S	BS in FH, CKLR in NH
11/5/99 7:16:21 AM	4	NH	CKLR	K	BS in FH, CKLR in NH
11/5/99 7:27:35 AM	3	NH	CKLR	L	BS in FH, CKLR in NH
11/5/99 7:38:48 AM	3	NH	CKLR	C	BS in FH, CKLR in NH
11/5/99 7:51:40 AM	3	FH	BS	B	BS in FH, CKLR in NH
11/5/99 8:02:06 AM	3	FH	BS	S	BS in FH, CKLR in NH
11/5/99 8:22:27 AM	2	NH	CKLR	R	BS in FH, CKLR in NH
11/5/99 8:46:43 AM	3	NH	CKLR	L	BS in FH, CKLR in NH
11/5/99 8:57:28 AM	3	NH	CKLR	C	BS in FH, CKLR in NH

11/5/99 9:08:56 AM	3	FH	BS	B	BS in FH, CKLR in NH
11/10/99 7:43:23 AM	5	NH	CRK	R	BLS in FH, CKR in NH
11/10/99 7:56:03 AM	5	NH	CRK	R	BLS in FH, CKR in NH
11/10/99 8:07:31 AM	4	FH	BSL	L	BLS in FH, CKR in NH
11/10/99 8:20:11 AM	4	NH	CRK	K	BLS in FH, CKR in NH
11/10/99 8:32:02 AM	4	FH	BSL	S	BLS in FH, CKR in NH
11/10/99 8:43:47 AM	3	NH	CRK	C	BLS in FH, CKR in NH
11/10/99 8:58:20 AM	4	FH	BSL	B	BLS in FH, CKR in NH
11/12/99 7:28:21 AM	4	NH	CKLR	C	BS in FH, CKLR in NH
11/12/99 7:41:03 AM	3	NH	CKLR	L	BS in FH, CKLR in NH
11/12/99 7:52:04 AM	3	FH	BS	B	BS in FH, CKLR in NH
11/12/99 8:04:34 AM	3	NH	CKLR	K	BS in FH, CKLR in NH
11/12/99 8:29:17 AM	3	FH	BS	S	BS in FH, CKLR in NH
11/12/99 8:41:03 AM	3	NH	CKLR	R	BS in FH, CKLR in NH
11/12/99 8:51:34 AM	4	FH	BS	S	BS in FH, CKLR in NH
11/12/99 9:02:26 AM	4	FH	BS	B	BS in FH, CKLR in NH
11/15/99 7:27:12 AM	6	NH/FH	BCKLRS	S	
11/15/99 7:38:06 AM	5	NH/FH	BCKLRS	B	
11/15/99 7:48:38 AM	5	NH/FH	BCKLRS	C	
11/15/99 7:59:40 AM	4	NH/FH	BCKLRS	L	
11/15/99 8:11:54 AM	3	NH/FH	BCKLRS	K	
11/15/99 8:26:34 AM	3	NH/FH	BCKLRS	R	
11/15/99 8:38:53 AM	3	NH/FH	BCKLRS	C	
11/18/99 7:31:27 AM	8	NH/FH	BCKLRS	S	
11/18/99 7:43:30 AM	7	NH/FH	BCKLRS	R	
11/18/99 7:55:30 AM	6	NH/FH	BCKLRS	L	
11/18/99 8:06:49 AM	6	NH/FH	BCKLRS	B	
11/18/99 8:22:10 AM	7	NH/FH	BCKLRS	C	
11/18/99 8:33:04 AM	6	NH/FH	BCKLRS	K	
11/18/99 8:45:17 AM	7	NH/FH	BCKLRS	R	
11/19/99 7:17:23 AM	2	NH/FH	BCKLRS	B	
11/19/99 7:28:14 AM	2	NH/FH	BCKLRS	L	
11/19/99 7:39:39 AM	2	NH/FH	BCKLRS	S	
11/19/99 7:50:29 AM	2	NH/FH	BCKLRS	C	
11/19/99 8:10:09 AM	3	NH/FH	BCKLRS	K	
11/19/99 8:20:13 AM	2	NH/FH	BCKLRS	R	
11/19/99 8:30:56 AM	2	NH/FH	BCKLRS	S	
11/19/99 8:41:23 AM	3	NH/FH	BCKLRS	C	
11/22/99 7:22:24 AM	3	NH/FH	BCKLRS	K	
11/22/99 7:33:33 AM	3	NH/FH	BCKLRS	B	
11/22/99 7:43:57 AM	2	NH/FH	BCKLRS	L	
11/22/99 7:55:51 AM	2	NH/FH	BCKLRS	C	

11/22/99 8:14:28 AM	1	NH/FH	BCKLRS	R	
11/22/99 8:25:18 AM	1	NH/FH	BCKLRS	S	
11/22/99 8:36:33 AM	1	NH/FH	BCKLRS	B	Did only 3 min session
11/22/99 8:42:26 AM	1	NH/FH	BCKLRS	B	
11/23/99 7:00:49 AM	3	NH/FH	BCKLRS	S	
11/23/99 7:15:48 AM	2	NH/FH	BCKLRS	L	
11/23/99 7:26:17 AM	2	NH/FH	BCKLRS	R	
11/23/99 7:36:57 AM	2	NH/FH	BCKLRS	K	
11/23/99 7:47:20 AM	2	NH/FH	BCKLRS	C	
11/23/99 8:04:44 AM	1	NH/FH	BCKLRS	B	
11/23/99 8:15:56 AM	1	NH/FH	BCKLRS	B	
11/23/99 8:27:02 AM	1	NH/FH	BCKLRS	S	
11/23/99 8:38:30 AM	1	NH/FH	BCKLRS	L	
11/23/99 8:48:56 AM	1	NH/FH	BCKLRS	R	
11/24/99 7:12:52 AM	2	NH/FH	BCKLRS	C	Sargasso weed present
11/24/99 7:23:14 AM	2	NH/FH	BCKLRS	K	
11/24/99 7:33:37 AM	2	NH/FH	BCKLRS	L	
11/24/99 7:45:46 AM	2	NH/FH	BCKLRS	B	
11/24/99 7:56:33 AM	2	NH/FH	BCKLRS	S	
11/24/99 8:14:46 AM	1	NH/FH	BCKLRS	R	
11/24/99 8:25:17 AM	1	NH/FH	BCKLRS	B	
11/24/99 8:36:26 AM	1	NH/FH	BCKLRS	R	
12/1/99 7:38:12 AM	4	NH/FH	BCKLRS	C	
12/1/99 7:49:22 AM	4	NH/FH	BCKLRS	K	
12/1/99 8:00:28 AM	4	NH/FH	BCKLRS	R	
12/1/99 8:11:17 AM	4	NH/FH	BCKLRS	B	
12/1/99 8:22:13 AM	3	NH/FH	BCKLRS	S	
12/1/99 8:41:14 AM	3	NH/FH	BCKLRS	L	
12/1/99 8:51:46 AM	3	NH/FH	BCKLRS	K	
12/6/99 8:10:48 AM	8	NH	BCKLRS	K	
12/6/99 8:22:06 AM	8	NH	BCKLRS	L	
12/6/99 8:33:02 AM	8	NH	BCKLRS	S	
12/6/99 8:47:06 AM	8	NH	BCKLRS	C	
12/6/99 8:58:53 AM	7	NH	BCKLRS	B	
12/6/99 9:09:25 AM	7	NH	BCKLRS	R	
12/6/99 9:20:35 AM	7	NH	BCKLRS	K	
12/7/99 7:12:49 AM	7	NH/FH	BCKLRS	S	
12/7/99 7:24:07 AM	7	NH/FH	BCKLRS	C	
12/7/99 7:35:28 AM	7	NH/FH	BCKLRS	R	
12/7/99 7:46:18 AM	7	NH/FH	BCKLRS	L	
12/7/99 7:56:44 AM	7	NH/FH	BCKLRS	B	
12/7/99 8:19:47 AM	6	NH/FH	BCKLRS	K	Forgot to set beeps - only have #10

12/7/99 8:30:25 AM	6	NH/FH	BCKLRS	K	
12/7/99 8:44:14 AM	5	NH/FH	BCKLRS	R	
12/7/99 8:54:57 AM	5	NH/FH	BCKLRS	C	
12/7/99 9:06:27 AM	5	NH/FH	BCKLRS	S	
12/7/99 9:12:38 AM	5	NH/FH	BCKLRS	S	
12/9/99 7:09:55 AM	5	NH/FH	BCKLRS	L	
12/9/99 7:20:25 AM	5	NH/FH	BCKLRS	R	
12/9/99 7:30:53 AM	5	NH/FH	BCKLRS	B	
12/9/99 7:41:43 AM	5	NH/FH	BCKLRS	S	
12/9/99 7:52:15 AM	5	NH/FH	BCKLRS	K	
12/9/99 8:10:28 AM	5	NH/FH	BCKLRS	C	
12/9/99 8:20:56 AM	4	NH/FH	BCKLRS	B	
12/9/99 8:32:04 AM	4	NH/FH	BCKLRS	K	
12/9/99 8:42:32 AM	4	NH/FH	BCKLRS	L	
12/9/99 8:52:56 AM	4	NH/FH	BCKLRS	R	
12/9/09 9:05:20 AM	4	NH/FH	BCKLRS	C	
12/10/99 7:12:20 AM	4	NH/FH	BCKLRS	R	
12/10/99 7:23:16 AM	4	NH/FH	BCKLRS	S	
12/10/99 7:33:47 AM	4	NH/FH	BCKLRS	L	May have switched to Cirrus partway through,
12/10/99 7:45:21 AM	4	NH/FH	BCKLRS	B	
12/10/99 7:56:56 AM	4	NH/FH	BCKLRS	C	
12/10/99 8:12:47 AM	4	NH/FH	BCKLRS	K	
12/10/99 8:24:39 AM	4	NH/FH	BCKLRS	S	

Table 3.2. 2 Summary of sample sizes of behavior types stratified by focal animal

Behavioral Type	Bailey	Cirrus	Somers	Calf	Caliban	Khyber
Abrupt-Social	0	0	1	0	0	1
Abrupt-Solitary	83	6	14	1	79	24
Abrupt-Unknown	4	4	21	11	17	27
Affiliative	195	206	165	209	95	62
Affiliative -Event	50	30	32	18	17	11
Agonistic-Aggressive	7	23	43	45	21	142
Agonistic-Submissive	3	11	19	19	3	17
Agonistic-Unknown	2	6	56	23	6	55
Brief Touch	38	48	72	59	23	51
Bubble	1	0	2	0	1	3
Calf	4	1	1	1	0	0
Foraging	5	0	17	2	20	57
Genital Interest	9	20	16	12	4	11
Object	4	0	5	0	12	13
Sexual	0	16	1	12	0	0

Appendix 3.3

The percentage of time (in terms of interaction time) that vocalizations were used in agonistic interactions involving different types of agonistic behaviors was calculated for each vocalization type. The percentages are in terms of the total interaction time (of that specific combination of agonism) that vocalizations were present.

Table 3.3. 1 Use of vocalization types stratified by type of agonism involved in the interaction

Aggressive	Submissive	Unknown	Percent of Time of a Vocalization Type		
			Tonal (%)	Pulsed (%)	BPI (%)
X	?	?	2.9	3.6	0.8
?	**X**	?	3.6	6.6	1.6
?	?	**X**	3.5	4.5	0.6
X	**X**	?	3.6	7.0	2.2
X	?	**X**	4.4	4.8	0.7
?	**X**	**X**	4.8	5.9	0.6
X	**X**	**X**	5.1	3.7	0.9
X	O	O	1.4	1.3	0.5
O	**X**	O	0.7	3.0	1.1
O	O	**X**	2.2	3.6	0.6

Note: Percentage is in terms amount of the time of the agonistic interaction that the vocalization was present. ? indicates that the interaction may or may not have included that behavior type. O indicates that the interaction did not include that behavior type.

Table 3.3.1 shows the percentage of each vocalization type broken down by the agonistic interactions involving different types of agonistic behaviors. The percentages are in terms of total amount of time of occurrence of each vocalization type during any type of agonism. In the first 6 rows (with ?'s) the interaction inclusively includes that agonism type (possibly along with others). In the last three rows, the interaction exclusively includes that agonism type. For instance, in the first row, a tonal vocalization was present 2.9% of the time in an agonistic interaction that involved an aggressive behavior (and may or may not have involved a submissive or agonistic-unknown behavior). In the last row, a tonal vocalization was present 2.2% of the time in an interaction that involved only aggressive and no other agonistic behaviors.

