WHISTLE PRODUCTION RATES IN A GROUP OF MALE BOTTLENOSE DOLPHINS (*TURSIOPS TRUNCATUS*) OVER CHANGES IN COMPOSITION

BY

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Dedication

To Mercy
For teaching me my first great lessons
in non-human cognition

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Finally, to the dolphins of the world. May you lose some of your mystery, but never your charm.

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WHISTLE PRODUCTION RATES IN A GROUP OF MALE BOTTLENOSE DOLPHINS (*TURSIOPS TRUNCATUS*) OVER CHANGES IN COMPOSITION

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ABSTRACT

Bottlenose dolphins (*Tursiops truncatus*) are highly social animals with fine-tuned abilities in sound reception and production. Interesting aspects of their vocal behaviors such as signature whistles and vocal mimicry have been studied in detail. Little is known about their vocal behavior in general. Information such as normal vocal repertoire, or the conditions in which vocal behavior is most likely to occur, is absent from the literature. This study examines the whistle production rates of a group of male dolphins across changes in composition. One dolphin was present throughout the study. Whistle rates were analyzed before and after the death of one individual, following the introduction of another individual, after both animals were allowed mutual access, and following the introduction of yet another dolphin. Whistles were almost absent with one animal present and most common in the condition with three animals present. The latter effect seems to be partly attributable to the extensive vocalization rate of the newly-introduced animal. These results suggest that there is individual variation in whistle production rate between individual animals and that dolphins are more likely to vocalize in the presence of conspecifics.

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Dr. Heidi E. Harley

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Division of Social Sciences

In 1967 William Evans wrote, “It is safe to say that the complexity of cetacean vocalizations is exceeded only by the fervor of the research efforts of cetologists and behaviorists to explain their function.” Thirty-six years later, even Evans might be surprised at the exuberance that has been demonstrated by researchers hunting for functional significance in the diverse vocal repertoires of whales and dolphins. Vocal behavior of cetaceans, particularly bottlenose dolphins (*Tursiops truncatus*), has captured the attention of researchers and the imagination of the world for the past four decades. (Caldwell & Caldwell, 1965; Caldwell, Caldwell & Tyack, 1990; Smolker, Mann & Smuts, 1993; Janik, Dehnhardt & Todt, 1994; Janik & Slater, 1998; McCowan & Reiss, 2001; Miksis, Tyack & Buck, 2002). Despite these fervent efforts, there remains no overarching description of how these vocalizations are used. In fact, the literature at present does not include such basic information on vocal behavior as rate of production or factors which influence this rate. Establishing baselines of normal vocal behavior under circumstances encountered in research is a crucial step towards determining the functions of such behavior and filling the gaps in our knowledge of non-human communication systems.

The brain of the bottlenose dolphin

Bottlenose dolphins possess a variety of distinctive characteristics that attract interest in their vocal behavior. Bottlenose dolphins have unusually large brains, and they have a brain to-body ratio of roughly 4.5 (Woods & Evans, 1980). Brain-to-body ratio, or encephalization quotient (EQ), is the ratio of brain size to body size. The scale is designed with a ratio of one being expected, that is, a species with an EQ of one has a brain that is proportionate to its body. Humans have an EQ of 7. The relationship between EQ and cognitive ability is tenuous at best. Examining the brain's structure is more likely to provide insight into possible cognitive capabilities. Structurally, dolphins have unusually large cerebellums relative to total brain size (Marino, Rilling, Lin & Ridgway, 2000) and high cortical area relative to brain volume (Elias & Schwartz, 1969; Ridgway, 1986). One current theory about the function of the cerebellum is that it tracks the timing of sensory and motor information (Paulin, 1993). The primary function of the cerebral cortex seems to be elaborating or integrating sensory information.

Brain tissue requires a high investment of energy. Because most neurons cannot be replaced, they are protected from damaging infection by the blood-brain barrier. The same barrier that keeps viruses out also keeps out many nutrients. Thus glucose, which can be actively transported into the brain, is the main energy source for vertebrate neurons. Oxygen is important in processing glucose, and the maintenance of the brain requires much oxygen in proportion to other organs (Wong-Riley, 1989). Metabolically expensive structures are expected to serve purposes important enough to compensate for their energetic cost.

Several uses have been proposed to explain the unexpectedly large brains of dolphins. They may be used for processing the vast amount of acoustic information dolphins are exposed to in their environment (Ridgway, 1986; Wood & Evans, 1980), particularly the information they receive via their primary sensory modality, echolocation. Klinowska (1994) made the odd proposal that dolphins might need such relatively enormous brains in order to compensate for their lack of REM sleep. However, other animals with similar abilities (many species of bats also echolocate; the spiny anteater, *Tachyglossus aculeatus*, lacks REM sleep) do not have similarly large cerebra. Alternatively, a large part of the dolphin cortex may be required for tracking social relationships. Dolphins are gregarious, social creatures, and this makes them particularly interesting research subjects.

Among mammals with complex social relationships we find a pattern of well-developed cerebral structures. African elephants (*Loxodonta africana*) live and travel in groups of long-lived individuals forming long-term associations (Moss & Poole, 1983). They keep track of dominance rankings within herds, feeding orders between herds, varied sexual relationships, and long-distance communications between herds. Chimpanzees (*Pan troglodytes*) live in a world of sprawling familial and social structures that help them survive their harsh environment, and make them more effective predators, hunting in tandem and even learning population-specific simple tool use (Wrangham, McGrew, de Waal & Heltne, 1994). A closely related species of primate, *Homo sapiens*, has formed even more complex social structures, based not only familial and competitive relationships, but on ethereal concepts such as patriotism and religion. Finally, bottlenose dolphins live in large societies of variable structure, they hunt cooperatively and maintain long lasting relationships with both related and unrelated conspecifics.

Dolphin Societies

Bottlenose dolphins live in complex fission-fusion societies. In fission-fusion societies individuals associate in small groups within a larger closed community. These groups are not rigidly structured, and they change in composition over hours or days (Connor, Wells, Mann & Read, 2000). An individual in such a society can expect to find itself in groups of very different composition at different times, but generally with familiar conspecifics. Thus, there is much opportunity for an individual's behavior to change based on which other animals are present at any given time.

Bottlenose dolphin populations are found in a wide range of habitats around the world, and these differing environments impact their group structures. For example, group size in free-ranging bottlenose dolphins tends to vary with the openness of the surrounding environment. Larger groups of dolphins are found in deep water off-shore areas as compared to near-shore bays and coves. Bottlenose dolphins in coastal southern California have a mean group size of 18, in Corpus Christi Bay a mean group size of 6.10, and in South Africa they average 140 individuals per group (Shane, Wells & Würsig, 1986). Changes in group size related to time of day have also been noted and may be related to activity cycles. Reports of seasonal variation in group size are mixed.

Specifics of population structure vary with habitat structure and feeding strategy (Shane et al., 1986). Bottlenose dolphins may live for 40 or 50 years (Wells & Scott, 1999), and thus have a long span of time to develop relationships and experience the consequences of their social behavior. They can expect to see many changes in the individuals with which they associate over the course of their lives.

Bottlenose dolphins also take a long time to reach sexual maturity. Calves are not weaned until they are three to five years of age (Mann & Smuts, 1998), and are not fully mature until they are eight to twelve years old. Females give birth roughly every three to six years, starting when they are approximately twelve. Mothers with calves are often relatively solitary, perhaps to avoid close competition for resources. In other cases, females associate together based on reproductive condition, with mother-calf pairs swimming together (Wells, 1991). These different patterns of association may be related to feeding strategies. Subadults form mixed-sex groups, although with a disproportionate number of males. Subadult females are more likely to associate with adults than are subadult males, and males take longer to reach maturity (Wells, 1991).

Male bottlenose dolphins are known to form dyads and triads (Connor, Smolker & Richards, 1992). These are long-term associations between two or three specific individuals. Males in a dyad tend to spend 80% or more of their time together, often as much time as mothers spend with nursing calves. This is a very clear example of high investment in a relationship between individuals. Male dyads remain stable for at least ten years (Wells, 1991), often for the lifespan of the members. If a dolphin’s male-pair partner dies, it is possible for the dolphin eventually to acquire another partner.

Differences exist in male grouping between different populations of dolphins. In Shark Bay, male triads are common. Triads tend to be unbalanced, that is, a pair of animals associate most strongly with each other, and then second most strongly with the third animal. In Sarasota Bay, triads are extremely uncommon. In Shark Bay, male dyads or triads may team up, forming second order groupings or “coalitions” (Connor et al., 1992). This is the only known example of higher order groupings (that is, groups composed of smaller groups) besides those formed by humans.

Female dolphins do not form pair-bonds, but each female does tend to have a small group of regular associates. These relationships are not closed, but rather, each female is the center of a unique group that overlaps with several other females’ unique groups. For example, female A may associate with female B, and female B may associate with female C, yet females A and C do not associate with each other.

The complexity of bottlenose dolphins' social structures is highlighted by the influence differing environments have on their social behaviour. Success in such different lifestyles implies a capacity for flexible responding.

Acoustic information in a marine environment

In any discussion of dolphins we must consider the environment in which they dwell. The marine world is far removed from the terrestrial world. One significant difference is the lack of light at depth. Scattering and absorption reduce light intensity exponentially with increasing depth. Long (red) and short (ultraviolet) wavelengths of light are absorbed quickly. The remaining blue light is reduced by 90% for every 70 meters of depth, even in the clearest of water (Herring, 1996). A mere one kilometer down is a world of complete darkness lit only by the glow of bioluminescence. Moreover, water most often is not clear, but filled with some form of sediment — mud, sand and algae often severely limit visibility. For all of these reasons, vision is not likely to be the most important sense for a dolphin or other pelagic organism, nor the means through which the most important social information is communicated.

However, although a marine environment is hostile towards the propagation of visible light, sound travels roughly 4.5 times faster in water than in air and can rapidly cover great distances with little loss of power. Frequency modulated whistles are omnidirectional and can carry for some distance. Given the nature of the marine environment, it seems likely that sound carries a great deal of important social information, and is thus of immediate relevance in studying dolphins' lives.

Dolphins are skilled at acoustic processing, and make frequent use of this skill. Echolocation (or biosonar), which involves producing a series of broadband pulses and determining the characteristics of the surrounding environment based on the returning echoes, is one of the primary senses through which dolphins perceive their world. Dolphins have very good vision compared to other mammals, both in water and air (with an oil coating they can apply simply by blinking), although their visual capacity is unimpressive compared to the human range. While dolphins certainly do not use their echolocation continuously, the information provided about objects via echolocation seems to be more detailed than that from other sensory systems, such as vision. For example, a dolphin presented with an object and rewarded for selecting an identical object from a range of alternatives performed significantly better when the objects were exclusively presented for echolocation than when they were exclusively presented for vision (Harley, Roitblat & Nachtigall, 1996).

Dolphins hear well over a wide range of frequencies; they can finely discriminate among sounds ranging in frequency from 20 Hz to at least 140 kHz (Thompson & Herman, 1975). In comparison, the human hearing range is 20 Hz to 20 kHz in childhood (Schneider, Trehub, Morongiello & Thorpe, 1986) degrading to a range of 20 Hz to 15 kHz in adulthood. Fine discrimination in humans is possible only for frequencies less than 8 kHz.

Dolphins track a large number of changing social relationships while dwelling in an environment where sound is the predominant source of information. Given such an arrangement, it would be reasonable to expect dolphins to have an elaborate vocal communication system.

The vocal behavior of bottlenose dolphins has attracted considerable scientific attention over the past 40 years, and indeed, research in this area has been rewarding. Dolphins have a large repertoire of sounds, ranging from a great many variations on the familiar whistle to harsh clacks to the "buzzing" observed from hunting dolphins in Scotland. Moreover, dolphins are not restrained to the narrow frequencies of whistling, but are capable of producing broadband "burst-pulse sounds" which have spectrographic characteristics similar to human speech. A high-energy broad-band pulse described as a "crack" (and distinct from a jaw clap) has been associated with behaviors indicating a fright response, such as tight schooling and avoidance of a novel stimulus (Caldwell, Haugen, & Caldwell, 1962; Connor et al., 1992). A vocalization that consists of a whistle and a burst-pulse vocalization emitted simultaneously occurred in spotted dolphins (*Stenella frontalis*) during times of stress or excitement (Herzing, 1996). Morozov (1970, as reported in Saayman, Tayler & Bower, 1972) used underwater observations in association with auditory recording to determine that specific sounds are emitted by free-ranging dolphins at particular stages of feeding during fish-herding. Doubtless other meaningful vocalizations have not yet been described. On the other hand, one of the most unusual and intriguing dolphin vocalizations has been described in some detail.

Signature Whistles

Studies on both captive and free-ranging bottlenose dolphins have reported that individual dolphins possess unique, stereotyped vocalizations, known as "signature whistles" (Caldwell & Caldwell, 1965; Caldwell & Caldwell, 1968; Caldwell, Caldwell & Tyack, 1990). Signature vocalizations are unusual, and possibly unique. Some bats may have signature calls, but this has not yet been determined (Defanis & Jones, 1995). Signature whistles are narrow-band frequency-modulated sound emissions generally less than one second in duration. Different signature whistles have different frequency contours. Whistle characteristics specific to individual dolphins were first proposed in the literature in 1953 (Essapian), and first described in 1965 (Caldwell & Caldwell). The initial observation was that they accounted for 90% of dolphins’ vocalizations.

Bottlenose dolphin calves in captivity develop signature whistles by around six months of age (Caldwell & Caldwell, 1979). This may be typical of wild dolphins as well. All wild dolphins investigated when they were one-year-old or more had already developed a stable signature whistle (Sayigh, Tyack, Wells & Scott, 1990). Signature whistles in free-ranging dolphins can remain stable for at least 12 years (Sayigh et al.).

Signature whistles may be strongly influenced by each individual’s developmental history (Sayigh et al., 1990; Sayigh, Tyack, Wells, Scott & Irvine, 1995). During long-term studies of the bottlenose dolphin population in Sarasota Bay, Florida, the signature whistles of several mothers and their offspring were recorded. Spectrograms of the signature whistles of male young were strikingly similar to those of the signature whistles of their mothers. Female offspring, however, were much more likely to have quite different signature whistles. The researchers theorized that because young female dolphins often continue to associate with their mothers' pods well into their adulthoods, the females would need signature whistles which were notably different from their mothers' to avoid confusion within the group. However, males join separate groups and thus do not face the same problem. Returning males may also be able to determine that a female is a sibling due to the similarity of her whistle to their mother's whistle. This may serve to guard against incest.

Do "signature" whistles in fact communicate individually identifying information? For humans and other species, individual recognition is often possible based on general characteristics of an individual's vocalizations (Cheney & Seyfarth 1980, 1988; Lind, Dabelsteen & McGregor, 1996; Rendall, Rodman & Edmond, 1996). Dolphin vocalizations have long been thought to lack these characteristics. The nasal sacs dolphins use to produce vocalizations are altered by pressure changes at depth, and these changes may affect characteristics of the vocalizations (Tyack & Sayigh, 1997; Ridgway, Carder, Smith, Kamolnick & Elsberry, 1997). High levels of background noise may also serve to obscure vocal characteristics. Signature whistles may then be a way of allowing individual recognition in the absence of such general characteristics. On the other hand, one study does report individual differences for whistles with the same frequency contours (McCowan & Reiss, 2001). This same study reports the complete absence of individual-specific signature whistles.

Experimental evidence suggests that dolphins associate signature whistles with specific individuals (Sayigh et al., 1999). Temporarily captured wild mother and independent offspring (offspring no longer dependent on the mother) pairs were used as subjects. Recordings of signature whistles from independent offspring were paired with those from dolphins of similar age known to be familiar to the mother subjects. Likewise, recordings of signature whistles from mothers were paired with those from female adults known to be familiar to the offspring subjects. Vocalizers were known to associate with subjects at similar levels; that is, the subject could not simply select the whistle that it heard more often. Human observers held each subject in the water, and a playback speaker was placed at a right angle to the subject. Number of head turns towards the speaker was used as a measure of response to each whistle. Subjects responded significantly more strongly to playback of kin whistles. This result suggests that subjects recognized kin whistles as being associated with kin. It provides stronger support for the idea that signature whistles serve an identifying function.

Possible spontaneous mimicry of signature whistles has been reported (Tyack, 1986). Two bottlenose dolphins were recorded with a telemetry device to identify which dolphin produced which sounds. Analysis of the recordings suggested that each dolphin had a primary whistle (possibly a signature whistle) that it produced for roughly two-thirds of its vocalizations, and another secondary whistle that it produced the remainder of the time. Interestingly, one dolphin’s primary whistle was the other’s secondary whistle, and vice versa. Given evidence that individual bottlenose dolphins do not share a large number of stereotyped whistles, it was concluded that the dolphins in this study may have been mimicking each other’s signature whistles. Mimicry of signature whistles may be a means of addressing a particular individual (Tyack, 1986).

Other studies have found imitation of signature whistles to be rare (Janik & Slater, 1998; Smolker, Mann & Smuts, 1993). Imitation of signature whistles, if it occurs, presents a challenge to the hypothesis that they are used for individual recognition. If dolphin A mimics the signature whistle of dolphin B, does dolphin C assume that B is whistling? Several factors could negate that confusion. If only two animals are present, there is no problem—dolphin B will know that it did not produce the whistle. If the location of different individuals was already known, localization of sound source may be sufficient for identification. If general vocal characteristics are present and available for dolphins, then again there is no problem, as dolphin A's "voice" will signal the vocalizer. Finally, some form of response on the part of dolphin B could inform dolphin C that the previous whistle was an imitation. In fact, wild dolphins in Moray Firth, Scotland match each other's whistles: one dolphin will produce a whistle and a different dolphin will repeat the same whistle almost immediately, often within one second (Janik, 2000).

In an attempt to determine the context in which signature whistles were actually used, a study was conducted wherein recordings were made of a group of four captive bottlenose dolphins (Janik & Slater, 1998). The dolphins were housed in two connected pools. Recordings from occasions when an individual had spontaneously separated from the group in an undisturbed context and entered the other pool were compared with recordings from occasions when the group was intact. Signature whistles were most commonly produced when individuals were separated from the group, both by the separated individual, and by the remaining three members of the group. Signature whistles were otherwise rare in undisturbed contexts, although it did occur. These findings suggest that signature whistles may serve to maintain group cohesion. Signature whistle mimicry was noted very rarely in this study, although it could only be recorded when the copy was produced by a separated individual due to the difficulties in determining which individual was vocalizing when they were grouped. In the five cases in which mimicry occurred, the signature whistle mimicked had been produced by a member of the group within a minute prior to the mimicry, and was produced again within a minute afterwards. There was no difference in whistle rates per individual when an individual was separated from the group versus when recordings were taken from the group as a whole.