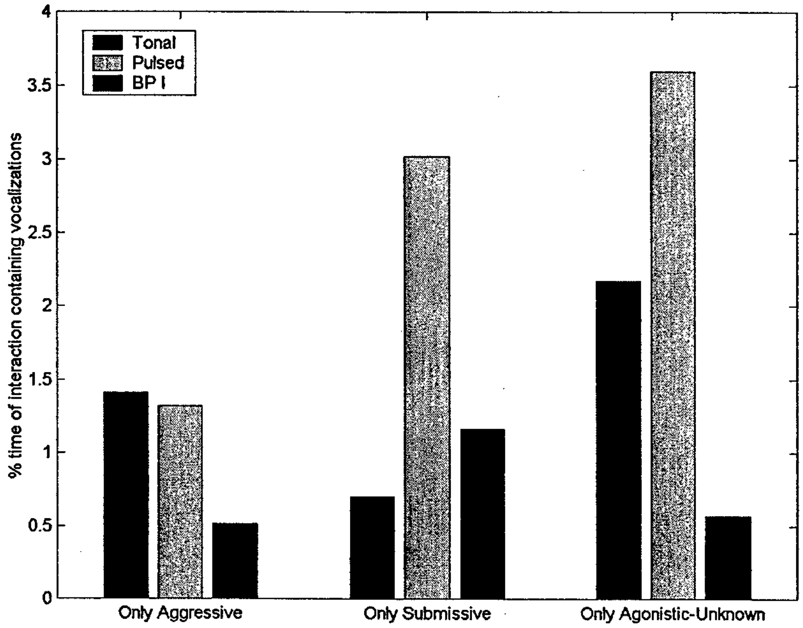

Figure 3.3. 1 Percent of time of the agonistic interaction during which the vocalization type was present

The bar plot in Fig. 3.3.1 shows the data from the last 3 rows in Table 3.3.1. These are the data where the agonistic interactions contain exclusively aggression, exclusively submission, or exclusively agonistic-unknown behaviors. That is, the aggressive interactions used in Fig. 3.3.1 are agonistic interactions that involved *only* aggressive behaviors and no submissive or unknown behaviors. As agonistic-unknown behaviors are probably a combination of aggressive and submissive behaviors (see Appendix 3.4), the focus of this plot should be on the aggressive and submissive categories.

What is of interest is the difference in usage of vocalization types across the agonism types. For instance, it appears as though pulsed calls may be used more often in interactions containing only submissive behaviors than those containing only aggressive behaviors.

Appendix 3.4

3.4.1 Relating behavioral events (methods):

Components of Agonistic interactions:

Agonistic interactions are composed of aggressive and submissive interactions. For purposes of this study an additional category, "agonistic-unknown" was also defined for times when the animals were engaged in an agonistic interaction, but the observer could not see clearly what was going on (see Appendix 3.1). For this analysis, an agonistic interaction was defined to be a series (1 or more) of agonistic behaviors where each behavior occurred within 10 s of another. The 10 s chain rule was used to allow relation of this method to following methods where 20 s windows (± 10 s) were used. The number of agonistic interactions containing (at least) each type of agonism were tallied, and presented as the percent of total agonistic interactions.

3.4.2 Relating behavior events (results)

Components of Agonistic interactions:

If we define an agonistic interaction to be a series (1 or more) of agonistic behaviors that each occurred within 10 s of another (chain rule), we get 239 separate interactions. As shown in Table 3.4.1, about 52% of all the interactions have agonistic aggressive behaviors, 22% have agonistic-submissive behaviors, and 48 % have agonistic-unknown behaviors (note that the first 6 rows are not mutually exclusive). About 6% of all the interactions have both agonistic-aggressive and agonistic-submissive behaviors, about 16% have both agonistic-aggressive and agonistic-unknown behaviors, and about 4 % have both agonistic-submissive behaviors and agonistic-unknown behaviors. About 1 % of the interactions have all three of the types of agonistic behaviors: agonistic-aggressive, agonistic-submissive, and agonistic-unknown behaviors. Thus 44 out of 239 (18.4 %) agonistic interactions have at least two different types of agonistic behaviors. This would contribute to the agonistic behaviors tending to be jointly associated with vocalization types.

Table 3.4.1 Agonistic interactions involving combinations of types of agonism

Aggressive	Submissive	Unknown	Percent of Total Interactions
X	?	?	125/239=**52.3%**
?	**X**	?	53/239 = **22.2%**
?	?	**X**	107/239 = **44.8%**
X	**X**	?	14//239 = **5.9%**
X	?	**X**	24/239=**10.0%**
?	**X**	**X**	10/239 = **4.2%**
X	**X**	**X**	2/239 = **0.8%**
X	O	**X**	87/239 =**36.4%**
O	**X**	O	30/239=**12.6%**
O	O	**X**	72/239=**30.1%**

Note: Percentage is in terms amount of the time of the agonistic interaction that the vocalization was present. ? indicates that the interaction may or may not have included that behavior type. O indicates that the interaction did not include that behavior type.

Appendix 3.5

3.5.1 Relating sound detections (methods)

Call overlap:

The amount of time that call types overlapped as well as the amount of time that call types didn't overlap was calculated. As BP type I calls were a subset of the pulsed call category, all of the BP type I calls overlapped with the pulsed calls.

3.5.2 Relating Sound Detections (results)

Call overlap:

The overlap in time of tonal signals with pulsed calls and BP Type I calls is shown in Table 3.5.1. Note that as BP Type I calls are a subset of pulsed calls, the 100% overlap of BP Type I calls with pulsed signals is not shown.

Table 3.5.1 Overlap in time (s) of signal types

	Tonal Signals	**Pulsed Calls**	**BP Type I calls**
Tonal Signals	--------	274.7 (*232.6*)	22.6 (*31.7*)
Pulsed Calls		--------	267.1
BP Type 1 calls			---------

3.5.3 Autocorrelations of Tonal and BP I parameters:

Autocorrelation of Tonal parameter:

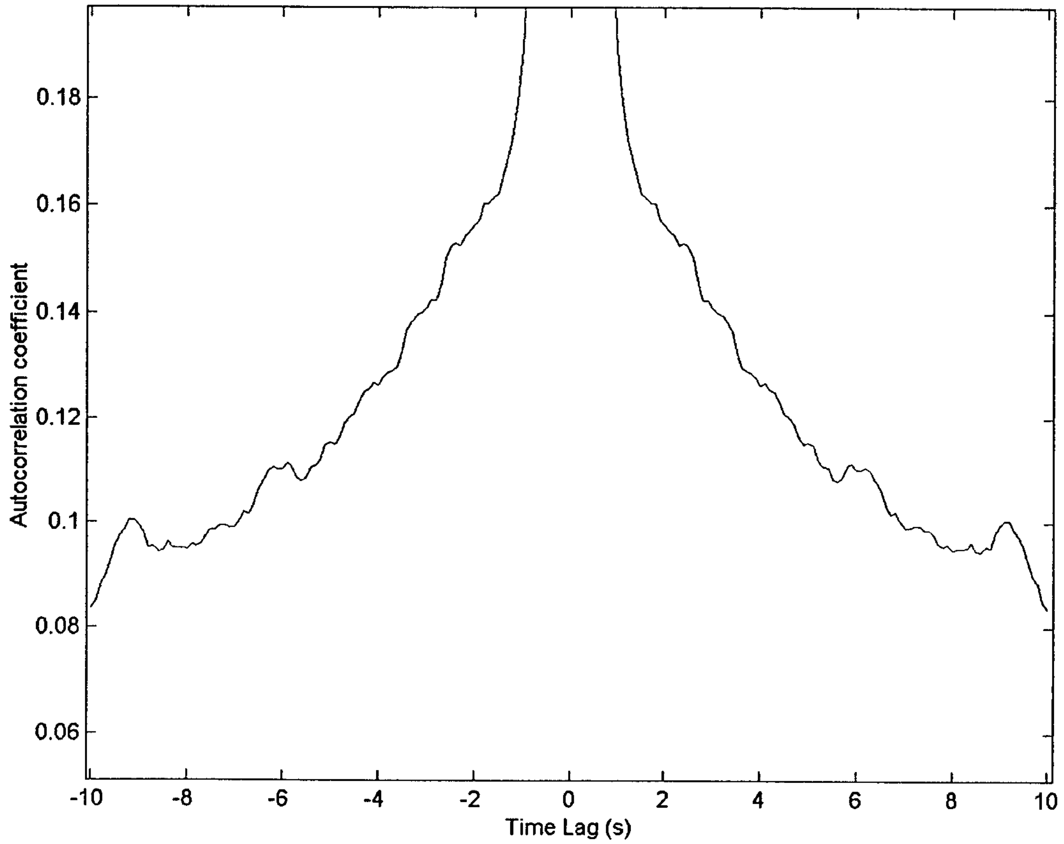

Figure 3.5.1 Autocorrelation of the tonal parameter series

The autocorrelation of the tonal parameter decays slowly from zero, indicating that when there is one whistle, there is likely to have been a whistle around it in time. The lack of sharp side peaks indicates that the neighboring whistle(s) does not always occur at specific time lags.

Autocorrelation of BP I parameter:

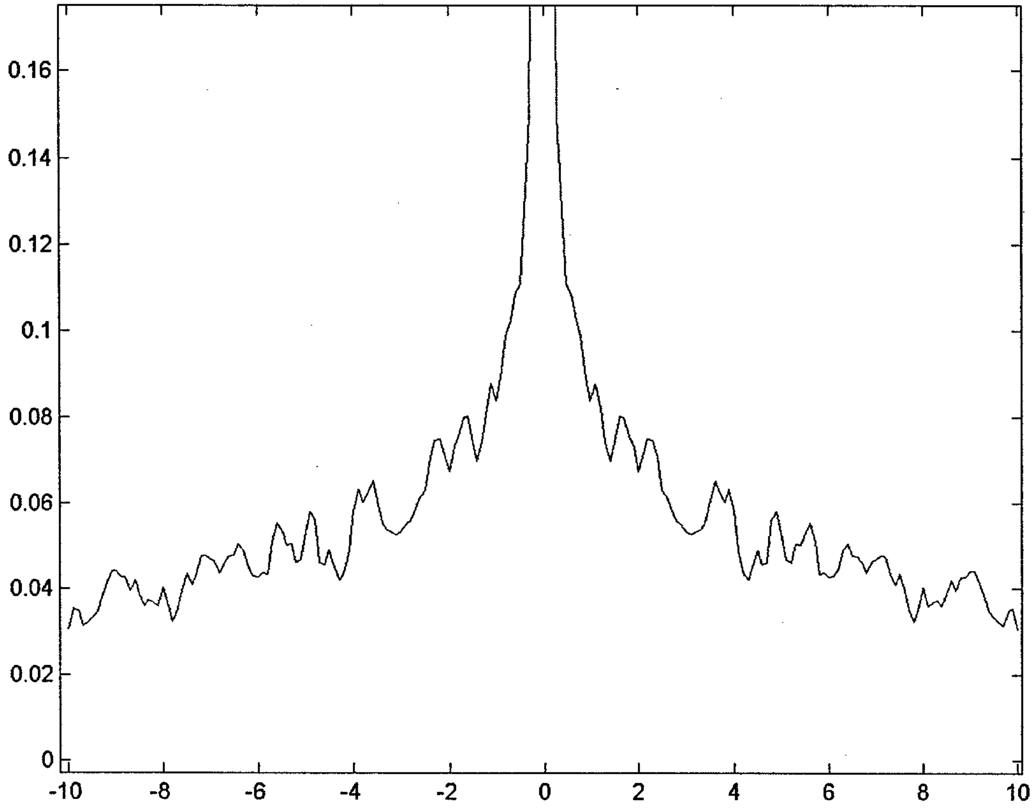

Figure 3.5.2 Autocorrelation of the BP I parameter series

The autocorrelation of the BP I parameter decays fairly sharply in time, indicating that while other BP I calls may tend to occur within a few seconds, the probability falls off sharply with time. There do not appear to be any distinct side peaks indicating that BP I calls do not tend to occur after one another at specific time lags.

Chapter 4: Functional analysis of repertoire elements using linked vocalizations and concurrent agonistic behavior

4.1 Introduction:

4.1.1 Studying the group vs. the interaction

Studies of animal communication often separate communication into several components: the signaler, the signal being transmitted, and the receiver. The signal may be entirely contained in one modality, or may combine several modalities. The critical aspect of the signal is that it transmits information. The research tradition in terrestrial animals historically has differed from that of marine animals in that the signaler in studies of terrestrial animals is usually easy to identify, and observers can use their eyes and ears to associate visual and acoustic displays with individual signalers. Due to low visibility in the ocean, many studies of marine mammal communication have treated acoustic signals as completely separate from elements of social behavior that are visible to observers above water (group size, composition, aerial displays).

As detailed in Chapters 1 and 2, determining identity of the vocalizing animal can be difficult with marine mammals. This makes it particularly difficult to integrate visual and acoustic information at the level of the individual signaler. For this reason, many studies have focused on analyses of vocalizations pooled across the group, and relate these to a measure of group-wide activity. In practice marine mammal researchers often will follow a group of animals, observing visual behaviors, and recording sounds when possible, assuming that recorded sounds come from the group under observation.