Strengthening the idea that signature whistles serve to maintain cohesion is the finding that signature whistles may be used to initiate reunions between individuals. Wild bottlenose dolphin mothers and calves living around Shark Bay, Australia, were observed and recorded during separations of a pair (Smolker et al., 1993). Whistling occurred most often by calves during separations, often beginning when the distance between the two was at its greatest, which is to say, preceding the initiation of a reunion. Anecdotal evidence suggests that in some cases a signature whistle may prompt waiting behavior by the receiver, who will stop or slow down until the whistler catches up.

As well as identifying specific individuals and maintaining contact between those individuals and their associates, signature whistles may also provide context-specific information. Variations on the same frequency contours may provide clues about the state of the individuals producing them. To test this hypothesis, a study was conducted comparing the signature whistle vocalizations of captive bottlenose dolphins under different circumstances (Janik, Dehnhardt & Todt, 1994). Vocalizations were recorded when the dolphins were isolated, when they were performing a trained discrimination task and had performed correctly, and when they were performing the discrimination and had just performed incorrectly. Frequency range was found to vary by these contexts, suggesting that some form of context-specific information is embedded in signature whistles.

Much about dolphin vocalizations is still not understood. Even aspects as thoroughly studied as signature whistles provoke numerous unanswered questions. Recently, some researchers suggest that their centrality has been overemphasized, even going so far as to suggest that they do not actually exist.

McCowan and Reiss (1995) categorized the whistles of groups of captive bottlenose dolphins at three facilities, and found that individuals in all facilities had diverse whistle repertoires, and shared many whistles among them. Because of difficulties in recording whistles and associating them with individuals, most early experiments on signature whistles occurred with dolphins temporarily isolated from conspecifics. This seems to be a context in which frequent signature whistles are very likely (Janik & Slater, 1998). In contrast to experiments with isolated animals, the study across different facilities identified vocalizers by assuming that a dolphin seen to be emitting a bubble-stream was producing any whistle recorded at the same time. However, bubble-streams can occur in the absence of whistles, and whistles can occur in the absence of bubble-streams, so it is possible that whistles were attributed incorrectly. Furthermore, bubble-stream emissions are relatively rare, although they are more common in juveniles than in adults. In this study, less than twenty whistles were collected for each animal.

Vocal Mimicry

Bottlenose dolphins possess another particularly interesting vocal ability. No terrestrial mammals other than humans are known to be capable of vocal mimicry (Tyack, 2000). In birds, vocal mimicry is much more common, and has been observed in several species, including the mockingbird (*Mimus polyglottos*), European starling (*Sturnus vulgaris*), and the spotted bowerbird (*Chlamydera maculata*). Roughly 15-20% of bird species in most regions practice vocal mimicry. The leading hypothesis to explain vocal mimicry in birds is that it is an easy way to increase vocal repertoire. This may be important because intensity of birds' responses to songs decline as they are repeated; thus, a large repertoire will maintain response interest. It is not known whether mimicry may serve this function in dolphins as well.

The earliest formal report of vocal mimicry from bottlenose dolphins dates back to 1965 (Lilly). In this study, three bottlenose dolphins were trained via operant conditioning to respond to sounds produced by human trainers with in-air vocalizations that "resembled" the humans' sounds. A set of randomly-generated syllables consisting of a consonant sound followed by a vowel sound were arbitrarily organized into groups of one to ten syllables, which were read aloud by an experimenter. The dolphins responded with bursts of sound. Any vocalizations which "resembled" the syllables read by the experimenter were reinforced. Ninety-two percent of dolphins' responses were numerically accurate to within one count of the number of syllables presented by the experimenter. These data suggested that dolphins could mimic at least one aspect of sound, specifically enumeration of syllables.

In a later study a young female bottlenose dolphin was trained via operant conditioning to mimic computer-generated whistles (Richards, Wolz & Herman, 1984). She could faithfully mimic the stimuli and had a concept of mimicry such that she would replicate novel auditory features and features that she was not specifically being rewarded to mimic. Once those criteria had been reached, an attempt was made to teach her computer-generated whistle "labels" for five familiar objects. The first method used was to present an object, displayed in air, and then present the sound associated with it. As the dolphin learned the sounds, they were gradually faded out to induce the dolphin to produce the labels on her own. Unfortunately with regard to the question of labeling, the dolphin mimicked the fading of the sounds as well as she had mimicked the sounds themselves. A later method gradually decreased the percentage of time that the model of the sound was presented along with the object. This method was successful. This labeling indicated an ability to learn an association between an arbitrary sound and an object.

A different study attempted to give the dolphins more flexibility in responding to sounds. An underwater “keyboard” consisting of keys composed of plastic shapes was constructed and placed in the environment of a pair of young male dolphins (Reiss & McCowan, 1993). Instead of being trained in the traditional sense, the dolphins were given free access to the keyboard. The activation of any key resulted in a distinct computer-generated whistle that was quickly followed by the introduction of a particular object or event, such as the presentation of a ball or a ring, a fish, or rubbing from the experimenter. The keyboard was only placed in the water when experimenters were present to fulfill these roles. The dolphins were reported to begin imitating these sounds rapidly--the first mimicry occurred after only thirteen exposures to the target sound, another after only nine. A later sound was mimicked after only two exposures. According to the researchers, the dolphins began by mimicking the end of the whistle, then the beginning, and then the whistle as a whole. These dolphins also appeared to combine whistles, running the whistles associated with ring and with ball into each other. The subjects spontaneously produced whistles in appropriate contexts, producing the ball whistle while physically playing with the ball or the rub whistle while being rubbed. This spontaneous associative labeling suggests that similar behaviors may occur in the wild, and provides further evidence that signature whistles can be associated with individual dolphins.

At most captive dolphin facilities, trainers use a dog whistle as a secondary reinforcer. The whistle typically produces a simple sound easily within dolphins' production capabilities (narrow band, typically near 8 kHz with no frequency variation). It is repeated frequently in the dolphins' environment, and it is particularly relevant to the animals because it predicts primary reinforcement in the form of fish. Spontaneous mimicry of a training whistle by an isolated juvenile male has been reported (Caldwell & Caldwell, 1972). In addition, dolphins raised in captivity seem to develop whistles with less frequency variation than free-ranging dolphins (Miksis, Tyack & Buck, 2002). This may be the result of constant exposure to the flat (single-frequency) training whistle.

Variable vocal behavior under different conditions

How often do bottlenose dolphins normally vocalize? The answer to that question is likely complex, depending on a number of factors, such as the environmental factors discussed above. A better question is, how often do bottlenose dolphins vocalize under different conditions? This question has only been partially addressed.

At present, there is only one direct report of whistle rate in terms of number of whistles, amount of recording time, and number of dolphins present (Tyack, 1986). "Altogether, 1083 whistles were recorded in five sessions from 0930 to 1600." That is 1083 whistles in 32.5 hours, or 0.28 whistle/dolphin/min. These dolphins were a wild-caught adult male and a wild-caught adult female. At the time of the study they had been at the same facility for 7 years. Little context exists in which to embed these numbers.

We know that rates of vocalizations may be related to time of day or activities. Dolphins brought into captivity change their circadian vocalization patterns (Richards, Bauer, Wolz & Herman, n.d.). Feeding schedules have influenced vocalizations in at least two facilities. In one facility, a peak in vocalizations was observed shortly before sunrise, following a lull throughout the early part of the evening (Powell, 1966). Captive dolphin whistle production in another group was found to occur with marked variability relative to time of day, although it was consistently infrequent in the morning and seemed to occur infrequently at night as well (Saayman, Tayler & Bower, 1973).

Powell (1966) specifically addressed the relationship between vocal behavior and time of day. Two young females, a young male of recent capture, and one mature male bred in captivity were maintained in a round community tank and were fed 15 pounds of fish per animal at random times during the day. The vocal activity of the dolphins was carefully monitored for seven days, and the raw data were analyzed at five minute intervals. If "vocal events" exceeded six occasions per minute, an interval was considered to be "filled" with vocal activity, although rates as high as 30 "vocal events" per minute were recorded. Roughly 770 mean minutes of vocalization occurred throughout the 24-hour (1440 minute) day in the group of five dolphins.

Conclusions from the above and three other conditions (with different sets of animals and feeding schedules) were that vocal activity was periodic, and at least in animals fed during daylight hours, vocal activity was related to a 24-hour day. Nighttime feeding changed the periodicity markedly, prompting much more vocalization at night. In addition, an isolated wild-caught female, estimated to be six years old at the time of the study, showed marked vocal stereotypy.

A different group of researchers (Saayman et al., 1973) observed dolphins at different times of day. The four captive Indian Ocean bottlenose dolphins (a adult male, two adult females, and a female calf) lived in a 4,742,400 liter tank at a public oceanarium. At 1100 and 1530 hours each day for five days each week between 5th March and 17th November 1970, the dolphins took part in half-hour long public displays during which they were fed "to capacity." The researchers undertook two observation periods of these dolphins each day, randomly determining when to begin each session and gaining at least one sample of each half-hour period between 0600 and 1730. The hydrophone recordings of the dolphins' acoustic activities were analyzed by listeners using earphones. The researchers observed no clear relationship between the rate of vocalization and the time of the day, although it was reported that the dolphins were fairly quiet in the early morning. There was no systematic analysis of the dolphins' vocalizations after sunset.

Although night-time whistles were not examined in this study (Saayman et al., 1973), the activity levels given resemble those of one group in Powell, in as much as there is a very low morning rate which rises to a midmorning peak, drops moderately for the afternoon, reaches its highest peak in the early evening, and then apparently falls for the night.

During a wild dolphin study from 1990 (Dos Santos, Caporin, Moreira, Ferreira & Coelho), a small resident population of around 40 bottlenose dolphins, usually found in groups of 15 or so, was monitored with hydrophones. Monitoring lasted for 76 hours over the course of 30 sightings and resulted in 342 minutes of taped footage. Analysis of these tapes revealed that whistles occurred in all activity patterns but were especially abundant when animals were surface feeding or engaged in social behaviors at the surface. Both of these patterns involved a high level of arousal, with numerous other calls, presumably burst-pulse vocalizations, being noted along with a range of whistles. Unfortunately, the study does not list the number of vocalizations or the amounts of time spent vocalizing, focusing instead on the categorization of sound contours.

Richards et al. (n.d.) noted that the relationship between time of day and whistle rate seemed to change over time for a pair of newly captured dolphins. Two subadult female dolphins were periodically recorded and observed during their first year in captivity (beginning in August 1978, two months after their capture) in order to establish a baseline for a playback experiment. Ten hours of recordings were made under a variety of conditions. Four hours of the recordings were five-minute hourly samples of twenty-four hour periods between August 1978 and January 1979. The remaining six hours consisted of training session tapes from a language study, recordings from weighings and vaccinations, and a few samples of social play between dolphins under various conditions. A series of 79 or 80 playback studies immediately followed the collection of this baseline data, and a comparison between the two sets of recordings revealed changes in the vocal output of the dolphins over time. Shortly after capture, the two dolphins seemed to vary their acoustic activity considerably throughout the day, producing no great profusions of sound at any particular times. Within six months, however, their whistles became especially concentrated during feeding sessions. Within a year of their capture, the two dolphins appeared to engage in vocalizations only before and during feeding time.

A factor that could directly affect vocalization rate based on social context is that dolphins exhibit phonoresponse: they often respond to hearing a sound by producing one (Richards, et al., n.d.). This is also characteristic of some birds and some species of insects including tarbrush grasshoppers (Minckley, Greenfield & Tourtellot, 1995). This tendency in common dolphins *Delphinus delphis*, was considered striking (Caldwell & Caldwell, 1968, p. 1122): “Two opposing tendencies in whistling are demonstrated in analyses of the data on time versus contour: the most obvious is excitation of a whistle, or response, by one or more animals after another animal’s whistle; the second is a strong tendency toward inhibition of the response until after termination of the first animal’s vocalization.” Caldwell and Caldwell (1968, p. 1122) also observed that “as the size of the group increases, the number of phonations per animal per hour tends to increase geometrically rather than arithmetically.” Recordings began on the animals discussed in that study after only two days in captivity. Recordings were made of a group of four dolphins before and on the day of the removal of one individual. Actual rates of vocalization were not reported, although the researchers state (p. 1121) that "After … removal of a female, both the loudness and frequency of occurrence of sound emissions were reduced." At the time of this study, possible time of day/feeding effects had not yet been reported.

Given how little is known about dolphin vocal behavior outside of signature whistles, establishing basic information is an obvious step. Outlining a baseline of whistle production under different conditions would allow researchers to concentrate efforts on conditions in which vocal production is common and may be particularly important. It may also allow researchers to identify rare vocal behaviors that may otherwise be overlooked. Furthermore, changes in vocal behavior during different activities or in different contexts may provide a strong indication of the functions of vocal behaviors.

From what is known about dolphins' social behavior, social factors may be more likely to influence vocal production rate than time of day or perhaps even activity. It is possible that this factor has been confounded in studies that have examined the relationship between activity and vocal production, since relationships likely exist between activity and group structure. To what extent is vocal production related to which individuals are present? Several factors could account for variations in vocalization rate related to group composition. Phonoresponse was mentioned above, and is known to occur. Individual differences in vocal production may exist. These could be related to demographic factors such as age or sex, which could suggest possible functions of vocalizations. For example, if males were found to vocalize more frequently than females, perhaps these vocalizations serve a function in maintaining male-pair bonds. On the other hand, individual variation may not be tied to any other particular attribute. In this case, it may be worthwhile to look for differences between noisy and quiet dolphins, such as differences in social relations or in health.

The present study attempts to fill in some of the gaps in general knowledge about bottlenose dolphin vocal behavior by examining rates of whistle production in a group of dolphins with different composition at different times. We know that dolphins are highly social animals and that their patterns of vocal production display much variability. We know that some vocal behaviors, such as signature whistles, are strongly influenced by social factors, such as temporary separations between individuals. There is some indication that broader vocal behavior is affected by social context, however, we do not know how social context affects vocal behavior in general. Information about that relationship would promote a better understanding of the function of bottlenose dolphin vocalizations.

The dolphins in the present study were all adult males, and were all recorded at one facility, with factors such as schedule and recording equipment held constant. In this study, group composition changed over a broad span of time. The changes did not result from short-term interaction patterns or temporary separations, but rather were long-term changes resulting from the death of an individual and the introduction of other individuals. This method allowed certain questions to be addressed, such as whether vocal rate increased predictably based on number of individuals present in the group and whether presence or absence of individual animals strongly influenced group vocal rate.

Method

Subjects

A total of four captive male bottlenose dolphins were recorded at one location, The Living Seas in Disney World's Epcot Center in Orlando, Florida. The main tank at The Living Seas is a circular aquarium 61m in diameter, 8m deep, with a volume of 22 million liters. It contains artificial reefs, hundreds of marine animals, and an underwater viewing area. It is connected via separate gates to two smaller concrete tanks out of the public's view, denoted as tank A and tank B. These back tanks are each rectangular, 6.1m by 7.62m and 1.83m deep. Figure 1 shows the relative sizes and placements of the tanks.

Each subject lived at the Seas for different amounts of time. Bob and Toby were wild-caught from the Gulf Coast of Mexico in 1985; aside from a brief quarantine period in the Florida Keys immediately after capture, their entire captive periods had been spent at The Living Seas at the time of this study. Bob was estimated to be 22 years old as of 2003. Toby was estimated to be 21 years old as of his death in 2002. Bob and Toby had been participating in experimental research on a daily basis for 14 years at the time the study began. Ranier was wild-caught from the Gulf of Mississippi in the 1980s, and had lived at three facilities before being brought to the Seas in 2002 during this study. Ranier was estimated to be in his early 20s as of 2003. Calvin was born in 1994 under human care and has an unusual history. He was orphaned at four months of age at which time he was living with four female dolphins with nursing calves. Calvin nursed from all four females, as well as being fed fish by human caregivers. He lived at two other facilities before being brought to the Seas in 2003 during this study. None of these animals were known to be related.

For purposes of comparison, three captive female bottlenose dolphins were recorded from another facility, The Mirage Hotel in Las Vegas, Nevada. Picabo was captive-born, and was seven years and two months old as of the time of recording (2001). She gave birth on the day of the recording. Duchess was wild-caught, estimated to be 26 years old as of 2001. Huf was captive born and was one year and two months old as of 2001.

Vocal Recordings

At the Living Seas, subjects were recorded at times of day ranging from 0900 to 1800 during the spring of 2002 and the spring of 2003, although recording was sporadic before the introduction of Ranier. After the introduction of Ranier, recordings were taken at the same times each day, roughly one hour each starting at 0900, 1200, 1500 and 1800.

Subjects were recorded under five conditions of conspecific company over particular dates (see Table 1). In condition B+T, Bob and Toby were present at the facility, with full access to each other and to all tanks. Condition B+T recordings span March 4th 2002 through May 10th 2002. In condition B, following the death of Toby, Bob was alone at the facility, with full access to all tanks. Condition B recordings exist from May 10th, May 26th, and July 2nd of 2002. In condition B|R, Ranier was introduced, and Bob and Ranier were in separate tanks, with open metal gratings between them. Their positions were rotated, but they did not have physical access to each other. Condition B|R recordings span July 9th 2002 through July 11th 2002. In condition B+R, Bob and Ranier had full access to each other and to all tanks. Condition B+R recordings span July 12th 2002 through July 17th 2002. In condition B|R+C, Calvin was introduced and Ranier and Calvin had full access to each other with Bob in a separate tank. Condition B|R+C recordings span February 8th 2003 through February 19th 2003. The comparison recording from the Mirage Hotel took place on 15 May 2001.

In all conditions at the Living Seas, acoustic and video information were recorded simultaneously. In the main tank, a BM 121 E (TR) Hydrophone/Projector (manufactured by Don Norris) was used. Receiving sensitivity was approximately -165dB re 1 volt/uPascal from about 18Hz to about 40kHz. Spatial response was omni-directional in a plane at right angles to the cable exit. Recordings were made on a Sony GV-D1000 MiniDV Digital Video Cassette Recorder. In tank A, a model 8234 hydrophone/projector (manufactured by Don Norris) was used. Receiving sensitivity was approximately -176dB re 1 volt/uPascal from about 18Hz to about 140kHz. Spatial response was omni-directional in a plane at right angles to the cable exit. In tank B, a Cetacean Research Technology model #C53 hydrophone was used. Recordings in both the A and B tanks were made with a Panasonic PV-DV401D MiniDV Palmcorder. These recordings were transferred from mini-DV format to DVD format for analysis.