A major focus of this thesis was the development of a technique to link visually observed behavior with vocalizations, and to identify which individual produced which visual and acoustic displays. The goal of this method was to enable analysis of specific patterns of signal and response in animals that were interacting. Hinde (1976) argues that the interaction between one or more animals can be thought of as the basic building block for studying social behavior and structure. In this framework, relationships are inferred based upon observations of interactions, and the social structure is inferred from the patterning of relationships. Most work on social behavior among terrestrial animals follows this framework, but following individual interactions can be very difficult for some cetacean species. For this reason, many cetacean researchers follow the "gambit of the group," and assume that individuals who are in the group are interacting with each other (Whitehead *et al.* 2000). Whitehead *et al.* (2000) assert that this assumption may or may not be reasonable depending on whether the groups are spaced further apart than the maximal range of communication.

The "gambit of the group" is often used for cetaceans as the group is often easier to follow than the individual, and the behavior doesn't need to be stratified by individual. Disadvantages of this method were initially described by Altmann (1974) and were detailed by Mann (2000) for cetacean research. One major disadvantage of this approach is that although the group as a whole is being analyzed, each individual animal follows an individual strategy, and uses signals related to that strategy. A group analysis lumps all these strategies together, potentially blurring or obscuring the functional significance of the signals. In addition, the group analysis has little power for studying specific interactions between one signaler and one receiver within the group. The gambit of the group implicitly assumes that the signaler is broadcasting the signal equally to all members of the group, but the Hinde view of the interaction assumes that when an animal signals within a group, it is likely to be directing the display to a particular receiver.

The initial question I addressed in this chapter concerns the question of whether social behavior in captive dolphins can be studied on a group level, or whether it is more appropriate to analyze social behavior in terms of dyadic interactions between animals within a group. I used the localization technique described in Chapter 2 to integrate visual information about displays with data on the vocalizations of particular animals.

4.1.2 Are particular vocalizations used in specific functional contexts of the interaction?

The message being transmitted in an animal's signal could contain a variety of kinds of information, such as internal state of the signaler (e.g. reproductive or hunger state, future intentions) or external information such as availability of food, presence of predators, etc. In order to understand the function of the signal, it is important to know under what context the signal was made. Many studies of communication in wild cetaceans stratify behavior by group activities such as feeding, traveling, resting or socializing (e.g. (Ford 1989)). They then compare the rates of production of different types of vocalization when groups are in different activity states. Sounds produced during feeding might be described as feeding calls (Janik 2000), those produced during social activity might be called social sounds (Silber 1986).

In this chapter, I attempt to study functional contexts of vocalization within the context of specific interactions within a group. One obvious source of information involves the age and sex class of the vocalizer. For example, behavioral ecologists may conclude that if a signal is made by males during the breeding season, it may be a reproductive advertisement display. It is also important to observe who responds to the signal and how they respond. To continue the previous example, observations that females select such a signaling male for mating obviously would strengthen the interpretation that the signal functions for reproductive advertisement. Even better would be experiments that demonstrate that females select a male from other males based upon some acoustic features of the signal.

I have categorized my visual observations of interactions by functional categories such as affiliative, aggressive and sexual behaviors. The standard method for analyzing functional context of vocalizations is a simple cross tabulation of usage by category. The analysis divides vocalizations into whistles, pulsed calls, and BP I calls. A specific behavior type was chosen for in-depth study. Agonistic-submissive behaviors were chosen as the behavioral focus of this chapter for several reasons. Agonistic interactions are better studied than any other kinds of dolphin interaction. Samuels and Gifford (1997) have used focal animal sampling to study changes in agonistic relations in a captive group.

Several results from Chapter 3 also suggest a focus on agonistic interactions. The conditional probability analyses in Chapter 3 showed that vocalizations were very likely to occur within 10 s of a submissive behavior. Sexual behaviors were another candidate for study, but the probability of BP type I calls occurring within 10 seconds of sexual behaviors was not high. The sample size of sexual behaviors was also low (24). With a larger sample size (66), and a strong association for each call type, the results in Chapter 3 indicated that agonistic-submissive behaviors were promising for a more in-depth study of how call types relate to specific behaviors.

The second part of this chapter will analyze whether dolphins use specific call types differently depending upon the nature of the agonistic interaction.

4.1.3 Sequence dependence

Analysis of which signals tend to be made in a particular functional context can help identify the function of a signal, but this kind of analysis is relatively coarse for studying the dynamics of communicative interactions. An important tool for analyzing patterns of signal and response involves analyzing the sequences of signal and response using sequential analyses. An emphasis on analyzing sequences of behavior relates to the idea that interactions may be made up of a series of communicative acts in which one signal may trigger a response in the receiver that provides a new signal to the initial signaler. One of the classic models in ethology of sequential behavior is Tinbergen's description of courtship behavior of the three-spined stickleback, in which he describes a complex interaction as a chain of these stimulus-response pairs (Fig. 4.1) (Tinbergen 1976). In this model, the behavior sequence is deterministic, with one behavior always following another. One behavior serves as a releasing mechanism for the next, so that the "zigzag dance" by the male always leads to courting by the female, etc. While sequences of behavior need not be this well determined to be modeled, sequences of behavior in an interaction may be very important for the outcome of the interaction. Sequential models of interaction suggest that the probability of a signal depends upon the previous signal. If vocalizations serve as an acoustic component of the interaction, we might expect a sequence-dependent usage of vocalizations as well.

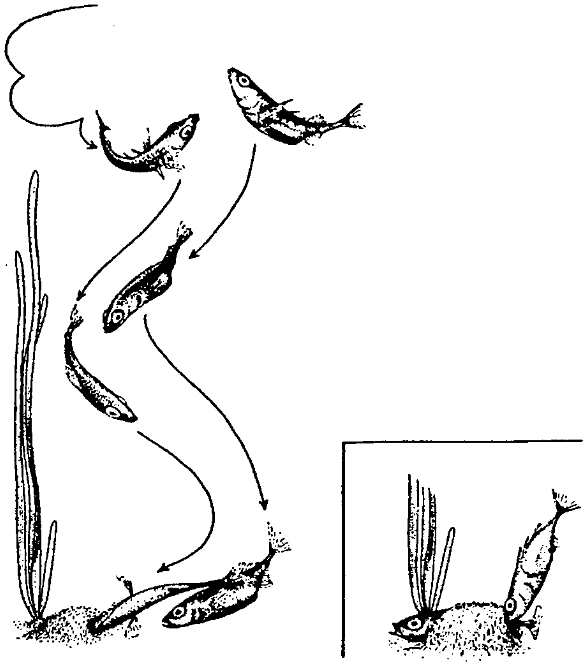

FIG. 47. The mating behaviour of the three-spined stickleback.

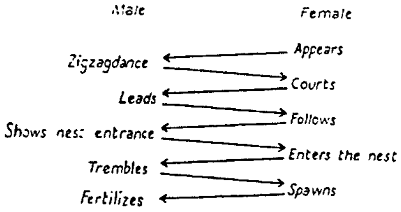

FIG. 48. Schematic representation of the relations between male and female three-spined stickleback. After Tinbergen, 1942.

Figure 4. 1 Tinbergen's model of the sequential nature of three-spined stickleback courtship

In the sequential-assessment model of escalation of agonistic interactions, animals may gradually acquire information about the fighting ability and motivational level of their opponent (Bradbury and Vehrencamp 1998). Each animal may have a "bid" beyond which it will not exceed, but how can it assess whether the "bid" of its rival exceeds its own? One hypothesis as to how animals might achieve this is the "escalation-level" hypothesis. This hypothesis states that variation in signal displays can communicate motivation for different levels of contest escalation (Krebs *et al.* 1981). In species where individual recognition exists, assessing motivational level rather than fighting ability may be the primary goal of the assessment. At each stage of the contest, animals may be able to communicate motivation for escalation and de-escalation using minimal or perhaps even no physical contact.

Bottlenose dolphin agonistic interactions have been hypothesized to follow this model of graded escalation of aggressive behaviors (Overstrom 1983). In the study by Overstrom (1983), jaw-clap behavior was used as an index of aggressive motivation. The sound produced by a jaw-clap is often associated with open mouth threats (Samuels and Gifford 1997). Jaw-clap behavior (aggressive motivation) was associated more often with burst-pulsed emissions than with other sounds, indicating that burst-pulsed sounds may be associated with agonism. Overstrom also found that the intensity of aggressive motivation increased with increasing duration of burst-pulse sounds. Overstrom proposed a model of graded escalation of aggressive behavior involving both visual displays and acoustic cues (Fig.4.2). He suggested that agonistic interactions may start with an initiating dolphin emitting subtle threat cues and pulsed signals. The responding dolphin would return the threat and pulsed sounds. The initiator might then respond with an open mouth threat and burst-pulse sounds. The dolphins would gradually increase the intensity of the interaction, both in terms of visual displays and acoustic signals, trading escalating signals back and forth. However, until further data are available, Overstrom's (1989) model should be viewed more as a hypothesis than a definitive result.

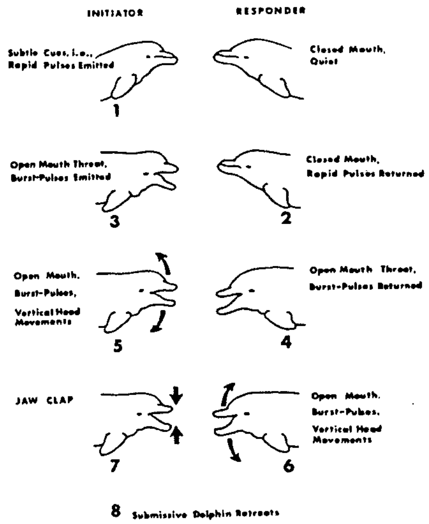

Figure 4. 2 Overstrom's model of graded escalation of aggression

Overstrom's model is similar to Tinbergen's model of stickleback courtship in that it has an inherently sequential nature. In the sections so far, we have not discussed the dependence of vocalizations on the sequential nature of the interaction. The final part of this chapter will explore whether the probability of vocalizations occurring close in time to a particular kind of interaction depends strongly upon the timing of the interaction.

4.2 Group vs. Interaction

The analysis conducted in Chapter 3 tested for relationships between any vocalization recorded in the pool with specific behaviors observed with just one focal animal. This analysis found significantly higher rates of vocalization when the focal animal was engaged in an interaction with one, or occasionally two, other dolphins, particularly when the interactants were engaged in aggressive or sexual behaviors. It is somewhat surprising how strong the association is of timing of lagoon-wide vocalizations with timing of specific behaviors, such as submissive events, since most interactions involved only 2 of 6 dolphins in the pool. For interactions involving two animals, we might expect only a 33% (2 of 6) chance that a vocalizing animal is the focal dolphin or is interacting with the focal dolphin.

One reason that the correlation of vocalizations with focal interactions is surprising is that the focal dolphin was chosen at random, and all dolphins were observed equally often, so there is no reason to expect the focal to be more likely to be involved in interactions than any of the other dolphins in the pool. The frequency of occurrence of these other interactions that may lead to increased vocalizing must also be considered. If these interactions are common, then vocalizations emitted by animals not involved in the interaction with the focal animal may have been emitted by animals that were in another interaction. The probability of any one individual in the lagoon being involved in a social interaction that includes all affiliative, aggressive, sexual, and other behaviors not included in swim-together or rest-together, is 0.09. This is calculated from point sample data, collected at regular one minute intervals during the focal session, and these are appropriate data for calculating activity budgets (Altmann 1974). The times when the focal animal was out of sight were removed from the total as it was not known what the animal was doing. Why not include swim-togethers and rest-togethers with the other social behaviors? The probability of any one animal being involved in a swim-together or rest-together is 0.52. Most of that number comes from the swim-together, as the probability of any one animal being involved in a swim-together is 0.50. From chapter 3, (Table 3.7) it was demonstrated that vocalizations are less frequent than expected during affiliative states (mainly swim-together behaviors). Rest-together behaviors are similar to swim-together behaviors, except that the animals are not moving, and might be expected to show a similar decrease in vocalization rate. As the percent occurrence of rest together behaviors is low (2 %), this is also unlikely to affect the results.

So the probability of occurrence of interactions that may lead to increased vocalizing can be considered to be 0.09. That means at any moment, any one animal in the pool will probably be in an interaction involving increased vocalization 9 % of the time. The probability that two of these interactions will be going on at the same time will be on the order of magnitude of 0.09 x 0.09, which is less than 0.01. This is assuming that the probabilities of there being two separate interactions occurring at the same time are independent. So we can probably assume that when an interaction by the focal animal is occurring, the other animals not in that interaction are unlikely to be engaged in an interaction themselves and can be classified as the acoustic audience, or non-interactants.

The analysis in Chapter 3 did not involve identifying which animal made each vocalization. Therefore we cannot discriminate whether the vocalizations were produced by the interactants and therefore intimately involved in the interaction, or whether the interaction might have stimulated vocalizations from non-interactants. These two situations would lead to very different interpretations of the function of the calls. For instance, whistles were shown to be associated with agonism. What is the role of whistles in agonism? Is the whistle used by one of the animals involved in the agonistic interaction? Or is the whistle made by an animal not involved in the interaction, e.g. as a mother signaling her calf to return to her and distance itself from the interaction? In all these situations, knowing the identity of the vocalizer would at least narrow down the possible functions of the vocalizations.