Software

Audio and video information were played back with Intervideo's WinDVD 4 (2002). VOB sound files were converted to WAV format with ac3dec 0.8.21. WAV files were then displayed as spectrograms using Avisoft's SASLab Lite 3.74 (1999).

Procedures

Samples were drawn from a total of 60 hours of recordings. Recording times were different in each condition (see Table 1). Additionally, recordings of three of the subjects were collected when the subjects were isolated from conspecifics.

In the auditory coding method, all audio/video data were played back together in real time. One experimenter coded the entire sample, indicating track-time of both whistles and burst pulse sounds (the latter are not included in the present analysis). A grouping of many vocalizations would not be individually time-stamped, but a time-stamp would be provided at least every 60 seconds.

In the visual coding method, samples were coded by looking at the spectrogram displays of the WAV translations of the VOB files in SASLab Lite. Resolution was set at half-seconds.

Reliability checks were run on a sample of ten percent of the total 60-hour data set. Samples were ten minutes long and were chosen randomly within each condition using the random number generator in Excel 2000. Reliability samples from each condition were proportional, that is, ten percent of the total time of each condition was included for reliability. The checker was trained by the original coder until he could identify whistles, burst-pulse sounds and click trains and distinguish them from background noises. Presence or absence of vocalizations in a segment was fairly reliable. Of eleven 10-minute segments coded by the primary coder as being devoid of vocalizations, the checker coded eight the same way. Coder/checker reliability numbers are graphed in Figure 2. Agreement as to the number of whistles over the entire 6 hour sample was 81%. The average agreement for each 10-minute segment in which both coders agreed that whistles were present was 63%. This low number can be attributed to the small number of whistles in many samples (for example, a disagreement of only 3 whistles produces a percent agreement of 25% for the segment, if the segment is coded as having one versus four whistles). Differences in whistle counts could be fairly wide. In the most extreme example, coder and checker disagreed by a count of 62 whistles (153 versus 91).

A clear relationship existed between the coder and checker results, despite the variability of actual numbers. When analyzed based on rank order, the reliability results produced a Spearman correlation of $r_s = 0.87$, $p < 0.01$. This indicated that actual numbers should be interpreted cautiously, but relative low or high values can be considered robust.

To allow comparisons between conditions, a sample of 100 minutes from each condition was excerpted. These samples were taken from samples recorded between 1000 and 1400 hours to control for possible time-of-day or feeding schedule effects. Two segments were chosen randomly during the designated time frame within each condition using the random number generator in Excel 2000, although recordings from that time window in condition B were analyzed in their entirety (100 minutes).

Not all previous studies examining dolphin vocalizations have included information about time of day or schedule. To allow comparisons with other studies and to produce an overall idea of actual whistle rate over most of the day (as opposed to whistle rate over just the afternoon), a larger 445-minute sample was taken from each condition. This included times between 0900 and 1900 hours for each condition. These were not matched precisely across conditions, but were similar; see Table 2 for start-times. This 445-minute set entirely excluded condition B, which totaled only 150 minutes. The 445-minute sample was coded using both the auditory and visual methods.

Whistle counts derived from the auditory and the visual methods are compared in Figure 3. Correlating ranked values of whistle counts for these segments with the Spearman correlation was less successful than the reliability check run on two different coders both using the auditory method. This correlation was significant ($r_s = 0.58$, $p < 0.01$), but because the auditory method was more reliable, whistle counts determined via visual coding were not used in analyses.

In order to place results in a broader perspective, the 82-minute segment of hydrophone recordings from the Mirage hotel in Las Vegas was analyzed using the auditory coding method.

Spectrograms of whistles were sorted into categories by human sorters. Other studies have shown that this is at least as effective as any computerized sorting methods yet devised (Janik, 1999).

Results

Figure 4 displays the estimated number of whistles (derived through the auditory method) per condition for the 100-minute samples. Only four whistles (0.4/dolphin/10min) were found in condition B (with Bob alone). Moderate levels of whistles were found in conditions B+T (16; 0.8/dolphin/10min) and B|R (21; 1.05/dolphin/10min). Much higher levels (109; 5.45/dolphin/10min) were found in condition B+R, and the most whistles were found in condition B|R+C (219; 7.3/dolphin/10min).

During the 82-minute segment from the Mirage Hotel (with three animals present) 231 whistles (9.4/dolphin/10min) occurred.

Figure 5 displays the estimated number of whistles (derived through the auditory method) per condition for the 445-minute samples. Some differences existed between the 100- and 445-minute samples. The 445-minute sample showed much less difference between conditions B|R and B+R than the 100-minute sample, and the rate of whistling in condition B|R+C was twice that from the 100-minute sample. In the 445-minute sample, condition B+T had 87 (1/dolphin/10min) whistles, condition B|R had 207

(2.3/dolphin/10min), condition B+R had 167 (1.9/dolphin/10min) and condition B|R+C had 1930 (14.5/dolphin/10min).

Whistles recorded from temporarily isolated individuals are shown in Figure 7. In those cases it is possible to determine which subject produced the vocalizations; furthermore, this is thought to be a circumstance that is very likely to elicit signature whistles. Only one whistle was recorded from Calvin when he was alone. Many more recordings were taken from Bob in isolation, and those whistles showed some variability. The contour shown recurred several times and was the most common, but was not the only contour to occur more than once. Several whistles were recorded from Rainer as well, but contours of his whistles showed much less variation.

Categorization of spectrograms in an initial analysis reveal one particular whistle (see Figure 8 for two examples) that seems to recur frequently in condition B|R+C and not to occur in the other conditions. For example, one ten-minute segment from condition B|R+C contains 198 examples of this contour out of a total of 273 observed whistles. This whistle was found throughout condition B|R+C.

Discussion

Whistle Rates and Group Size

Condition B|R+C, the three dolphin condition, consistently had more vocalizations than any other condition. Assuming that all dolphins whistle at similar, stable rates, we would expect an increase of 50% when going from a condition with two animals to a condition with three. The consideration of social facilitation or phonoresponse predicts a greater increase, because each individual present would vocalize more often. Finally, if wide variation exists between different individuals' whistle rates, it is difficult to predict the number of vocalizations, but this number may be quite different from a 150% increase.

The results allow the first possibility to be discarded immediately. The difference in number of whistles from the three-animal condition (B|R+C) was not simply 150% of the whistles in the two-animal conditions (B+T, B|R or B+R). Condition B|R+C would then have a predicted 30 versus an actual 109 whistles the 100-minute sample and a predicted 300 versus an actual 1930 whistles in the 445-minute sample.

The second possibility is that in larger groups, each individual will vocalize more often. This is supported by the change in number of whistles from condition B (4 whistles) to conditions B+T (16 whistles) and B|R (21 whistles). In both cases, the addition of an animal produced a similar increase of 300-400%. It is further supported by the still higher numbers of whistles from both B|R+C and from the Mirage sample, which both had three animals present.

The third possibility is that the added individual was particularly vocal, and that there exists notable variation between individuals' vocal rates. Since one whistle was extremely common in condition B|R+C and has not been found in the other conditions, it is possible that this whistle is specific to Calvin (who was present in condition B|R+C but not in the other conditions). If this is the case, then the high number of vocalizations in condition B|R+C can be partly attributed to one individual, suggesting that individual variation in whistle rate does exist. Calvin is known to have had an unusual history (as described in the Subjects section); this may have influenced his vocal behavior. Of course, effects from social facilitation and individual variation are not mutually exclusive; both effects may in fact be present simultaneously to account for large increases in whistling in larger groups.

Signature whistles?

The whistle recorded from Calvin in isolation (Figure 7) has a different contour than the whistle common exclusively in the B|R+C condition (Figure 8). This common whistle may be related to the rise or upsweep whistle previously reported in the literature (McCowan & Reiss, 2001). Isolation conditions in other animals showed predominant whistles (Figure 7), but also several other contours. Considerable variation existed in the contours produced in group situations. Thus it was not possible to determine subjects' signature whistles, but the results of this study should be expected to apply to whistle production in general, not just to signature whistles.

Whistle Rates in Novel Social Situations

The 100-minute sample revealed an apparent difference between conditions B|R and B+R, whereas the 445-minute sample did not. In the 445-minute sample, no difference in number of whistles existed between conditions B+T, B|R and B+R (the conditions with two animals present). The lack of a difference in number of whistles between conditions B|R and B+R suggests that tactile interaction may not facilitate vocal interaction. However, a close examination of the data does reveal a large increase in vocal rate immediately following physical contact (see Figure 6). On the other hand, a similarly high vocal rate occurs on July 9th 2002, which was the day following Ranier's arrival at the facility. This suggests that increased vocal behavior may be associated with novel or "exciting" situations, perhaps novel social situations in particular. Novel social situations could affect vocal behavior for several reasons. The introduction of individuals may prompt behaviors for the purpose of gaining information about the new individual and establishing a social relationship. Whether relationship-establishing behaviors are agonistic or affiliative, they could be vocally mediated. In dolphins, the introduction of a new animal also provides a new source of sounds which may be learned and mimicked, which could produce a temporary increase in vocal activity.