A basic result from Chapter 3 was that the rate of vocalization was higher than expected in the 10 seconds around agonistic or sexual behaviors. The logic of the "gambit of the group" would suggest that these behaviors signify that the behavioral state of the entire groups has changed, and that the change in vocalizations is associated with this change in group activity pattern. Alternatively, analysis of dyadic interactions would focus just on the interactants, and would assume that the vocalizations were more likely produced by the interactants than by what might be viewed as a passive audience.

The first basic issue to be addressed in this chapter is whether vocalizations associated with an agonistic interaction are more likely than expected to be produced by the interactants.

4.2.1 Are the vocalizations produced during interactions made by the entire group or more specifically by the interactants?

As with Hinde's (1976) framework for studying social structure, the interaction will be used as the basic unit of analysis. Dolphins engaged in agonistic interactions were often less than a body length apart and therefore closer together than the resolution given by the localization/video system. Because of this, vocalizations could usually only be determined to come from one of the interactants, but not from which specific individual. Interactions were usually dyadic, although they were sometimes triadic. For dyadic interactions, 33.3% of the animals in the pool were engaged in the interaction (2 of 6). For triadic interactions, 50% of the animals in the pool were engaged in the interaction (3 of 6). Thus, if vocalization rates are unrelated to participation in the interaction, it would be expected that 33.3% of the vocalizations during dyadic interactions involving the focal animal would come from one of the interactants, and 66.7% from the non-interactants. For triadic interactions, this would be 50% from the interactants and 50% from the non-interactants as well. To determine whether vocalization rates were related to participation in the interaction, it should be determined whether the number of vocalizations emitted by the interactants vs. non-interactants varied from expected for each call type. Therefore, analysis will be performed on each call type used in Chapter 3 (tonal, pulsed, and BP Type I) to determine if the number of calls associated with submissive behaviors that were emitted by one of the animals in the interactions is different than expected.

Test 1: **The number of vocalizations of all types associated with submissive behaviors that were emitted by one of the animals in the interaction vs. emitted by an animal not in the interaction is different than expected.**

If the test shows a negative result, then the increase in vocalization rate associated with the interaction is due to increased vocalizing by all animals in the lagoon, and the gambit of the group may be appropriate, although analyses by individual would likely still prove even more fruitful. If the test shows a positive result, the increase in vocalization rate associated with the interaction is due to increased vocalizing by interactants, and the focus on dyadic interactions is necessary to make sense out of interactions occurring between a few individuals within the group.

General Methods: The times of occurrence of all submissive behaviors (flinches and flees) were determined from the continuous behavior data set described in Chapter 3. A 10 s chain rule as described in Chapter 3 was used to group the submissive behaviors into interactions. I localized vocalizations within a ±10 sec window of the time of occurrence of the submissive behavior of the focal dolphin. The ±10 s time period was selected to match that used in Chapter 3. I did not attempt to localize all vocalizations, as not all vocalizations were suitable for use by the localization algorithm. Localization was not attempted on vocalizations that overlapped with vocalizations that appeared to come from a different dolphin (based upon visual inspection of the time delays), vocalizations that were too faint to show up across a majority of channels, and vocalizations that were excessively contaminated by snapping shrimp clicks.

In general, it requires a longer duration sound cut to localize a whistle than to localize a pulsed sound. This is because pulsed sounds tend to contain broadband energy packed into a short amount of time, while the broadband (frequency modulated) character of whistles that enables localization is realized over a longer period of time. This makes whistles more susceptible to contamination by impulsive noises like snapping shrimp.

Whistles may therefore be more difficult to localize. Therefore, frequencies of occurrence of whistles and pulsed calls should not be compared across categories.

After I selected vocalizations in time and frequency, the vocalizations were localized and overlayed onto the corresponding video clip for viewing. By inspecting the overlayed video clip, I determined for each localized vocalization whether the vocalization appeared to localize to any animal in view in the lagoon. I then determined whether it came from one of the dolphins involved in the agonistic-submissive interaction, from a dolphin apparently not involved in the interaction, or whether it was unclear whether the vocalization came from an interactant or a non-interactant. The latter might be the case if other animals were in close proximity to the interactants but were not directly involved in the interaction. I also classified each cut as a tonal call, pulsed call, or BP Type I call based upon the vocalization types used in Chapter 3. For this analysis, BP Type I calls were not included as pulsed calls, but were taken out as a separate category.

Methods for Test I:

The number of calls in each call type category were summed by functional identity of vocalizer (interactant vs. non-interactant). A chi-squared test (with a Bonferroni correction on the significance level) was performed for each call type to determine whether calls were emitted significantly more often than expected by interactants or non-interactants.

Results for Test I:

40 interactions with submissive behaviors were determined to be of high enough acoustic and behavioral quality (e.g. animal was visible on video) to attempt localization of vocalizations within ± 10 sec of the submissive behavior(s). Of these, 23 interactions contained at least one vocalization that could be localized to an interactant, non-interactant, or "unclear" animal. Results from this analysis are shown in Figure 4.3,

along with the expected number of vocalizations for each vocalization type and interaction involvement. The "unclear" category was not analyzed for significance but was used for later interpretation of the data. A total of 422 localizations were attempted.

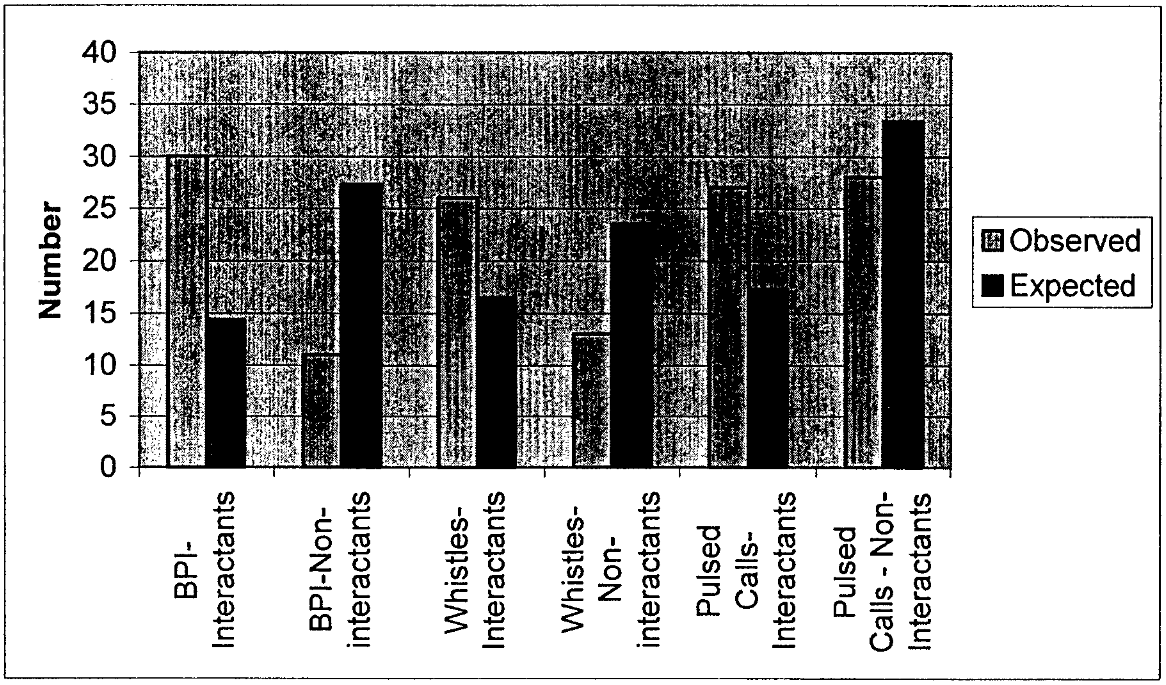

Figure 4. 3 Numbers of observed and expected localizations of call types to interactants and non-interactants

The emission of vocalizations by interactants vs. non-interactants is significantly different than expected for each vocalization type (Fig. 4.3). Whistle emission patterns by interactants and non-interactants were significantly different than expected (p<0.002) (Fig. 4.3). Whistles were emitted more often than expected by interactants and less often than expected by non-interactants. BP Type I emission patterns by interactants and non-interactants were significantly different than expected (p<<0.001). BP Type I calls were emitted more by interactants than non-interactants. Pulsed call emission patterns by interactants and non-interactants were also significantly different than expected, with pulsed calls being emitted more by interactants more often than expected and by non-interactants less often than expected ($p<.015$). (Including Bonferroni adjustments to allow for repeated testing, the p values for all vocalization types are still less than $p= .05/3 = .0167$).

Discussion for Test I:

The positive results from test 1 support the interpretation that the increase in vocalization probability in the context of the agonistic-submissive interaction is due to vocalizing by the interactants. This result suggests that it is important to analyze behavior on the level of the interaction rather than on the level of the group. Although the "gambit of the group" may be appropriate for some situations or species, Hinde's (1976) framework with the interaction as its foundation is more appropriate for bottlenose dolphins in a captive environment.

4.3 Functional contexts of vocalizations

4.3.1 Identification of vocalizer: whistle usage

The localization technique allows me to identify specific sounds produced by dolphins engaged in specific agonistic interactions. These are the kind of observations typically used by behavioral ecologists to identify the functional context of vocalization and therefore to infer the potential function of the call. Identification of the age and sex class of the signaler can often inform analysis of the function of vocalizations. I analyzed which animals made whistles during submissive interactions in order to address this point.

Signature whistles have been shown to play a role in mediating mother-calf reunions, and might serve a role in the context of soliciting support as well. Data from Smolker (Smolker et *al*. 1993) indicated that signature whistles occur when mother-infant pairs are separated, and that the probability of whistles increases during separations. Data also indicate that mothers may not whistle as frequently during separations as infants. Therefore it might be expected that whistles would be produced more often in interactions involving a calf and an adult than in interactions involving only adults. In interactions involving a calf and an adult, the calf is likely to be separated from its mother. Even if the interaction is between the calf and the mother, separations may still occur. During agonistic interactions, which may involve potentially damaging behaviors such as a bite or a body slam, it may be additionally important that the mother and calf stay in acoustic contact.

The number of interactions containing whistles that could be localized to the interactants was compared for calf/adult and adult/adult dyadic interactions. The sample size is low, so statistical analyses were not performed. Thus the hypothesis that whistles are produced more often in calf/adult than adult/adult interactions cannot be disproved using this data set, but the data may indicate potential for further study.

Test 2: **Whistle usage varies by age class, with the number of interactions containing whistles localized to the interactants being higher for calf/adult than for adult/adult dyadic interactions.**

Methods for Test 2:

Whistle usage by interactants in calf/adult vs. adult/adult interactions involving submission were compared. Only dyadic interactions involving submission that were between a calf and an adult, or between an adult and an adult were used. The numbers of interactions containing whistles localized to the interactants were totaled for the calf/adult and adult/adult interactions involving submission. The total number of whistles localized to interactions used in each age/sex class interaction was also determined.

Results of Test 2:

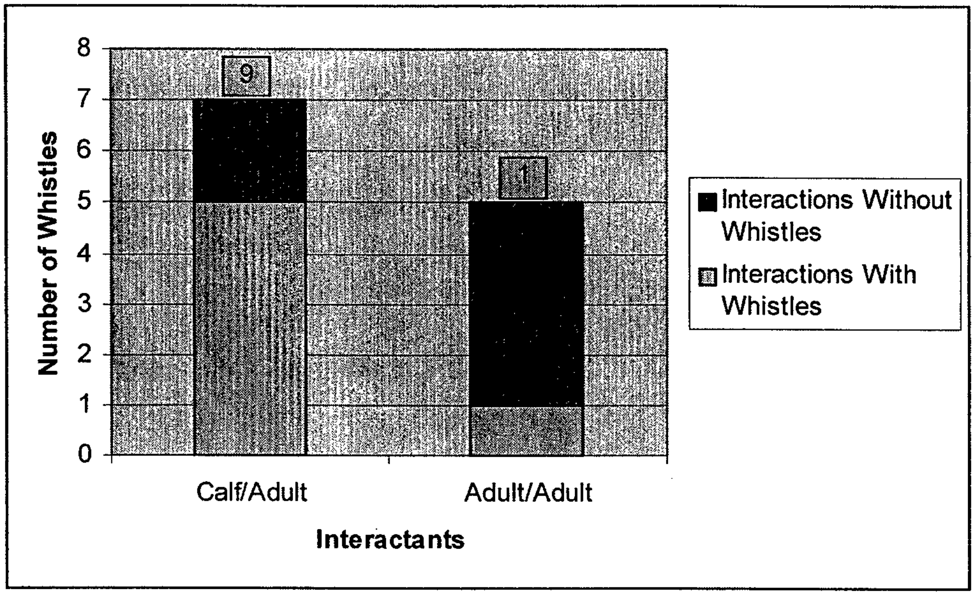

Figure 4. 4 Number of interactions in which whistles did and did not localize to an interactant for calf/adult and adult/adult dyadic interactions.

Note: Only dyadic interactions between a calf (Nimbus or Somers) and an adult or between two adults were considered. The total numbers of whistles used in conjunction with calf/adult and adult/adult interactions are shown above each bar.

Adult-adult interactions:

Of the 5 interactions between only adults, only 1 interaction (Caliban/Khyber) had a whistle localized to an interactant, and then only 1 whistle.

Adult-calf interactions:

Of the 7 interactions between only a calf (Nimbus or Somers) and an adult, 5 of the 7 have whistles localized to one of the interactants (for a total of 9 whistles) (Fig. 4.4). Only in 1 case could the whistle be localized to a specific interactant, and it was Nimbus. The interactions which appeared to have the most whistles localized to the interactant were among Cirrus, her calf Nimbus, and Khyber, but as these were triadic interactions, they were not considered in the analysis. Of the two interactions (involving submission) between a mother and her calf, 1 interaction had no whistles localized to an interactant, and the other interaction had 4.

Discussion for Test 2:

The sample sizes are low, but in general the result that there were more interactions containing whistles in calf/adult interaction than adult/adult interaction appears to support use of whistles by calves either to elicit support or to help keep track of mother or calf locations during interactions. A larger sample size as well as data linking signature whistles to individuals are needed to more fully determine the possible role of whistles is agonistic interactions involving submission.

4.3.2 Context-dependent usage: variation in vocalizations depending upon other agonistic behaviors associated with submission

The initial result from the previous chapter showed a strong association of each of the three vocalization types with submissive behaviors. These associations were seen both in the conditional probability results (Figs. 3.10– 3.12) and in the cross-correlation results (Figs. 3.13 – 3.15). The analysis from the previous section shows that these vocalizations tend to be produced by the interactants. Here I would like to investigate more subtle aspects of the association of vocalizations with agonistic interactions. Vocalization usage with respect to the submissive behavior might be influenced by other behaviors that are themselves linked to submission. As shown in Chapter 3 (Appendix 3.4), different forms of agonistic behaviors often appear together in agonistic interactions. To test whether presence of other agonistic behavior types within the interaction influences vocalization usage, I will test whether or not the vocalization rate varies with the presence of other agonistic behaviors in the interaction.

Test 3: **Does the vocalization rate differ among call types depending on the presence of other agonistic behaviors in the interaction?**

Methods for Test 3:

Interactions involving submission often include both submissive and aggressive behaviors. Appendix 3.4 in Chapter 3 shows that this was also common for this study. To determine whether the presence of other agonistic behaviors in the interaction had an effect on vocalization usage, rates of vocalizations that were localized to the interactants were compared for interactions that had both submissive and aggressive (or agonistic-unknown) behaviors within 10 s of the submissive behavior to interactions that did not have other agonism within 10 s of the submissive behavior. Agonistic-unknown behaviors were high-energy agonistic interactions (white water and deep water) that probably included both aggressive and submissive behaviors. These could not be segregated into aggressive and submissive behaviors because the observer could see some but not all of the specific behaviors in the agonistic interaction. Analyses were performed for each call type, and a Bonferroni correction for the significance level was used with each t-test.

Results for Test 3:

Submissive behaviors often occur in conjunction with aggressive behaviors within an interaction. The rate of BP I vocalizations that were attributed to interactants varied according to whether the interaction contained aggressive behaviors in addition to the submissive behavior (t-test, $p< .0005$; Bonferroni adjustment requires $p<.0166$ for significance) (Fig. 4.5). The rates of tonal and pulsed calls did not vary significantly depending on the additional presence of other agonistic behaviors (t-test, tonal calls, $p = .93$, pulsed calls, $p = .37$). The details of the interactions are in Table 4.1 and are separated by the presence or absence of other agonism. Included are the other behaviors associated with the interaction, separated into time blocks before and after the submissive behavior (see Appendix 3.1 for behavior codes). Non-agonistic behaviors are included in parentheses. Also included are the specific submissive behavior including interactants, whether the interaction was decided or undecided (calculated as in Samuels (1997)), the winner of the interaction (if any) and the number of each call type that localized to the interactants for each interaction.

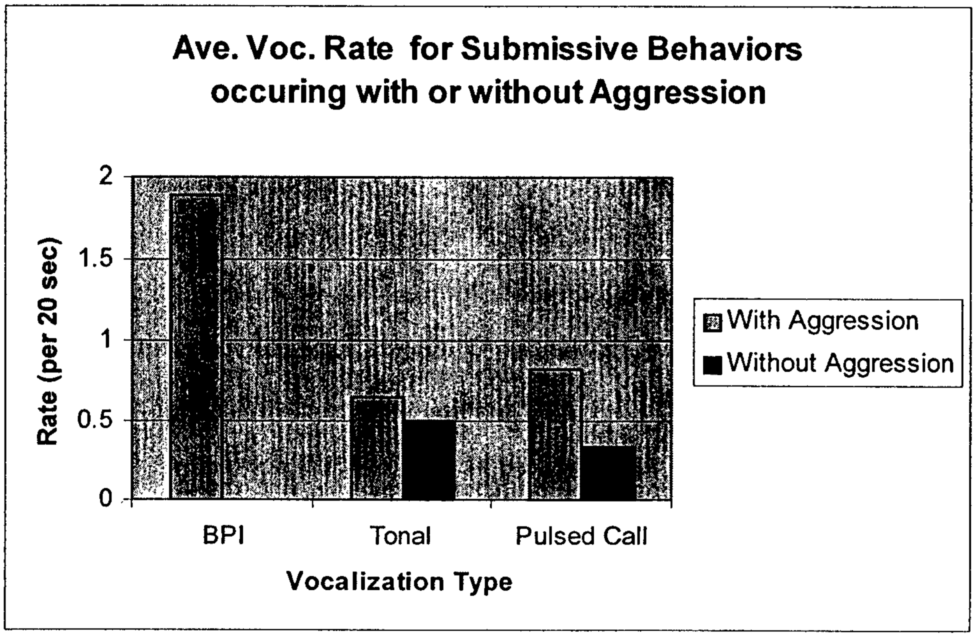

Figure 4. 5 Rate (per 20 s) of vocalizations emitted by an interactant for interactions with and without aggressive behaviors

Note: These results are based upon interactions that contained at least one submissive behavior.

Table 4. 1 Call types from interactants with respect to presence/absence of other agonism in the interaction

Association with other agonism					Who		Winner?	Decided?	Session	Vocalization Type		
-10 s (before submissive behavior)	-20s	In between FL's (or during FE for CK4FE2)	+10s (after submissive behavior)	+20s						*BPI*	*Tonal*	*Pulsed Call*
With other Agonism												
	(CS/ST)		WW		CK		?	D	17C4FL	*3*	*0*	*0*
TS (CT,SB)		TS, (SB)	BS (SG)	(ST)	C|S FL		NA	U	15C5FL0	*5*	*0*	*0*
WW	TS			TH,HI,TS	L|K FL		NA	U	15K6FL	*0*	*1*	*3*
MO	HI,MO		HI	HI,MO	R|K FL		NA	U	11aK4	*3*	*0*	*0*
WW (QS)	HI		WW		S|K FE		NA	?	20S5FE	*3*	*0*	*0*
	AL - Distance threats		AL - mutual RK MO		CR|K FL		NA	?	11bC3	*2*	*0*	*5*
TS,MO,TH, PO(away)		(PO)	DW	(ST)	S|K FL	2	NA	U	18aS1FLs	*0*	*0*	*1*
MO,HI (SB)	MO (CT)		MO (SG)	MO,BI	R|K FL		NA	U	17K1FL	*3*	*0*	*0*
CH,HT	HI,WW			HT	CR|K FE		NA	U	6K4FE3	*0*	*1*	*0*
(SB)	(CV)	DW,TH, (SB,PO)	DW,MO (SB)	MT	S|K FL	1	K	D	18aS1FLs	*0*	*0*	*0*
	(CS/ST)			WW	S|K FL		NA	?	17bS6FL	*5*	*4*	*4*
(SG)		(SB,SG)	HI (SG)		C|R FL		NA	U	19R8FLs	*0*	*0*	*0*
(SB)			CH,WW		S|K FL		NA	?	18aK4FL	*3*	*0*	*0*
(SB)			DW		S|K FL		NA	?	15S1	*1*	*1*	*1*
CH	DW				C|L FL		L	D	15C5	*0*	*0*	*0*
(UU =not sure)	(ST)		WW	WW	CR|K FL		NA	?	6K4FL3	*3*	*4*	*0*
DW,CH	HI	TH,HI,(BU,PO,ST)		(UU=not sure, FL)	CR|K FE		NA	U	6K4FE2	*1*	*0*	*0*
									Total	*32*	*11*	*14*
									Average	*1.8824*	*0.647*	*0.82*

Without other Agonism												
(CT)	TS(SB)		(CT)	(ST)	C|R FL		R	D	15C5FL1	0	0	0
(QS)	(SB)				C|K FL		K	D	20C1FL2	0	0	0
(ST)				(CS/ST,ST)	C|K FE		K	D	20C1FL1 (FE)	0	0	0
(SB,BR)	(SG,ST)				S|R FL	3	R	D	18aS1FLs	0	1	1
					S|L FL		L	D	17L3FL	0	0	0
		(SB)		(ST)	C|R FL,FE		R	D	15R7FL	0	2	1
									Total	0	3	2
									Average	0	0.5	0.33

Discussion for Test 3:

Test 3 is positive; therefore vocalization rate differs among call types depending on the presence of other agonistic behaviors in the interaction, indicating a dependence of vocalization usage on context. Specifically, the rate of BP type I calls attributed to the interactants was significantly different in interactions that contained other forms of agonism within 10 s vs. those that did not. The rates of tonal and pulsed call types (not including BP type I) were not significantly different. This differential use of call types based upon the presence of other forms of agonism suggests that BP I vocalizations play a different role in agonistic interaction than the other call types. These results agree with findings of Overstrom (1983) in suggesting that burst-pulse vocalizations are a signal specifically associated with aggressive behaviors.

4.4 Sequence dependence

The association of BP I calls within 10 s of an interaction containing both aggressive and submissive components suggests that this call is more likely to function in this kind of interaction than the other calls, but this analysis does little to tease apart the fine grained patterns of signal and response that may make up these interactions. If signals actually tend to elicit a response from an interactant, then one would expect a specific order in which the signal comes before the reaction. The previous analysis lumped 10 s before and 10 s after into one 20 s window. This loses the ability of investigating order effects.

This final section of the chapter uses techniques of sequential analysis to investigate these more subtle and fine grained aspects of communicative interactions.

4.4.1 Does sequence affect vocalization usage, or are vocalizations merely context-dependent?

Calculation of vocalization rates before and after the submissive behavior will be the primary method of evaluating this question, and cross-correlation and lag sequential analyses will be used to aid interpretation of these results.

Test 4: **The rate of vocalizations (per ± 10 s window) emitted by the interactants associated with submissive behaviors is as expected (the same before and after the behavior.)**

Methods for Test 4:

For instances when only one submissive behavior was performed within 20 s, the "before" period was the 10 s period before the submissive behavior, and the "after" period was the 10 s period after the submissive behavior. For instances where the focal animal performed submissive behaviors less than 20 seconds apart, the "before" period was the 10 s period before the first submissive behavior, and the "after" period was the 10 s period after the last submissive behavior. The number of each vocalization type was summed for before and after periods. The analysis was performed over all call types. A chi-squared test was used to determine significance.

Results for Test 4:

A total of 178 localizations were attempted before the (first) submissive behavior, and 159 were attempted after the (last) submissive behavior. The number of vocalizations over all call types that localized to an interactant before the submissive behavior was significantly less than the number of vocalizations that localized to an interactant after the submissive behavior (Fig. 4.6), (p = .04).

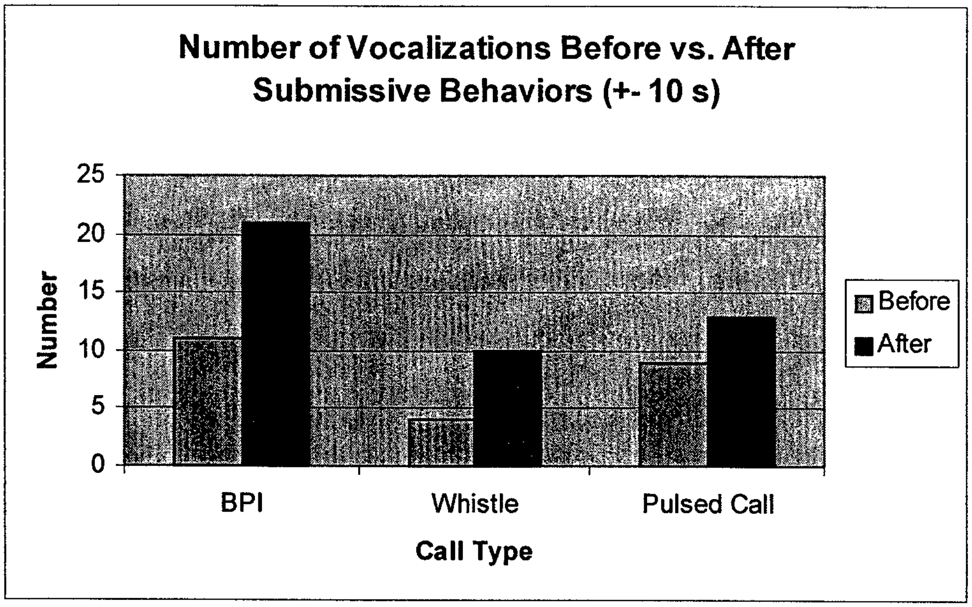

Figure 4. 6 Numbers of vocalizations (within ± 10 s of submissive behaviors) that occurred before vs. after the submissive behavior

If vocalization rates change with the presence of other agonism in the agonistic interaction, the cross-correlation function may aid in interpreting why. The aggressive behavior time series is used alone without the agonistic-unknown behavior time series as the agonistic-unknown behaviors are specifically a catch-all definition for when the observer cannot clearly see the agonistic interaction due to roiled water, etc.