The idea that tactile interaction may increase vocal production should not be abandoned until actual behaviors can be associated with vocal production. It should be noted that during one period of frequent contact behaviors, the rate of burst-pulse sound production was unusually high. This should be examined more closely in the future.

The 445-minute sample had a much higher rate of whistling in condition B|R+C (14.5/dolphin/10min) than the 100-minute sample had in the same condition (7.3/dolphin/10min). The rate from the 445-minute sample is more representative of the rate for the entire 571-minute set of B|R+C data (15.0/dolphin/10min). This difference can probably be attributed to schedule effects. Although this study tried to control for time-of-day effects, previous research suggests that feeding has a strong effect on whistle rate. While feeding schedule was controlled for in the Living Seas environment, no information existed regarding the previous feeding schedules of newly introduced animals (Ranier and Calvin).

As in previous work on dolphin vocalizations (Caldwell & Caldwell, 1968), the subjects in this study were unlikely to vocalize simultaneously. Simultaneous whistles were most obvious when using the visual coding method, and were very rare, occurring 5 times out of 925 analyzed whistles.

Future Research

Reliability of whistle count data was an unexpected problem during this study. The initial assumption was that a count of whistles and burst-pulse sounds would be fairly straightforward. A very reliable method for counting vocalizations needs to be developed, along with a reliable method of categorizing them. Once this method is refined, samples from a variety of different captive environments should be examined in this way. Large differences between whistle counts from visual and auditory coding methods suggest that both methods have different strengths and weaknesses; a combination of auditory and visual methods may produce more stable counts, as may manipulations such as filtering out background noise.

Individual variation in whistle production which is not related to demographic factors appears to exist. This should be studied in terms of its relationship to individual social interactions and fitness to further define the interaction between vocal and social behaviors.

Based on this study, it also seems likely that larger groups facilitate higher whistle production in all members. Individual variation obscures the extent to which this is true, but if individual whistle rates were determined, the effects of group size would be made clearer.

Increased whistle production in novel social situations could be related to a number of factors, as discussed above. Vocal behavior during introductions of individuals should be examined and compared to vocal behavior during meetings between free-ranging dolphins.

Finally, casual observation during this study suggests that burst-pulse vocalizations may be associated with high-energy, high-social-contact behaviors. Burst-pulse sounds have received less attention than whistles. The situation must change if we are to achieve a broad understanding of the function of bottlenose dolphins' vocal behaviors.

The results of this study reinforce the idea that general whistle production in bottlenose dolphins is closely tied to social functioning. Further describing the use of whistles burst-pulse vocalizations to mediate social behavior will provide insight as to how dolphins establish and maintain social bonds. Examining vocal and social behavior may one day provide a comprehensive account of the function of dolphins' unusual vocal abilities.

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Table 1.

Recording information for each condition.

	B+T	**B**	**B|R**	**B+R**	**B|C+R**
Rec. start/end dates	04 Mar 02 - 10 May 02	10 May 02 02 Jul 02	09 Jul 02 17 Jul 02	12 Jul 02 17 Jul 02	08 Feb 03 19 Feb 03
Rec. Time (hrs):	8.6	2.5	15.2	17.9	11.9
Rec. Time (min):	514 min	151 min	915 min	1407 min	571 min

Table 2.

Start times for all segments included in the sample with 445 minutes per condition, to show times of day covered. Condition B was not included in the 445-min sample. Segments were approximately 60 minutes long.

B+T	B|R	B+R	B|R+C
1000	0900	0900	0919
1015	0900	0900	1000
1048	1130	1000	1150
1200	1130	1200	1242
1300	1200		1330
1400	1500	1500	1410
1500	1800	1500	1450
1600	1800	1800	1802
1615	1800	1800	

Figure 1.

Epcot Living Seas tank diagram.

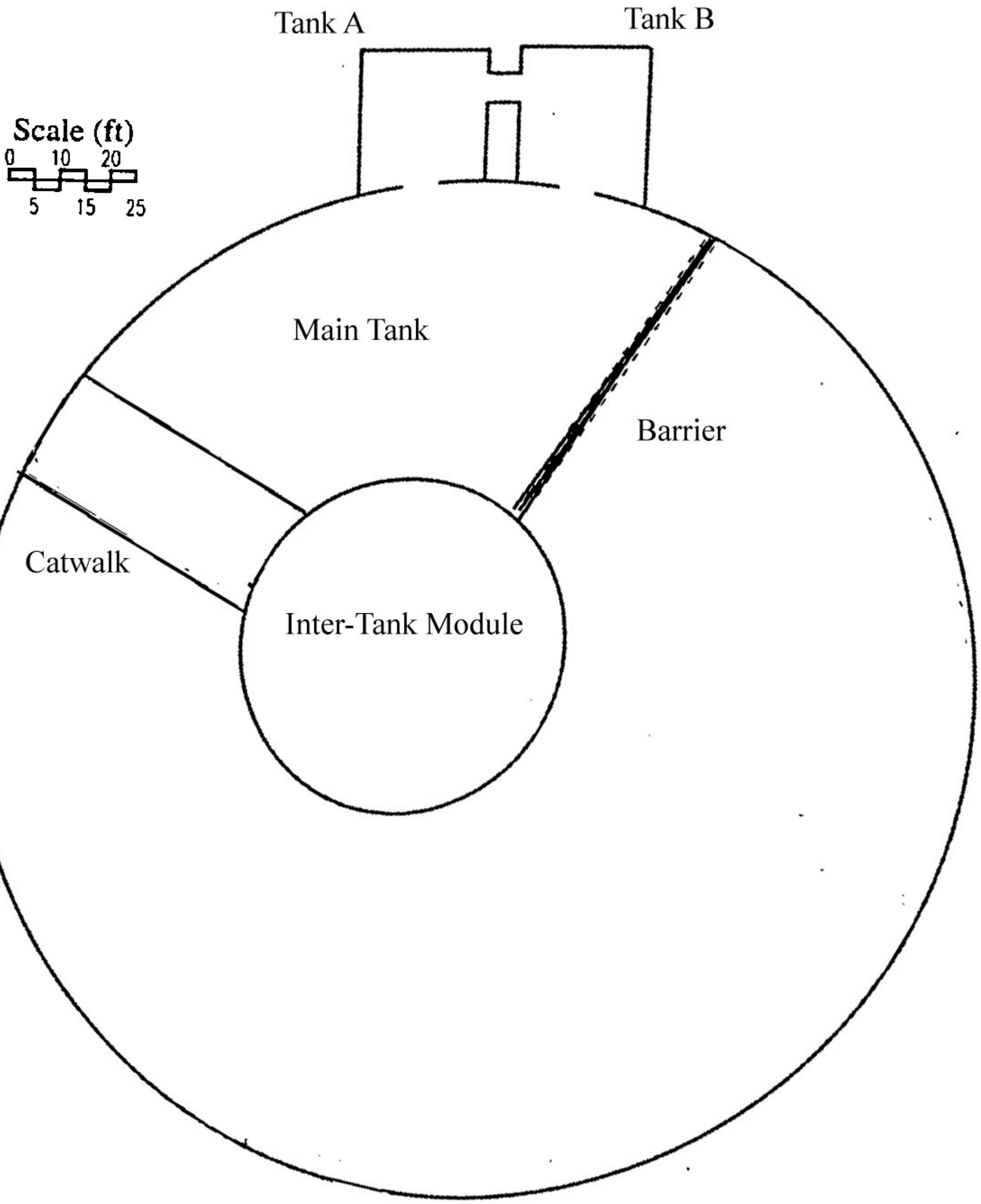


Figure 2.

Graph of coder and checker reliability for number of whistles. Each data point is a ten-minute segment. Eight segments coded as silent by both coder and checker have been excluded from this graph. Agreement over the entire six-hour sample was 81%.

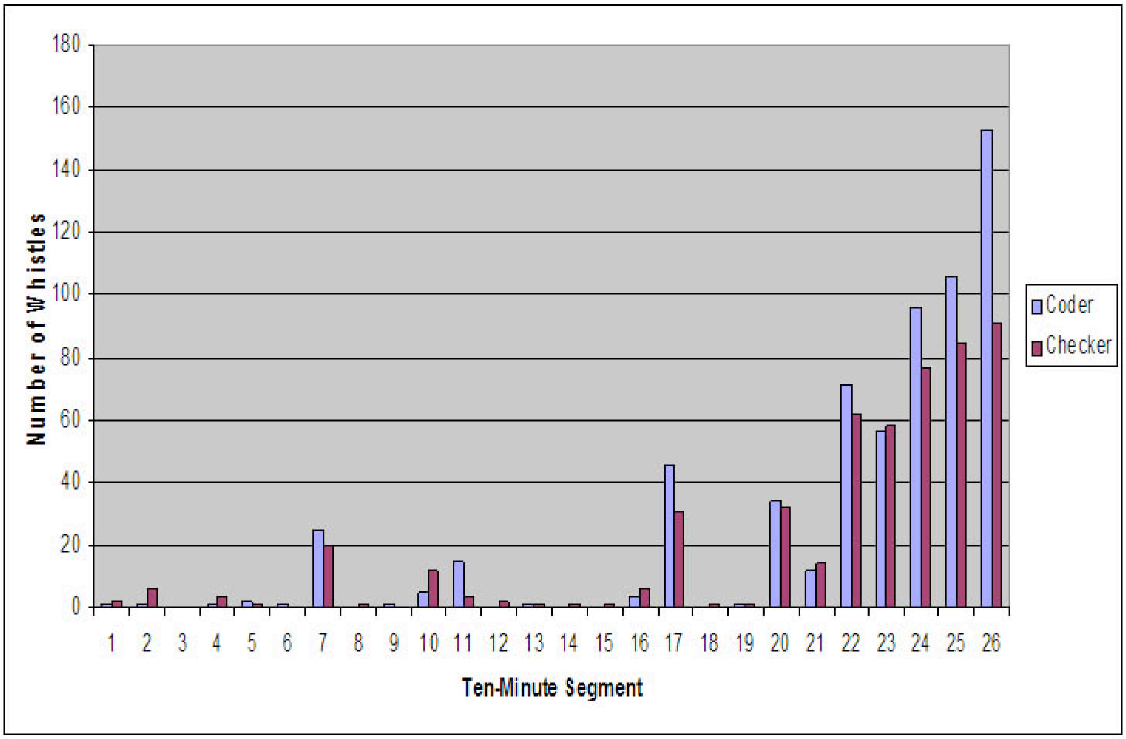


Figure 3.