Cross-correlation methods:

As introduced in chapter 3, cross-correlation techniques can illuminate the time dependencies between two time series. An introduction to this method was provided in van Hooff's review (1982) of methods in analyzing sequences of behavior, although van Hoof describes Heiligenberg's (1973) use of this method for studying interindividual dependencies of social behavior in male zebra fish as "unconventional." Although this method has great potential for use in analysis of time-dependent behavior series, it has received little use. The cross-correlation function can show whether or not the aggressive and behavior time series are tightly linked, and at what time lags associations occur. In the present study the continuous follows of behavior were transformed into a binary time series as described in Chapter 3. Standard cross-correlations and auto-correlations of the behavior time series were performed (MathWorks 1984-1999).

Cross-correlation results:

The cross-correlation of the aggressive and submissive behavior time series is shown in Fig. 4.7. Lags to the right of 0 indicate that the submissive behavior happened before the aggressive behavior. Lags to the left of 0 indicate that the aggressive behavior happened first. There is a strong peak at a time lag of 0, which indicates that aggressive and submissive behaviors tend to occur together at the same time. The set of peaks around zero seems skewed to the left, which indicates that there may be a tendency for a submissive behavior to occur after aggressive behaviors, although this is by no means deterministic. It should also be kept in mind that correlation does not imply cause and effect.

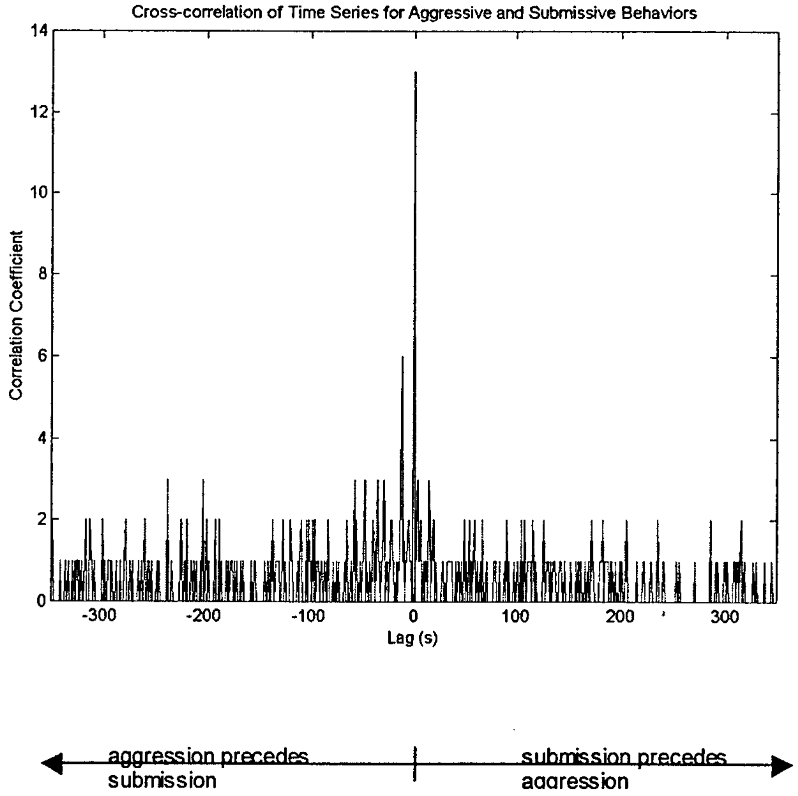

Figure 4. 7 Cross-correlation of the aggressive and submissive behavior time series

Lag sequential methods:

Lag sequential analysis was also used to look at the relation in timing of submissive behaviors to affiliative-state (mainly swim-together) behaviors to look for possibilities of vocalizations mediating reunions or eliciting support. Lag sequential analysis calculates transition probabilities over longer time periods than one transition. Lag sequential analyses are fairly widely used and are described in van Hoof (1982) and Bakeman and Gottman (1997). If vocalizations are used to solicit support, then we might expect an increase in the probability of the individual being in a affiliative-state behavior (swim together) after the agonistic interaction.

The conditional probability that the focal animal would be in an affiliative-state behavior at time lag t given that it has just completed a submissive behavior was calculated for time lags t = -90 to 90 seconds.

Lag sequential analysis results:

Lags to the left of 0 indicate that the affiliative-state behavior would have occurred before the submissive behavior. Lags to the right of 0 indicate that the affiliative-state behavior would have occurred after the submissive behavior.

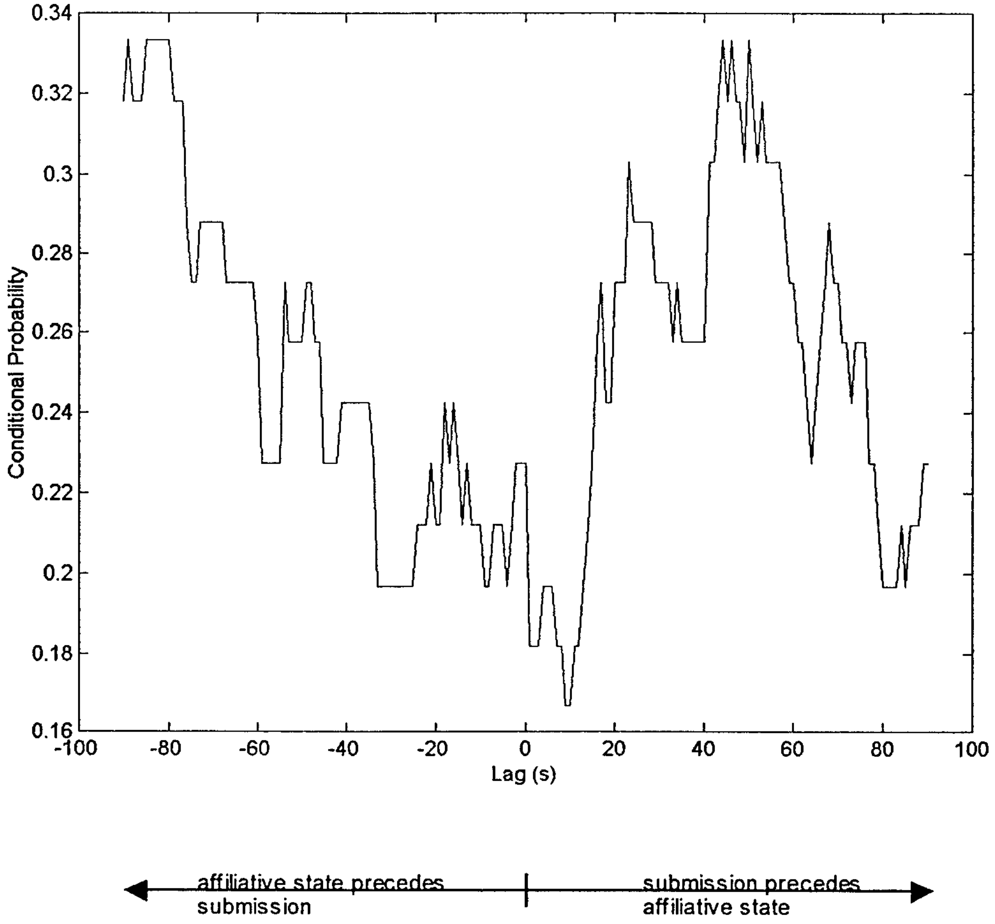

Figure 4. 8 Lag-sequential analysis of the occurrence of being in an affiliative-state (swim together) behavior in relation to submissive behaviors.

There are two major peaks in the plot (Fig. 4.8), one at about -90 s, and one at about +45 s. There is a minimum around a time lag of 0 seconds, which indicates that submissive behaviors and affiliative-state behaviors tend not to co-occur. The peak at -90 s, with the gradual slope to 0, indicates that animals leave an affiliative state up to 90 s before the submissive behavior occurs in the agonistic interaction. The peak at 45 s, with a sub-peak around 20 s, indicates that an individual tends to return to an affiliative-state behavior by around 20 s after the submissive behavior in the agonistic interaction, and if it is going to return will probably have done so by 45 s. Since the only agonistic interactions considered involved the focal, the dolphin engaged in the affiliative state is necessarily one of the dolphins involved in the agonistic interaction.

Test 4 Discussion:

Test 4 shows that number of vocalizations emitted by interactants across all vocalization types before vs. after the submissive behavior is significantly different than expected, with more vocalizations being emitted after the submissive behavior than before. This supports the hypothesis that vocalization usage varies with sequence in the interaction. The question remains as to why interactants would emit more vocalizations after the submissive behavior than before.

We should first consider that this may be related to biases inherent in the localization and identification process, rather than resulting from behavioral processes. Many vocalizations were deemed unsuitable for localization, and of those that were deemed suitable, many of these could not be identified as coming from an animal in view on the video image. Therefore many vocalizations coming from both the interactants and non-interactants were not used for this analysis. If there were a bias between which vocalizations could and could not be used for analysis, this might have biased the results.

One possible reason for the result that more vocalizations were found to the emitted by the interactants after than before the submissive behavior might be that more localizations were attempted on vocalizations occurring after than before the submissive behavior. However, the column showing "attempted locs" in Table 4.1.1 (see Appendix 4.1) shows that this is not the case, and in actuality 159 vocalizations were attempted after submissive behaviors vs. 178 before.

Another possibility that the results might stem from biases inherent in the localization process is that conditions might have been better for localization after the submissive behavior than before. This might occur if animals were closer together before the submissive behavior and further apart afterwards, allowing more vocalizations to be localized to the interactants before than after. If this were so, we would expect that there would be fewer “unclear” localizations after the behavior, and more “non-interactant” localizations after the behavior. In actuality, there were 19 “unclear” localizations before compared to 24 after, and 25 “non-interactant” localizations before, compared to 15 after.

So the data do not support this possibility either. Another possibility is that the animals in the lagoon tended not to overlap their vocalizations as much after the submissive behavior, or fewer animals were vocalizing after the submissive behavior. This might occur if the non-interacting animals were listening to the interactants or were waiting for calls eliciting support or for victory/loser calls. This possibility is more difficult to test. Yet another possibility related to call overlap might be that overlapping of calls is used to target the interactant, or as an aggressive display as in birds (Dabelsteen *et al.* 1997). This might be used more often in the beginning stages of an interaction. Since overlapping calls are more difficult to localize, there might appear to be fewer calls from the interactants in earlier stages of the interaction. All of the above possibilities are somehow related to biases in the localization process, although they may be related to behavioral processes as well. The following possibilities are more closely tied to the behavioral interaction.

As mentioned before, it is possible that vocalizations are used as a victory call or as a "badge of status" (Rohwer 1975, 1982) call after the interaction is decided. Unfortunately, the sample size of decided and undecided interactions is too low to determine this if other factors are to be taken into account. One confounding factor is that interactions with only submissive behaviors are more likely to be decided, and interactions with only submissive behaviors tend to have fewer BP type I vocalizations (Fig.4.4). For example, the data set contained only 1 undecided agonistic interaction that did not contain aggressive or agonistic-unknown behaviors.

In addition, since the submissive behaviors scored in this study, flinches and flees, often occur both before and after other aggressive behaviors, the vocalizations may be related to the aggressive behaviors (or other behaviors) occurring immediately afterwards. (In contrast to possible expectations, flinches and flees do not appear to signal the end of an agonistic interaction, as is usually expected for a signal of submission). There is also the possibility of these vocalizations being related to behaviors that occur minutes later. There are also reasons specific to each call type which may have led to the result of more vocalizations being produced by the interactants after the behavior than before.

If BP type I calls function in de-escalation of the agonistic interaction, they might be used more frequently in the latter stages of the interaction. In order to determine this, we would need a larger sample size of vocalizations from the interactants related to each specific stage of the interaction. Individuals might be more likely to call for support, possibly using signature whistles, after the submissive behavior if agonism is still occurring and de-escalation has not occurred. Identification of signature whistles, and the age/sex classes (e.g. mother/calf) of the animals in the interaction might help determine the feasibility of the possibility.

The results from the cross-correlation and lag sequential analysis shed interesting light on some of these possibilities. The skewed peak at negative time lags in the cross-correlation of the aggressive and submissive time series may indicate that even though aggressive behaviors do sometimes occur after submissive behaviors, there may be a tendency for submissive behaviors to occur after aggressive behaviors, and thus possibly signal de-escalation of the interaction. Therefore the increase in vocalization rate after the submissive behavior may be partially associated with de-escalation. It would be very useful to know which animal in the interaction produced which vocalization, but the resolution of the current system generally did not allow for this discrimination.