Comparison of the auditory and visual methods for coding number of whistles from segments from the 445-minute sample. Each data point is a full segment, approximately 60 minutes in length.

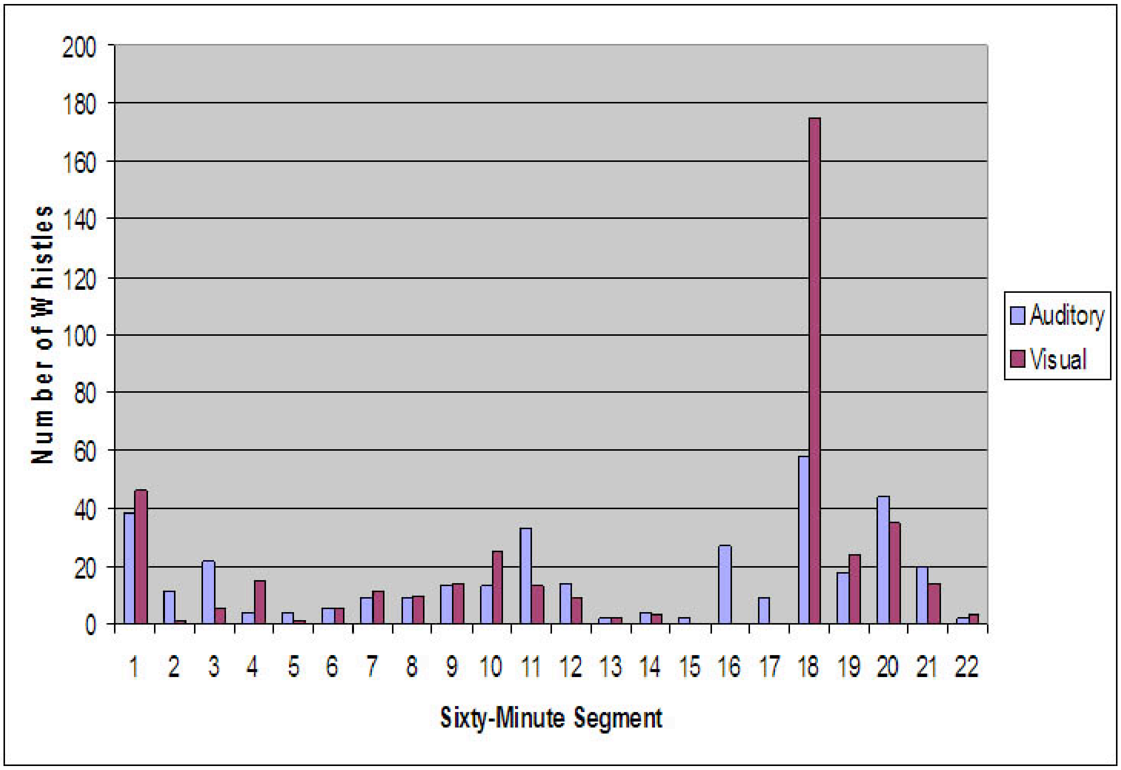


Figure 4.

Number of whistles per condition from the sample with 100 minutes in each condition.

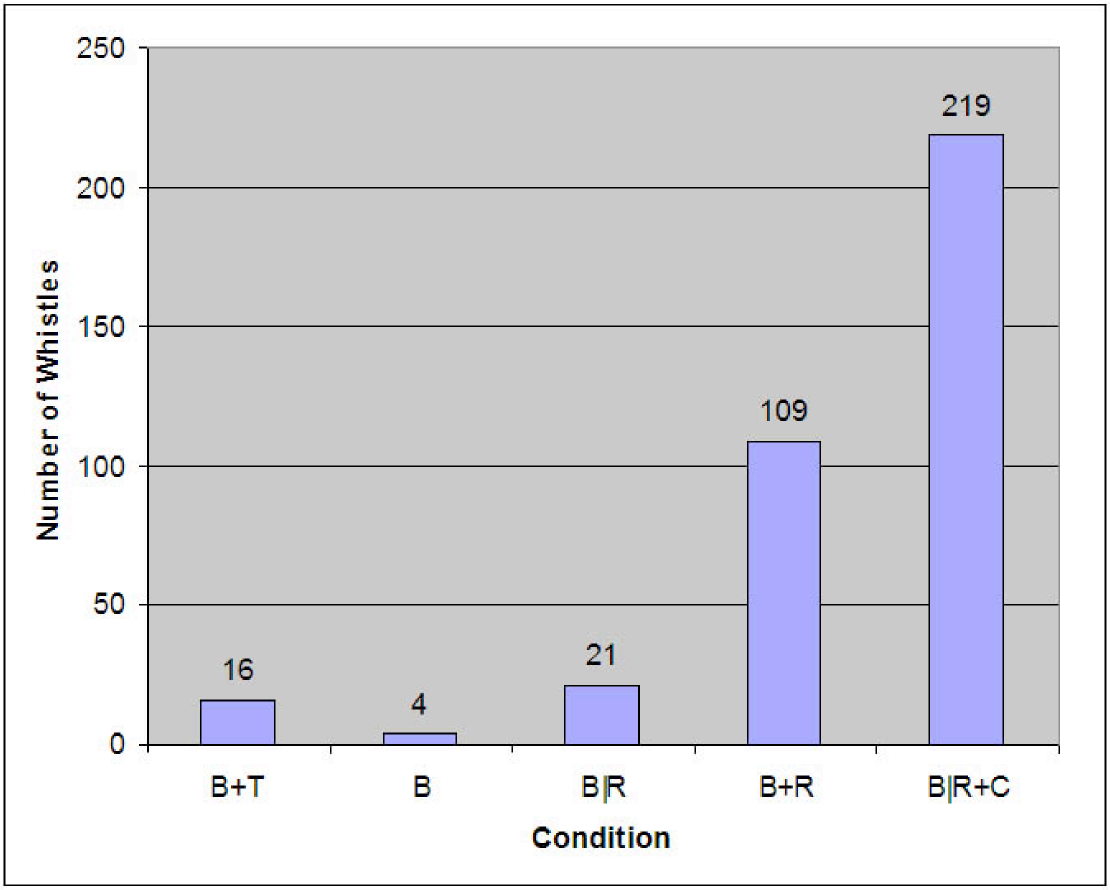


Figure 5.

Number of whistles per condition from the sample with 445 minutes in each condition.