The lag sequential analysis shows that individuals tend not to perform submissive behaviors while in an affiliative state. It also shows that animals may tend to leave an affiliative state up to 90 s before the submissive behavior. If individuals return to an affiliative state after the agonistic interaction, they will tend to have done so within 20 - 45 s. This may have implications for use of vocalizations to solicit support or to elicit a reunion.

4.5 Summary:

The results from all models and the whistle usage study are summarized and discussed below. Separating results by both presence of other agonistic behaviors as well as by before and after the submissive behavior yields sample sizes too low for each category, so statistical analyses were not performed. The plots are for purposes of synthesis of the data analysis models only.

4.5.1 Results:

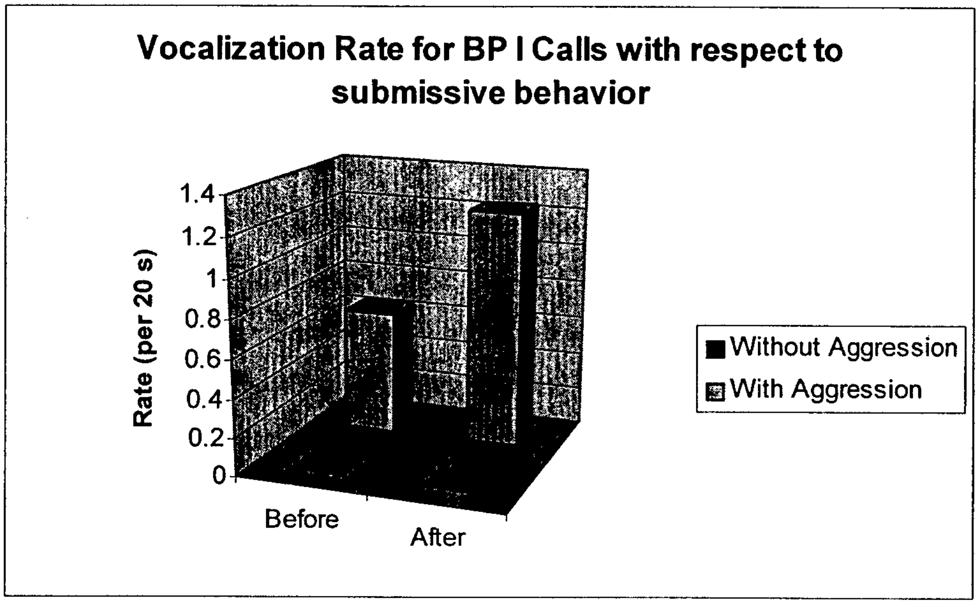

Figure 4. 9 Rate (per 20 sec) of BP I calls emitted by an interactant for interactions with and without aggressive behaviors

Note: These results are based upon interactions that contained at least one submissive behavior), both before and after the submissive behavior.

BP I calls: For submissive behaviors without aggression, the rate of BP type I calls by the interactants was low before and after the submissive behavior (Fig. 4.9). The number of BP I calls was greater in interactions containing aggression in addition to submission. For submissive behaviors with aggression, the rate of BP I calls was higher after the submissive behavior than before.

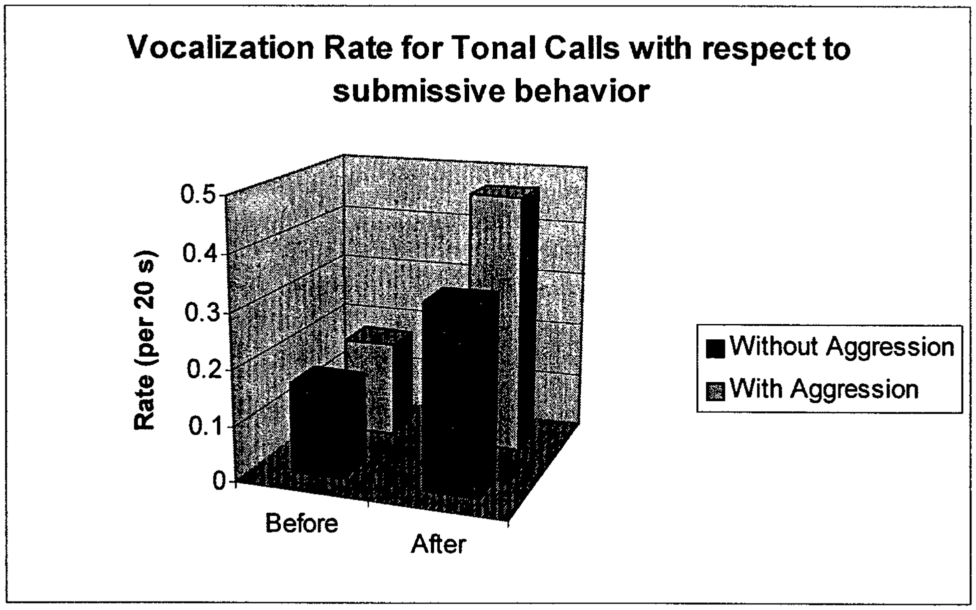

Figure 4. 10 Rate (per 20 sec) of tonal calls emitted by an interactant for interactions with and without aggressive behaviors

Note: These results are based upon interactions that contained at least one submissive behavior), both before and after the submissive behavior.

Tonal calls: Vocalization rates for tonal calls were similar whether the interaction contained aggressive behaviors or not, and more tonal calls occurred after the submissive behavior regardless of the presence of aggressive behaviors in the interaction (Fig. 4.10).

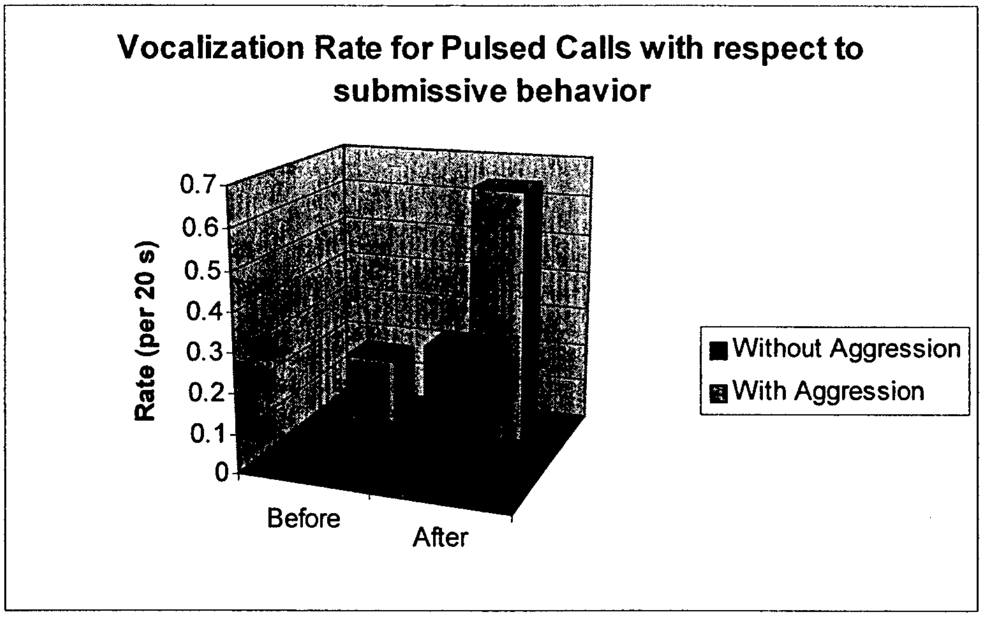

Figure 4. 11 Rate (per 20 sec) of pulsed calls emitted by an interactant for interactions with and without aggressive behaviors

Note: These results are based upon interactions that contained at least one submissive behavior), both before and after the submissive behavior.

Pulsed Calls: The trend in vocalization rates for pulsed calls was that there were more vocalizations when the interaction contained aggressive behaviors (Fig. 4.11), and more vocalizations after the submissive behavior than before.

4.5.2 Discussion:

Test 1 shows that the overall level of all call types during an interaction containing submission increased due to vocalizing by the interactants. Therefore using the "gambit of the group" to study captive bottlenose dolphins is not appropriate, and studies of vocalization function should focus on the level of the interaction, although subsequent analyses indicate that the level of the individual is also important. The general increase in vocalization number might have been due to arousal from the intensity of interaction. However, from the results from tests 3 and 4, contextual and sequential factors are probably also at work. If arousal were the only factor affecting call rate, we might expect a uniform increase in all call types in all contexts. However, the difference in call rates between BP Type I calls vs. whistles and pulsed calls during interactions with aggressive and agonistic-unknown behaviors contradicts this. We should thus also look to factors associated with each call type to explain the increase in vocalizing.

It should also be kept in mind that most of these interactions involved a calf (Somers or Nimbus) and may not follow the normal rules for agonistic interactions among adults. This may actually help explain the results from the lag sequential analysis showing that dolphins tend to be in an affiliative state (swim together) both before (90 s) and after (45 s) a submissive event. Nimbus and Somers were a in a swim-together with another dolphin 79% (Nimbus) and 60% (Somers) of the time they were in sight. Therefore, it may be that for the two calves, being in a swim-together was their normal routine, and the agonistic interaction was the aberration in their routine.

It should also be noted that most (16 of 23) of the agonistic interactions involved Khyber, the juvenile male. The agonistic interactions studied may not reflect typical adult interactions, but may be more indicative of agonistic interactions among juveniles and may also be idiosyncratic due to the involvement of the same dolphin in most of the agonistic interactions. In addition, since the adult male was removed from the social group shortly before the beginning of this study, any discipline that an adult male might have provided was absent for this study. Therefore, these results should be interpreted and generalized with caution.

The association of BP I calls with agonistic interactions containing aggressive and agonistic-unknown behaviors, but not submissive behaviors, is striking, although not surprising. Burst-pulsed calls have been previously shown to be associated with agonistic interactions involving aggression. As mentioned earlier, Overstrom (1983) showed that production and duration of burst-pulsed calls increased with the level of aggressive motivation, quantified as jaw-clap production.

More vocalizations in general were produced by the interactants after the submissive behavior than before. If BP I calls are produced in the later stages of agonistic interactions, they may be used in the de-escalation of the agonistic interaction.

Alternatively, they may be used in specific contexts in relation to timing of aggressive behaviors. To determine this, more data are needed linking BP Type I calls to timing of agonistic interactions involving aggression. These could be obtained by looking at all agonistic interactions in the data set, not just those containing submission. More data might need to be collected to attain a suitable sample size. A larger sample size of vocalizations could also be obtained if the localization method were improved to achieve better resolution, or if overlapping vocalizations could be vocalized. In this way, more vocalizations could be identified to individual. If vocalizations from the interactants could be obtained at each stage of the agonistic interaction, the vocalizations could then be related to their specific function in escalation and de-escalation of agonism.

Whistles, unlike BP Type I calls, may not be specifically associated with aggression but more with submission, as whistle rate was not significantly different among interactions containing vs. not containing other forms of agonism. The possibility that signature whistles may function in reunions or soliciting support appears to be supported by the preliminary results that whistles are used more often in calf/adult than adult/adult interactions. The mothers of both calves were in the lagoon, and signature whistles have been shown to mediate reunions of mothers and calves (Smolker et *al.* 1993). The increase in conditional probability of being in an affiliative state after the submissive behavior also supports the possibility of whistles mediating reunions or solicitation of support after the agonistic interaction. To determine the possible role of whistles in reunions after agonistic interactions, a larger sample size would be needed. In addition, data on approaches and leaves of one dolphin to another would be helpful, including which animal initiates the approach or leave towards which animal, as well as timing of the approach or leave in relation to other behaviors.

The role of pulsed calls may be more complicated, with social burst-pulsed calls possibly playing a role in the submissive interaction, and rates of echolocation by the interactants increasing in the context of the interaction. Splitting the pulsed calls into more categories might help resolve this issue.

4.6 Contributions:

Contributions of this chapter to the field include:

Group vs. Interactant Analysis: For this setting, analysis of group vocalizations in relation to focal animal behavior was not appropriate, rather a focus on vocalizations from interactants (or individuals) was more appropriate.