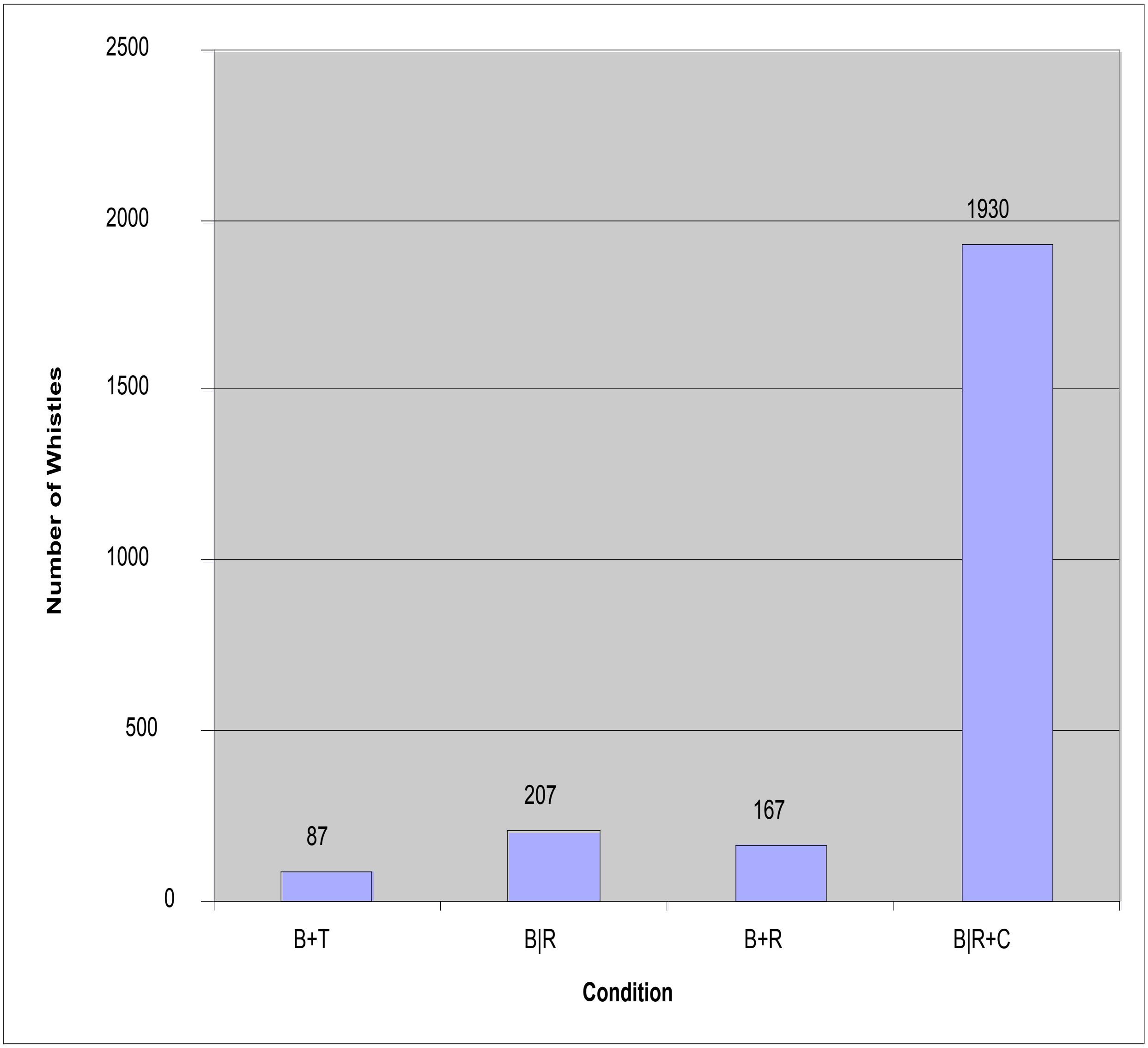


Figure 6.

Average number of whistles per hour by date. Ranier was introduced on 8 July 2003 and Bob and Ranier were permitted direct contact on 12 July 2003.

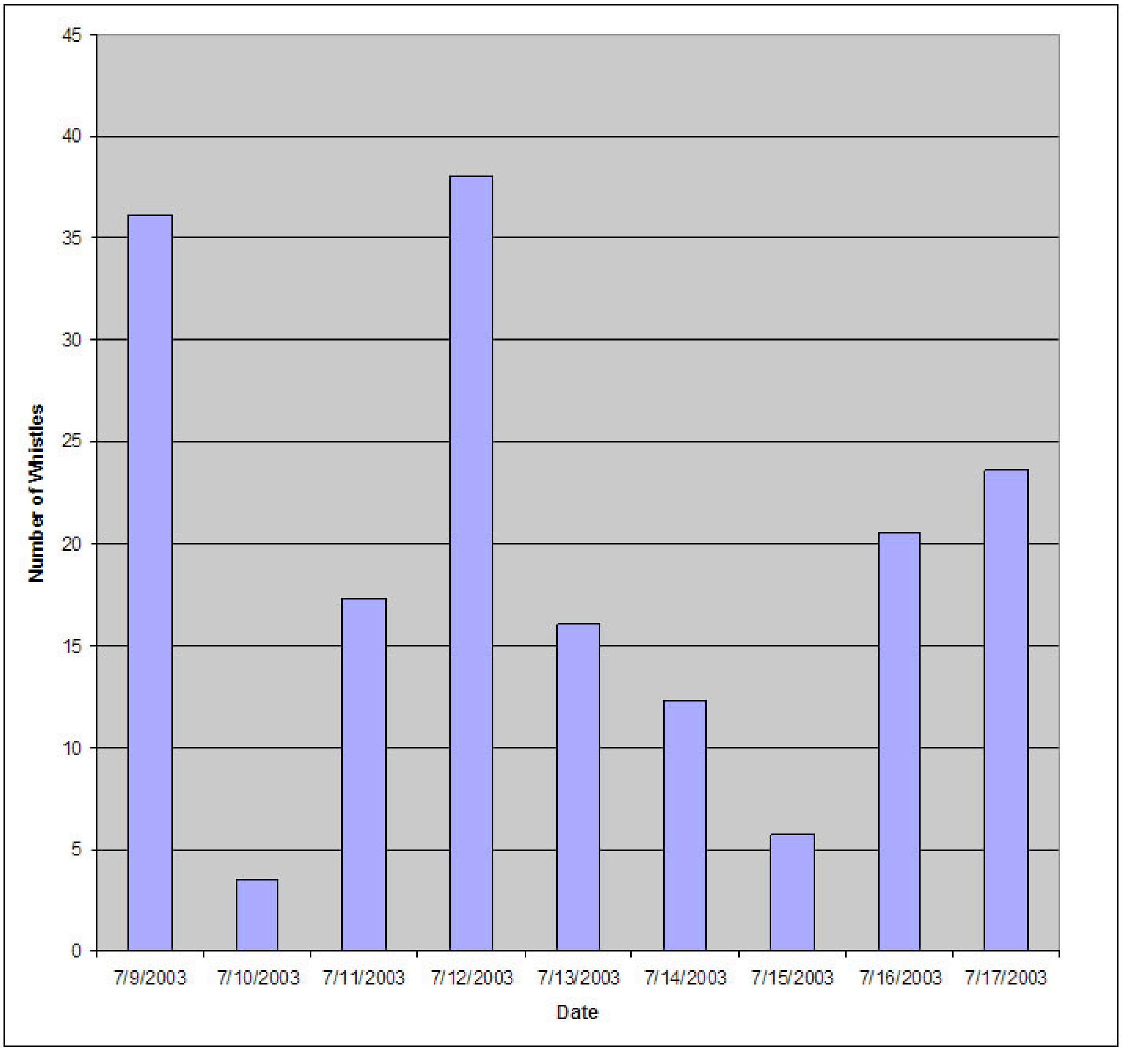
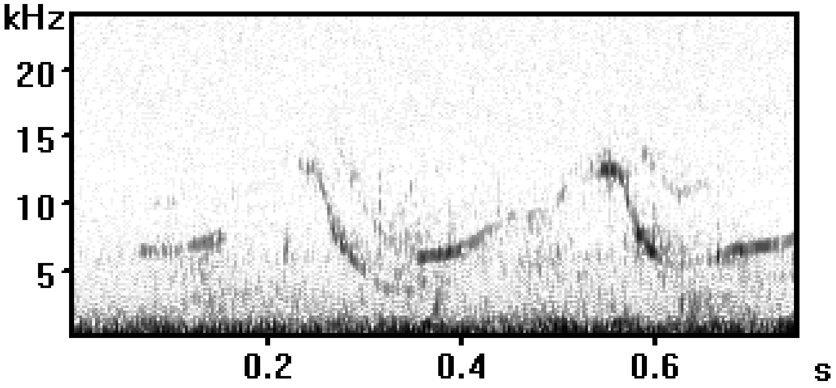


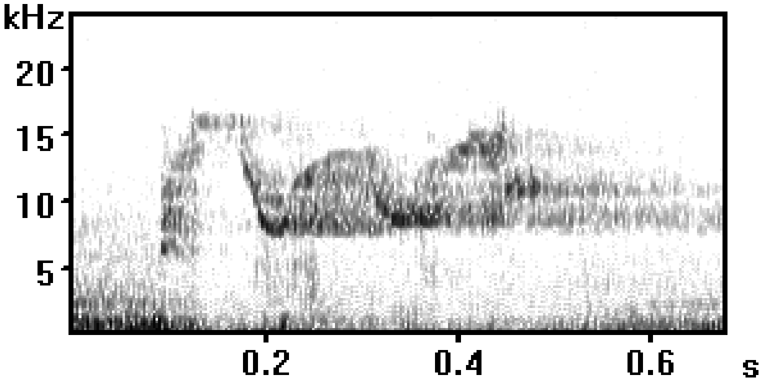
Figure 7.

Spectrograms of whistles from subjects in temporary isolation.

Calvin



Bob



Ranier

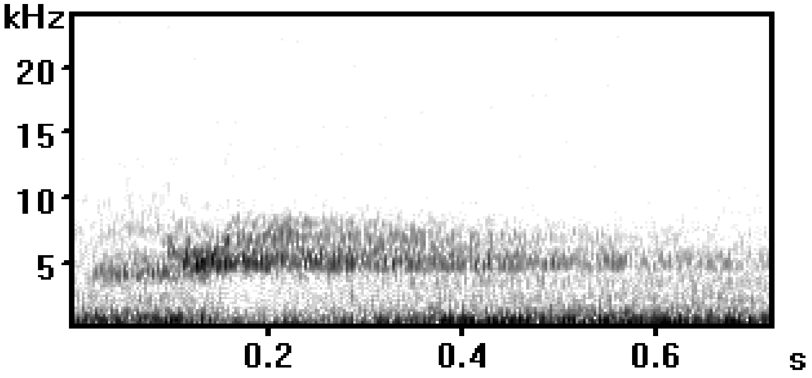


Figure 8.

Spectrogram of two instances of whistle exclusive to and prevalent in condition B|R+C.