I. Vocalizations were made more often than expected by interactants, and less by non-interactants (in relation to agonistic interactions)
II. Vocalization usage varied with respect to other behaviors in the interaction
III. BP I calls were used more often when interactions involved aggression and submission rather than just submission.
IV. When analyzing vocalization usage with respect to (agonistic) behavioral interactions, sequence in the interaction matters.
V. More vocalizations of all types were produced by the interactants after a submissive behavior than before

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Appendix 4.1:

Table 4.1.1 Timing of vocalizations with relation to submissive behavior

		Before							After							Total
		BPI	*Whistle*	*Pulsed Call*	To Non-Interactant	Unclear	Attempted BPI total	Attempted locs	*BPI*	*Whistle*	*Pulsed Call*	To Non-Interactant	Unclear	Attempted BPI total	Attempted locs	Attempted Locs
	From:															
	20S5FE	*1*	*0*	*0*		0	16	17	*2*	*0*	*0*			10	8	25
	20C1FL2	*0*	*0*	*0*		5		11	*0*	*0*	*0*		1		0	11
	20C1FL1	*0*	*0*	*0*	8			12	*0*	*0*	*0*				5	17
	19R8FLs	*0*	*0*	*0*				13	*0*	*0*	*0*				1	31
	18aK4FL	2	*0*	*0*			2	5	*1*	*0*	*0*			9	9	14
1	18aS1FLs	*0*	*0*	*0*	1			3	*0*	*0*	*0*				5	12
2	18aS1FLs	*0*	*0*	*0*	3			6	*0*	*0*	*1*				2	16
3	18aS1FLs	*0*	*1*	*0*	5			6	*0*	*0*	*1*	5			10	16
	17bS6FL	*0*	2	*1*			1	4	5	2	3			7	15	19
	17C4FL	*0*	*0*	*0*			6	8	3	*0*	*0*			14	17	15
	17L3FL	*0*	*0*	*0*				5	*0*	*0*	*0*	1			2	7
	17K1FL	3	*0*	*0*		4	15	16	*0*	*0*	*0*		4	4	5	21
	15S1	*1*	*1*	*1*	3		3	13	*0*	*0*	*0*		1	1	2	15
	15C5	*0*	*0*	*0*	1	2	1	6	*0*	*0*	*0*				1	18

	15C5FL0	*1*	*0*	*0*		2	4	5	*4*	*0*	*0*	2	5	14	15	15
	15C5FL1	*0*	*0*	*0*		4	6	12	*0*	*0*	*0*	1	6	7	12	24
	15R7FLa	*0*	*0*	*0*	4		4	9	*0*	*0*	*0*	3		2	5	16
	15R7FLb	*0*	*0*	*6*				9	*0*	*2*	*1*				8	20
	15K6FL	*0*	*0*	*1*				4	*0*	*1*	*2*				5	9
	11aK4	*1*	*0*	*0*			5	6	*2*	*0*	*0*		2	9	12	18
	11bC3	*1*	*0*	*0*			1	2	*1*	*0*	*5*			5	0	2
	6K4FE3	*0*	*0*	*0*				1	*0*	*1*	*0*	3			6	14
	6K4FL3	*0*	*0*	*0*			1	1	*3*	*4*	*0*		4	4	18	48
	6K4FE2	*1*	*0*	*0*		2		13	*0*	*0*	*0*		1		1	19
	Total	*11*	*4*	*9*	25	19	65	187	*21*	*10*	*13*	15	24	86	164	422

Chapter 5: Summary and Conclusions

5.1 Summary:

The goal of this thesis was to develop methods to analyze the function of vocalizations of the bottlenose dolphin, *Tursiops truncatus* on the level of the interaction. Past researchers have experienced many impediments in determining the function of elements of the bottlenose dolphin vocal repertoire. These impediments have included difficulty in determining the identity of the vocalizer and lack of a coherent and complete quantitative analysis of the vocal repertoire. Thus this thesis presents methods to address these problems as well as results obtained from these methods. Most of the results are preliminary or exploratory, but they confirm the value of the techniques for resolving long-standing problems.

Chapter 2 demonstrated a method for determining identity of the vocalizing animal in a lagoon. This method combined passive acoustic localization with video sampling to determine which animal vocalized. The resolution of the passive acoustic localization system for an artificial sound source was 1.5 m, the resolution of the video system projected onto real-world coordinates was 2.1 m, and the overall resolution of the localization/video system was 2.1 m. Analysis of the performance of the system for dolphin vocalizations was measured in terms of three vocalization types: echolocation clicks, whistles, and burst pulsed calls. The mean errors for these were 0.8 m, 1.3 m, and 1.3 m respectively. The 95 % confidence bound for all vocalizations was 2.8 m, roughly the length of an adult bottlenose dolphin. The algorithm localized a vocalization to an individual dolphin for about 39% of the attempted localizations. The algorithm localized a vocalization to a group of dolphins, but not to an individual dolphin, for about 45% of the attempted localizations. This method fills an urgent need for unbiased identification of vocalizations of undisturbed dolphins where the details of social interactions can be followed without affecting the behavior of the subjects (Tyack 1998).

Chapter 5: Summary and Conclusions

Chapter 3 described the current state of analysis of the bottlenose dolphin acoustic repertoire, showing the clear need for a detailed quantitative and consistent study of the repertoire. Rather than identify fixed categories of vocalization, this chapter develops parameters to detect signals from the two different modes in which dolphins vocalize: tonal whistles and broadband pulses. This chapter does not attempt to do a comprehensive repertoire study, but uses several new quantitative methods to relate vocalizations and behavior from dolphins to look at functions of broad vocalization types. The results from Chapter 3 are based on a combination of confirmatory and exploratory analyses. The primary confirmatory result from Chapter 3 is that vocalizations in the lagoon tend to occur around the time of onset of behaviors produced by the focal dolphin. A comparison of vocalizations during affiliative and agonistic interactions revealed that this association of group vocalizations with focal behaviors is related to agonistic but not affiliative interactions. Further analyses were performed to explore the relation of specific vocalization types to specific behavior types. From these analyses it appears that one type of burst-pulsed sound, BP Type I, was closely associated with agonistic behaviors. The pulsed calls in general were associated with agonistic as well as foraging behaviors. Tonal vocalizations were also associated with agonism. As the analysis involved vocalizations from the entire lagoon, it was not clear whether these associations of vocalizations to behavior types were a result of vocalizing by animals who were involved in the behavioral interaction, or were a result of vocalizing by the entire group.

In order to address this question in more detail, Chapter 4 focused on vocalization usage in relation to a specific behavior type, submissive behaviors. Using the localization/video method described in Chapter 2, vocalizations in a ±10 s window around submissive behaviors were localized and classified as having come from either dolphins engaged in the interaction or dolphins not engaged in the interaction. This ascribing of vocalizations to interactants versus non-interactants instead of to individual was performed since interacting animals were usually closer together than the resolution of the localization/video system. Vocalizations were emitted by interactants more often than expected, and by non-interactants less often than expected. Therefore the "gambit of the group," in which all animals in a group can be assumed to be interacting, is not appropriate for this case. Rather, it is more appropriate to focus on the level of the interaction or individual. Use of different vocalization types was found to vary depending on the context of the agonistic interaction. Interactions containing aggression as well as submission contained more BP Type I vocalizations emitted by the interactants than interactions only containing submission. In addition, not only context but sequence within the interaction mattered. More vocalizations were emitted by the interactants in the 10 s period after a submissive behavior was performed than in the 10 s period before the behavior. Taken together, the results from Chapter 4 affirmed the need for developing the acoustic localization/video method by demonstrating that group-based analyses are insufficient and one must use techniques suited to studying interactions within a group in order to study communication and social behavior in dolphins. They showed that patterns of usage of specific vocalizations depended both upon the behavioral context and were sensitive to timing and sequence of previous behaviors on a variety of time scales.

5.2 Contributions:

Contributions by this thesis to the field include:

I. **Acoustic Localization/Video technique:**
    a. Capability for localization of vocalizations of captive dolphins to vocalizing dolphin, or group of possible vocalizing dolphins
    b. Capability for studying vocalizations from an individual (or a group of closely spaced dolphins) in an unbiased social setting (in captivity).

II. **Quantitative Methods:** Used quantitative and replicable methods for parameterizing vocalizations and relating them to observed behavior.
    a. Developed methods for relating vocalization parameters to focal behavior
        i. Parameterization of vocalizations into tonal and pulsed parameters

   b. Relating time series of vocalization parameters to time series of behavior
      i. Conditional probability analyses with time window
      ii. Cross-correlation analyses
   c. Focus on *quantitative* and *objective* techniques

III. **Group vocalization usage during affiliative states and agonistic interactions:**
   a. *Fewer* vocalizations of all types (produced by the group in general) occurred during affiliative states (involving the focal) and *more* occurred during agonistic interactions (involving the focal).

IV. **Group vs. Interactant Analysis:** For this setting, analysis of group vocalizations in relation to focal animal behavior was not appropriate, rather a focus on vocalizations from interactants (or individuals) was more appropriate.
   a. Vocalizations were made more often than expected by interactants, and less by non-interactants (in relation to agonistic interactions)
   b. Vocalization usage varied with respect to other behaviors in the interaction
      i. BP I calls were used more often when interactions involved aggression and submission rather than just submission.
   c. When analyzing vocalization usage with respect to (agonistic) behavioral interactions, sequence in the interaction matters.
   d. More vocalizations of all types were produced by the interactants after a submissive behavior than before

V. **BP Type I** was isolated as a distinct call type (subset of pulsed, or burst-pulsed calls)

5.3 Future Research:

The methods developed in this thesis have helped open up more avenues for future research. The ability to identify the vocalizer in an unbiased social setting (in captivity), even if only to the level of interactant versus non-interactant, is a major advance. Performing similar analyses to those in Chapter 4, except focusing on aggressive behaviors, sexual behaviors, and affiliative behaviors seems especially promising. Studying a larger cross-section of age and sex classes of dolphins, over longer time periods, would probably prove very fruitful. If a larger sample size were available, lumping across age/sex classes would not be necessary. Not having the blurring of results that sometimes occurs when age/sex classes are lumped might further clarify the function of specific vocalization types. For instance, having more data on whistle usage by mother/calf pairs might allow exploration of signature whistle usage by calves during agonistic interactions.

The results in this thesis illuminate some very promising areas for future study. The results from the localization/video system in Chapter 2 demonstrate that resolution of the system could be enhanced by improving the video calibration. Improvement of the localization/video system might allow more precise assigning of vocalizations to the vocalizer than the interaction/non-interactant system used in Chapter 4.

Reducing the amount of time necessary for performing the acoustic localization and identification of vocalizer step would be extremely useful. Several months of extracting appropriate vocalizations, localizing, and perusing the video record were required to obtain the data used in the analyses of Chapter 4. The extraction and localization step would likely prove easiest to automate, although would by no means be trivial. Replacing the human component in determining identity of the dolphin on the video record would likely prove difficult. In addition, replacing the human observer who records behavior would be extremely difficult without loss of resolution.

The results from Chapter 3 analyzing the association of vocalization type with behavior type would benefit from further exploration into different classifications of behavior types. For instance, separating the aggressive behaviors into the individual behaviors, such as bite, mouth open threat, etc. might generate interesting results when compared to vocalization types. For instance, it might be fruitful to look in more detail at the association of snout-to-genital behaviors with vocalizations, or the use of echolocation to target animals for a swim-together or a rub. Separating or rearranging the behavior groups used in this thesis into different groups or sub-groups based upon frequency of co-occurrence of behaviors might also prove fruitful. In addition, it might be possible to break down the tonal and pulsed parameters into smaller categories and test the functional significance of these categories by relating them to their association with behavior types. Further exploration into hypotheses formed from the exploratory analyses (conditional probabilities and cross-correlations) would allow for statistical inference. One such possibility would be exploring the timing of sexual behaviors to types of pulsed calls.

The results in Chapter 4 demonstrate the power of the methods developed in this thesis. However, applying these methods on a broader scale, both in terms of behavior and additional data sets, might help further explain some of the interesting results obtained in Chapter 4. Some of the preliminary results could be confirmed or denied by increasing the sample size or collecting more data with more animals and across age/sex classes. Whistle usage by mothers and calves is one example of this. Looking over more agonistic interactions in the current data set, as well as collecting data on approaches and leaves, might help clarify whether whistles are used by mothers and calves for reunions and/or for soliciting support. More data linking BP Type I calls to timing of agonistic interactions involving aggression would help determine more clearly the role of BP type I calls in agonistic interactions. Studying social groups with adult males might be particularly helpful for obtaining a more complete picture of a typical bottlenose dolphin social group, especially for studying agonism, sex, and interactions of bonded male pairs. If resolution of the localization/video system were increased, then analyses on the role of the individual in agonistic interactions could also be explored.

5.4 References:

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6. Abstract (Limit: 200 words)

This thesis presents methods to analyze the function of vocalizations of the bottlenose dolphin, *Tursiops truncatus.* It uses the social interaction as the basic unit of analysis, and maintains a deliberate focus on quantitative and replicable analyses throughout.

A method for determining identities of vocalizing animals in a lagoon was developed. This method combined passive acoustic localization with video sampling to determine which animal vocalized in a captive lagoon. It fills an urgent need for unbiased identification of vocalizations of undisturbed dolphins where details of social interactions can be followed without affecting the behavior of the subjects.

This thesis uses several new quantitative methods to parameterize vocalizations and relate these to behavior from dolphins. Vocalizations within the lagoon tended to occur around the time of onset of behaviors produced by the focal dolphin. A comparison of vocalizations during affiliative and agonistic interactions revealed that this was related to agonistic but not affiliative interactions.

Vocalizations in a time window around submissive interactions were localized and found to be emitted by interactants (vs. non-interactants) more often than expected. Use of different vocalization types varied depending on the context of the agonistic interaction, with more vocalizations occurring after the submissive behaviors than before.

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